**A Thesis Submitted for the Degree of PhD at the University of Warwick**

# Modelling weed population dynamics: Impact of cultural control and climate change

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# Preface

Instead of nose diving straight into the research, I would like to share with the reader my reflections on what I've learned from this Phd. After all, this thesis is the culmination of 4 years of research and will turn me into a 'Doctor of Philosophy', an honorary title indeed.

Over the course of these four years I have increased my understanding in plant ecology, agronomy and modelling biological systems. One of the most important things that I have learned is that successfully carrying out a research project requires determination, patience and time-management. The latter can only be successful if one knows fully well the direction in which to go, (which is an alien concept to most fresh Phd students), the time it takes to fulfill the tasks ahead and the willingness to choose those options that correspond with the time that is available.

Without previous experience in modelling I taught myself how to program in Matlab, something of which I am proud. What was more important however, was the 'How much' question. What level of detail, how much complexity should be incorporated to derive answers? Crucial to and representative of this insight are two quotes that together should be the guiding principles in any modelling project:

***"Essentially, all models are wrong, but some are useful."*** (George E.P. Box)
***"Everything should be made as simple as possible, but not simpler."*** (A. Einstein)

The first quote does not qualify when or which types of models are useful, merely that some models, despite being wrong, can still produce valuable results. Adding Einstein's interpretation of the value of complexity to it suggests, by way of inverting the argument, that only up to a certain point is it useful to add complexity. Modelers are thus urged to make parsimonious models that capture enough detail to answer the question(s) at hand, but do not overburden a model with details that do not fundamentally change the behaviour of the system. The latter aspect immediately highlights a challenge, *a priori* it is often unknown which aspects are most important in regulating a particular biological system. Nevertheless, I would like to believe that, when reading the description of the model components, the reader of this thesis will recognise the compass effect of these rules.

# Acknowledgements

There are many people that I would like to thank for their contribution to the work that is presented in this thesis. In the first place my advisors Andrea Grundy and Andrew Mead who were always available for advice and our discussions significantly contributed to my enthusiasm for the research. Paul Neve, a research fellow that was appointed on the project at the same time as I started my Phd, has been an inspiration in his organised approach and realistic time-management.

Many other people at Warwick HRI have facilitated or helped me at some point during the experiments. Sally Mann, Julian Brandreth and Colin Jones of the Horticultural Staff in Wellesbourne have always been friendly and very helpful in accommodating my protocols for field experiments. Andy Bradshaw did a tremendous job in manufacturing the framework with which the soil samples were excavated (see Chapter 3). Judith Shields and Tracey Overs have been invaluable in retrieving the plastic beads from my soil samples. From the staff over at HRI Kirton I would like to specifically mention Geoff Clark who carried out the fort-nightly parallel measurements on ‘soil slumping’ after ploughing as well as helping me with the field preparation. A warm thank you to Peter Brooks who, apart from being an excellent librarian, could easily be a member of the mental support staff for Phd students that are writing up.

Both Dirk Kurstjens (previously Wageningen University) and Nathalie Colbach (INRA) have given useful advice in the pre-stages of the experimental work on cultivation. Preben Klarskov Hansen (Researchcentre Flakkebjerg, Denmark) wrote and provided me with the original file for the image analysis in MatLab which I then adapted. Tanja Koch, a student from Germany, helped me with the image analysis of the many acquired photos in MatLab. I want to express my gratitude to the consultants Cathy Knott, Carl Sharp and Tom Will and the carrot growers, Andrew Francis from Elveden Estate in particular, who kindly provided me with practical information that gave me a better understanding of ‘the real world out there’.

Thanks also to my parents, brothers and sisters and their lovely postcards from the Netherlands. Last but certainly not least, I can not imagine how I would have fared if not for the financial, mental and even physical support during some experiments of my wife, Marianne. You made life so much easier, in particular during the 4th year. Not even half a year of washing up would make up for this!

# Declaration

I declare that this thesis and the research that is being contained therein is the sole work of the author, that it does not contain any material that was published previously, and that none of this work has been presented for another degree. If the author collaborated with colleagues, used or adapted methodologies originally established by fellow academics, this is fully acknowledged in the relevant part of the text.

SIGNED DATE:

# Abstract

Over the last three decades, concern about food safety and the management of natural resources has increased. Instigated by the previous EU pesticide review, (EU 91/414) carrot growers in particular have been hit by the revocation of several post-emergence herbicides. There is real concern among growers that this may impair profits. To identify alternative weed control strategies, a modelling framework capable of simulating the impact of alternative weed management strategies on long-term weed population dynamics, was proposed. Scentless mayweed (*Tripleurospermum inodorum*) was chosen as model weed species. The system represented in ECOSEDYN (Effects of Cultural control and climate On SEedbank DYNamics), comprises a six-year crop rotation: one year of carrot and five years winter wheat and repeated four times. The weed management strategies consist of combinations of cultural control measures (sowing time and crop maturity time). In addition, the interaction of climate with the cultural control measures was assessed by implementing two future climate scenarios, ('No change' vs 'Heating up') based on weather data over the last 18 years.

For each component model in ECOSEDYN the literature was reviewed to identify the best mathematical representation and then the model was parameterised. To improve accuracy of model projections and address gaps in knowledge, field experiments were conducted in two areas: soil cultivation, and plant growth and reproduction. The results of the cultivation experiments revealed that key assumptions in models for weed seed re-distribution are incorrect. The experiments focusing on plant growth and reproduction resulted in a novel approach to the modeling of biomass increase, flowering and seed shedding where the different processes were quantitatively and temporally linked using Beta functions.

The results of the ECOSEDYN simulations showed that, regardless of the prevailing climate, choosing a fast maturing carrot cultivar is by far the most important factor in maintaining the weed seedbank low. In addition, the risk for higher seedbank levels in the long-term under 'Heating up' climate is largest if carrot is continuously sown late.

# 1 General Introduction

## 1.1 *Motivation for study*

Out of all the harmful organisms (pathogens, viruses, animal pests and weeds) that impair crop performance, weeds have the biggest potential to reduce crop yield (Oerke, 2006). The good news is that, compared to the other pests, there is a wider range of measures available to counteract weeds, and therefore the actual crop yield loss is reduced to a much larger extent (see Figure 1-1, after Oerke, 2006).

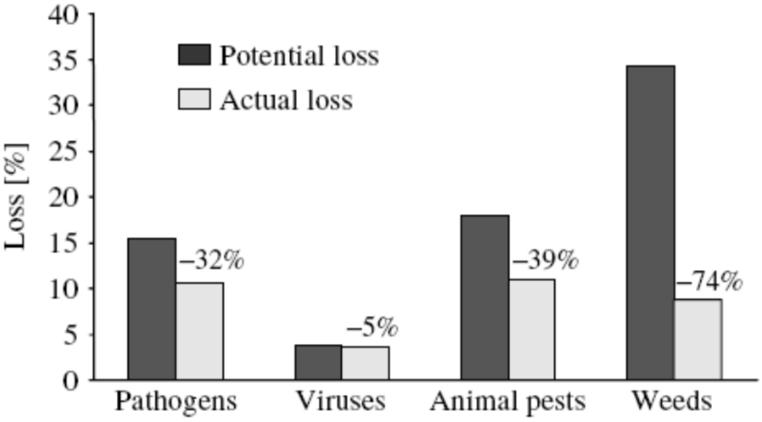


**Figure 1-1** Average efficacy of pest control practices worldwide in reducing loss potential of pathogens, viruses, animal pests and weeds, respectively. Reduction rates calculated from estimates of monetary production losses in barley, cottonseed, maize, oilseed rape, potatoes, rice, soybean, cotton, sugar beet, tomatoes and wheat in 2001-03. Data and figure after Oerke (2006).

Since the discovery of phenoxy-acetic herbicides from 1942-1944, herbicides have been used worldwide in controlling weeds (Timmons, 2005), mainly because they were both inexpensive to produce and effective for weed control (Buhler, 1999; Naylor, 2002; Håkansson, 2003). Squire *et al.* (2003) showed that seedbank populations in research and commercial fields measured before the rise in chemical herbicide use were substantially larger than thereafter (see Figure 1-2.). Because other farm management practices intensified as well over this period, the effect of herbicides on the weed seedbank is confounded but it is generally assumed that herbicides greatly contributed to the decline in weeds (e.g. Gianessi and Reigner, 2007).

However, since the 1980s, the public has become more aware of and concerned about the effects of pesticides on food safety and the environment (Curry, 2002; Kudsk and Streibig, 2003; 't Mannetje *et al.*, 2005). Agricultural policy at EU, national and regional scale now pays far more attention to producing food in a sustainable manner. The change in agricultural policy resulted in a shift from a policy emphasising production towards a policy advocating the sustainable management of natural resources and the landscape.

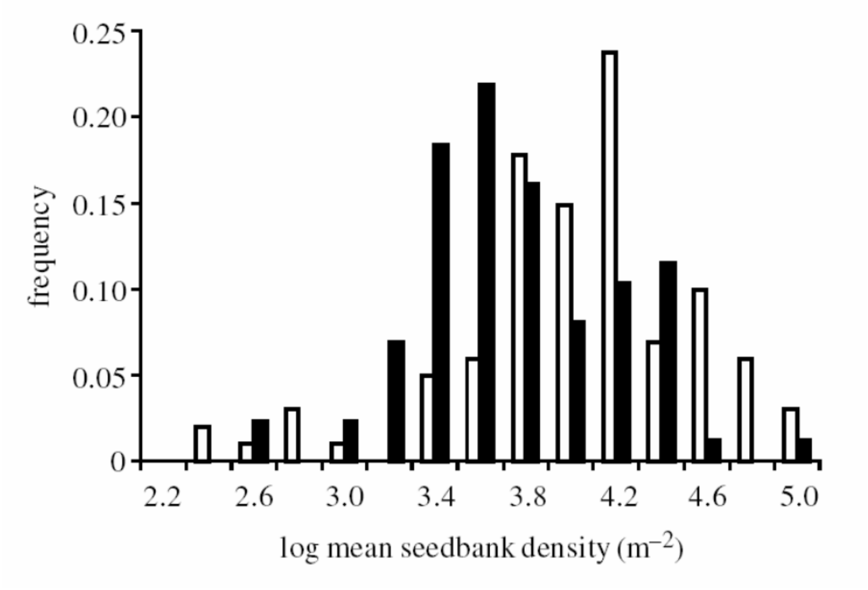


**Figure 1-2** Frequency histogram of seedbank density, expressed as the logarithm of the number of seeds per square metre of field, for fields in Great Britain sampled in the periods before (1915-1950) and after (1966-1990) rapid intensification of field management (e.g. herbicide use). The x-axis labels refer to the upper limit of bin width. 1915–1950 (mean of 101 fields, open bars) - 1966–1990 (mean of 87 fields, closed bars). Data originate from various published seedbank records and were amalgamated by Squire *et al.* (2003; see their Table 1c).

In the late eighties and early nineties weed management started being viewed as a problem to which ecological principles should be applied (Navas, 1991; Hess, 1994; Cousens and Mortimer, 1995) and this has steadily continued (Buhler, 1999; Mortensen *et al.*, 2000; Blackshaw *et al.*, 2006). Recent weed science textbooks (Liebman *et al.*, 2001; Booth *et al.*, 2003; Håkansson, 2003) and peer reviewed papers in 'Weed Research' testify that research has indeed moved in this direction (Kropff and Walter, 2000). Despite consumer preference for a reduction in the amount of applied pesticides, to avoid financial losses any reduction must be achieved without consequent reductions in crop quality. In terms of weight of product applied, herbicides form the biggest contributor of pesticides in outdoor vegetables overall (see Figure 1-3) and in each vegetable crop except onions and leeks that receive more fungicides (Garthwaite *et al.*, 2004). The situation is similar for all arable crops except oats and potatoes that received more growth regulators and desiccants respectively (Garthwaite *et al.*, 2006).

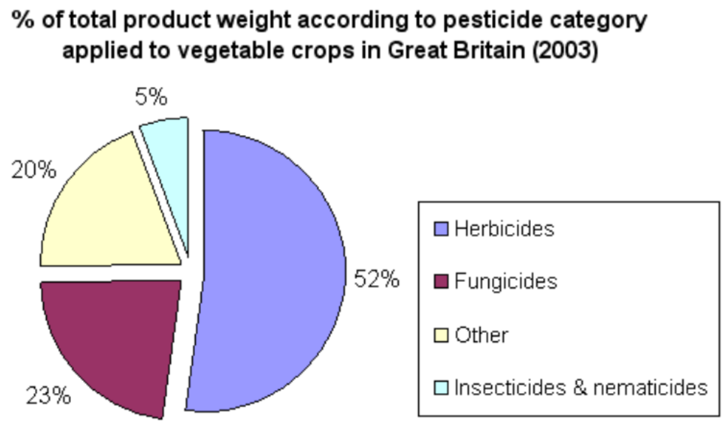


**Figure 1-3** Herbicides as a proportion of the total weight of pesticides applied to vegetable crops in Great Britain in 2003. Data from Pesticide Usage Survey Report (Garthwaite *et al.*, 2004).

Through various environmental policies, the British Government has stepped up the pressure to reduce pesticide use. One of the explicit aims of the 1990 Government White Paper ‘This Common Inheritance’ was to "limit the amount of pesticide use to the minimum necessary for the effective control of pests compatible with the protection of human health and the environment" (Department of the Environment, 1990). Since then it has been extended into various other policies, for example as a key sustainability indicator in ‘Towards Sustainable Agriculture – a Pilot Set of Indicators’ (2000) and through the implementation of the ‘National Pesticides Strategy’ (Pesticides Safety Directorate *et al.*, 2006). In 2001, the Voluntary Initiative was introduced by the Crop Protection Association in response to a Government plan to introduce eco tax on pesticides. Collaborating with other farming, countryside and crop protection organisations, a 5-year programme of voluntary measures to minimise the environmental impacts of pesticides was initiated (Goldsworthy, 2007).

With regards to weed management, one of the ways in which reducing pesticides is realized is by adopting reduced herbicide doses. The number of treatments a crop requires is positively correlated with the length of the critical weed-free period, i.e. the period a crop has to be kept free of weeds to avoid yield loss. Longer critical weed-free periods are typical for slow growing, low competitive crops such as carrot and onion (van Heemst, 1985). The number of herbicide treatments to carrots and parsnips has increased remarkably – see Figure 1-4, left, as derived from data from the website from Central Science Laboratory (2008) over the last 15 years. Despite this, a reduction in the amount of herbicide applied per unit area, confirming that reduced dose-rates are indeed being used (see Figure 1-4, right).

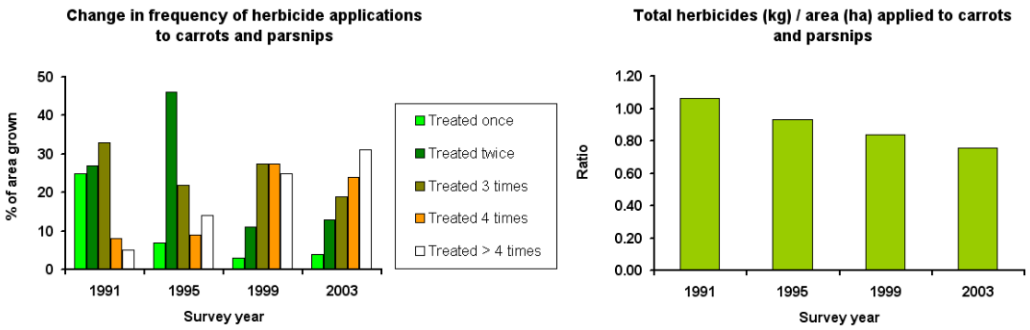


**Figure 1-4** Data from Central Science Laboratory on pesticide usage in carrots and parsnips over the period 1991-2003, showing that despite an increased number of herbicide applications per season, the overall amount of herbicides per unit area (ha) has decreased.

For weeds that are highly outcrossing, continuous application of reduced herbicide doses may result in the gradual accumulation of resistance through multiple genes, also called ‘creeping resistance’ (Gressel, 1995; Neve and Powles, 2005; Beckie and Gill, 2006). Although there is no consensus among weed scientists whether or not continuous reduced herbicide rates are indeed responsible for herbicide resistance as observed in the field (Neve, 2007), weed scientists seem to agree that where continuous reduced rates are applied in field situations this should be part of an integrated weed management strategy (Beckie and Gill, 2006; Blackshaw *et al.*, 2006).

Growers are not only under pressure to reduce pesticide usage, they are also facing a decrease in available herbicide products. After the last EU pesticide review (Directive 91/414/EEC) a number of important herbicides for horticultural crops were blacklisted to be phased out. For vegetable growers, new herbicides are unlikely to come to the market soon as agrochemical companies concentrate their search mainly on compounds which will be effective for the major crops due to increased development costs and stricter approval conditions (Copping, 2002; Grundy *et al.*, 2003). If no approval can be negotiated for alternative herbicides, serious gaps in weed control for growers of more specialist crops will be the result (Grundy *et al.*, 2003; Pesticides Safety Directorate, 2004).

Carrots are perceived to be the crop hardest hit. At the 2004 Annual Conference of the British Carrot Growers’ Association, Julian Davies (Stockbridge Technology Centre) said “The old ADAS booklet on weed control in brassicas and root vegetables ran to

62 pages of information on herbicides. By 2007 you might be able to write about all the available herbicides for carrots on the back of a fag packet." (Knott, 2004a). Indeed, after 31 December 2007 carrot growers for example, can no longer use herbicides based on the active ingredients metoxuron, prometryn, pentanochlor. In addition, a reduced maximum rate has been announced for linuron and is expected for new labels of pendimethalin after 2008 (Hamilton, 2007). Up until 31 December 2007, weeds were not regarded as a problem by most conventional carrot growers (personal communication, Cathy Knott) but especially the loss of Dosaflo (metoxuron) and Gesagard (prometryn) are regarded as creating a real gap in the herbicide armoury (Knott, 2004b; Martin, 2005).

In onions, herbicides based on the active ingredients cyanazine, prometryn and sodium mono-chloracetate have been revoked (Assured Produce, 2006; ADAS, 2007). The R&D Committee of the British Onion Producers Association (BOPA) gave a high priority to the search for new active ingredients and new weed management systems as a consequence of the loss of these herbicides after 2007 (BOPA, 2006).

With fewer herbicides available to vegetable growers there is a risk for certain weed species to escape the control operations and cause serious yield reduction. For example, in carrots and onions, Dosaflo (metoxuron) was used in combination with linuron to specifically target mayweeds and volunteer potatoes whereas Gesagard (prometryn) was used to control *Fumaria* spp. (ADAS, 2003). The Horticultural Development Council has funded trials (e.g. Knott, 2004b; Knott, 2006) to find new (programmes of) herbicides that can cover the gap, but this is a lengthy process and not without hurdles. Even when an alternative herbicide is proving successful in trials (e.g. aclonifen), it still has to acquire approval status in the UK. A new herbicide may not cover the range of weeds controlled by its revoked predecessors, e.g. off-label approval (SOLA) for Defy (prosulfocarb) is expected for 2008 which would guarantee control of *Fumaria* spp. but not *Matricaria* spp. / *Tripleurospermum inodorum* and *Senecio vulgaris* (Pesticides Safety Directorate, 2004).

The revocation of herbicides is not limited to a few crops but covers both arable and vegetable crops. Given that outdoor vegetables such as carrots and brassicas are often grown on land rented from arable farmers (Sly, 1978; ADAS, 2007), this leads to the reliance on an overall narrowing range of products and active ingredients. For example, herbicides based on the active ingredients isoproturon and trifluralin are used to tackle grass weeds and especially blackgrass (*Alopecurus myosuroides*) in cereal crops. Trifluralin has on-label approval in vegetable brassicas and carrots as well and no resistance to trifluralin has been encountered so far (WRAG, 2007). In 2007 the PSD announced that these herbicides were to be banned after failing to receive Annex I approval in the latest EC Review (Farmers Weekly Interactive, 2007), due to their perceived risk to aquatic life. The Weed Resistance Action Group (2007) said in a statement that “fewer herbicides mean there is greater pressure, both for resistance and on risk of those being used reaching water (as a direct effect of the area sprayed).”

In 2006 a new pre-emergent herbicide Defy (prosulfocarb) was approved for use in winter cereals (and potatoes) that could fill the gap left by isoproturon. Over a year later, specific off-label approval (SOLA) has been granted for use in a range of arable crops (spring barley, rye and triticale, winter field beans), outdoor grown vegetable (leeks, bulb and salad onions, carrots and parsnips, celery, celeriac) and a number of herbs (Pesticides Safety Directorate, 2008). Because of the lack of herbicides available to growers of minor crops, these SOLA’s are vital. In a recent study it was considered that “without them some crops could either not be grown, or it would be uneconomic to do so” (Grundy *et al.*, 2003). However, since many outdoor vegetables are effectively grown in a crop rotation with arable crops, granting SOLA’s for a particular herbicide to a wide range of crops inevitably leads to an increased frequency of application of that herbicide to the weed population. It is well recognized that the frequency of herbicide use is one of the factors contributing to the selection pressure for herbicide resistance (Maxwell and Mortimer, 1994) and several studies, though not all, reveal a positive correlation between frequency of use and herbicide resistance (Beckie and Jana, 2000; Légère *et al.*, 2000; Moss and Perryman, 2007).

At a conference focusing on the future of cereal weed control, experts warned against relying on a single product (Atlantis) too much after the loss of IPU and trifluralin and urged growers to use herbicides only as one component of an integrated weed management strategy (Farmers Guardian, 2007). Unfortunately, farmers tend to adopt integrated measures only after detection of herbicide resistance rather than as a preventative strategy (Clarke *et al.*, 1997; Beckie and Gill, 2006). One of the reasons for this is that the costs to prevent or delay herbicide resistance are perceived to be equal to the cost for managing a population where herbicide resistance is actually diagnosed. This suggestion has been corroborated in some scenarios (e.g. Powles *et al.*, 2001) and introducing cultural control measures as part of a strategy to prevent resistance will undoubtedly increase financial costs initially. However, Orson (1999) showed that preventative management can cost significantly less than the measures necessary once herbicide resistance is a reality (see Figure 1-5).

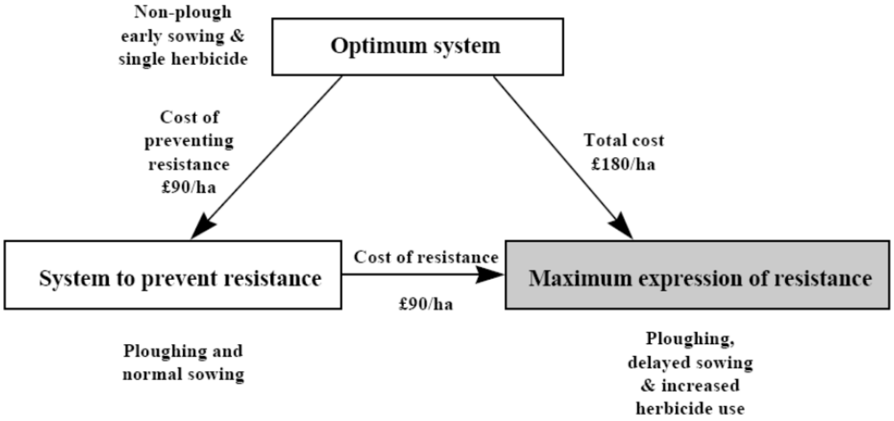


**Figure 1-5** The cost of a system aimed at preventing herbicide resistance vs. the cost of a system facing the consequences of herbicide resistance in blackgrass (*Alopecurus myosuroides*) – data after Orson (1999) and figure obtained from Clarke (1998).

This has led to an official endorsement to integrate herbicides with alternative measures by research and industrial partners alike. In 2003, the Weed Resistance Action Group (WRAG) produced a set of guidelines called ‘Managing and preventing herbicide resistance in weeds’; in it they emphasized “the need for cultural control to reduce the need for herbicides and the risk of resistance developing”.

Cultural control measures constitute:

manipulating crop-related aspects, for example, increasing sowing rate (Beckie and Kirkland, 2003) or breeding more competitive crop varieties so that reliance on herbicides is reduced (O'Donovan *et al.*, 2007)

manipulating the timing and nature of crop management practices, for example, through reduced fertilizer input or alternative cultivation regimes (Moonen and Barberi, 2004).

Measures recommended by the WRAG include set aside, a diverse cropping rotation and ploughing instead of minimal cultivation. Importantly, this message is supported by big companies such as Bayer, the manufacturers of herbicides who advocate the use of more integrated control strategies to protect and optimise the existing chemical options (WeedFocus, 2008).

Unlike arable crops where herbicide resistance in a few grass weeds is now considered a serious problem, no serious resistance problems currently exist in broadleaf weeds in outdoor vegetables in the UK (Moss, 2003). Herbicide sequences, herbicide mixtures and sometimes additional mechanical weeding are practiced in outdoor vegetables such as carrots and onions and it is possible that these strategies together are sufficient to prevent the development of resistance. However it would be unwise to take this for granted for the future especially given the recent revocation of a number of key herbicides. In addition, selection for resistance occurs long before herbicides visibly fail in the field (Moss, 2006) and it is suggested that resistance problems are “most unlikely” to be detected before 30% of the population consists of resistant biotypes (Gressel and Segel, 1978).

## 1.2 Study objectives

In the previous section it was concluded that there is both an increasing pressure on growers to deliver agricultural products that are produced in a sustainable way and at the same time a risk that a decreasing portfolio of herbicides or continuous use of reduced herbicide rates might jeopardise weed management and economic profits in the future. There is now a broad recognition that weed management strategies have to be diversified to meet these challenges and cultural control is increasingly seen as a vital part of integrated weed management.

The general objective of this study therefore was to evaluate the relative merit of weed management strategies based on cultural control on the long term development of weed populations.

Within the DEFRA project ‘Understanding the relative establishment times of crops and weeds within the changing seedbed’ - HH3406SX, of which this Phd research was part, carrot and onion had been chosen as target crops. The former because it is the vegetable crop hardest hit by herbicide loss and the latter since it is particularly vulnerable to yield loss if weeds are insufficiently controlled. The value of home produced carrots represents by far the highest value for all field vegetables (£167 million in 2005), whereas onions are less important in terms of value but constitute a relatively high proportion of the vegetable planted area (DEFRA, 2006). Two problematic weed species, *Stellaria media* (L.) Vill. and *Tripleurospermum inodorum* (L.) Schultz Bip. (see Figure 1-6) were initially chosen as model species.

**Figure 1-6** Two weed species frequent in many crops and chosen as ‘model’ species; on the left *Stellaria media* and on the right *Tripleurospermum inodorum*.

Scentless mayweed is often referred to as *Matricaria perforata* but this thesis will follow Stace (1997) and use *Tripleurospermum inodorum*. The weed species have been chosen as both are quite prevalent in field vegetables (see Table 1.2 in Grundy *et* *al.*, 2003), because for both weeds considerable amounts of biological data is available from other studies and because they possess contrasting life history characteristics (see Table 1-1).

**Table 1-1** Key contrasting life history characteristics of the two model species

| | *Stellaria media* | *Tripleurospermum inodorum* |
|---|---|---|
| Depth-mediated germination | practically no germination if seeds are located > 5 cm. | practically no germination if seeds are located > 2 cm. |
| Plant morphology | prostrate | upright |
| Flowering induction | not sensitive to daylength | sensitive to daylength |

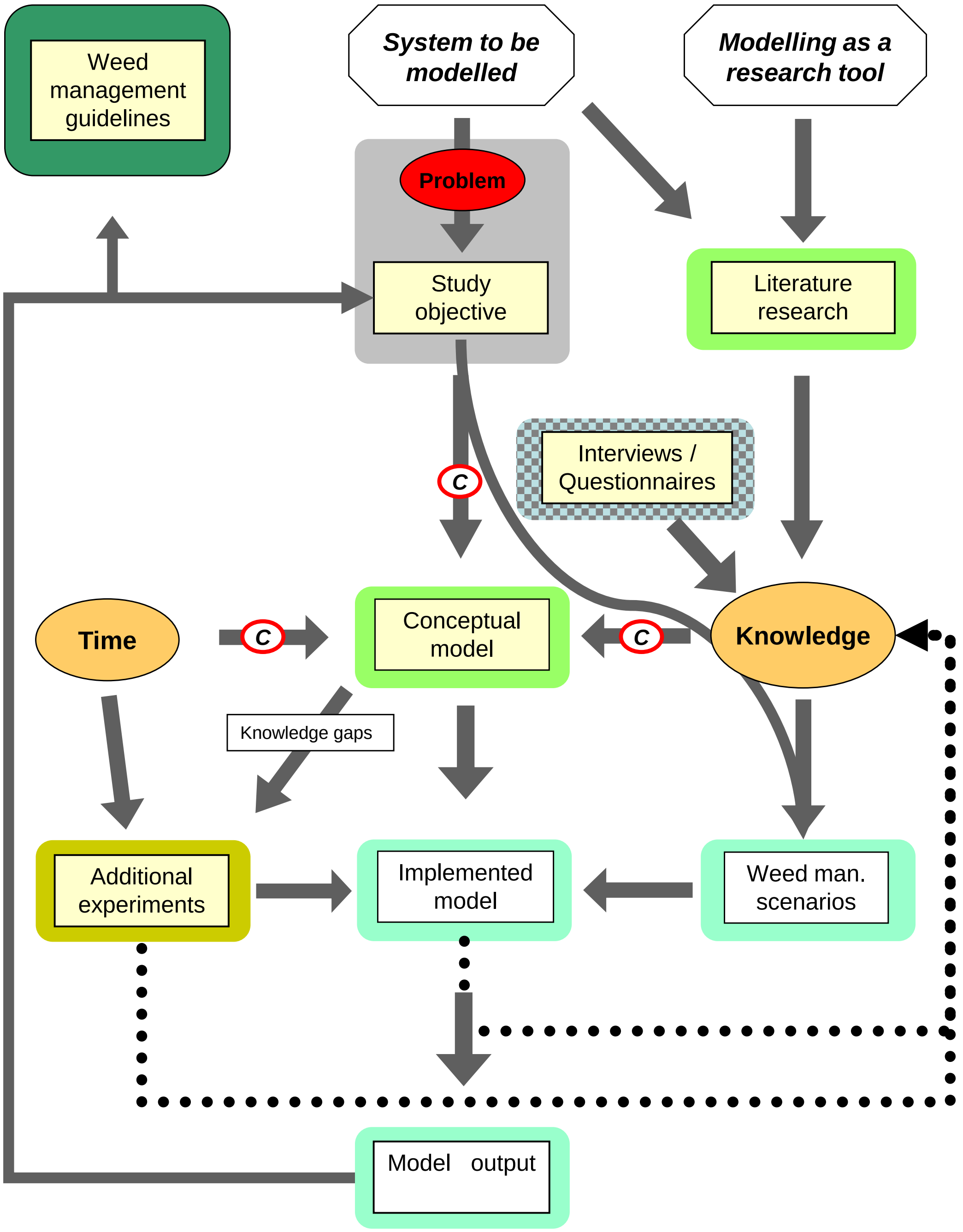
Due to the buffering effect of the weed seedbank, the evaluation of weed management strategies typically requires long-term field studies (Norris and Légère, 2004; Thomas *et al.*, 2004), especially if it involves crops grown in rotation. Such long-term trials are often not economically feasible. Population dynamic models on the other hand, are an efficient tool to compare the effect of weed management strategies on the long-term population dynamics (Kropff *et al.*, 1999) and carry a number of advantages. In a multi-component system a model brings together the knowledge of the parts and provides a coherent view of the behaviour of the complete system. Once a model is in place, more targeted, instead of ad hoc, experimentation can be planned (France and Thornley, 1984) and using sensitivity analysis 'Achilles heels' can be identified in a weed's lifecycle that can then be specifically targeted (Davis *et al.*, 2003).

Climate change provides both threats and opportunities to agriculture (Anonymous, 2005) and when proposing alternative weed management strategies it is important to understand how changing climate conditions might affect and interact with these strategies. It has been suggested that weeds may respond stronger than crops to resource changes (light, water, nutrients or carbon dioxide) due to their larger genetic diversity (Ziska, 2004).

Specifically then, the objective of this study was to develop a modelling framework, capable of simulating the impacts of (weed management strategies based on) cultural control and climate on the long-term population dynamics of weeds in field vegetable systems. The intended aim of the model is as a management aid. The modelling framework will be further referred to in the thesis as ECOSEDYN which stands for: Effects of Cultural control and climate On SEedbank DYNamics.

## 1.3 *Study approach and outline of the thesis*

At the start, literature reviews were carried out to select promising cultural control components for the weed management scenarios and to make sure that the weed biology was represented as accurately as possible in ECOSEDYN (see further Chapter 2). The approach followed to meet the objectives is graphically presented in Figure 1-7.



In addition a questionnaire (see Appendix 1) was sent out to 10 carrot growers and to an agronomist at the Allium & Brassica Centre (Carl Sharp) to find out about current common practices of commercial carrot and onion growers in the UK. The questions related to cropping system characteristics and the nature and timing of farming practices (weed management and cultivation). A further visit to three large commercial carrot growers (Elveden Estate, Isleham Fresh Produce and Watton Produce), going through the same questions, yielded additional information.

It is important to emphasize that the development of a model is not a one-way process but an iterative process of revisiting previous stages when flaws are identified and new insights gained (Balci, 1994; Jackson *et al.*, 2000). This aspect is represented graphically by the dashed arrows (feedback loops) in Figure 1-7. This feature also made it inevitable that in the thesis forward and backward references to sections of other chapters are given on several occasions. The study approach is narrated over the next paragraphs through outlining the content of the different chapters.

**Chapter 2** documents the conceptual modelling phase. The literature was thoroughly reviewed to get a comprehensive understanding of the system, to evaluate the different ways in which system components have been and can be modeled and to select the cultural control options that would form the components for the weed management scenarios. Together this resulted in the conceptual model (Robinson, 2006), a description of the simulation model addressing the biological aspects of the system. The assumptions, mathematical representation and parameterisation of those model components that operated independently of the weed management scenarios are presented in this chapter. Evaluation of available model components and parameters resulted in the identification of key areas for additional research which led to several field experiments being conducted that are discussed in the next chapters.

With the project progressing, the understanding of the system increased and this inevitably led to new areas for potential research. However due to time constraints these gaps could not be addressed through experiments and therefore had to be bridged by additional assumptions in the model.

In Chapter 3 and 4, experiments are described that were aimed at evaluating existing and formulating new model components. To continue the flow of the text, model implementation is presented at the end of each chapter. If the representation depends on the specifics of other model components or the weed management scenarios this will be referred to in the text.

**Chapter 3** explores the validity and robustness of the present ways in which seed movement by cultivation is modelled. The validity of the algebraic approach (multiplication of transition matrices) of modelling seed movement when multiple implements are involved and the assumptions in the more mechanistic models for ploughing as proposed by Colbach *et al.* (2000) and Roger-Estrade *et al.* (2001) were empirically evaluated. To compliment the experimental work that led to the transition matrices of the four implements by Mead *et al.* (1998), a transition matrix for the plough was generated. This chapter provides the theoretical justification, but not the exact implementation, for modelling vertical seed distribution. The model implementation of vertical seed distribution due to cultivation and harvest is given at the end of the chapter.

**Chapter 4** deals with the theme ‘Plant growth and reproduction’. Experiments identify:

- the environmental variable that best explains biomass increase of weeds during early growth
- the onset and increase of flowers relative to biomass increase
- the biomass – seed relationship for plants of different ages
- the relationship between timing and duration of flowering and plant biomass

Together the results lead to the formulation of a set of model components for biomass increase, flower production and seed production over time. The mathematical representation and parameterisation of the component models for Biomass increase, Flowering and Seed production are presented in the last section of the chapter.

**Chapter 5** represents the second part of the modelling process. First the specifics and hypotheses regarding the weed management and climate change scenarios are given. Then the modelling methodology, e.g. the model structure and the analysis of model output, is explained. Lastly the results of the model simulations in ECOSEDYN are presented and discussed.

In **Chapter 6** a summary of the experimental research achievements is given first. I then reflect on model development, provide explicit weed management guidelines based on model output and discuss where future work on ECOSEDYN should be focused and how this fits in with the future of weed research in general.

The key content of the chapters and the way the chapters relate to each other is graphically represented in Figure 1-8.

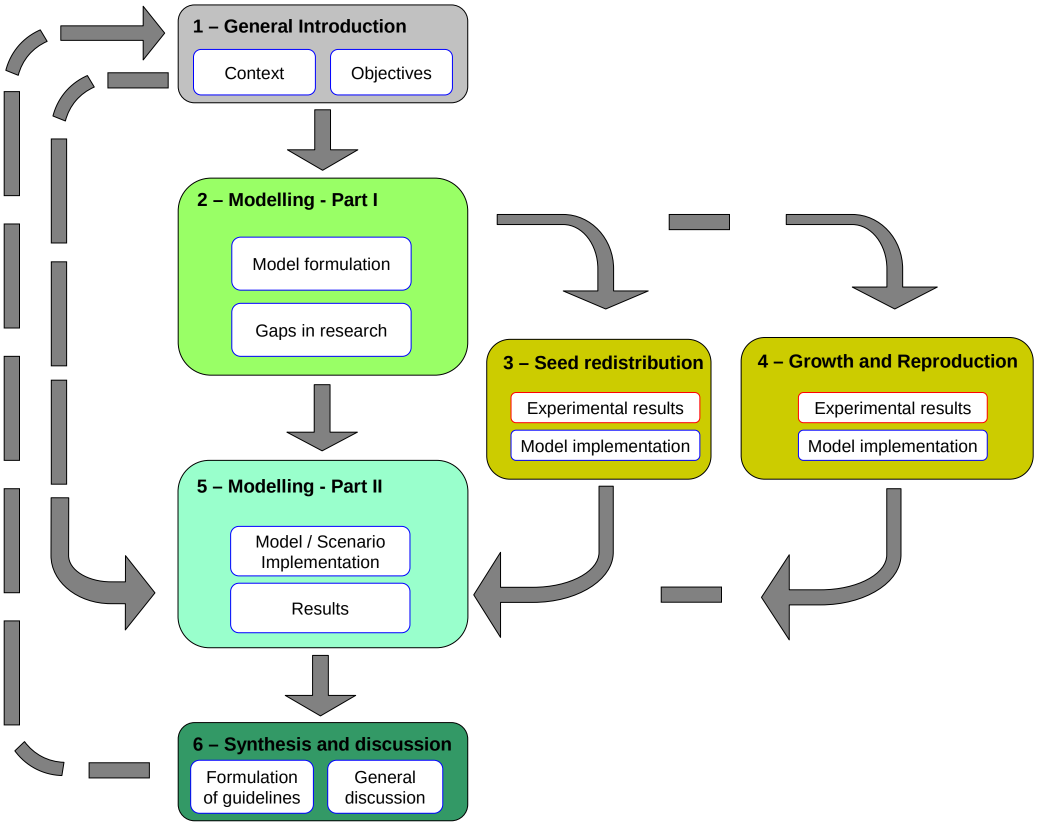


**Figure 1-8** Thesis-structure and key contents of the six chapters

# 2 Modelling – Part 1: Conceptualisation

## 2.1 *Introduction*

In Chapter 1 the ‘Why’ question, the rationale for a modelling approach, has been addressed. In order to choose the right modelling approach, the “What” and “How” questions are addressed in this chapter. This indispensable process is often described as the conceptual modelling phase (Jackson *et al.*, 2000).

This chapter consists of four sections and the way they relate to each other is shown in Figure 2-1. In section 2.2 a blue-print of the system is given. In Section 2.3 the implementation of the cultural control options that were chosen as the components in the weed management scenarios and the climate scenarios are presented. Having defined the weed management scenarios, Section 2.4 addresses model formulation; most importantly, the degree of complexity (abstraction, space, time, random events) at which the system should be represented. Section 2.5 contains the mathematical representation of the component models: the relevant processes, the in- and outputs of the component models and the chosen parameters. These parameters were collected through literature searches (weed biology) and interviews (agronomists and growers).

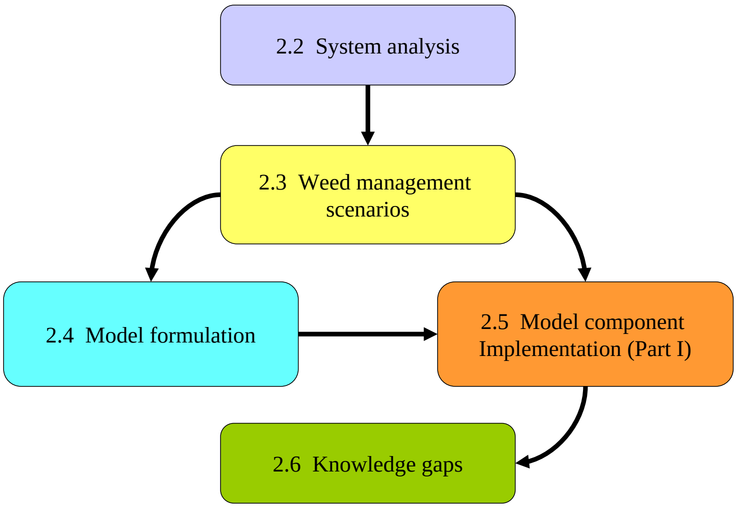


**Figure 2-1** Structure of Chapter 2 and relationships between the 5 remaining sections.

The last section, 2.6, highlights the areas that were identified as knowledge gaps. It functions as the connection to Chapters 3 and 4 in which the experimental work on weed seed redistribution in the soil (Chapter 3), and plant growth and reproduction (Chapter 4), is presented first, followed by the particular model components that were developed as a result of the work.

## *2.2 System analysis*

A precursor to modelling is an understanding of the system to be modelled. The system comprises the object of study and its regulating factors. Here, the object of study is an annual weed population occurring as seeds and plants in an agricultural field. The development of the population over time is regulated by interactions amongst individuals and by factors intrinsic and extrinsic to the population (Cousens and Mortimer, 1995).

### 2.2.1 Life history of an annual weed

Weed science has long focused on targeting only the above ground individuals of a weed population, which is understandable from a crop yield loss point of view. However, considering that most species spend more time as seeds in the soil than as plants, from a weed management point of view it makes sense to explore the possibilities to target the weed seedbank (Gallandt, 2006). Processes that affect seeds are very different from those that affect plants. Equally, the impact of agronomic practices (e.g. efficiency of weed control) can not be considered independent of plant lifestage (see Section 2.2.3.9). Hence, from a modelling point of view there is ample reason to break the lifecycle of an annual plant down into lifestages (see Figure 2-2).

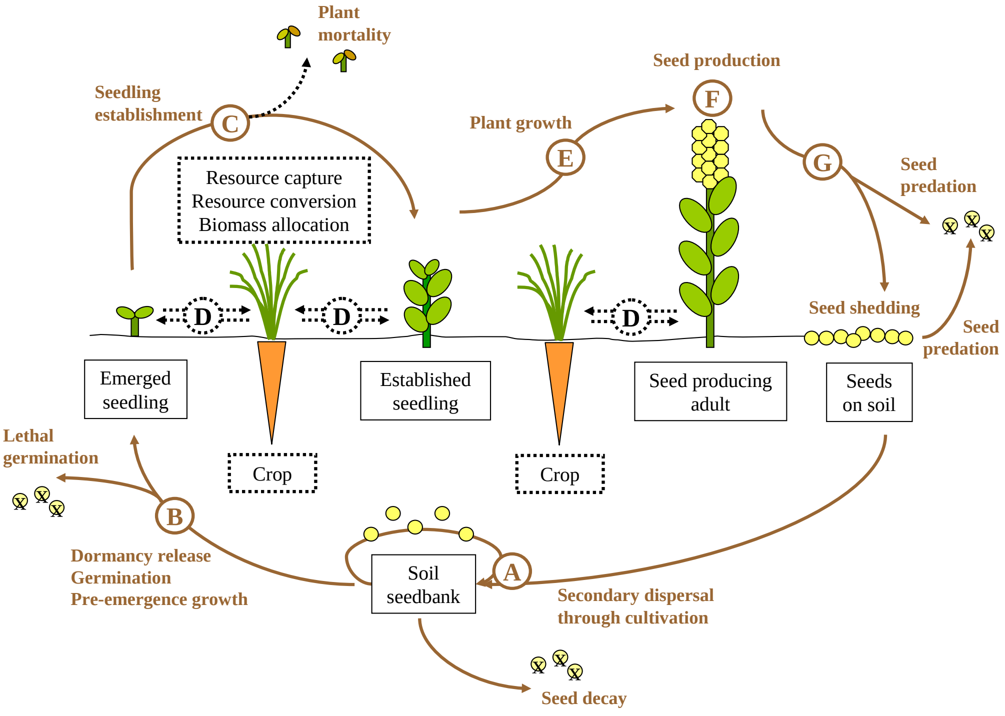


**Figure 2-2** Lifecycle and life stages of an annual weed in a crop habitat. The processes A-G are referred to and elaborated on in the main text.

The depth of a seed in the soil is of paramount importance since it determines whether or not the specific conditions necessary to start germination can be met. Several studies have shown the depth-dependent relationship between proportion emergence and vertical position in the soil (Benvenuti *et al.*, 2001a; Grundy *et al.*, 2003a; Mennan and Zandstra, 2006). In general, the proportion emergence decreases with increasing soil depth, but the rate with which this happens is species specific. Not all seeds emerge successfully though; in the ‘white thread’ stage the seedlings are vulnerable to pathogens, desiccation or simply a failure of the hypocotyls to reach the soil surface. The probability of fatal germination increases over the depth range over which the relevant weed species can germinate and emerge (Grundy *et al.*, 2003b) but decreases beyond this depth due to depth-mediated induction of dormancy (Benvenuti *et al.*, 2001a)

The depth distribution of the seedbank is mainly determined by the cultivations (Process A in Figure 2-2) the seeds have experienced (Grundy *et al.*, 1996). For example, ploughing buries seeds that were initially on the surface whilst bringing buried seed up towards the surface.

Seeds in the seedbank can be dormant, i.e. in a physiological state that prevents the seed from germinating, for a certain time in the year. The release of dormancy is a continuous process which enables the seed to germinate over an increasing range of conditions (Vleeshouwers and Bouwmeester, 2001). When non-dormant seeds do not germinate, they may go ‘back’ into the dormant state again. The seasonal dormancy cycles, i.e. release and induction of dormancy, are regulated largely by temperature (Vleeshouwers *et al.*, 1995; Bradford, 2002). If conditions for germination are conducive, the seeds in the seedbank that are non-dormant will germinate and emerge (Process B in Figure 2-2), thus forming the above-ground part of the population. Soil disturbance through cultivations is an important trigger for seeds to germinate (Roberts and Potter, 1980). This is used in the stale seedbed technique where a series of cultivations is performed to deplete the germinable fraction of the seedbank, which can alleviate weed problems in the crop that is subsequently sown or transplanted. Cultivation in the dark may reduce or delay the number of weed seeds that germinate, but this depends on a

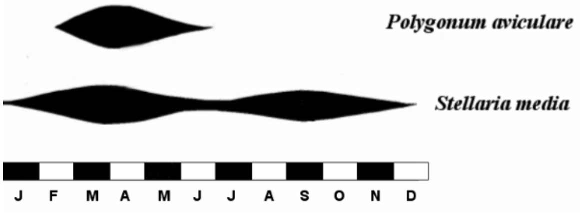


**Figure 2-3** Two contrasting patterns of emergence over the season. Adapted from Naylor (2002).

number of factors, notably soil moisture (Botto *et al.*, 2000) and required light sensitivity (Juroszek and Gerhards, 2004).

The periodicity of emergence of a given weed species can give an indication of whether seeds are inhibited from germination primarily by dormancy or by unfavourable climatic circumstances. In the former case, peaks of emergence may be observed in spring but not in autumn despite the weather conditions being very similar. This is the case for so-called summer annuals (e.g. *Polygonum aviculare*, see Figure 2-3) that require low temperatures to release dormancy but where high temperatures induce dormancy. Other species exhibit a pattern where emergence peaks are both seen in spring and autumn, mainly regulated by temperature and, to a lesser extent, soil moisture (Grundy and Mead, 2000).

Studies have shown that emergence can be reduced under a developing crop canopy for some but not all species (Rees and Brown, 1991; Leblanc *et al.*, 2002; Norsworthy, 2004). In a developing canopy, both thermal amplitude (Benech Arnold *et al.*, 1989) and the ratio of R:FR light (Holmes and Smith, 1977) decrease, the chlorophyll in the leaves acting as a filter to the light and the canopy layer as a buffer against temperature fluctuations.

The extent to which the crop canopy can affect the release of dormancy, will depend on the density of the crop canopy before and during the 'periodicity of emergence' (Kruk *et al.*, 2006). Whether dormancy release is impeded is also species specific; R:FR ratios between 0.5-0.8 had to be imposed to inhibit seed germination of *Lolium multiflorum* (Deregibus *et al.*, 1994) whereas only slight reductions in R:FR ratio from natural light were sufficient to influence the emergence pattern of *Brassica campestris* and *Silene gallica* (Batlla *et al.*, 2000). The effects of thermal amplitude and decline in R:FR ratio sharply decrease in magnitude with seed burial depth. Kruk *et al.* (2006) found that when seeds of six weed species had been buried in the soil there was no effect of the incipient canopy on the number of emerged seedlings for any of the weed species. However, for some weed species, emergence was reduced if the seeds were placed on the surface.

The time of emergence of a weed seedling relative to the sowing or transplanting date of the crop is important in determining the <u>growth rate and probability of survival</u> (Process C in Figure 2-2). It is important to realise that, relative to the uniform emergence of a sown or transplanted crop, the emergence of weeds is spread over a long period. As with other life history characteristics, variability is one of the survival strategies of a weed population as a whole, in an insecure habitat. Without weed management, earlier emerging weeds would have had ideal establishment conditions giving them a head start over the crop. However, these weeds would be most detrimental to crop yield and therefore, the majority of weed management in any crop is concentrated around the establishment phase of the crop, with the seeds germinating in that period more likely to be killed. Weed seedlings emerging after the main weed management window may have a higher chance of survival, but, on the other hand, the quality of the habitat is lower as competition for resources will start earlier. Competition for resources (Process D in Figure 2-2) implies that either one or both of the plant species cannot utilise as much resources as when grown in isolation. A reduction in the available resources is reflected in a decrease in the accumulated biomass of the plant. For a grower this simply means that the more weeds, the higher is the crop yield loss. Thus, the size of a plant is largely regulated by the number of plants (crop + weeds) per unit area. The density and relative timing of establishment of neighbours can affect the allocation of biomass to stems vs. leaves (Rohrig and Stutzel, 2001; Steinmaus and Norris, 2002) and the vertical distribution of leaves in the canopy (Baumann *et al.*, 2001), in other words, the efficiency of resource uptake. In addition, for some weed species it has been observed that competition for light tends to reduce the allocation of biomass to reproductive structures in favour of vegetative structures (Baumann *et al.*, 2001; Knezevic *et al.*, 2001).

After a period of vegetative growth (Process E in Figure 2-2) an annual plant starts allocating biomass to reproductive structures (Process F in Figure 2-2). The timing of this switch is not so much affected by the size of the plant but rather by accumulated thermal time (Swanton *et al.*, 1999) or a combination of day length and accumulated thermal time in short- and long-day plants. The size of the plant is important in that it determines the reproductive output. In other words, bigger plants produce more seeds.

After seeds have accumulated enough thermal time they are mature and may be shed on the soil surface or dispersed by the wind (Process G in Figure 2-2). Once on the soil surface they may be predated. Maternal environment during maturation, age of the mother plant during maturation and position of the seed on the plant (Kegode and Pearce, 1998) are aspects known to affect the dormancy status of a seed (Andersson and Milberg, 1998).

### 2.2.2 Regulating factors

The primary concern of this study is to create a model where the regulating effect of weed management strategies on population dynamics can be simulated. It is clear that cropping systems and specific farming practices can strongly influence the composition of the weed community, the abundance of individual species within this community and the development of the population of a certain weed species. For example, Albrecht (2005) reported that 6 years after conversion from conventional to organic farming, 31 out of 44 species had increased and 3 species had decreased relative to two years prior to the conversion.

On the other hand, changes in plant population size can occur regardless of management practices. An example is the increase, especially over the last two decades, in thermophilic plant species in the Netherlands that has been attributed to climate change (Tamis *et al.*, 2005).

Similarly, other extrinsic factors (i.e. weather and other organisms) interact with weed management. For example, a number of arable weed species in the UK, once common, are now considered rare. In the case of *Agrostemma githago* (Firbank, 1988) it was improved seed cleaning that brought about the decline (Bond and Turner, 2004). Looking at the distribution maps of rare arable weeds in the UK reveals that their presence is gravitating towards the south of the UK, where calcareous soils prevail (Wilson and King, 2008). The UK represents the northern boundary of the geographical distribution of *A. githago* and it is still quite common in the more central area of its distribution, such as Spain. This shows that edaphic, climate and management factor are interacting forces in shaping the dynamics of weed populations. In conclusion, at any one time, population dynamics are subject to change due to extrinsic factors, to causes intrinsic to the population (e.g. density dependent regulation), to the interaction between both types of factors and to interactions

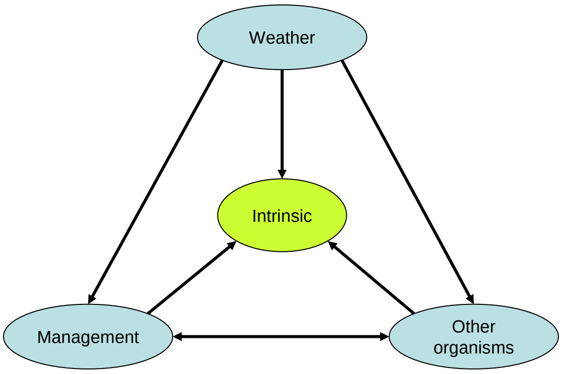


**Figure 2-4** Diagrammatic representation of the interaction between intrinsic population processes and extrinsic factors (after Cousens and Mortimer, 1995).

amongst individuals in the population (Cousens and Mortimer, 1995) (see Figure 2-4). Understanding the key factors regulating weed population dynamics requires integrating the perspectives of two fields, agronomy and plant ecology.

#### 2.2.2.1 Density dependence

Density-dependent factors regulate population growth in such a way that the impact of these factors per individual changes with population size. One of the best examples of density-dependent processes in plant ecology is competition for limited resources (Firbank and Watkinson, 1986). By increasing plant density, total yield will increase towards an asymptote whereas the average weight of an individual plant decreases according to a negative hyperbole (see Figure 2-5).

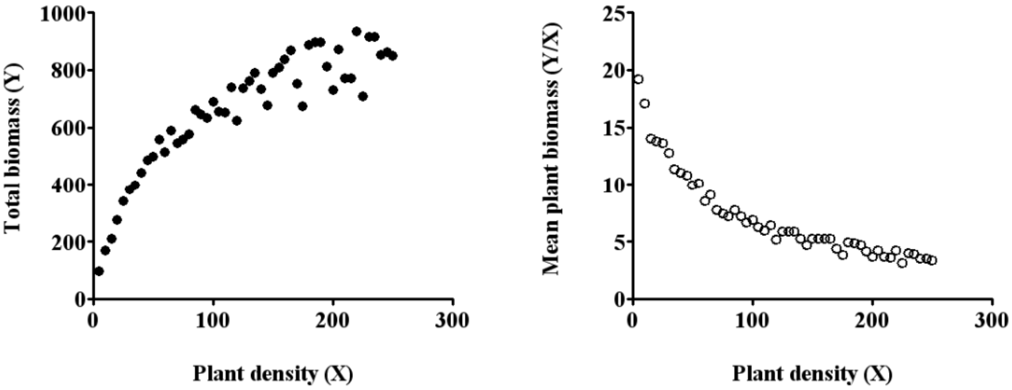


**Figure 2-5** Production-density curves (left graph showing total biomass and right graph individual plant biomass) describing a hypothetical single-species stand. Curves are based on Håkansson (2003). Left curve is of the form Y = X/(a + bX) with a = 0.05 and b = 0.001. Random noise was added to the resulting Y values to mimic real data.

Density-dependent effects often tend to work as ‘inhibitory checks’ on the population, but positive density-dependence (also called Allee effects or facilitation) has been observed as well (Cappuccino, 2004; Davis *et al.*, 2004a).

In contrast, the impact of density independent factors (such as weather) remains constant per individual, regardless of population density. Without density-dependent regulation a population would either exponentially increase forever or go extinct. Hence, ignoring density-dependence in population dynamic models may lead to over-estimation of the population size.

Most population dynamic models that include density-dependence have singled out weed seed production as the life-stage through which it is assumed to operate (Holst *et al.*, 2007). For many plant populations this may be true, but studies have shown that density-dependence operates on other areas, for example recruitment and mortality as well (Crawley, 1990; Silvertown and Charlesworth, 2001). Lintell Smith *et al.* (1999) found that density-dependent recruitment stabilised populations to such an extent that hardly any density-dependent fecundity could be observed. Several authors have shown that density-dependence at different 'locations' in the life-cycle can produce different dynamics (Watkinson *et al.*, 1989; Gillman *et al.*, 1993; Buckley *et al.*, 2001). Westerman *et al.* (2007) compared three scenarios where density-dependence was included at different stages in the lifecycle (seedling emergence, seedling survival or seed production) of a population of the parasitic weed *Striga hermonthica*. The mean seed production per individual plant below which the population would go extinct was three times higher if (only) seed production was density-dependent as compared to if (only) seedling emergence was density-dependent. Hence, arbitrarily choosing density-dependence might result in spurious projections of population size and dynamics.

Goldberg *et al.* (2001) argued that density mediated population regulation is not a within-species matter but rather a mechanism that operates on the level of the entire community. They provided evidence that support this hypothesis from desert annual plants in Israel. At all three life history stages studied (emergence, survival, and final size) strong evidence of community-level density dependence was detected. As the crop either possesses most biomass or is the most abundant species in the 'crop-weed community', it makes sense to evaluate the density-mediated effects of the crop on life stages of weeds.

Weeds that survive weed control will be competing for light and possibly also for water and nutrients with crop plants and this in itself is a density-dependent process. Numerous studies have shown that by increasing crop density and decreasing row distances the total and/or mean individual weed biomass could be reduced (Wilson *et al.*, 1988; Wilson *et al.*, 1995; Murphy *et al.*, 1996; Weiner *et al.*, 2001; Mertens and Jansen, 2002).

Density-dependence due to intra- or interspecific weed competition only occurs above a certain weed population threshold size. Unless fields are extremely weedy and/or weed control operations around crop sowing are somehow unsuccessful, the weed population is heavily reduced and may be well below this threshold. For example, Medd (1996) reported that no clear density dependence could be detected for fecundity below a density of 40 individuals of wild oat / m$^2$. Even in a wheat crop sown at a high density of 150 plants / m$^2$ to boost competitiveness, yield losses of around 15-20% would be incurred from densities of up to 40 wild oat plants / m$^2$

(Martin *et al.*, 1987). This is well above the economic threshold (ET) range of 9 – 13 plants $m^{-2}$ (Jones and Medd, 2000). Therefore, if weed control is successful, the importance of intra- and inter-specific weed competition may be minor. Indeed, Debaeke (1988) showed that a density independent model predicted weed population development well in a three-crop rotation system. The way density dependence is actually represented in most population dynamic model depends on how competition for light between crop and weeds and weed seed production are modelled. If biomass is accounted for, then in fact plant biomass is density-dependent. Alternatively, seed production can be modelled as a function of density.

#### 2.2.2.2 Agronomical aspects: cultural control

Organic as well as conventional farmers in the UK are advised to grow carrots and onions in a 5-7 year rotation (Assured Produce, 2008). This is mainly to avoid the build-up of soil-borne diseases such as white rot in the case of onion (Soil Association, 1999b), and cavity spot and violet root rot for carrots (Soil Association, 1999a; Assured Produce, 2007). The questionnaires and further interviews with carrot growers (see Appendix 1) and crop consultants (Carl Sharp and Tom Will) highlighted that growers often rent a field from arable farmers once every five to eight years. In the other years, a range of arable crops are grown by the arable farmers.

Different crops in the rotation may vary in three key aspects; timing (e.g. sowing time) and type of farming practices (e.g. cultivation), crop competitiveness and weed management strategy. These aspects will affect the performance of the weed species in the seedbank. Different cultivation regimes prior to crop sowing may generate different vertical distribution patterns of weed seeds in the soil, thereby regulating the recruitment of weeds (Froud-Williams *et al.*, 1983; Feldman *et al.*, 1998; Vanhala and Pitkanen, 1998). Various studies have shown that weeds produce more biomass and seeds in one crop or crop cultivar than another because of differences in relative emergence, relative crop competitiveness and/or harvest time (van Acker *et al.*, 1997; Lutman, 2002; Sester *et al.*, 2004; Weaver *et al.*, 2006). Weeds belonging to the same botanical genus or family as the crop can have an advantage over other weeds since they can not be targeted by selective herbicides as that would damage the crop as well.

Not surprisingly, therefore, weed demographic rates are crop / cultivar -specific which may lead to different population densities; for example *Convolvulus arvensis* density was higher in wheat years than in sunflower years (Jurado Exposito *et al.*, 2004). Moreover, when considering crop rotations, demographic rates in one crop may be affected by the previous crop. For example, fewer weed seedlings were observed in corn when alfalfa was the preceding crop as compared to continuous corn in a low-input system without herbicides (Clay and Aguilar, 1998). Long-term field experiments have shown that the development of the weed flora composition, and with it the abundance of individual weed species, can depend on the type of crops in a crop rotation (Ball, 1992; Liebman and Dyck, 1993; Sosnoskie *et al.*, 2006). Even for crop rotations of the same length and consisting of the same crops, different annual mean weed population growth rates may result depending on crop order (Mertens *et al.*, 2002) or timing of cultivation (Davis *et al.*, 2004b).

The timing of emergence of the weed relative to that of crop plants is paramount as it determines growth and yield of both crop and weed. Early weed cohorts cause higher crop yield loss than later cohorts (Knezevic *et al.*, 1997; O'Donovan and McClay, 2002; Hock *et al.*, 2006). Moreover, early-emerged weed cohorts produce more biomass and seeds than late-emerged weed cohorts (Brainard and Bellinder, 2004; Willenborg *et al.*, 2005; Walsh and Minkey, 2006). This can even fundamentally change the population growth rate; Selman (1970) as cited in Cousens and Mortimer (1995), showed that the ratio of population size between two years of *Avena fatua* was higher ($\lambda = 2.74$) when sowing of spring barley was early than when sowing was delayed ($\lambda = 0.40$).

Scursoni *et al.* (1999) showed that twice as many *Avena fatua* seeds entered the seedbank in a wheat crop compared to a barley crop due to the later harvest time of wheat. Bennett and Shaw (2000) showed that early maturing soybean cultivars resulted in lower seed production by *Ipomoea lacunosa* and reduced germination of *Sesbania exaltata* seeds due to harvesting prior to physiological maturity. Finally, Hansson *et al.* (2001) studied the influence of harvest time (and stubble height) on weed seedling recruitment in barley grown for silage. In the absence of weed control, the later barley was harvested, the higher the percentage of weed seeds that had shed at harvest time. Consequently, the number of weed seeds in the soil at the time of harvest (as well as the number of weed seedlings in the following year) increased with progressive harvest time (see Figure 2-6).

For the plots where barley was harvested early for 6 years the selection pressure was favourable to fast reproducing species; *Stellaria media* increased considerably over the 6 year course in comparison with late reproducing weeds.

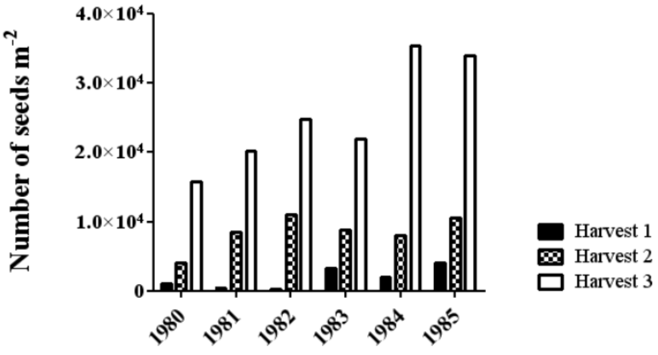


**Figure 2-6** Annual changes in the total number of weed seeds recovered from the soil after harvesting barley at three progressive stages of grain maturity and leaving 10 cm stubble (redrawn from Hansson *et al.* (2001). Harvest times: H1 was at grain-water content 50-60%, H2 was at grain-water content 35-45% and H3 was at grain-water content 18-32%. Number of days from H1 to H3 varies between 17 and 26.

Although substantial experimental work was conducted relating to cultivation (see Chapter 3), this was in order to evaluate the individual cultivation models available rather than as an effort to use cultivation as a separate component of cultural control.

## 2.3 *Weed management scenario implementation*

In the previous section it was concluded that crop rotations are an essential feature of carrot and onion production and as such the crop rotation feature has to be implemented in ECOSEDYN. When it comes to crop rotations there is no such thing as standard practice. The questionnaires and interviews with carrot growers and crop consultants (Carl Sharp and Tom Will) highlighted that a range of different crops are grown by the landowners on the land that is rented out but cereals are often grown in several years of the rotation. It was impossible to collect parameters for the entire range of crops grown in commercial fields, and for simplicity winter wheat was chosen as the single arable crop in rotation with carrot. More than 90% of wheat in the UK is now sown in autumn rather in spring (Robinson and Sutherland, 2002). Therefore, a simplified crop rotation is proposed for ECOSEDYN, consisting of one year of vegetable (carrot / onion) and five years of autumn sown wheat. On the one hand, simplifying the "system" results in a concession to the practical value of the model predictions. On the other hand, a simplified system is more easily comprehended and by understanding the basic principles, guidelines can still be given for more complex systems. The aim was to compare the weed seedbank after a total length of 24 years, i.e. 4 complete crop rotations, had passed.

The cultural control methods chosen as components for the weed management scenarios are:

- Crop sowing time
- Crop variety (maturity time)

Crop sowing time was chosen as the first cultural control component because the Defra project of which this Phd studentship was part, had as a primary aim to gain a better understanding of the importance of relative crop and weed emergence timing. Crop variety (maturity time) was chosen as the second cultural crop component because the few studies that explicitly included different times from sowing to harvesting show substantial effects on weed seed production.

If the availability and efficacy of weed management options for carrots is sufficient, then growers do not need to consider the weed management of the field in the years that the arable crop is grown. However, the diminishing range of post-emergence herbicides has contributed to an attitude where a more holistic or integrated view of weed management is being considered more positively (pers. communication Tom Will). Approximately 85% of the land that commercial vegetable growers use for growing carrots is rented land (pers. communication Tom Will) and this shared ownership does not facilitate the integration of weed management. The selected components are therefore applied in both the vegetable as the arable phase of the crop rotation. The cultural control options are to be combined in a factorial to give a range of weed management scenarios assuming a ‘worst-case’ scenario for weed control (i.e. with herbicide efficacy values being 75% of normal efficacy values). Scenario components are referred to in this way: V_ST, V_MT, A_ST, A_MT where the prefix ‘A’ or ‘V’ indicates whether the vegetable or arable crop is concerned and the postfix ‘ST’ and ‘MT’ stands for sowing time and maturity time respectively. A particular weed management scenario might for example consist of V_ST=1, V_MT=3, A_ST=2, A_MT=3.

In comparing the weed management scenarios two main questions were posed:

1. Which cultural control practice, sowing time or crop variety, and applied in which crop, has most potential in alleviating long term weed seedbank levels?
2. Can cultural control practices applied in one crop (carrot or winter wheat) maintain sufficient low weed seedbank levels or is the application in both crops required?

A more thorough explanation of the weed management scenarios and specific hypotheses are given in Chapter 5.

### 2.3.1 Implementation of crop sowing time

Five different sowing dates for carrot and onion and three for winter wheat were included in the weed management scenarios. Crop sowing and consequently seedbed preparation times vary markedly, both to provide carrots throughout the year and according to the type of market outlet (processing or fresh). Early carrots are sown from October to February and are grown under polythene. ‘Maincrop’ carrots are sown from April to mid June at densities of 600 to 800 thousand seeds / acre, approximately twice the density at which early carrots are sown (Elsoms, 2007c). In ECOSEDYN, early carrots (grown under polythene) will not be considered as no information is available about the effects of polythene on weed biology.

Sowing dates follow general practice in the UK and were obtained through the catalogues of breeding companies (Elsoms, 2007b (carrots); Elsoms, 2007a (onions)) from literature (Spink *et al.*, 2000 (winter wheat)) and from trials from the Home-Grown Cereals Authority (HGCA, 2002 (winter wheat)), and are given in Table 2-1.

**Table 2-1** Sowing dates and symbols used in ECOSEDYN to identify scenarios for the different crops in the crop rotation

| **Symbol** | **Carrot / Onion** | | **Symbol** | **Winter wheat** | |
|---|---|---|---|---|---|
| | Date | Day | | Date | Day |
| V_ST = 1 | 1 March | 152 | A_ST = 1 | 1 October | 1 |
| V_ST = 2 | 15 March | 166 | A_ST = 2 | 19 October | 19 |
| V_ST = 3 | 29 March | 180 | A_ST = 3 | 8 November | 37 |
| V_ST = 4 | 12 April | 194 | | | |
| V_ST = 5 | 26 April | 208 | | | |

## 2.3.2 Implementation of crop variety (maturity time)

Three different crop varieties (maturity times) were selected. For carrot, the online product catalogue of Elsoms (2007b) was used to choose realistic values for the time from sowing to maturity: in the Nantes group, early (e.g. Norwich F1), intermediate (e.g. Nairobi F1) and late (e.g. Nerac F1) maturing varieties take between 98 and 130 days from sowing to maturity. Data on onion varieties is available from studies at Wageningen University (van den Broek, 2002). The variation in harvest time ranges between 115 and 129 days from sowing to 50% foliage senescence for an early and late maturing variety respectively. The time from sowing to harvest varied between winter wheat varieties by about 14 days (Gleadell, 2007; HGCA, 2007). Sowing and harvest dates varied depending on the location in the UK and resulted in a range of 301 to 349 days from sowing to harvest with an average of 320 days (HGCA, 2002). The maturity times are given in Table 2-2.

**Table 2-2** Maturity times (days after sowing, DAS) and symbols used in ECOSEDYN to identify scenarios for the different crops in the crop rotation

| **Symbol** | **Carrot (DAS)** | **Onion (DAS)** | **Symbol** | **Winter wheat (DAS)** |
|---|---|---|---|---|
| V_MT = 1 | 98 | 115 | A_MT = 1 | 313 |
| V_MT = 2 | 112 | 122 | A_MT = 2 | 320 |
| V_MT = 3 | 130 | 129 | A_MT = 3 | 327 |

It was assumed that the difference in time to maturity would be constant at each sowing time. It has to be emphasized that the values do not represent particular varieties since this assumption is unlikely to hold for specific crop varieties, i.e. variety A may mature 14 days earlier than variety B at ST = 1 but only 7 days earlier at ST = 3. The particular way in which the crop harvest date is determined in ECOSEDYN is explained in Section 4.7.1.2, after the novel modelling approach for 'Biomass Increase' has been explained.

In conclusion, given the various levels of sowing time and maturity time, a full factorial of combinations of cultural control could be created resulting in 135 weed management scenarios: V_ST (5) x V_MT (3) x A_ST (3) x A_MT (3).

### 2.3.3 Climate scenarios

As indicated in Section 2.1.2, plant populations are regulated by several factors that interact and changing climatic conditions are likely to interact with the effect of weed management scenarios. Weather projections for the UK estimate the annual temperature to rise between 2˚C and 3.5 ˚C by 2080, winters to become wetter and summers likely to become drier (Hulme *et al.*, 2002).

Weather data collected at Warwick HRI were examined and 17 weather years (October-September) since 1989 selected (weather year 2001-2002 was omitted due to missing values for solar radiation). Over this interval no change in monthly or yearly rainfall could be detected although, contrary to the projections by Hulme *et al.* (2002) there was a trend for the summer months May – August to be wetter (see Figure 2-7, left). There was a significant rise in temperature over the last 18 years

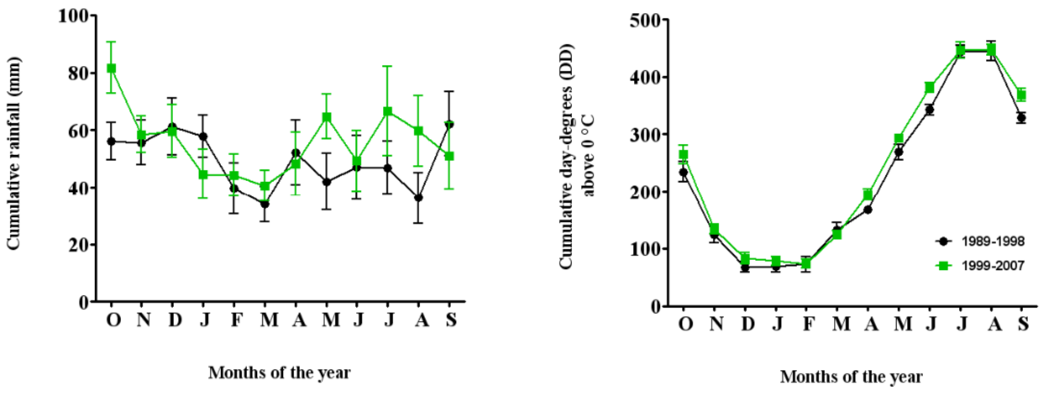


**Figure 2-7** Cumulative rainfall (left) and cumulative day-degrees (right) measured at Warwick HRI over the year (October – September) split over the periods 1989-1998 (black line) and 1998-2007 (green line). Bars represent standard error.

(paired T-test, two-tailed: P=0.0051) with the largest differences for the months April-June and September-October (see Figure 2-7, right). The last six years belonged to the nine years with the highest monthly accumulated day-degrees. Two climate scenarios were therefore created based on the total accumulated day-degrees per year:

1. **Scenario 1 - 'No change':** Given that the total length of the simulation in ECOSEDYN was 24 years and only 17 weather years were available, 7 weather years were randomly drawn from the 17 and added to the pool of 17 weather years. The 24 weather years were then permutated and this sequence was applied to each weed management scenario.
2. **Scenario 2 - 'Heating up':** The eight years with the highest accumulated day-degrees above 0˚C from 1 April to the end of September were selected. The eight years selected were: 1994/95, 1996/97, 1998/99, 2002/03, 2003/04, 2004/05, 2005/06, 2006/07. Seven of the eight years would have been selected too if the cumulative day-degrees would have been based on the period from October to the end of September. Each of the eight years was then selected three times and a randomised sequence of 24 weather years was generated from this pool. The aim of including these two climate scenarios is to examine whether under the 'Heating up' scenario different combinations of cultural control should be applied compared to the default 'No change' scenario.

Since the weed management scenarios were run under both climate scenarios, the question was whether the questions as posed for the weed management scenarios (see pg. 29) would be any different under the two climate scenarios.

## *2.4 The modelling process – Model formulation*

The (complete) modelling process can be divided in several phases: Formulation, Implementation, Verification, Calibration, Analysis and Evaluation (Haefner, 2005). This section deals with the most fundamental tenet of model formulation, i.e. to what kind of detail the system should be represented in ECOSEDYN in order to provide a reasonable tool by which the effect of various weed management scenarios on the long-term weed seedbank can be compared.

### 2.4.1 Traditional modelling approaches

The first efforts to project weed population development over time were made by Sagar and Mortimer (1976) in the form of demographic models. The basic structure of the model consists of the lifecycle of an annual plant, usually divided into four states or stages; seeds in the soil (seed bank), seedlings, mature plants, seeds on parent plant. Demographic processes (germination, reproduction, survival, death) are expressed as transition and mortality rates (usually % per year). Cousens and Mortimer (1995) classify these models as multi-stage single cohort models and since 1976, many studies have followed this approach (Vidotto *et al.*, 2001; Gonzalez Andujar and Fernandez Quintanilla, 2004; Puricelli *et al.*, 2007). The values for transition rates (e.g. germination) and mortality rates in these models are obtained through conducting field experiments.

Similarly, projection matrices (van Groenendael *et al.*, 1988; Caswell, 2001) have been used in identifying points in the life cycle that are of particular interest for designing intervention strategies (Parker, 2000; Davis *et al.*, 2003; Westerman *et al.*, 2007). Alternatively, these matrix models were used to forecast the development of (mostly perennial) weed populations over time given different cropping systems (Pino *et al.*, 1998; Davis *et al.*, 2004b) or weed management options. The transition rates between the distinguished life stages consist of the multiplication of so-called lower-level parameters.

It is essential to appreciate that in the case of difference equations and projection matrix models, the 'rates' constitute the combined effect of all agronomic and biological factors with their interactions. Large inter-annual differences of demographic rates have been reported (Reader, 1985; Bierzychudek, 1999; Fernandez Quintanilla *et al.*, 2000; Davis *et al.*, 2004b) often linked to contrasting weather patterns. The current increase in extreme weather events only increases that probability. Another factor that compromises the use of ‘rate-based’ models is that certain ‘vital rates’ are not independent from each other (van Tienderen, 1995; Ramula and Lehtila, 2005). Hence, correlated rates ought to be assessed simultaneously and over a number of years.

By replacing the ‘rates’ with components that represent the mechanisms, including the effect of the weather if relevant, these two disadvantages can be avoided (Colbach and Debaeke, 1998). The construction of population dynamic models by integrating a range of component models, each representing the best available empirical or mechanistic models is a recent trend (Rasmussen and Holst, 2003; Colbach *et al.*, 2006) that looks very promising, both from a research as well as an agronomic point of view.

## 2.4.2 Defining appropriate level of complexity

Models never attain the complexity of the ‘real’ system and one of the most important choices to be made regards the way and the detail in which various aspects of the system are mathematically represented in ECOSEDYN. For example, should processes be represented by empirical or mechanistic models, should ECOSEDYN include spatial aspects and if so in which processes (component models) should it be incorporated and at what level of detail? These characteristics affect the way the component models operate and interact with each other.

To answer these questions, the objectives of a study, the understanding of the system and the data availability have to be considered. To come to a sound decision regarding the complexity warranted in ECOSEDYN, the relevant literature was thoroughly scrutinised and is summarised in the following sections.

### 2.4.2.1 Process abstraction

The hierarchical level at which the processes of the ‘system’ are represented mathematically is one of the key factors to distinguish between models. On the one hand a group of models exist that include little or none of the mechanisms responsible for a particular behaviour but merely consist of statistical models fitted to experimentally derived data. These are usually referred to as descriptive (Penning de Vries *et al.*, 1989), empirical or phenomenological models (France and Thornley, 1984; Haefner, 2005). In the second group of models – referred to as explanatory, mechanistic or process-oriented models - phenomena are separated into individual processes that are then represented quantitatively. Similarly to empirical models, the parameters of the equations are derived from experiments. For the sake of clarity, this thesis will use the terminology of empirical vs. mechanistic models. In practice a large group of models are somewhere in between these two ends (Russell, 1996). Azam-Ali (1994) referred to this group as semi-empirical or ‘index’ models. In these models, an index value with a clear biological meaning is defined whose value is related to parameters that will mechanistically influence the output. The index value is then experimentally derived for a number of different situations. For example, some crop growth models use an index parameter called the harvest index (seed biomass as a proportion of total crop biomass), to simulate crop seed growth over time (e.g. Bindi *et al.*, 1999).

The value of an empirical model is determined by the quality of the data input. Despite data quality, an empirical model may provide a poor description in conditions other than it was developed for. Substituting an empirical model for a mechanistic model generally implies disentangling the various processes that are then each represented by mechanistic or empirical models themselves (France and Thornley, 1984). The net result is a model with increased process representation and usually more parameters. Mechanistic models that represent processes that are insufficiently understood or for which no data was available to test and calibrate have to include assumptions to cover this void. Hence, a mechanistic model is not just constrained by the quality of the data but also by the inherent assumptions present in the model (see Figure 2-8).

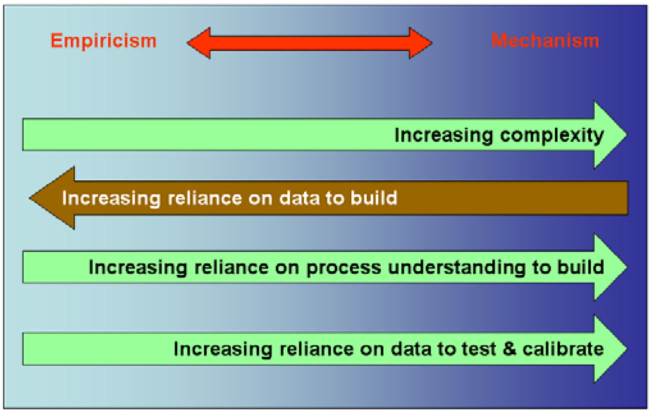


**Figure 2-8** Model features along the ‘empiricism – mechanism’ axis (redrawn from 2005)

Recent reviews of both weed population dynamics and individual component models have argued against ‘black box’ approaches and for the distinction between different processes (Forcella *et al.*, 2000; Colbach *et al.*, 2005). To an extent this is being realized as, for example, considerable progress has been made over the last decade on the ‘dormancy – germination - pre-emergence growth' pathway (Vleeshouwers and Kropff, 2000). On the other hand, Colbach *et al.* (2005) argued for realism in deciding upon the level of complexity in models:

> *"Biological aspects and environmental effects should only be specified if they interact with cropping systems"*

> *"Model structures should not be overburdened with processes and complexities that have no immediate bearing on their use"*

In general, a narrow-focussed research project on modelling seed dormancy justifies the construction of a more mechanistic model than a project seeking to evaluate the effect of weed management strategies on long-term weed population dynamics.

The three guiding principles in choosing the structure of the overall framework and the mathematical representation of components were therefore: the objective of ECOSEDYN (weed management scenarios), the system to be modelled and the data, knowledge and time available. For example, given that crop sowing time was one of the components of the weed management scenarios to be tested, a model structure was needed that could deal with flexible sowing times.

#### 2.4.2.2 Time

Models without an explicit representation of future states are usually referred to as static models whereas their counterparts are called dynamic models (Haefner, 2005). Given that the objective of this study is to build a model that is able to project the population development given certain management strategies, the factor time has to be included. Static models have to be replaced by dynamic ones, for example, the relationship between plant biomass and seed production is normally determined at crop harvest and is commonly modelled by a linear regression of plant biomass against seed weight. To incorporate time in this model requires experiments that assess the relationship between seed production and plant biomass at several times in the lifecycle of a plant (see Chapter 4).

The real question is: At what time-scale does ECOSEDYN need to simulate population dynamics? This depends on the objectives (weed management scenarios) and the time-scale over which the related regulating factors operate. Processes can be represented at different time resolutions in ECOSEDYN only if they are unrelated. Otherwise the time-scale at the finest resolution that is required for one process will dictate the time-scale of the related processes as well. The weed management scenarios proposed focus on crop sowing time and crop cultivar (maturity time). Each of the cultural control factors has the potential to affect weed population dynamics. Studies exploring the relative time of emergence of crop and weed show that emerging a few days earlier can tip the balance in favour of either crop or weeds. It is unsure if the advantage of harvesting the crop a few days earlier can have the same effect as the crop emerging a few days earlier than the weeds. It is possible that when weed emergence is expressed on a weekly basis that the resolution of relative differences in time are being lost. The (smallest) time-scale at which ECOSEDYN operates is therefore on a **daily** time step.

#### 2.4.2.3 Space

Spatially homogeneous models do not include an explicit representation of space whereas heterogeneous or spatially explicit models do, either in a discrete way such as cellular automata models (Wang *et al.*, 2003) or in a continuous way as in diffusion equations (Haefner, 2005).

Weed and seedbank populations tend to have a patchy distribution at the field scale. This spatial heterogeneity is the result of uneven effects of biotic (humped dispersal curve), abiotic (soil properties) and management factors (cultivation, weed control) and their interactions (Blanco Moreno *et al.*, 2004). Brain and Cousens (1990) showed mathematically that if weeds in a field had a patchy distribution, crop yield would be underestimated by assuming a random distribution, especially under high weed densities. In more aggregated weed distributions, on average each weed individual exerts more competition on surrounding weed plants and less on surrounding crop plants. However, unless weed density exceeded the economic threshold this was unlikely to have a major effect on crop yield, regardless of spatial distribution. On the other hand, Garrett and Dixon (1998) showed that for less competitive weeds, with aggregation at small scale, weed spatial pattern is important and large shifts of the weed threshold density may occur as a consequence.

Most population dynamic models have ignored the spatial distribution of weeds and their dispersal curves (Holst *et al.*, 2007), but see (Gonzalez Andujar *et al.*, 1999; Richter *et al.*, 2002; Dicke *et al.*, 2007). Alternatively, heterogeneity in weed distribution can be simulated by dividing the field into a number of smaller areas where the density of weeds is allowed to vary according to a negative binomial distribution (Buckley *et al.*, 2003).

Leaving spatial aspects out of a weed population-dynamics model can be justified under two assumptions. The first assumption is that ignoring the spatial distribution *within* the study area (more or less aggregated) is not fundamentally jeopardising the objective of the study. Fields where carrots are grown are subject to one of the most rigorous cultivation regimes present: among other operations the field is ridged and soil passes through a stone-and-clod separator (see Chapter 5). The net effect is that seeds are very unlikely to have a patchy distribution and therefore the need to account for increased intraspecific competition is reduced.

The second assumption is that immigration *to* and emigration *from* the study area is negligible. The scale at which ECOSEDYN operates is the field level or lower. If substantial dispersal occurs between fields, or from the field margin to the field, possibly enhanced by different intensities of weed control, then ignoring such source-sink effects could lead to spurious predictions of population size (Perry and Gonzalez Andujar, 1993). For *Bromus sterilis* this assumption was invalidated (Theaker *et al.*, 1995), as the field edges functioned as an important source of replenishment. However, Marshall (1989) found that only 30% of the common species in arable field boundaries also occurred in the crop, mostly within 2.5 meters from the edge. More specifically, field boundaries were a highly unfavourable habitat for *T. inodorum* whilst *S. media* was found to some extent in the edges of the field but their prostrate growth and lack of wind-dispersal predict a short-tailed seed dispersal curve. Other studies have also concluded that the dispersal of seeds from plants in the field margins to the field is minor (Fogelfors, 1985; Blumenthal and Jordan, 2001). One of the suggested reasons for this is that the combine harvester usually harvests the crop-strip most prone to weed infestation along the field boundary in a parallel rather than a perpendicular way (Rew *et al.*, 1996).

There can be substantial seed dispersal between fields for wind-dispersed species (Dauer *et al.*, 2007) and for such weeds dispersal ought to be taken into consideration in terms of the structure of the population dynamics model. Without cleaning the combine harvester before proceeding with the harvest of cereals in the next field, for some grass weeds, seed dispersal between fields is a realistic possibility (Ballaré *et al.*, 1987; McCanny and Cavers, 1988). Apart from these two categories, inter-field dispersal of weeds has been shown to be trivial (Jones and Naylor, 1992; Theaker *et* *al.*, 1995; Bischoff, 2005). Neither *S. media* nor *T. inodorum* are wind-dispersed. Both have very small seeds (ca. 0.8-1.3 mm.) and therefore are unlikely to be moved great distances by a combine harvester.

**In conclusion**: spatial aspects only need to be included in a model to account for inter-field dispersal of wind-dispersed species and a few other weeds that are known to be able to spread from the field margins. Many of the problematic weeds in field vegetable crops, including the two model weed species, do not belong to these categories. Therefore, spatial aspects on the horizontal plane were not included in ECOSEDYN.

#### 2.4.2.4 Random events

Three forms of stochasticity can affect data on (weed) population dynamics (Lande *et al.,* 2003): demographic stochasticity, extrinsic stochasticity and measurement error. Demographic stochasticity consists of random events related to births and death. It is cancelled out as being a relevant source of variation in this study because in general only small populations are sensitive to demographic stochasticity. Temperature and rainfall are extremely important in regulating the emergence patterns of weeds but are accounted for as driving variables.

Stochastic models are more complex than their deterministic counterparts and from a parsimony principle “there is little point in complicating a model just for the sake of it” (Cousens and Mortimer, 1995). The value of using a stochastic model over a deterministic model depends on how much information is available, on the shape of the probability distribution function of the parameter(s) in question (Cousens and Mortimer, 1995). In deciding on whether to make parameters stochastic a number of aspects need to be taken into consideration:

Objectives of the project; the use of a stochastic model is warranted over a deterministic model if the project objectives require an estimate of the variability of the system (Grant *et al.*, 2000) or the time to extinction or eradication under a given management regime (Lande *et al.*, 2003). Ignoring stochasticity may lead to an under estimation of the time to extinction of the population of the organism under study

Understanding of the system and / or the mathematical representation of a model; an empirical model is better suited to describe the data than a mechanistic model if the processes that regulate a system are not sufficiently well understood. The more mechanistic a model, the lower the role of stochasticity. If collected data is subject to considerable variation without any knowledge to which process this variation can be attributed to, then a stochastic model may be more appropriate.

**In conclusion:** the aim of this model is not to estimate the time to eradication or extinction, as referred to as one of the conditions for stochasticity. Whether enough knowledge is available about certain biological processes (e.g. dormancy, seed predation) is species-specific. The default position was not to include stochasticity in ECOSEDYN unless no general principles could be derived from the literature.

## *2.5 Model implementation: mathematical representation and parameterisation of component models*

After providing the agronomic context against which the weed population is developing, the proceeding sections relate to the biological processes within the lifecycle of an annual weed. Each section contains a brief overview of the key factors that need to be modelled, the mathematical representation of the processes and is completed with the parameterisation. Component input sources are either set by the weed management scenarios (e.g. crop rotation length is 4 years), by species-specific parameters or parameter files embedded in the component or by other components.

### 2.5.1 Nomenclature

ECOSEDYN distinguishes state, rate and driving variables (Rabbinge and de Wit, 1989). The state variables represent a quantitative measure at any given time of the population characteristic that is modelled, in this case numbers of seeds (S), pre-emerged seedlings (G), plants (P) and the weight of plants (W). Subscripts are used to identify the status and position of seeds (S) in the soil and the size-cohorts of plants (P); e.g. the total amount of seeds in the surface layer is indicated by $S_{tot-1}$, and the number of emerged seedlings until the 2nd true leaf stage is represented by $P_1$. To acknowledge that weed seedlings are separated into different weed cohorts and that within a crop different habitats are characterised, the notation for plants and seeds will be followed by the characteristic ‘c’ and/or ‘h’ between brackets whenever required.

Driving variables are environmental variables that regulate important processes; e.g. plant growth is regulated by solar radiation and temperature, seed germination by temperature and soil moisture. They will be indicated with capital letters (e.g. effective day-degrees, EDD).

A year in ECOSEDYN runs for 365 simulation days (no leap years) from the 1st of October to the end of September to accommodate the farming activities associated with growing winter wheat, which is sown in October and harvested in August the next year. A random simulation day is represented by $d_{sim}$ whereas specific days such as for example sowing day are indicated as $d_{sowing}$.

## 2.5.2 Dormancy evolution

### 2.5.2.1 Background

Only recently have researchers started to include dormancy in models of population dynamics. One of the reasons is that the factors influencing the dormancy status of seeds pre- and post dispersal are not fully understood for most species. The dormancy status is not simply a binary condition but rather is measured on a continuous scale; the temperature range over which germination can occur increases during dormancy release and reduces during dormancy induction (Vleeshouwers *et al.*, 1995; Baskin and Baskin, 2006). An essential feature of dormancy is that it prevents a viable seed from germinating even if the actual environmental conditions (temperature, soil moisture) would allow successful germination. For some species, germination may be restricted more by environmental conditions rather than internal conditions. Although this model aimed to have a generic purpose, without the detailed data it was impossible to create a generic component for dormancy. Instead species-specific accounts of the biology were created and implemented into simple mathematical equations.

In representing dormancy in ECOSEDYN, the intent was not to represent the relevant processes at the mechanistic level, e.g. factors that control phytochrome changes in seeds which cause the seeds to be more or less sensitive to light (Hartmann *et al.*, 2005). However, key aspects that impact on the probability of germination were implemented to reflect their importance. Neither *S. media* nor *T. inodorum* displays an annual dormancy cycle but rather a decrease in dormancy over time.

A recent review on the outcome of day-time as compared to night-time cultivations showed that, although the results are very variable, *S. media* and *T. inodorum* belong to a small subset of species where germination is more often than not reduced by night-time cultivations (Juroszek and Gerhards, 2004). Seeds of both species display temporally variable levels of light requirement, a manifestation of dormancy. Whereas the ability to germinate in light relates to seeds located in the top surface layer, a flash of light as received during cultivation can trigger germination at any depth. The ability to germinate after so-called short duration light exposure (SDLE) is included as well to account for germination after cultivation.

In the species account of *S. media* below the parts of the review that address the implementation of the principles, based on findings of the literature as discussed in the preceding part of the text, are indented for clarity.

### 2.5.2.2 Species specific parameterisation: *S. media*

The germinability of seeds from *S. media* is determined by two processes and both act upon young seeds only: an afterripening requirement to germinate and cold stratification that can either reduce or enhance germination in dark or light.

**Afterripening**

Many studies have shown that fresh seeds of *Stellaria media* are primary dormant (Roberts and Lockett, 1975; Baskin and Baskin, 1976; van der Vegte, 1978; Froud Williams *et al.*, 1984; Grundy, 1997). When tested over a range of temperatures, fresh seeds collected in May, June or October did not germinate in dark and a maximum of 5% germinated in light (Roberts and Lockett, 1975). Grundy (1997) found that after 6 weeks of dry storage at laboratory temperatures only 40% of seeds germinated. After 5 weeks of storage at room temperature followed by 8 months of cold storage (over which the percentage germination did not change) 95% of fresh seeds germinated both in light and dark (Noronha *et al.*, 1997).

Wesson and Wareing (1969) noticed some inhibition of germination in 1 month old seeds germinated in light ($\approx$25%) as compared to dark ($\approx$40%) and the same response can be observed in seeds from two of the three populations in the study by Milberg and Andersson (1998); percentage germination in dark / light was 51 / 38, 29 / 18, and 98 / 97 respectively after 7 weeks of dry storage. Population variability and seasonal differences are likely to play a role in the germinability (capacity to germinate) of fresh seeds. Perhaps populations differ in the rate with which they afterripen and growing plants from different populations in a common environment could shed light on this issue. Interestingly, in both populations where germination was high (afterripening completed) (Noronha *et al.*, 1997; Milberg and Andersson, 1998) there was no appreciable difference between germination in light and dark. It is assumed therefore that the inhibition to germinate in light is alleviated once afterripening is completed.

Roberts and Lockett (1975) showed that afterripening was complete after 14 weeks for seeds shed and buried in May and June but not for those in October. Baskin and Baskin (1976; 1986) showed that there is a clear relationship between temperature and afterripening; high temperatures increase the rate and extent of afterripening but below 10 ˚C afterripening was inhibited.

It is postulated therefore that prior to the winter season (cold stratification), afterripening progresses based on the accumulation of day-degrees. Complete afterripening requires a certain ‘heat sum’, the accumulated day degrees above a base temperature of 10.0 ˚C. It was further assumed that dormancy loss is a linear function of accumulated day degrees.

Roberts and Lockett (1975) tested germinability of seeds after 4 and 14 weeks of burial; after 4 weeks, only about 50% seeds germinated but after 14 weeks all seeds germinated over a broad range of temperatures. Quite possibly afterripening was already completed earlier.

It was assumed that the minimum period in which the heatsum could be reached was after 9 weeks. The interval that spans the period with highest temperatures in England roughly starts the 1st of July. The number of accumulated day-degrees above 10.0 ˚C over the 9 weeks was determined for each of the 17 weather years used for the climate scenarios (see Chapter 5, Section 5.3). The average value (471 DD) was then calculated and this taken as the reference heatsum to complete afterripening.

To account for the initial inhibition of germination in light, separate equations for the proportion of the population that can germinate in dark and light were generated, approximately reflecting the results as observed by Milberg and Andersson (1998) and Wesson and Wareing (1969); 20% and 5% of freshly shed seeds can germinate in dark and light respectively and this increases to a maximum of 95%, the rate a function of accumulated DD.

Van der Vegte (1978) showed that fresh seeds from plants grown at 7˚C had higher dormancy than seeds grown at 20 ˚C which suggests that the temperature whilst seeds are still on the motherplant contributes to the heatsum as well.

Therefore the heatsum should be initiated two weeks before seed shedding (i.e. the heatsum is initiated on the day of seed shedding as the accumulated heatsum over the previous two weeks). The linear functions of the germinability of seeds in dark and light against accumulated degrees then become:

**Equation 2-1:** $$s_{\mathrm{g-dark}}\left(\mathrm{d_{sim}}\right) = 0.001592 * \mathrm{DD_{aft-acc}}\left(\mathrm{d_{sim}}\right) + 0.20$$

**Equation 2-2:** $$s_{\mathrm{g-light}}\left(\mathrm{d_{sim}}\right) = 0.001911 * \mathrm{DD_{aft-acc}}\left(\mathrm{d_{sim}}\right) + 0.05$$

where $s_{\mathrm{g-dark}}$ and $\mathrm{s_{g-light}}$ are the proportions of seeds that can germinate in dark and light respectively, and $\mathrm{DD_{aft-acc}}$ is the accumulated thermal time from two weeks prior to seed shedding on a certain simulation day.

**Stratification**

Milberg and Andersson (1998) showed that seeds of two populations that germinated only to a low extent ($\approx$18-38 %) in light prior to cold stratification, germinated very well after cold stratification ($\approx$79-92 %). However, a third population for which the seeds germinated to a high extent in light prior to stratification (97%), retained a high germinability afterwards (95%). On the other hand, Noronha *et al.* (1997) found that germinability decreased from 95% prior to stratification to between 40-60% afterwards. Similar results were presented by Froud Williams *et al.* (1984).

Not all studies included before-and-after comparisons of germinability, which makes it more difficult to understand the processes. Studies have reported both low and high germination in light after stratification; 46% (Milberg *et al.*, 1996) and 80-95% (Andersson *et al.*, 1997). Froud-Williams *et al.* (1984) found that after soil stratification the proportion of seeds germinating in light varied over the season but no other studies were found in the literature that could corroborate the observed seasonal pattern.

When germination in dark, light and under SDLE (short duration light exposure) following cold stratification was compared, the proportion of seeds that germinated was highest under SDLE (Milberg *et al.*, 1996; Andersson *et al.*, 1997).

After cold stratification over the winter period, the proportion of seeds that can germinate in the dark is low: 1-36% (Milberg *et al.*, 1996), 30-35% (Andersson *et al.*, 1997) and decreases compared to before cold stratification: approximately from 70 to 20 % (Froud Williams *et al.*, 1984) decreasing further in the summer and autumn of the following season. Noronha *et al.* (1997) showed that under laboratory conditions (constant low temperature of 3.2 C) the proportion of seeds that can germinate in darkness decreased from 95% to 10% in only 42 days.

**In conclusion:** it appears that if seeds had low dormancy before cold stratification, then dormancy actually increases with the reverse taking place if there was high dormancy. Perhaps these are features of summer and winter populations.

The period of cold stratification was set from the 1st of December until the end of February; over this interval 95% of the days, when averaged over the 17 weather years, did not contribute to the afterripening heatsum which had a base temperature of 10 ˚C.

**Proposed decision rules for dormancy regulation of *S. media*:**

1. For seeds produced between the 1st of March and the end of November:
    - Dormancy behaviour between the 1st of March and the end of November: seeds germinate better in dark than in light, but this difference eventually disappears according to the degree that afterripening progresses, as calculated in Equations 2-1 and 2-2.
    - Dormancy behaviour between the 1st of December and the end of February: (day 62-151): the proportion of seeds that can germinate in light increases or decreases (according to the extent that primary dormancy was lost prior to the 1st of December) linearly to 60% and remains constant from start of March. The proportion of seeds that can germinate in dark decreases linearly to 20% and remains constant afterwards.

2. For seeds produced between the 1st of December and the end of February:
    - Dormancy behaviour between the 1st of December and the end of February: since temperatures are low the progress of afterripening is slow and the difference between light and dark germination remains present until the end of the interval.
    - Dormancy behaviour between the 1st of March and the end of November: similar to seeds produced between March and November with afterripening progressing from the level that was accumulated in the previous interval.

### 2.5.2.3 Species specific parameterisation: *T. inodorum*

The germinability of seeds from *T. inodorum* is determined by two processes and both act upon the young seeds (<2 years) only: a light requirement to germinate and cold stratification that can either reduce or enhance germination in dark or light. Afterripening is not a requirement in *T. inodorum*.

**Light requirement**

Buried seeds exhibit no annual dormancy cycle and, provided conditions with ample light and optimum temperature are fulfilled, germination can start immediately after maturation (Lonchamp *et al.*, 1984; Thomas *et al.*, 1994; Bowes *et al.*, 1995). In dark, however, 'fresh' seeds can only germinate to a very limited extent (<5%).

Various studies have shown that after burial in soil, seeds gradually lose this light requirement (Lonchamp *et al.*, 1984; Kessler, 1989; Bowes *et al.*, 1995; Milberg and Andersson, 1997). However, the period after which seeds start to lose the light requirement and the rate with which this occurred, varied (see Table 2-1).

**Table 2-3** Available studies / parameters on the loss of light requirement in *T. inodorum*

| **Study** | | **Loss of light requirement** | |
|---|---|---|---|
| | Burial | Start (months after burial) | Duration (months) |
| Lonchamp *et al.* (1984) | October | December (2) | 8 |
| Kessler (1989) | November | July (8) | 12 |
| Bowes *et al.* (1995) | November | August (9) | ≥15 |
| Milberg & Andersson (1997) | November | November (12) | 6 |

In the two studies from Canada (Kessler, 1989; Bowes *et al.*, 1995) seeds started to lose their light requirement in summer with a gradual loss over the next 12-15 months. In the two studies in Europe loss of light requirement happened in winter but in Sweden (Milberg and Andersson, 1997) the population started to lose light requirement a complete season later than in France (Lonchamp *et al.*, 1984). If these two studies represent true geographic differences then one would expect night-time tillage in Sweden to be more effective than in France. Although results of light vs. nighttime cultivations are variable (Hartmann *et al.*, 1997), *T. inodorum* is one of the weed species for which the largest reductions in germination have been reported after cultivation in dark compared to cultivations in light (Juroszek *et al.*, 2002). This suggests that a considerable proportion of the seedbank still has a light requirement at least after the first winter. In the study by Lonchamp *et al.* (1984) only 50% of the previous years seed had a light requirement at the start of spring and this was completely lost at the end of summer whereas in the study by Milberg and Andersson (1997) the proportion with a light requirement remained >90% over the entire growing season.

### Stratification

Cold stratification in the soil does not alter the proportion of seeds that can germinate in light but for fresh seeds the first cold stratification event slightly reduced the proportion that can germinate in dark (Milberg and Andersson, 1997; Milberg and Andersson, 1998). Once seeds have lost their light requirement, no annual changes in the germination rate in light or dark has been observed.

The response to short duration light exposure (SDLE) after cold stratification varies: after 18 weeks at 3 ºC in the laboratory only 0.5-10.8% germinated (Milberg *et al.*, 1996) but when stratified for the same period outside in soil, 47-99% of seeds germinated (Andersson *et al.*, 1997). In another experiment, around 80-90% of seeds germinated after burial over winter but germinability then decreased over the spring and summer period only to increase to previous levels in the next winter (Milberg and Andersson, 1997).

### Implemented decision rules for dormancy regulation of *T. inodorum* in ECOSEDYN:

Since the phenomenon of light requirement was better documented than that of stratification, only the former was implemented in the model. Without studies confirming the length of the light requirement of *T. inodorum* seeds in the soil in the UK, the study by Milberg and Andersson (1997) was taken as a reference in ECOSEDYN. The data from Milberg *et al.* (1997) were applied in the following way: in ECOSEDYN the seedbank consists of seeds in two germinable states: seeds either germinate only after having received a sufficient light response, $s_{g-light}$ or both in dark and light $s_{g-dark}$. Since the proportion of seeds in each of these two states varies with the age of seeds, this is implemented by representing the seedbank as a matrix with four arrays. Each array consists of 16 rows and 3 columns where the rows represent the soil layers and the columns the ‘total number of seeds’ and the seeds in both germinable states respectively. The soil layers distinguished in the seedbank are: ‘Surface’, 0-5, 5-10, 10-15, 15-20, 20-25, 25-30 mm, then every 3 cm down to 30 cm. The reason that the first 3 cm layer is split up in six 5 mm layers is that the germination response by *T. inodorum* seeds is extremely sensitive to depth.

Array 1 contains the seeds that are produced from June to 30 September in simulation year X (which runs from 1 October to 30 September). Freshly produced seeds are transferred to array 2 at the end of simulation year X. Whilst seeds are in array 1 or 2, 95% of the ‘fresh’ seedbank is able to germinate in light, but only 5% of the ‘fresh’ seedbank is able to germinate in both light and dark. Hence, 90% of the seeds germinate only after receiving a light trigger, $\mathrm{s}_{\mathrm{g-light}} = 0.9$, but only 5% is able to germinate in dark. The seeds in array 2 are transferred to array 3 at the end of simulation year X+1. In simulation year X+2 the seeds in array 3 start to lose the light requirement over the interval 1 November – 30 April (181 days) in a linear way so that on the last day of April, 95% of the seeds can germinate in both dark and light. At the time of seed shedding, 5% of the seeds are discarded as unviable. This removes the need to keep taking account of seeds that can not germinate and ensures that:

$s_{\mathrm{g-dark}} + s_{\mathrm{g-light}} = 1$.

The maximum proportion of the *T. inodorum* seedbank that can germinate both in dark and light, $s_{\text{g-dark}}$ ($\mathrm{d}_{\mathrm{sim}}$), is a function of the simulation day number ($\mathrm{d}_{\mathrm{sim}} = 1$ on the 1$^{\mathrm{st}}$ of October) and is represented thus:

**Equation 2-3:**

$$\begin{cases} \text{if } \mathrm{d}_{\mathrm{sim}} \le 31 & s_{\mathrm{g-dark}} = 0.05/0.95 \\ \text{if } 31 < \mathrm{d}_{\mathrm{sim}} \le 212 & s_{\mathrm{g-dark}} = 0.0052 * \mathrm{d}_{\mathrm{sim}} - 0.110 \\ \text{if } \mathrm{d}_{\mathrm{sim}} > 212 & s_{\mathrm{g-dark}} = 1.00 \end{cases}$$

As a consequence, the proportion of the *T. inodorum* seedbank that can only germinate in light, $s_{\text{g-light}}$ ($\mathrm{d}_{\mathrm{sim}}$), can be simply expressed as:

**Equation 2-4:**

$$\mathrm{s}_{\mathrm{g-light}} = 1 - \mathrm{s}_{\mathrm{g-dark}}$$

At the end of simulation year X+2, seeds are transferred to array 4 which experiences no temporal changes in light requirement, i.e. all seeds can germinate in both light and dark: $\mathrm{s}_{\text{g-dark}} = 1.00$

## 2.5.3 Germination and emergence

### 2.5.3.1 Background

As part of the objectives for DEFRA, extensive work was conducted by Paul Neve to characterise weed seed populations of different origins of *S. media* and *T. inodorum* in terms of base-water potential and base temperature. In addition, studies were conducted in which the parameters for pre-emergence growth were derived. The derived information was implemented and added to an existing model for carrot germination so that the effect of relative crop and weed emergence could be studied in detail.

It was impossible from a time point of view to implement that data in ECOSEDYN as developed within this Phd. There were two alternatives: either implement a much simpler germination model component or use the more accurate model to produce output that could be used in some way as input data in ECOSEDYN as developed within this Phd.

In terms of answering the research questions, the germination model component that delivers the most accurate data should be preferred but considering the construction of a modelling framework of different components the inclusion of an autonomous germination component is preferable. Since designing and implementing a simpler conceptual component model for germination and pre-emergence was deemed to be more time-consuming than using the output produced by the more complex germination and pre-emergence model as developed by Finch-Savage *et al.* (1998) and Rowse and Finch-Savage (2003) at the Seed Science Group at Warwick HRI the latter option was chosen.

The germination and emergence model as produced by the Seed Science Group at Warwick HRI (2008) predicts the daily number of germinated seeds based on hydrothermal time (HTT) (Gummerson, 1986) or on the principles as implemented in the ‘Virtual Osmotic Potential’ model (Rowse *et al.*, 1999) and the number of emerged seedlings based on post-germination seedling growth (Whalley *et al.*, 1999). For the crop and weed seed germination scenarios only the HTT option was used. The model runs on the assumption that weed seed germination occurs predominantly as a consequence of seedbed preparation. The day of seedbed preparation therefore is set as the ‘trigger’ from which hydrothermal time is accumulated.

#### 2.5.3.2 Parameterisation and implementation

**Carrot**

For each of the 85 weather year - sowing time combinations the number of emerged carrot seedlings / day was recorded and saved in tables. Each simulation comprised 500 carrot seeds sown at a dept of 12 mm. ± 2.0 (standard deviation). The simulation lasted from the day of sowing (seedbed preparation) until 60 days later. Regarding the other settings in the model: the parameterized carrot germination data originated from Paul Neve, 'Option 1' was checked and was fitted using the HTT method as implemented by 'Carole'. In fact, after all the simulations had been completed it became clear that the final percentage carrot germination did not vary much and the only characteristic that was assumed to impact on weed population dynamics was the day at which 50% of the carrot crop had emerged, $d_{Cs}$. This was calculated from the data in the tables using MatLab.

**Winter wheat**

The model has not been parameterized for winter wheat and therefore a simplified set of decision rules was implemented. In principal the timing of 50% emergence was timed to take place after 150 day degrees (above a base temperature, Tb, of 0) had been accumulated (Hodges and Ritchie, 1991). If within the interval of one week prior to crop sowing to one week after crop sowing the cumulative amount of rainfall was less than 10 mm or more than 50 mm, a delay of 7 days was imposed.

**Weed**

Although parameterized hydrothermal time models were available for *T. inodorum* the soil depth structure (single point, e.g. 1.5 cm deep) of the germination and emergence model did not match with the soil depth structure (layer, e.g. 0.5-1.0 cm deep) in ECOSEDYN. The germination model requires specifying a depth and 'spread' and then allocates a seed distribution according to a normal distribution. The maximum depth from which *T. inodorum* can germinate is roughly 15 mm (Grundy *et al.*, 2003a). By overlapping normal distributions with the same standard deviation but different means, a uniform distribution can be generated over most of the relevant interval. Using an Excel spreadsheet, seed depth distributions were generated with different combinations of mean (seed depth) and standard deviation ('spread') and initial depth to explore the ideal combination. In the model any seeds allocated above the soil surface are in fact allocated to the surface. An unrealistic number of seeds at the surface is likely to affect the germination and emergence results. Therefore the ‘shallowest’ normal distribution should contain a ‘mean’ and ‘standard deviation’ such that results in as low a number of seeds at the surface as possible. The best compromise between the uniformity of the distribution and the number of seeds at the surface was found when the first normal distribution had a mean of 1 mm and a standard deviation of 0.4, the mean soil depth of the remaining normal distributions was every 1 mm down to 15 mm. For each soil depth there were 136 simulations (17 weather years, 8 sowing times (carrot + winter wheat). In total there were 2040 simulations with 500 seeds each of the non-dormant *T. inodorum* population as characterized and implemented in the model by Paul Neve.

The number of germinated and emerged seedlings / day was initially converted to a proportion / day relative to the total number of germinated seeds / emerged seedlings at the end of the 60 days. This is however re-calculated in MatLab to a daily proportion relative to the size of yesterday’s seedbank. The daily germination and emergence proportions for the 1 to 5 mm, 6 to 10 mm and 11 to 15 mm depths were then averaged to get an estimate for the 0-5, 6-10 and 11-15 mm soil layers in ECOSEDYN.

In raised bed systems the seeds experience severe soil compaction in the tramlines but no soil compaction within the beds. Weed species emergence due to soil compaction is variable with both positive (Jurik and Zhang, 1999; Boyd and van Acker, 2004) as negative effects (San Roman and Fernandez, 1991) reported. Compared to other weeds, *T. inodorum* seeds have one of the narrowest depth ranges over which they can emerge. This implies that the seedling does not have enough vigour to be able to emerge from other depths. It is therefore likely that soil compaction also reduces the number of seeds that can emerge. Two seedbanks are distinguished, the between-bed area (BB) and the within-bed area (WB). From the BB area fewer seeds are likely to germinate due to severe compaction. On the other hand, compaction would bring some seeds at a distance from where they could emerge whereas they could not before. Without data to indicate which effect would be more important, no reduction of germination in the BB area was applied. No distinction was made either between the within-row and between-row areas in the WB area.

In ECOSEDYN decision rules were introduced to reduce the predicted proportion of germination. Firstly, it was imperative to apply a depth-dependent germination reduction scaler. If the temperature and soil moisture are sufficient, the model estimates that if *T. inodorum* seeds are placed at 3 cm depth or deeper, around 80% of the seeds will still germinate, which would result in 100% fatal germination and thus a massive depletion of the seedbank. Seedbanks of *T. inodorum* are relatively persistent (Thompson *et al.*, 1997) which suggests that the seeds possess a depth-mediated germination response.

A germination reduction factor (GRF) based on seed depth was calculated based on a Beta distribution function:

**Equation 2-5** $$\mathrm{GRF}(\mathrm{depth}) = \mathrm{GRF}_{\max}\left(1+\frac{\mathrm{depth}_e-\mathrm{depth}}{\mathrm{depth}_e-\mathrm{depth}_m}\right)\left(\frac{\mathrm{depth}-\mathrm{depth}_s}{\mathrm{depth}_e-\mathrm{depth}_s}\right)^{\left(\frac{\mathrm{depth}_e-\mathrm{depth}_s}{\mathrm{depth}_e-\mathrm{depth}_m}\right)}$$

where the maximum reduction of germination ($\mathrm{GRF}_{\max}$) was 0.9 and was reached at 16 mm depth ($\mathrm{depth}_e$). The starting depth at which germination was assumed to become reduced ($\mathrm{depth}_s$) was at 6 mm. and the point at which germination reduction increases fastest ($\mathrm{depth}_m$) was assumed to be at 12 mm.

Fatal germination levels vary between 5 and 40% of the total proportion germination, depending on weed species, soil depth and presence of pathogens (Benvenuti *et al.*, 2001b; Benvenuti *et al.*, 2001a; Davis and Renner, 2007). In ECOSEDYN the value for fatal germination of *T. inodorum* below the layers for which germination and emergence was calculated by the germination and emergence simulation model (Seed Science Group, 2008) was set at 15% and 5%, in carrot and winter wheat respectively, over the 60 day interval over which germination and emergence was simulated to occur.

Secondly, the degree of crop development determines to what extent weed germination is suppressed. A germination suppression factor increased linearly from 0.0 to 1.0 over the interval of critical period of crop competition (0.20 – 0.52 of growing period). The shorter the time from sowing to harvest, the earlier the critical period of weed competition is initiated. Hence, when comparing equal sowing times for varieties with different times of sowing to maturity, the shorter the time from sowing to maturity, the more germination is suppressed and therefore the lower the weed density in the crop.

The germination and emergence model gives one value for the proportion germination whereas in ECOSEDYN two seed states, $s_{g-\mathrm{light}}$ and $s_{g-\mathrm{dark}}$, and four seed ages are considered. Since seeds of the first age have not been produced yet at the time of seed germination there are in fact six separate seed categories that all contribute to the overall daily germination. To ensure that each of the six seed categories is reduced by the appropriate proportion of germination the following calculation is carried out per soil layer:

1. The number of available seeds is calculated for each of the six groups (three seed ages, two seed states, $s_{g-light}$ and $s_{g-dark}$). Due to the more intensive seedbed preparation for a carrot crop as compared to a winter wheat crop, it was assumed that 75% of the seeds that can germinate only after receiving a light trigger, $s_{g-light}$, are 'excited', i.e. available, during carrot seedbed preparation but only 25% are excited during the winterwheat seedbed preparation. In contrast, all seeds in the $s_{g-dark}$ state are available.
2. For each of the two seed states the number of seeds per seed age is expressed as a proportion of the total number of seeds of that seed state. For example, 65% of '$s_{g-light}$' seeds are 1 year old and 35% are 2 years old (since all seeds lose the light requirement at the end of the $2^{nd}$ year (see Section 2.5.1.3 in thesis), there are no '$s_{g-light}$' seeds that are 3 years old).
3. The daily proportion germination as calculated by the 'Germination and Emergence' model is multiplied with the proportion that each seed age of a particular seed state represents of the total number of seeds of that seed state (as calculated in 2) to obtain the total number of seeds that germinated.
4. This number is subtracted from the relevant category (seed age, seed state) of the seedbank.

The number of emerged seedlings per soil layer was calculated by multiplying the predicted number of emerged seedlings per soil layer by the 'Germination and Emergence' model with one minus the proportion pre-emergence mortality due to linuron application (see Section 2.5.4). This was repeated for the other two soil layers and the number of emerged seedlings was then summed. According to the 'Germination and Emergence' model the maximum period over which germination was predicted to continue after seedbed preparation was 60 days. Rather than account for the emerged seedlings on each day individually, a maximum of 12 weed cohorts were created by grouping the weeds of each 5-day period together. The median date of each interval was then assigned to be the day of emergence, $d_{Ws}$.

### 2.5.4 Seedbank mortality

#### 2.5.4.1 Background and mathematical representation

Seed banks decline due to dispersal, post-dispersal seed predation, fatal germination, successful emergence, pathogen attack and embryo death due to ageing (Gallandt *et al.*, 1999; Forcella, 2003). The persistence of weed seed banks ranges from transient (<1 yr), through short-term persistent (between 1 and 5 years) to long-term persistent (>5 years) (Thompson *et al.*, 1993). By mixing a known quantity of seeds with a volume of soil, retrieving the viable seeds in the soil over time whilst preventing emerged weeds from reproducing, decline rates have been established for many weed species, see for example Wilson and Lawson (1992). A negative exponential function is by far the most used model to estimate the numbers of viable seed numbers over time (Roberts and Feast, 1973; Roberts and Boddrell, 1983; Lawson *et al.*, 1993; Sanchez del Arco *et al.*, 1995) though occasionally other declining negative functions have been fitted as well (Donald, 1993). Discontinuous or linear declines have been reported, however, for within-year observations (Puricelli *et al.*, 2005; Sester *et al.*, 2006).

Seedbank decline has been assessed through various ways but it is important to appreciate that the nature of the assessment can affect the decline rate through eliminating, or not distinguishing between some of the factors responsible for seedbank decline. Seed predators predominantly target seeds on the soil surface (Scopel *et al.*, 1988; Orrock and Damschen, 2007). Hence, persistence studies that mix seeds through the soil do not account for losses of fresh seeds due to seed predation. Some persistence studies do not record emerged seedlings and therefore establish an ‘all-in’ decline rate, not a ‘mortality-only’ rate (e.g. 2002; Westerman *et al.*, 2003a).

Seed predation, emergence and fatal germination are accounted for in ECOSEDYN by other model components. Hence, for ECOSEDYN seedbank decline-rates that include all factors responsible for seedbank decline are not useful. Instead, the decline of the seedbank due to seed embryo death caused by ageing and seed death from pathogen attack is the parameter required. In practice it is often impossible to distinguish seed mortality due to fatal germination from seed mortality due to decay. Although it could be argued that fatal germination is already being accounted for by the ‘Germination and Emergence’ model (see Section 2.5.2), the fact is that in reality plenty of *T. inodorum* seeds germinate outside the window in which germination and emergence is assumed to happen in ECOSEDYN. Even if these seeds successfully emerge, then the seedlings are likely to die or be killed prior to setting seeds and therefore represent a substantial extra mortality factor. Seedbank mortality studies in which emergence was explicitly recorded and seeds were not scattered freely on the surface were considered the most relevant.

Empirical studies evaluating the fate of weed seeds over the soil volume found no (consistent) relationship between seed mortality and depth in the soil (Lapham and Drennan, 1990; Mohler, 1993) except for seeds close to the soil surface that either die faster (Carmona and Boas, 2001; Gulden *et al.*, 2004; Puricelli *et al.*, 2005; Peachey and Mallory-Smith, 2007) or slower (Taylor *et al.*, 2005). Due to the inconsistency in results, it was assumed that seed mortality is independent of depth in the soil. Three more assumptions were made in the 'seedbank mortality' component of ECOSEDYN:

- the proportion mortality in each year is the same regardless of the age distribution or the proportional dormancy of the seed bank.
- seedbank mortality is independent of crop type.
- seeds in Array 1, i.e. freshly produced seeds that are on the surface, are only dying because of seed predation and not from decay.

If the value for annual seedbank mortality is extrapolated to daily seed mortality then the net annual seedbank mortality is lower, since seeds that disappear from the seedbank due to seed predation, fatal germination or successful emergence can not die from 'seedbank mortality'. To minimise this effect, yet at the same time acknowledge that seeds die throughout the season, seedbank mortality is calculated on a weekly basis. The proportion weekly mortality is calculated from the annual seedbank persistence:

**Equation 2-6:** $$m_{\mathrm{d-S}}(\mathrm{w}) = 1 - \sqrt[53]{1 - m_{\mathrm{d-S}}(\mathrm{a})}$$

and the proportion weekly survival multiplied with the seedbank resulting in an exponential decline.

**Equation 2-7:** $$\mathrm{S}_{\mathrm{tot}}(\mathrm{t}+1) = (1 - m_{\mathrm{d-S}}(\mathrm{w})) * \mathrm{S}_{\mathrm{tot}}(\mathrm{t}) = \mathrm{S}_{\mathrm{tot}}(\mathrm{t}+1) = \sqrt[53]{1 - m_{\mathrm{d-S}}(\mathrm{a})} * \mathrm{S}_{\mathrm{tot}}(\mathrm{t})$$

#### 2.5.4.2 Parameterisation and implementation

Seedbanks decline due to mortality and successful emergence. When considering studies for parameterisation it is important to discern to which degree these two processes have been distinguished.

***T. inodorum***

Measurements on persistence in the soil have been conducted in various ways: buried in mesh envelopes at certain depths (Method 1), mixed with soil and buried in pots (Method 2), spread over soil surface followed by cultivation (Method 3). Interestingly the various methods gave rather different results for annual decline rates. When seeds are stored in nylon mesh envelopes (Method 1), the annual decline values are much lower than for the other methodologies (see Table 2.4). Van Mourik *et al.* (2005) warned that high seed densities in mesh envelopes could overestimate decline rates, but from the review here it seems that mesh envelopes may exclude certain mortality factors and therefore lead to an underestimation of the depletion rate.

The highest 'all-in' decline rates are reported from studies where seeds were broadcast in the field and the field then cultivated (Method 3). Barralis *et al.* (1988) reported a staggering 88% decline for *T. inodorum* in the first year and Roller and Albrecht (2006) found values in the same range, with, on average the seedbank declining 75% after 25 months under various cultivation regimes.

Intermediate values are reported from Harold Roberts' experiments where he mixed seeds with soil in pots that were buried in the field (Method 2) (Roberts, 1964; Roberts and Feast, 1972; Roberts and Feast, 1973). In these experiments there was evidence for an exponential decrease of viable seeds and therefore annual decline values were calculated as follows: if 't' is the length of the experimental period in years then over the course of the experimental period a proportion of the seeds emerge, $e_{\mathrm{S}}(\mathrm{t})$, a proportion dies, $m_{\mathrm{d\text{-}S}}(\mathrm{t})$, and a proportion survives, $s_{\mathrm{S}}(\mathrm{t})$.

**Table 2-4** Experimental results from literature, where annual decline rates of *T. inodorum* were measured. C/U stands for cultivated vs uncultivated soil. Shading implies the use of these values for the parameter in ECOSEDYN.

| | | | | | | Annual decline rate (%) | |
|---|---|---|---|---|---|---|---|
| Study | | Method | Years | Depth (cm) | C/U | 'All-in' | 'Mortality-only' |
| Lewis (1973) | | 1 | 1 | 13 | U | 13.0 | -- |
| | | | | 26 | | 18.0 | -- |
| | | | | 39 | | 18.0 | -- |
| | | | 4 | 13 | U | 7.9 | -- |
| | | | | 26 | | 14.7 | -- |
| | | | | 39 | | 13.9 | -- |
| Lonchamp *et al.* (1984) | | 1 | 2 | 10 + 25 | C | 17.0 | -- |
| Roberts (1964) | 1952 | 2 | 3 | 0-7.5 | C | 55.9 | 30.4 |
| | 1953 | | 5 | | | 50.7 | 22.9 |
| | 1954 | | 5 | | | 52.7 | 32.5 |
| | 1955 | | 5 | | | 48.3 | 17.9 |
| Roberts and Feast (1972) | | 2 | 5 | 0-2.5 | C | 43.0 | 19.2 |
| | | | | 0-7.5 | | 41.2 | 25.2 |
| | | | | 0-15.0 | | 35.7 | 22.9 |
| | | | | 0-2.5 | U | 39.7 | 25.0 |
| | | | | 0-7.5 | | 27.5 | 20.6 |
| | | | | 0-15.0 | | 23.0 | 20.5 |
| Roberts and Feast (1973) | | 2 | 6 | 0-15 | C | 31.9 | 20.6 |
| | | | | | U | 21.7 | 18.6 |
| Barralis *et al.* (1988) | | 3 | 1 | 0 - ± 30 | C | 88.0 | -- |
| | | | 2 | | | 70.9 | -- |
| | | | 3 | | | 55.9 | -- |
| | | | 5 | | | 64.0 | → 54.0[1] |
| Roller and Albrecht (2006) | | 3 | 1 | Variable | C | 81.4 | -- |
| | | | 2 | variable | | 75.4 | → 69.4[1] |

[1] Based on experimental results obtained via literature it was assumed that the annual emergence rate was 10%

The aim is to calculate the annual proportion of the seedbank that dies to causes other than emergence and seed predation, most likely *decay*, $m_{\text{d-S}}(\text{a})$, which can be calculated as:

**Equation 2-8:** $$m_{\text{d}-\text{S}}(\text{a}) = 1 - s_{\text{S}}(\text{a}) - e_{\text{S}}(\text{a})$$

The annual survival rate, $s_{\mathrm{S}}(\mathrm{a})$, can be calculated from the total proportion surviving and the length of the experimental period, t, as follows:

**Equation 2-9:**

$$s_{\mathrm{S}}(\mathrm{t}) = s_{\mathrm{S}}(\mathrm{a})^{\mathrm{t}} \Rightarrow s_{\mathrm{S}} = \sqrt[\mathrm{t}]{s_{\mathrm{S}}(\mathrm{t})}$$

The annual emergence rate, $e_{\mathrm{S}}(\mathrm{a})$, can be calculated by expressing the aggregate proportion of all emerged seedlings at the end of the experiment, $e_{\mathrm{S}}(\mathrm{t})$:

**Equation 2-10:**

$$e_{\mathrm{S}}(\mathrm{t}) = \sum_{1}^{\mathrm{t}} e_{\mathrm{S}}(\mathrm{a}) * s_{\mathrm{S}}(\mathrm{a})^{\mathrm{t}-1} \Rightarrow e_{\mathrm{S}}(\mathrm{a}) = \frac{e_{\mathrm{S}}(\mathrm{t})}{\sum_{0}^{\mathrm{t}-1} s_{\mathrm{S}}(\mathrm{a})^{\mathrm{t}}}$$

The discrepancy in the ‘all-in’ decline rates of the studies using Method 2 and 3 is striking. In field studies the annual percentage of the total weed seedbank that emerges is usually lower than 10% (Zhang *et al.*, 1998) whereas in Harold Roberts’ studies this is considerably higher (21% for ‘cultivated’ plots), on the one hand because of the more frequent disturbances of the soil and on the other hand because the seeds are distributed over a shallower depth. It could be argued that Harold Roberts’ studies underestimate field-mortality as more seeds are encouraged to germinate and emerge than would have done so in the field and this precocious emergence will keep the proportion of the seedbank that dies due to pathogen attack or other hazards much lower. If it was assumed that 10% of the seedbank emerged in the studies using Method 3, then the ‘mortality-only’ rates are still double that of Harold Roberts’ studies. It is not impossible that methodological issues have contributed to the high figure for seedbank mortality in the studies using Method 3 but it would be unreasonable to dismiss the results out of hand.

The parameter to be used in ECOSEDYN was calculated as follows: values derived using Method 1 were left out as they are felt to be an unrealistic assessment of seedbank mortality in annually cultivated soils. For the same reason, results of undisturbed soil in the Roberts studies (Method 2) were left out, as well as the results of mortality if seeds were mixed with soil depth between 0-2.5 cm. The average ‘mortality-only’ rate was then calculated for Method 2 (24.6) and Method 3 (59.70) and the mean of these two values (42.2) chosen as the annual seedbank decline parameter, $m_{\mathrm{d\text{-}S}}(\mathrm{a})$, for *T. inodorum*.

### *S. media*

The trend observed for the *T. inodorum* data was not seen in the data for *S. media*; the 'all-in' decline rates found in Roberts studies (Method 2) are larger than most of the fieldstudies that employed Method 3 (see Table 2-5). Lawson *et al.* (1993) mention that in two experiments only 1.1% and 3.6% of the *S. media* seedbank produced seedlings. Similar figures were given elsewhere (Lutman, 2006). It appears that plenty more seeds emerged in the studies using Method 2 than in the studies using

**Table 2-5** Experimental results from literature where annual decline rates of *S. media* were measured. C/U stands for cultivated vs uncultivated soil. Shading implies the use of these values for the parameter in ECOSEDYN.

| | | | | | | Annual decline rate (%) | |
|---|---|---|---|---|---|---|---|
| Study | | Method | Years | Depth (cm) | C/U | 'All-in' | 'Mortality-only' |
| Roberts (1964) | 1952 | 2 | 3 | 0-7.5 | C | 63.1 | 16.2 |
| | 1953 | | 5 | | | 61.9 | 21.2 |
| | 1954 | | 5 | | | 61.9 | 23.2 |
| | 1955 | | 5 | | | 53.4 | 17.5 |
| Roberts and Feast (1972) | | 2 | 5 | 0-2.5 | C | 66.0 | 22.9 |
| | | | | 0-7.5 | | 54.3 | 16.1 |
| | | | | 0-15.0 | | 54.3 | 24.9 |
| | | | | 0-2.5 | U | 60.2 | 21.3 |
| | | | | 0-7.5 | | 43.0 | 29.3 |
| | | | | 0-15.0 | | 31.6 | 24.5 |
| Roberts and Feast (1973) | | 2 | 6 | 0-15.0 | C | 41.5 | 19.9 |
| | | | | | U | 22.3 | 18.0 |
| Roberts (1962) | | 3 | 4 | 0-15 | C | 49.0 | → 44.0 [1] |
| Roberts and Dawkins (1967) | | 3 | | 0-23 | C | 56.0 | → 51.0 [1] |
| | | | | | U | 30 | -- |
| Lawson *et al.* (1993) | | 3 | 4 | 0 - ± 20 | C | 41.9 | → 36.9 [1] |
| | | | 3 | | | 27.1 | → 22.1 [1] |
| Lutman *et al.* (2002) | | 3 | 6 | variable | C | 33.1 | → 28.1 [1] |
| | | | 3 | variable | | 36.3 | → 31.3 [1] |
| Lutman *et al.* (2003) | | 3 | 4 | variable | C | 30.0 | → 25.0 [1] |
| | | | | variable | | 45.0 | → 40.0 [1] |
| Roller and Albrecht (2006) | | 3 | 1 | variable | C | 87.1 | -- |
| | | | 2 | variable | | 79.4 | → 74.4 [1] |

[1] Based on experimental results obtained via literature it was assumed that the annual emergence rate was 5%

Method 3. It was decided to subtract 5% of each of the 'all-in' values of the studies for which no 'mortality-only' value was available. The average 'mortality-only' rate was then calculated for Method 2 (19.63) and Method 3 (39.20) and the mean of these two values (29.41) chosen as the annual seedbank decline parameter, $m_{\text{d-S}}(\text{a})$, for *S. media*.

## 2.5.5 Plant mortality due to weed control

### 2.5.5.1 Background and mathematical representation

**Pre-emergence weed control**

For a conventional carrot grower, pre-emergence treatment on mineral soils consists of the application of a residual herbicide mixture (pendimethalin, linuron, clomazone) two-three days after crop sowing (personal comment Cathy Knott).

Persistent herbicides have a knock-on effect in killing pre-emerged seedlings (G) that germinate after application. The efficacy and persistence of the herbicide is product specific and most studies have shown an exponential decay of the herbicide efficacy (Rao, 2000). The proportion mortality of seedlings germinating on any day, $m_{\text{G-h}}(\text{d})$, after applying pre-emergent herbicides then becomes:

**Equation 2-11:** $$\mathrm{m}_{\mathrm{G-h}} = \mathrm{m}_{\mathrm{G-prwc}}(0) * \mathrm{e}^{\mathrm{h}*(\mathrm{d}_{\mathrm{sim}} - \mathrm{d}_{\mathrm{ha}})}$$

with $m_{\text{G-h}}$ decreasing as a function of the number of days after the day of herbicide application $\text{d}_{\text{ha}}$, the initial efficacy-rate, $m_{\text{G-h}}(0)$, and the parameter, $h$ that determines how fast the half-life is reached.

Although pre-emergence linuron rates have been restricted, growers indicated that they expected the pre-emergence program to remain more or less what it was and therefore no reduced rates for linuron need to be applied. It was assumed that the percentage of pre-emerged seedlings that survives the linuron treatment on the day of germination are not affected afterwards.

**Post-emergence weed control**

The efficacy of post-emergent mechanical weed control (Andersson, 1994; Fogelberg and Gustavsson, 1999) as well as herbicides (Boatman and Freeman, 1988; Buchanan *et al.*, 1990) is inversely related to growth stage. Herbicide efficacy is further dependent on dosage, nozzle type, weather conditions, soil type, adjuvants and crop competitiveness (Kudsk, 2002). To include all the factors involved is beyond the scope of this model and since plant (seedling) size is the single most important factor (personal communication Tom Will) this was the only factor that was included. An objective measure of plant size during early growth is true-leaf stage and weed control efficacy values are often based on this measure of plant size. Hence, there is a need to obtain realistic control efficacy values per true-leaf stage for the model weeds and to distinguish weed cohorts in ECOSEDYN according to true-leaf stage.

The timing of the post-emergence herbicide applications should take into consideration the size of crop plants since crop-weed competition is most severe during the early stages of crop growth. The timing of the post-emergence weed control operations was obtained from the interviews with the crop consultants.

### 2.5.5.2 Parameterisation and implementation

**Pre-emergence weed control**

Using the germination and pre-emergence growth model as developed by the Seed Science Group (2008), the timing of 50% crop emergence can be predicted.

The half-life value of linuron as retrieved from the MAUK website (Anonymous, 2003), was 13-82 days reflecting the variability in weather and soil conditions that impact upon herbicide degradation in the soil. The average value for half-life, 47 days, was assumed to be representative. Substituting this in Equation 2-11 gives:

1) $0.5 * m_{G-prwc} = m_{G-prwc}(0) * e^{h*(47)}$

2) $\ln(0.5) = 47 * h \Rightarrow h = -0.01475$

No species-specific information could be found for $m_{G\text{-}prwc}(0)$, the proportion mortality immediately after applying linuron. It was therefore assumed that the initial efficacy of linuron was 80% for both weed species. Hence the implemented model for pre-emergence weed control mortality was

**Equation 2-12:** $m_{G-prwc} = 0.8 * e^{-0.0148 * (d_{sim} - d_{ha})}$

In ECOSEDYN $d_{ha}$ was set at three days after sowing and on that day 80% of all pre-emerged seedlings died whereas for the following days only newly germinated seedlings died according to the reduced mortality rate valid for that specific day.

### Post-emergence weed control

A simple decision rule was implemented so that in carrot the first and second post-emergence applications were applied 28 and 56 days after the date with 50% crop emergence respectively.

For winter wheat the critical weed-free period, the interval over which the crop has to be weed-free to avoid yield loss, was kept as a guide line since that is more likely to give an accurate description than fixed dates given variable winter wheater. When assuming a 5% yield loss as acceptable, the critical weed free period in winter wheat was from 506 DD until 1023 DD (Welsh *et al.*, 1999). The timing of the first and second post-emergence herbicide applications were set at the start of the critical period and after 75% of the critical period has passed respectively.

Through the Danish site ‘Pl@nteInfo - Crop protection online’ (Faculty of Agricultural Sciences (Aarhus University Denmark), 2001), information about the weed control efficacy of herbicides on different growth stages is available. The information comes in the form of dose-response curves and is available for four growth stages: up to 2nd true-leave stage, 2nd to 4th true-leave stage, 4th to 6th true-leave stage and from the 6th true leave stage onwards (see also Section 4.7.1.2). Efficacy values are available for both weed species, *S. media* and *T. inodorum*, and for a number of herbicides. The calculated efficacies refer to the reduction of weed biomass (freshweight) 4-6 weeks after herbicide application. It is assumed that the efficacy values are a good reflection of proportion mortality in the field; i.e. 50% biomass reduction is 50% mortality. In reality, different (mixtures of) herbicide products are likely to be used in the carrot, onion and winter wheat crops but in ECOSEDYN the efficacy values of one product (Express ST) were chosen. Express ST was chosen because it gives an all-round good control of weed seedlings (see Table 2-6) which is representative of the situation before the revocation of the herbicides (personal communication Cathy Knott and Tom Will).

Post-emergence herbicide control in carrots and onions consists of several low-dose treatments (Knott, 2002; Garthwaite *et al.*, 2004) whereas in winter wheat one full dose in autumn and a reduced dose in spring is recommended (HGCA, 1997; Clarke, 2002).

It was shown in Chapter 1 (see Figure 1-4) that the number of treatments has increased but the total product applied has gone down. Therefore, for vegetable crops the efficacy values of ¼ dose and for winter wheat the efficacy values of a full dose in autumn / winter and a ½ dose in spring were applied. The efficacy values for reduced weed control as a consequence of fewer herbicide availability was assumed to approach only 75% of the efficacy values of those listed in Table 2-6. Reduced weed control was applied in the vegetable crop only.

**Table 2-6** Weed control efficacy values (%) per growth stage and herbicide dose (Express ST) for each of the weed species under standard weed control.

| | **Dose** | **0-2 leaves ($P_1$)** | **3-4 leaves ($P_2$)** | **4-6 leaves ($P_3$)** | **+ 6 leaves ($P_4$)** |
|---|---|---|---|---|---|
| ***Stellaria media*** | N | 97 | 96 | 95 | 94 |
| | ½ N | 95 | 94 | 92 | 90 |
| | ¼ N | 92 | 89 | 86 | 84 |
| ***T. inodorum*** | N | 94 | 92 | 90 | 89 |
| | ½ N | 90 | 87 | 84 | 81 |
| | ¼ N | 83 | 79 | 74 | 70 |

Plants in the tramlines suffer from additional mortality due to the wheels from the tractor with mounted sprayer. Assuming the boom width of the sprayer is 24 m it would extend over 13 beds / application. This implies that about 15% of weeds in the bb section (tramlines) are all being killed by the wheels and the remaining plants in the bb section (85%) die according to the efficacy of spray application. Following a herbicide application a proportion of seedlings will survive and it is assumed there is no additional negative effect on growth for those seedlings.

## 2.5.6 Seed predation

### 2.5.6.1 Background and mathematical representation

Losses due to seed predation can occur both prior to and after dispersal but the relative importance of each process is very species-specific; pre-dispersal seed predation has  been reported for *T. inodorum* (e.g. Fenner *et al.*, 2002) but not for *S. media*.

Ripe seeds can be retained on the plant but ripe seeds of most plants are shed from the motherplant. Upon shedding a proportion of the seeds become incorporated in the soil immediately and Westerman and co-authors (2006) estimated this could vary between 22% and 37% for a small-seeded weed (*Setaria faberi*) in crops with different vegetation structure. The rest of the seeds end up on the soil surface from where they face mortality through seed predation, may germinate or become incorporated in the soil. It is assumed that as soon as seeds are incorporated in the soil they are exempt from seed predation, which seems a reasonable assumption for small seeds (Hulme, 1994; Crawley, 1997). This means that the number of seeds that are predated is dependent on the combined burial and germination rate.

Data on seed predation are notoriously variable and are more often available for arable crops (Westerman *et al.*, 2003b; Mauchline *et al.*, 2005; Lutman, 2006) rather than for vegetable crops. It seems that the most constructive way of modelling seed predation is to look for principles that extend beyond empirical data collected in certain crops. Heggenstaller *et al.* (2006) found a positive correlation between canopy light interception (vegetative cover) and seed predation, which suggests temporal variation in seed predation is linked to crop development. These results are consistent with other studies (Reader, 1991; Povey *et al.*, 1993). Jones (1976) found that carabid abundance in the crop was dependent on development stage of the crop, the crop functioning as shelter against high temperatures and desiccation.

It appears from seed predation studies carried out over the length of the spring-summer season in winter wheat that temporal variation in proportion seed predation is not symmetric over time; high early in the season and then gradually decreasing towards harvest time (see Figure 2-8).

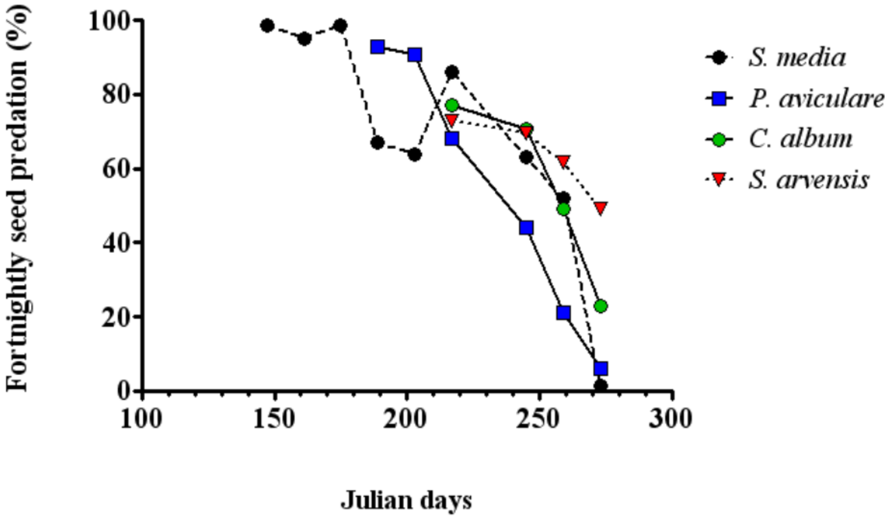


**Figure 2-9** Temporal variability in seed predation and how this affects species with different timing of seed shedding; the proportion of seed that is predated is high for early shed seeds and generally decreases over time, regardless of species (data after Mauchline *et al.* 2005).

The timing of crop sowing is a key factor regulating the timing that weed seeds start to shed their seeds and therefore the proportion of seeds that is predated. Seed predation increased after sowing autumn sown cereals in late September and remained considerable over the winter months (Lutman, 2006). It is likely that seed predation over that period is due to rodents or organisms other than carabids since most carabids are active between late April and the end of September (Jones, 1976).

Seed predation is a function of the availability of seeds of the target species, of the presence and abundance of seed predators, of alternative food sources of the seed predators and of the quality of the habitat for the seed predators. A detailed model of seed predation should model seed predation as a function of the dynamics of each of these factors and their interactions. Such complexity is not warranted here. In this model it was assumed that the factors that affect the proportion seed predation are crop type and timing of sowing and harvest. Carrots and onions are grown on beds with a number of rows per bed so some of the field area is left uncropped. Added to that is a general slow crop development, certainly for onion, and together this is likely to disfavour the presence of seed predators and therefore decrease seed predation compared to a winter wheat crop where some vegetation has already established around April-May. The temporal variation of the proportion seed predation can be represented by the following form of the Beta distribution (Ben Amar *et al.*, 2005) which is suitable for (a)symmetric patterns as observed in empirical studies. The function representing total daily seed predation can be written as:

**Equation 2-13:**

$$\begin{cases} \text{if } \mathrm{d}_{\mathrm{sim}} < \mathrm{d}_{\mathrm{ssp}} & m_{\mathrm{p-S}}(\mathrm{d}_{\mathrm{sim}}) = 0 \\ \text{if } \mathrm{d}_{\mathrm{ssp}} \le \mathrm{d}_{\mathrm{sim}} \le \mathrm{d}_{\mathrm{esp}} & m_{\mathrm{p-S}}(\mathrm{d}_{\mathrm{sim}}) = \dfrac{(\mathrm{d}_{\mathrm{sim}} - \mathrm{d}_{\mathrm{ssp}})^{\alpha} * (\mathrm{d}_{\mathrm{esp}} - \mathrm{d}_{\mathrm{sim}})^{\beta}}{n} \\ \text{if } \mathrm{d}_{\mathrm{sim}} > \mathrm{d}_{\mathrm{esp}} & m_{\mathrm{p-S}}(\mathrm{d}_{\mathrm{sim}}) = 0 \end{cases}$$

where $m_{\mathrm{p-S}}(\mathrm{d}_{\mathrm{sim}})$ is the daily proportion (mortality due to) seed predation, d is the day number, $\mathrm{d}_{\mathrm{ssp}}$ and $\mathrm{d}_{\mathrm{esp}}$ are the start and end dates of seed predation respectively, $\alpha, \beta$ are shape parameters and the additional parameter n is required to normalise the Beta distribution.

### 2.5.6.2 Parameterisation and model implementation

*Stellaria media* belongs in the top-category of plants visited by seed-eating birds (Marshall *et al.*, 2003). Several studies have shown that shed seeds are also heavily predated by rodents and carabids (Tooley *et al.*, 1999; Watson *et al.*, 2003; Westerman *et al.*, 2003c). Intensity of seed predation was variable in place and time but appears to be highest early in the summer (Westerman *et al.*, 2003b; Mauchline *et al.*, 2005). Since *S. media* is insensitive to photoperiod and has a very wide periodicity of emergence, seed production can span the period from April to November (van den Brand, 1987; Grundy *et al.*, 2003c). However, due to low temperature and solar radiation, the amount of biomass and flowers may well be negligible as compared to the spring – autumn period.

Between 19 and 72% of *T. inodorum* seeds were predated over a 3-week period, when dishes containing seeds were placed in different crops at 8 sites in Sweden (Andersson, 1998). A recent non-published study (Lutman, 2006) assessed the mean percentage seed predation pre- and post harvest in winter wheat and spring barley over a number of 14 day periods between May and February (see Table 2.2) which suggested *T. inodorum* lost more seeds pre-harvest than *S. media*.

**Table 2-7** Pre- and post harvest percentage seed predation in cereals (data Lutman, 2006)

| | **Timing** | **Winter wheat** | **Spring barley** |
|---|---|---|---|
| ***S. media*** | Pre-harvest | 42 | 42 |
| | Post-harvest | 45 | 47 |
| ***T. inodorum*** | Pre-harvest | 60 | 85 |
| | Post-harvest | 42 | 50 |

A recent study showed that when ground beetles (*Harpalus affinis* and *Harpalus distinguendus*) were offered seeds of 28 different species, *T. inodorum* seeds were preferred over 25 other seeds among which were *S. media* seeds (Honek *et al.*, 2006). For *T. inodorum* it can be assumed that total weed seed production is restricted to the interval from the beginning of May until the end of September. The reason is that at the end of September all flowering plants will be killed by ploughing / glyphosate spraying and any plants emerged after the end of July only flower in the next year (Roberts and Feast, 1974).

### Interval

The interval over which seed predation is implemented to occur is based on experimental studies of seed predation in crops (Westerman *et al.*, 2003b; Mauchline *et al.*, 2005) and an extensive study monitoring carabid activity throughout the season (Jones, 1976). Following the patterns observed in the seed predation studies (see Figure 2-9), it was assumed that the shape of the seed-predation-over-time curve is independent of weed species. The timing of seed shedding and the preference of seed predators for seeds is what regulates the total proportion of seeds that is predated. Assuming a constant seed proportion per day, the daily proportion seed predation $m_{\text{p-S}}(\text{d})$ can be calculated from the fortnightly seed predation figures:

**Equation 2-14:** $$m_{\text{p-S}}(\text{d}) = 1 - \sqrt[14]{1 - m_{\text{p-S}}(14\text{d})}$$

Since Westerman *et al.* (2003b) and Mauchline *et al.* (2005) did not record seed predation early in the season, no accurate parameter values could be estimated whilst fitting the Beta distribution in Equation 2-13. Arbitrary parameters were therefore chosen for $\text{d}_{\text{ssp}}$, $\text{d}_{\text{esp}}$, $\alpha$, $\beta$ and $n$ (see Table 2-8) that resulted in a pattern that roughly reflected the seed

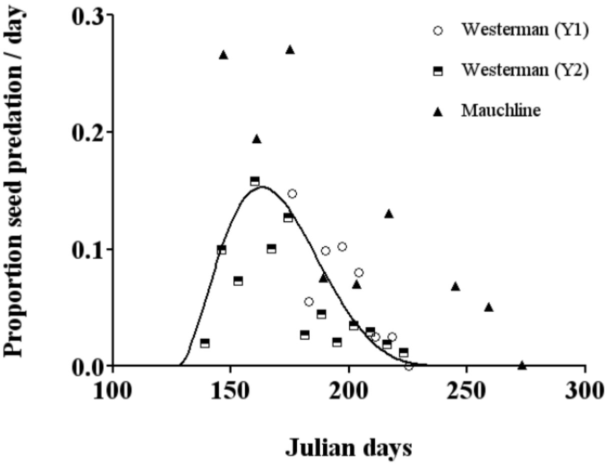


**Figure 2-10** Data points represent daily proportion seed predation of *S. media* from Westerman *et al.* (2003c) and Mauchline *et al.* (2005). Fitted line is the Beta distribution (see Eq. 2-13) and parameters are given in Table 2-8.

predation patterns for *S. media* as observed by these studies (see Figure 2-10). Even though this is a crude approach, it represents a more ecological approach to modelling seed predation than applying a constant daily proportion seed predation.

Data on the temporal variability of the proportion seed predation was available only for *S. media*. Since the data in the literature suggested that *T. inodorum* would be preferred over *S. media*, the fitted value of the parameter *n* in Equation 2-13 for *S. media* was multiplied by 4/5 to give the parameter *n* for *T. inodorum*.

**Table 2-8** Parameters for the Beta distribution function representing seed predation (Equation 2-13)

| | ***S. media*** | ***T. inodorum*** |
|---|---|---|
| $d_{ssp}$ | 127 | 127 |
| $_{desp}$ | 253 | 253 |
| $\alpha$ | 2.0 | 2.0 |
| $\beta$ | 5.0 | 5.0 |
| n | 5.0e+013 | 4.0e+013 |

## 2.5.7 Natural seed incorporation into the soil

### 2.5.7.1 Background and mathematical representation

Seguer Millàs (2002) assessed seed burial rate of a number of species with varying seed sizes. He found that burial rate is influenced mainly by the amount of rain in the preceding 24 hours and that small seeds disappear at a faster rate than larger seeds. Benvenuti (2007) did not correlate seed disappearance from the surface with daily rainfall but corroborated the relationship between seed burial rate and seed size. The effect of natural seed redistribution in the top soil during seed shedding due to rain is most probably trivial compared to the seed redistribution due to cultivation. In addition, germination and emergence of weed seeds in ECOSEDYN is assumed to happen only during the 60 days after seedbed cultivation, so the exact distribution of seeds during seed shedding is irrelevant.

### 2.5.7.2 Parameterisation and model implementation

The only aspect that was considered relevant in ECOSEDYN was the proportion of seeds that becomes incorporated in the soil immediately at seed shedding vs. the proportion that remains on the surface, and is therefore subject to seed predation. No information in the literature could be found that suggested that the proportion of seed remaining on the soil surface was different in a carrot crop as compared to a winter wheat crop. Shed seeds were distributed over the soil layers in the following way: 57% on the soil surface, 29% in the 0-5 mm and 14% in the 5-10 mm soil layer.

## *2.6 Knowledge gaps*

The model components presented in this Chapter (see Figure 2-11) were ‘mentally assembled’ and there was no time available to conduct experiments to validate the

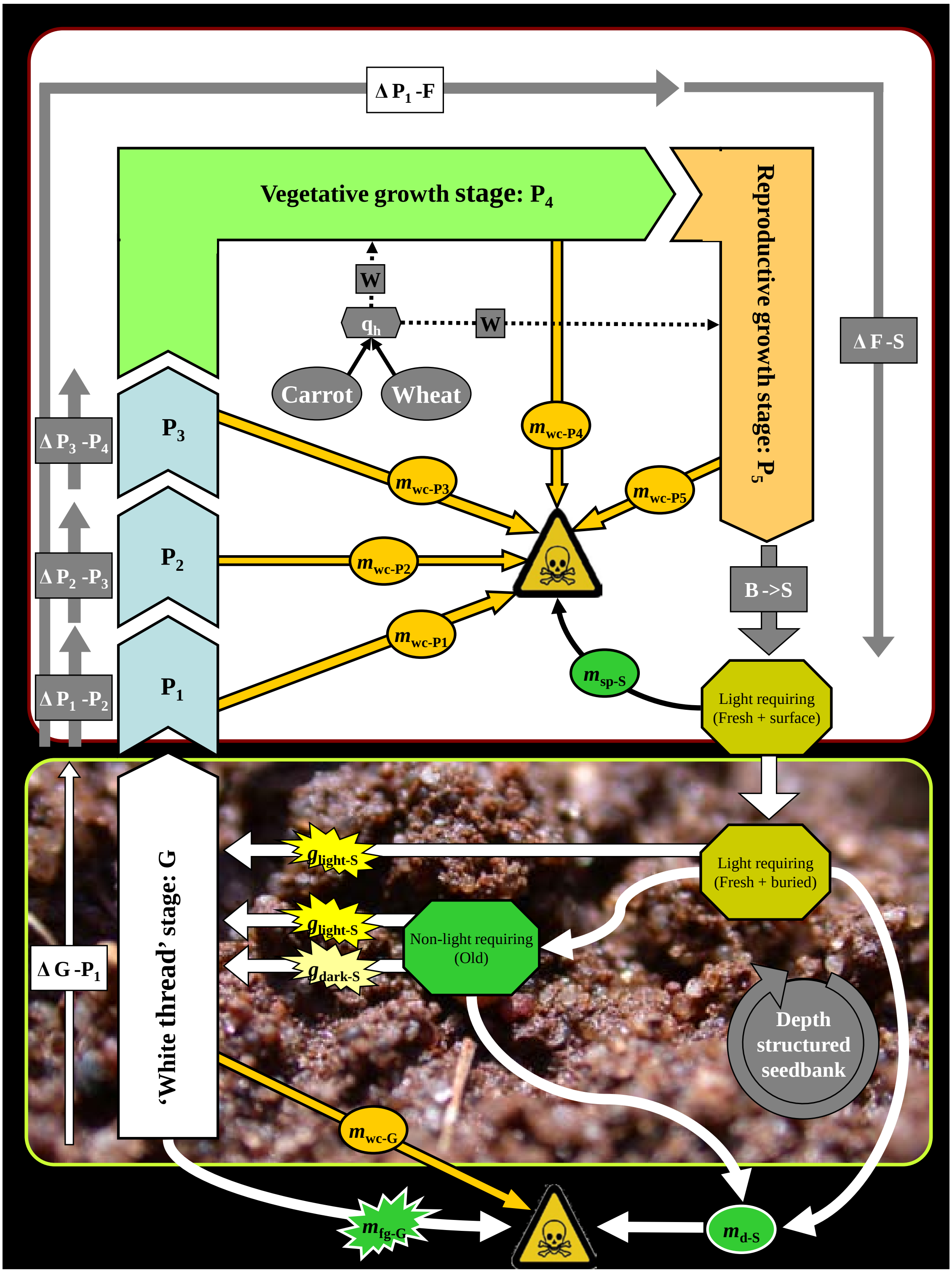


**Figure 2-11** Graphical representation of weed biology and regulating factors in ECOSEDYN. Model components (states and processes) that were addressed in Chapter 2 are highlighted in colour / white. Model components in grey are addressed in Chapter 3 and 4.

chosen parameter values. On the other hand, two areas of the system were identified early on, either because key assumptions of the available models had not been validated (vertical redistribution of seeds by cultivation) or otherwise because knowledge about the biology of the system was clearly lacking (growth and reproduction of the weed species).

### 2.6.1 Vertical re-distribution of seeds by cultivation

A mechanistic model for plough, both with and without skim-coulter, was developed by researchers at INRA (Colbach *et al.*, 2000; Roger-Estrade *et al.*, 2001). However, this model is considerably more complex and not straight forward to incorporate in the overall modelling framework. Although both models had been validated as part of the model construction by the authors, observations in the field raised some questions about the validity of the proposed movement of soil during ploughing.

Seedbed preparation often comprises two or more cultivation implements. In theory, multiplying the transition matrices of two different cultivation implements with each other and subsequently multiplying the resulting overall transition matrix with the vertical distribution prior to cultivation results in the vertical distribution post cultivation for that particular cultivation sequence. This is based on the assumption that there are essentially no changes in soil bulk density during cultivation, which has not been validated. If this assumption is true than it can save a lot of time since each implement only has to be parameterised on its own. However, if it is not, then the consequences are that each subsequent model component in the chain (germination and pre-emergence growth -> plant competition -> seed production) is receiving and therefore returning incorrect information as well. Therefore the assumptions underlying the transition matrix approach were tested through field experiments.

Another gap is that, though models were developed for several cultivation implements at Warwick HRI, no compatible model was available for the mouldboard plough which was a cultivation implement used in the crop rotation. The experiments that were conducted to verify the assumptions and to derive the model for the mouldboard plough are described in Chapter 3.

### 2.6.2 Plant growth and reproduction

No comprehensive model could be identified that combined the timing and qualitative relationship of dynamic processes such as plant growth, flowering and seed shedding and therefore experiments were set up to explore the relationship between these processes so that they could be represented in a simple but sound way. Since the model is to be a dynamic one, i.e. simulate processes on a fine time scale, there is a need to move beyond the current static biomass – seed relationship models (e.g. Lutman, 2002) and create models that simultaneously account for biomass increase and seed production. To create such models, an increased understanding of the phenology of both weed species was imperative. Several research questions were proposed and consequently addressed in field experiments.

Another piece of information that was missing was the phyllochron (days or thermal time to reach each true leaf pair). This is relevant as post-emergence weed control efficacy is normally expressed as a function of the the true-leave stage rather than the biomass of a plant. The research questions, the results of the experiments and the mathematical representation of the model components for biomass increase, flowering and seed shedding is given in Chapter 4.

# 3 Vertical re-distribution of weed seeds: experimental work and model implementation

## *3.1 Introduction*

The depth of seeds in the soil is a key regulator of weed emergence responses (Benvenuti *et al.*, 2001a; Grundy *et al.*, 2003a). Given the right weather conditions, the vertical distribution of seeds in the soil determines the proportion of the population that is in a position from where emergence is possible. However, the vertical distribution not only determines the number of emerged seedlings, it also affects the timing since mean time to germination increases with burial depth (Benvenuti, 2003). Not surprisingly then, reviews on emergence models have argued for the inclusion of components that predict vertical seed distribution (Forcella *et al.*, 2000; Grundy, 2003; Colbach *et al.*, 2005).

Rainfall and earthworms contribute to the incorporation of seeds into the soil seedbank (Chambers and MacMahon, 1994) and further re-distribution by earthworms has been documented as well (van der Reest and Rogaar, 1988; Smith *et al.*, 2005). However, as seed distribution patterns are often observed that are characteristic of the tillage regime practiced (e.g. Yenish *et al.*, 1992; Swanton *et al.*, 2000; Bàrberi and Cascio, 2001; Vasileiadis *et al.*, 2007), factors other than cultivation are generally assumed to be secondary. In fact, a key premise of including cultivation as a component of a weed management strategy is its effect on the vertical distribution of seeds. A good example is the development of the so-called ‘spot-plow’ which enables the complete inversion of furrows and thus maximises the percentage deep burial of seed (Shoji, 2007).

The realization that cultivation could play a key role in weed management led to the initiation of studies to explore the effect of cultivation on seed burial of fresh seeds. The first studies simulated the movement of seeds using beads or equivalent tracers that were spread out over the soil surface (Rottele and Koch, 1981; Moss, 1988; Staricka *et al.*, 1990; Dessaint *et al.*, 1996). Useful, mostly qualitative information can also be inferred from studies evaluating the depth and pattern of incorporation of fungicides (Kelpsas and Campbell, 1994; Juzwik *et al.*, 2002), herbicides (Walker *et al.*, 1976), nematicides (Woods *et al.*, 1999) and fungal spores (Ngugi *et al.*, 2002) from the soil surface by a range of different cultivation implements. However, seeds of the majority of weed species survive for a number of years in the soil seed bank so cultivations will not only distribute fresh seeds from the surface but also the surviving seeds in the soil. Hence, prediction should encompass both the movement of seeds freshly shed on the soil surface and the seeds produced and incorporated in the seedbank in previous seasons, located at any position over the cultivation depth.

The first study to tackle the problem of predicting the position of seeds after cultivation from both the soil surface and intermediate soil depths and translating this into a model was conducted by Cousens and Moss (1990). The experimental method comprised incorporation of plastic beads of different colours at known depths in the soil. The soil was then cultivated according to two different cultivation regimes; a mouldboard plough and two passes of a rigid tine. A shallow pass with a spring-tine cultivator + crumbler was used to level the soil for both cultivation regimes. Subsequently, soil cores were taken to establish the proportional distribution of recovered beads over the four 5 cm. sampling layers (0-5, 5-10, 10-15 and 15-20 cm). In this way a transition matrix was created consisting of the probabilities of a bead (seed) moving from its respective position before cultivation to each of four soil layers after cultivation. Multiplying a vector with the numbers of seeds in each different layer by the transition matrix gives the density of seeds after cultivation. Algebraically this is expressed as:

**Equation 3-1**
$$\begin{bmatrix} a_{11} & a_{21} & a_{31} & a_{41} \\ a_{12} & a_{22} & a_{32} & a_{42} \\ a_{13} & a_{23} & a_{33} & a_{43} \\ a_{14} & a_{24} & a_{34} & a_{44} \end{bmatrix} * \begin{bmatrix} S_{tot-1}(b) \\ S_{tot-2}(b) \\ S_{tot-3}(b) \\ S_{tot-4}(b) \end{bmatrix} = \begin{bmatrix} S_{tot-1}(a) \\ S_{tot-2}(a) \\ S_{tot-3}(a) \\ S_{tot-4}(a) \end{bmatrix}$$

where $a_{ij}$ is the probability of moving from layer i to layer j, $S_{tot-1}(b)$ is the number of seeds in layer 1 before cultivation and $S_{tot-1}(a)$ the number of seeds in layer 1 after cultivation. This approach was adopted later by Mead *et al.* (1998) to establish transition matrices for four different implements; spring tine, power harrow, rotovator and spader. Given a starting density and the availability of transition matrices for multiple cultivation implements, the vertical position of seeds in the soil can be calculated. For a sequence of two different cultivation implements this can be calculated as in Equation 3-2.

**Equation 3-2**
$$\begin{bmatrix} b_{11} & b_{21} & b_{31} & b_{41} \\ b_{12} & b_{22} & b_{32} & b_{42} \\ b_{13} & b_{23} & b_{33} & b_{43} \\ b_{14} & b_{24} & b_{34} & b_{44} \end{bmatrix} * \begin{bmatrix} a_{11} & a_{21} & a_{31} & a_{41} \\ a_{12} & a_{22} & a_{32} & a_{42} \\ a_{13} & a_{23} & a_{33} & a_{43} \\ a_{14} & a_{24} & a_{34} & a_{44} \end{bmatrix} * \begin{bmatrix} S_{tot-1}(b) \\ S_{tot-2}(b) \\ S_{tot-3}(b) \\ S_{tot-4}(b) \end{bmatrix} = \begin{bmatrix} S_{tot-1}(a) \\ S_{tot-2}(a) \\ S_{tot-3}(a) \\ S_{tot-4}(a) \end{bmatrix}$$

where $a_{ij}$ are the probabilities of moving from layer i to layer j associated with the first cultivation implement and $b_{ij}$ the probabilities for the second cultivation implement.

Arguing for simplicity, one might ask why multiple thin soil layers need to be distinguished deep in the profile from where no germination is occurring. The reason is that without this feature, the transition matrices would be reduced to stand-alone models for each cultivation implement, but without the ability to correctly multiply the transition matrices of several cultivation implements. For example, a transition matrix for a plough set up to plough at 24 cm could distinguish three layers 0-3, 3-6 and 6-24 cm. However, if the subsequent power harrow cultivation reached 15 cm deep, then this would result in a transition matrix with a 0-3, 3-6 and 6-15 cm layer and therefore these transition matrices would not be compatible.

The work on seed movement described in this chapter served two functions.

- Firstly, ploughing is still a common practice on land used for growing arable (winter wheat) and outdoor vegetable crops (carrot). The previous experimental work conducted at Warwick HRI (Mead *et al.*, 1998; Grundy *et al.*, 1999) focused on four cultivation implements, but not the mouldboard plough. A first aim of this study was therefore to obtain a model for the plough compatible with the previous models developed at Warwick HRI. The results of this work are presented in Section 3.2.
- Secondly, this study aimed to critically evaluate two published approaches to modelling seed movement:
    - transition matrices as pioneered by Cousens and Moss (1990) and applicable to any cultivation implement. More specifically, the 'multiplicativity hypothesis' will be addressed, i.e. the intuitive assumption that multiplying transition matrices of individual cultivation implements reflects an accurate way of predicting to where a seed moves when the relevant implements are used in sequence. The results of this study are presented in Section 3.3
    - mechanistic soil movement models of the effect of ploughing without and with skim-coulter as developed by Colbach *et al.* (2000) and Roger-Estrade *et al.* (2001) respectively. The results of this study are presented in Section 3.4

The conclusions that are drawn from the work presented in this chapter are given in Section 3.5. The implementation of vertical redistribution of weed seeds in

ECOSEDYN is then presented in Section 3.6. Hence, the work presented in this chapter is both providing the theoretical justification for how to represent vertical seed distribution in ECOSEDYN, as well as real data to ECOSEDYN.

## *3.2 Vertical seed re-distribution due to ploughing at two locations / soil types*

### 3.2.1 Introduction

Of all the cultivation implements commonly used on agricultural land, the plough has the highest burying potential for freshly shed weed seeds (e.g. Rahman *et al.*, 2000; Mohler *et al.*, 2006) and this has been realised since its inception (Guul-Simonsen *et al.*, 2002). Given that placing seeds at depths from where they can not germinate helps to alleviate weed emergence in future seasons, ploughing is a useful part of an integral weed management strategy.

Several studies have been conducted with the aim of quantitatively describing seed movement during ploughing. The earliest studies only considered the effects on surface applied beads or seeds (Moss, 1988; Staricka *et al.*, 1990; Dessaint *et al.*, 1996) but since Cousens and Moss's (1990) pioneering work, most studies have included movement from any position in the soil. The following studies were considered; the transition matrix models from Cousens and Moss (1990) and van Melick (1996) and the mechanistic models developed by Colbach (2000) and Roger-Estrade (2001). For reasons related to the methodology and/or soil type, the models / data were not considered suitable to be implemented as component in the overall modelling framework as explained below.

- Cousens and Moss (1990): Most importantly, 5 cm layers were used which is incompatible with the 3 cm layers used by Mead *et al.* (1998). Secondly, a spring-tine cultivator with crumbler attached was used to level the soil surface after ploughing, so in fact the transition matrix represents the probabilities of seed movement for [mouldboard plough + spring-tine cultivator + crumbler] rather than for [mouldboard plough]. If ploughing is followed by any other cultivation implement than the spring-tine cultivator + crumbler, the use of this transition matrix to represent the plough per se will be questionable. Lastly, the 1.5 x 1.5 m holes that were dug and over which the beads were scattered may have changed the soil structure relative to the surrounding soil.

- Van Melick (1996) conducted an experiment to compare the burial properties of an eco-plough designed for shallow ploughing 10-18 cm deep and two conventional ploughs. However, unlike Mead *et al.* (1998) they did not insert beads in the soil at fixed depths but as layers by mixing the beads with a volume of soil and then introducing them in the plough layer with an auger just before ploughing. Although this is a more straightforward way of creating a transition matrix that can be multiplied with a transition matrix of another cultivation implement over the same depth it is incompatible with the precision acquired from beads in layers for every 3 cm in the soil. In addition, only one replicate per plough treatment was realised.
- Colbach *et al.* (2000) and Roger-Estrade *et al.* (2001) modelled the effect of the plough in a mechanistic way and their model allows the creation of transition matrices that would be compatible with the transition matrices for other cultivation implements. However, the predictions of their models were not evaluated for sandy soil types as found at Warwick HRI. Secondly, compared to the straightforward use of transition matrices, the implementation of the processes is more complex, especially for the Roger-Estrade model which is most relevant due to the addition of a skim-coulter. Thirdly, the accuracy with which the model can predict the vertical coordinate after ploughing is sensitive to the number of slivers, especially if the number of slivers is low. This would require an additional soil model to estimate the number of slivers. Lastly, and the subject of study in section 3.4, the validity of the model is contentious as it seems to underestimate the soil height after ploughing.

In the agronomical context of the system to be modeled, three scenarios exist that include plough cultivation;

1 prior to secondary cultivation and sowing winter wheat, all in autumn
2 in autumn and leaving the field over winter to benefit soil structure, followed by secondary cultivation and carrot / onion drilling in spring
3 in early spring followed shortly afterwards by secondary cultivation and carrot / onion drilling

Although Scenario 1 and 3 are different in terms of timing it was assumed that ploughing in spring does not systematically differ from plouging in autumn and can be represented by the same transition matrix, ‘[Plough]’. Scenario 2 is different from

1 and 3 since leaving the soil over winter results in a redistribution of soil and a decrease in soil height. Therefore, at the time of secondary cultivation, the vertical distribution of seeds has changed relative to that immediately after ploughing and is represented by the transition matrix '[Plough + Soil settling]'. For species without winter emergence the '[Plough + Soil settling]' transition matrix can simply be used. However, for weed species such as *S. media* and *T. inodorum* a (small) proportion of seeds emerges over winter and these seedlings will be lost from the population due to secondary cultivation or glyphosate spraying in spring. The proportion that emerges over winter depends on the number of seeds in the top soil layer immediately after ploughing, which can be estimated from the [Plough] transition matrix.

Since the vertical distribution of beads is only measured at the start and end of the period of soil settling, the number of seeds (including germinated) in the zone from where emergence is possible at any point in time over this period will be assumed constant. The value for this constant is taken from the prediction for vertical seed distribution by the '[Plough]' transition matrix. Assuming that the 'multiplicativity' assumption is correct, the [Plough] transition matrix then has to be pre-multiplied with the '[Soil settling after ploughing]' transition matrix. Just prior to this multiplication, the cumulative number of germinated seedlings at the end of the period of soil settling should be deducted from the vertical distribution. The transition matrix '[Soil settling after ploughing]' can not be determined directly but instead has to be extracted from the '[Plough]' and '[Plough + Soil settling]' transition matrices using matrix algebra.

Therefore, the aim was to conduct an experiment from which the three transition matrices could be derived. A second goal was to assess how much an additional secondary cultivation, power harrowing, would change the vertical distribution of seeds after ploughing. The experiment was to be conducted at two locations (soil types) and at two plough depths to be able to compare the relative impact of these factors on the redistribution of seeds.

### 3.2.2 Preliminary experiment

Various approaches have been taken to introduce beads before cultivation and sample the soil after cultivation. To ensure compatibility it was anticipated to use the same methodology as used by Grundy *et al.* (1999); introducing beads in narrow layers every 3 cm down to the desired depth and sampling the soil after cultivation by taking soil cores with an auger (9 cm diameter). To decide over which area the soil cores should be taken, a preliminary experiment was conducted comparing different sampling designs.

The aims were:

- to determine the recovery rate for different sampling designs,
- to assess the distance and angle over which beads were displaced
- to assess whether this was different for beads at different depths prior to ploughing

#### 3.2.2.1 Methodology

Studies on soil erosion and weed seed movement have shown that soil and seed are diagonally displaced over an average distance of less than 50 cm (Marshall and Brain, 1999; Montgomery *et al.*, 1999; Kosmas *et al.*, 2001). The available soil corer had a diameter of 9 cm and some trials in freshly ploughed soil showed that the minimum possible distance between two soil cores without disturbing the soil was about 18 cm.

In one sampling design the horizontal and vertical distances were minimised (diagonal square or DS design) and in the other the diagonal distance was minimised (diagonal lattice or DL design), see Figure 3-1. Since the angle over which the soil was displaced was not known, a third sampling design included for each of the three plough bottoms a transect of 5 soil cores at different angles from the position of the beads in the soil (angle design or A design). The DL and DS designs were tested at one plough depth (24 cm) and the A sampling design was tested at two plough depths (16 cm and 24 cm). Since this was experiment only set out to evaluate the methodology it was considered satisfactory to assess just one replicate per treatment.

The experiment was conducted in November 2005 in Wellesbourne. To ensure proper rotation of the furrows in the experimental plot, a strip of land immediately adjacent to the experimental plot was ploughed first. Steel plates (150 cm. long, 2 mm. wide) were hammered in the soil at 10-12 cm distance from each other. Soil was then dug out over a length of ca. 110 cm and stored in a wheel barrow until the trench depth for the deepest layer of beads was reached. After the bottom of the trench was firmly pressed using a wooden plank and a light sledge hammer, 3000 beads of a specified colour were scattered evenly on the flattened surface. Fine soil was then taken out of the wheel barrow and carefully spread out on top of the beads. More soil was added until the next assigned depth was reached. Soil was carefully pressed and beads applied. This was repeated until the trench was filled to the soil surface.

For the experimental plots assigned to the DL and DS designs and one experimental plot assigned to the A sampling design (A-24), beads of different colours were applied at the surface, and depths of 4.5 cm, 10.5 cm 16.5 cm and 22.5 cm.

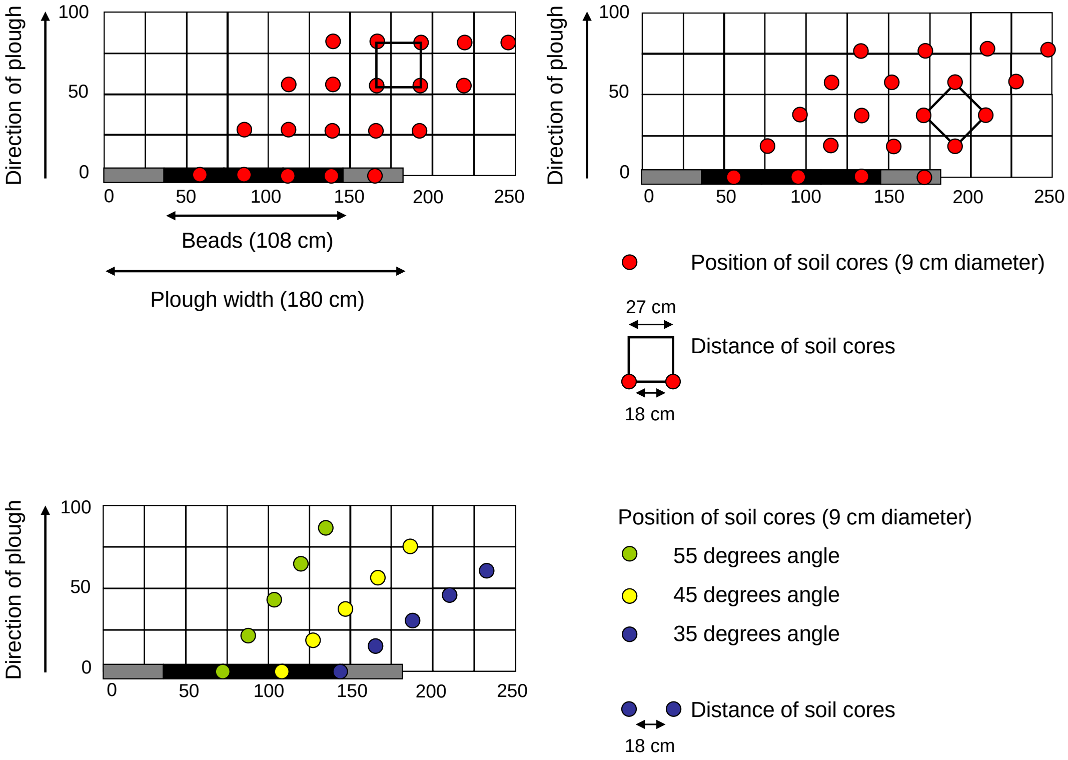


**Figure 3-1** ‘Diagonal square’ (top left), ‘Diagonal lattice’ (top right) and ‘Angle’ (bottom) sampling design and the position of soil cores within them after ploughing with a five-bottom plough (each 36 cm wide). Beads were positioned in the soil so that it matched the straight trajectory of the central three plough bottoms (the black area) with the outer plough bottoms representing the grey area.

In the other experimental plot with the A design (A-16), beads of different colours were applied at the surface and depths of 1.5 cm, 7.5 cm and 13.5 cm. The surface bead layer was applied just before the actual tillage operation. The beads were inserted in the soil in line with the path of the inner three plough bottoms (36 cm each) of a 5 bottom plough (Dowdeswell DP 8B Hydrawidth).

To mark the original position of the beads, sticks were put in the soil outside the ploughed strip in line with the beads. After ploughing the plots according to the assigned depth, soil samples were taken with the 9 cm. auger according to the sampling designs as illustrated in Figure 3-1. The soil samples were bagged and labelled in the field. Since the depth distribution per se was not of interest, entire soil cores were dispersed in water by manually mixing and stirring. Since the beads were made of low-density polythene and the soil was low in clay content, soil did not stick to the beads making them float to the surface from where they could be sieved off. For each soil core, beads were counted per colour. The following characteristics were determined: % recovery per starting depth, average % recovery, the number of recovered beads / soil sample at each position across the X-axis and Y-axis.

#### 3.2.2.2 Results

The most important observation from the preliminary experiment was that taking soil cores was not an appropriate way of sampling ploughed soil. Despite a relatively wide diameter of the auger (9 cm), the soil within the auger was compressed relative to the soil outside, obscuring the distribution of beads over depth. A second observation was that some soil clods had broken along the plane where the beads had been placed, in other words too many beads were being used. Average percentage bead recovery varied between 5.1 and 7.6 % for the sampling designs (see Table 3-1) which is within the range found by Mead *et al.* (1998) for the other four cultivation implements.

**Table 3-1** Average bead recovery per sampling design and over depth.

| ***Plough depth*** | ***24 cm*** | | | | ***16 cm*** |
|---|---|---|---|---|---|
| Sampling design | Lattice | Square | Angle | | Angle |
| ***Average*** | 5.1 % | 6.0 % | 7.6 % | | 6.4 % |
| ***Surface*** | 9.4 % | 3.9 % | 5.0 % | ***Surface*** | 5.3 % |
| ***4.5 cm*** | 2.2 % | 3.4 % | 3.5 % | ***1.5 cm*** | 3.8 % |
| ***10.5 cm*** | 2.0 % | 5.9 % | 10.0 % | ***7.5 cm*** | 5.8 % |
| ***16.5 cm*** | 1.8 % | 6.1 % | 9.0 % | ***13.5 cm*** | 10.8 % |
| ***22.5 cm*** | 10.2 % | 10.9 % | 10.5 % | | |

Proportionally more beads originally at 22.5 cm were recovered because the plough did not move all of these beads so that they were picked up by the soil samples targeting the original position of the beads. The cumulative percentage bead recovery for the transects in the ‘Angle’ sampling designs was much lower for the 55-degree transect than for the 45 and 35 degree transects (Figure 3-2 *left*). If data of all four plots were combined, 99% of the beads were recovered between X-coordinates 85.5 and 193.5, spanning exactly 108 cm (data not shown). With regard to forward movement (Y-axis), the peak of the bead distribution lies around 25 cm beyond the starting position and appeared not to be influenced by the vertical position of beads in the soil before ploughing (Figure 3-2 *right*).

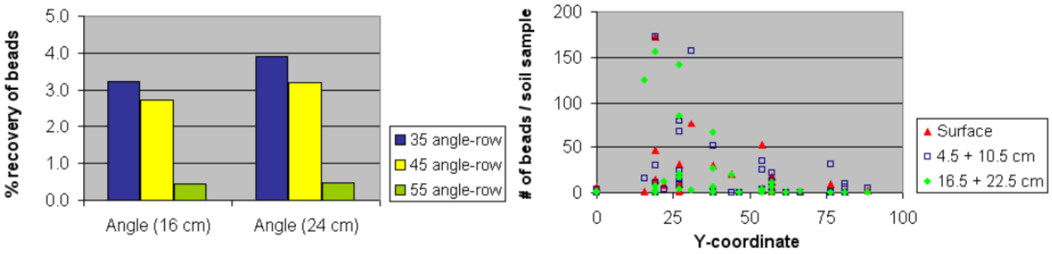


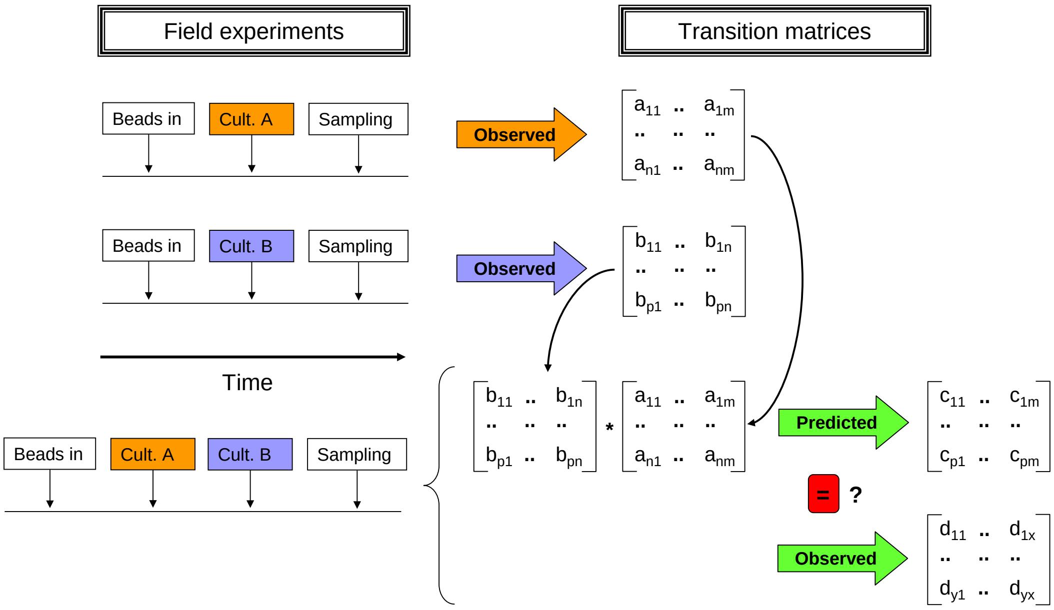
**Figure 3-2** *Left*: The percentage recovered beads for the soil sample transects at different angles from the line of beads (see Figure 3-1) for the plots ploughed at 16 and 24 cm.

*Right*: Distribution of bead displacement in the direction of ploughing (along Y-axis), distinguished by three depth groups before ploughing and pooled over the sampling designs DS, DL and A-24. Beads at 22.5 cm depth that had not been moved by the plough (i.e. Y-coordinate of soil sample is 0) have not been included.

### 3.2.3 Main experiment

The anticipated experimental design of the main experiment included three different plough treatments, [Plough], [Plough + Soil settling] and [Plough + Soil settling + Power harrow], each at two plough depths (16 and 24 cm) and replicated three times per treatment and at two locations (Kirton and Wellesbourne) (see Figure 3-4).

The preliminary study was conducted to find out *how*, not *if* a sampling design of soil cores be used. In the preliminary study it was observed that freshly ploughed soil was compressed within the auger, which made it unsuitable as a sampling tool. Hence, a sampling technique based on excavation of layers had to be created. Because there was not enough time left for an excavation framework to be designed and constructed before the start of the experiment, the [Plough] treatment, where sampling was to occur immediately after ploughing, had to be abandoned. This meant that the comparison of vertical distribution before and after soil settling could not be realised. Rather than cancelling the experiment altogether, it was decided to address the evaluation of modelling seed movement through transition matrices, more specifically, the so-called ‘multiplicativity’ assumption. The assumption can be evaluated by assessing two separate cultivation implements, as well as the sequence, so that a series of observed and predicted transition matrices can be created (see Figure 3-3).



$$\begin{bmatrix} a_{11} & .. & a_{1m} \\ .. & .. & .. \\ a_{n1} & .. & a_{nm} \end{bmatrix} \qquad \begin{bmatrix} b_{11} & .. & b_{1n} \\ .. & .. & .. \\ b_{p1} & .. & b_{pn} \end{bmatrix}$$

$$\begin{bmatrix} b_{11} & .. & b_{1n} \\ .. & .. & .. \\ b_{p1} & .. & b_{pn} \end{bmatrix} * \begin{bmatrix} a_{11} & .. & a_{1m} \\ .. & .. & .. \\ a_{n1} & .. & a_{nm} \end{bmatrix} \qquad \begin{bmatrix} c_{11} & .. & c_{1m} \\ .. & .. & .. \\ c_{p1} & .. & c_{pm} \end{bmatrix} \qquad \begin{bmatrix} d_{11} & .. & d_{1x} \\ .. & .. & .. \\ d_{y1} & .. & d_{yx} \end{bmatrix}$$

**Figure 3-3** Schematic explanation of the evaluation of the ‘multiplicativity’ assumption. It assumes that the vertical distribution of seeds after a sequence of cultivations is identical to the product of the multiplication of the individual transition matrices, i.e the d-matrix is identical to the c-matrix. Matrix element subscripts: ‘m’ and ‘p’ represent the number of bead layers before cultivation A and the number of soil layers after cultivation B respectively. To allow matrix multiplication, the number of soil layers after cultivation A, ‘n’, has to be equal to the number of bead layers before cultivation B. Similarly, for the d-matrix: x and y are the number of bead layers before and the number of sampled soil layers after cultivation respectively.

Clearly, the ‘multiplicativity’ assumption can be tested using a wide range of combinations. The cultivation sequence chosen was Plough – Soil settling – Power harrow, giving the following three treatments: [Plough + Soil settling], [Power harrow] and [Plough + Soil settling + Power harrow]. This sequence was chosen because of the following additional benefits:

- This experimental design consisted of the second and third treatments of the previous experimental design (see Figure 3-4), i.e. [Plough + Soil settling] and [Plough + Soil settling + Power harrow], for which preparations had already been taken
- It allowed the parallel evaluation of the Colbach and Roger-Estrade models (see Section 3.4) to be carried out.
- According to the expertise of farm staff at Warwick HRI (Julian Brandreth, Colin Jones), the Power Harrow was the cultivation implement most likely to

be used in spring on ploughed soil left over winter. Because of limited available time, a transition matrix already in existence for this implement (Mead *et al.*, 1998) and the power harrows used in Wellesbourne and Kirton being of exactly the same specification, no treatment was included to derive the [Power harrow] transition matrix again. It was assumed that the transition matrix derived previously for the Power harrow would be valid for use in this assessment both in Kirton and Wellesbourne.

#### 3.2.3.1 Methodology

**Experimental design**

Throughout the rest of this chapter, [Plough + Soil settling] and the [Plough + Soil settling + Power harrow] will be referred to as Treatment 1 (T1) and Treatment 2 (T2) respectively, plough depth will be abbreviated to 'pd'.

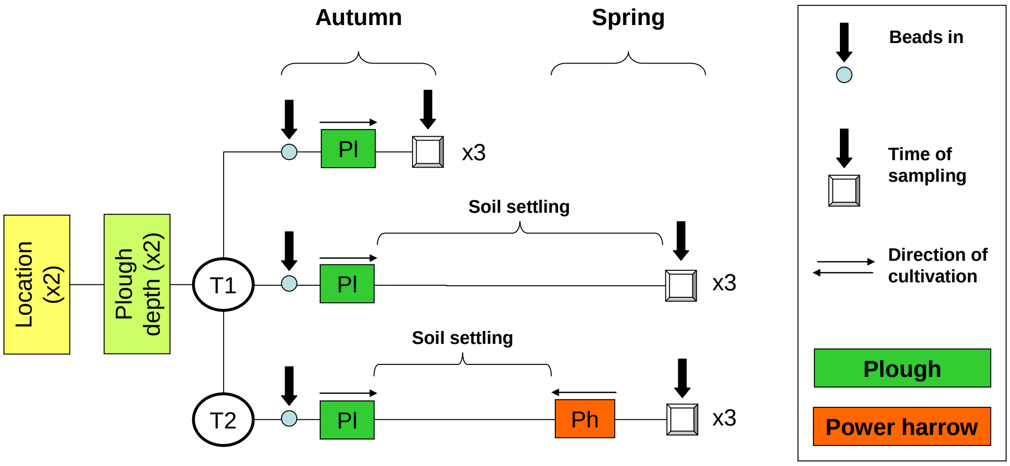


**Figure 3-4** Experimental design following initial study aim. The [Plough + Soil settling] and [Plough + Soil settling + Power harrow] were carried out. Locations were Warwick HRI research stations at Kirton and Wellesbourne and ploughs were set up at two depths: 16 and 24 cm.

To account for heterogeneous soil conditions, an incomplete Latin Square (3x4) was chosen as the experimental design to include three replicates of the four cultivation regimes (T1 and T2, each at two depths). Individual plots were 15 meters long and approximately 5 (Wellesbourne) or 5.5 meters (Kirton) wide (see Figure 3-5). Beads were available from previous work but to acquire the necessary number of colours, high density polyethylene (HDPE) granules with a density of 0.94-0.97 g/cm$^3$ and approximately 2 mm long were obtained from Begg & Co Thermoplastics Ltd. Beads were inserted in the plots as in the pilot experiment, except for the following details:

- Because beads varied slightly in weight and dimensions between colour, the colours were randomised between depths for each experimental plot.
- 1500 beads were mixed with 500 gram of fine sieved soil before scattering at the assigned depth in the soil to avoid the creation of soil fractures. The mixture was scattered over an area approximately 108 cm long and 10 cm wide.

Prior to ploughing, three soil samples were taken at different parts of the experimental area to measure the bulk density and gravimetric soil water content of the upper 15 cm of soil. The bulk density of the soil where the experiment was conducted was 1.88 ± 0.03 g / cm$^3$ and 1.69 ± 0.16 g / cm$^3$ in Wellesbourne and Kirton respectively. Soil water content was 16.7 ± 0.9 and 24.4 ± 0.2 % in Wellesbourne and Kirton respectively. Within 24-48 hrs after beads were inserted in the soil, plots were ploughed as shown schematically in Figure 3-5 and as explained below.

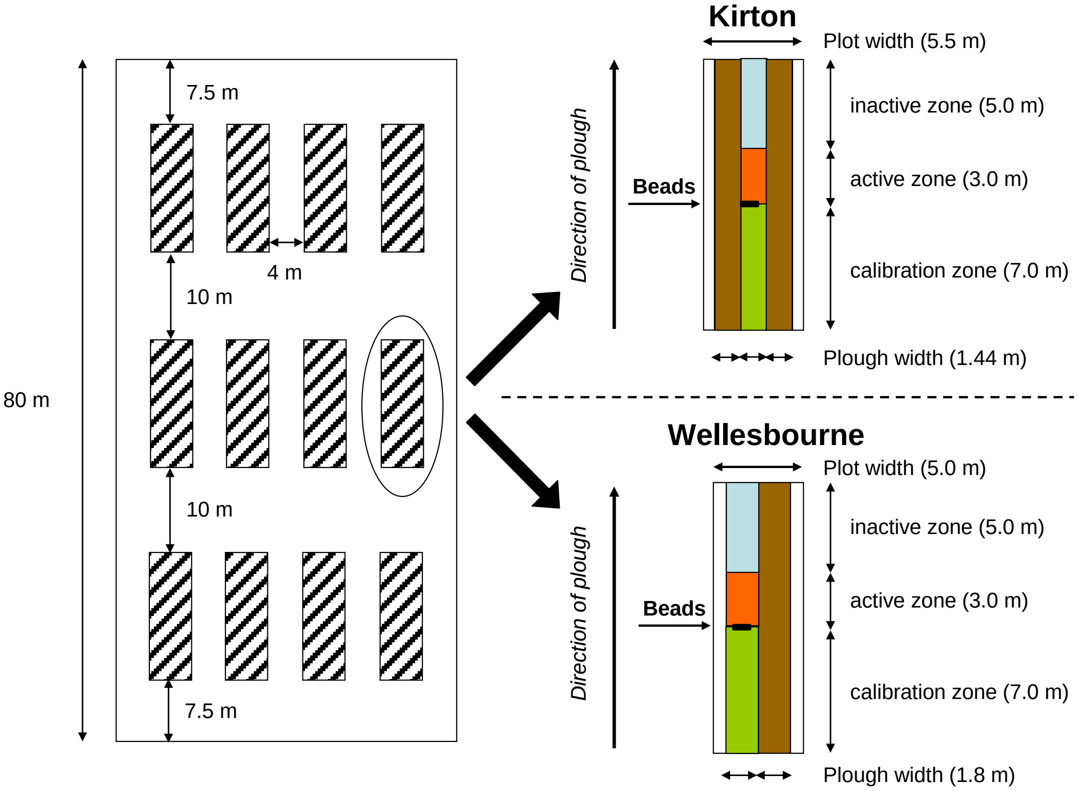


**Figure 3-5** Distances between, and layout and dimensions of, experimental plots. Brown 'zone' to the right of the beads was ploughed to ensure proper rotation of the furrows containing the beads. Brown zone to the left of the beads (only in Kirton) was ploughed to cover the outer left furrow which hit the left most section of the line of beads.

The ‘calibration zone’ is the area where the plough enters the soil and the tractor speed can be stabilised before the beads are hit by the plough at the start of the ‘active zone’ that continues for 3 m after which the plough was cleaned and visually inspected for any attached beads. The remaining section, the ‘inactive zone’, was ploughed to acquire even soil conditions for the treatments that were to receive a power harrow cultivation in opposite direction in spring. To facilitate furrow rotation, the soil strip immediately to the right of these zones was ploughed in advance. In Kirton the line of beads was hit by the three left most plough bottoms (of 4) instead of the three central plough bottoms (of 5) in Wellesbourne. To cover the outer left furrow, an additional stroke of soil to the left therefore was ploughed in Kirton (the brown zone to the left of the experimental area in Figure 3-5) but not in Wellesbourne. Actually the line of beads stretched out into the path of the left front and rear tyres so that the soil was compressed and surface beads possibly moved by the front and rear tyre before being moved by the plough. The shorter distance between the left and right tyre of the tractor used in Kirton meant that 34 cm of the line of beads was compressed whereas in Wellesbourne a 14 cm section was compressed. Because a reversible plough was used, one side was set up at 16 cm and the other at 24 cm deep. For T1 this resulted in diagonally opposite bead distribution patterns and sampling layouts (see Figure 3-7).

Due to time constraints not all plots could be ploughed before Christmas in Wellesbourne. Two replicates of all treatments were ploughed on the 12th of December 2005 and the remaining four plots were ploughed on the 6th of January 2006 using a 5 bottom mouldboard plough (Dowdeswell DP 8) with skim-coulter set at about 5 cm deep. In Kirton all plots were ploughed the 12th of January 2006 with a reversible 4 bottom mouldboard plough (Dowdeswell DP 8B Hydrawidth) with skim-coulter set at the same depth as in Wellesbourne. The area to be sampled and the adjacent area where soil settling was studied was sealed off with plastic meshed wirenetting to prevent hares, badgers and deer from disturbing the soil.

Power harrowing was carried out with a 1.83 m. wide Maschio Erpice DL 1500 in the second and third week of April 2006 in Kirton and Wellesbourne respectively. To prevent beads from being spread out of the sampling area, power harrowing was conducted:

- in one pass, encompassing the strip of soil that contained the beads
- in the opposite direction to ploughing.

### Sampling design

A steel height-adjustable framework (1.5x1.5 m) was constructed based on a design by Dirk Kurstjens (see van Melick, 1996), capable of excavating the soil (see Figure 3-6 left). It allows soil layers three cm deep to be excavated in 10x10 cm blocks using a scoop that slides over a steel groove. The groove was always positioned parallel to the original line of beads and can be divided into 10 cm sections (columns 1-15) using an insertable partitioner (see Figure 3-6 right). The groove rests on the excavation quadrat and can be moved forward and backward (along the direction of cultivation) and fixed at fifteen positions (rows A-O, beads in row O would have experienced maximum measurable forward movement).

**Figure 3-6** Left: excavation framework (1.5x1.5m) used to determine vertical distribution of beads after cultivations. The excavation quadrat is dropped 3 cm. each time soil in a horizontal plane has been excavated. Right: 10x10x3 cm soil blocks can be collected separately using a scoop and an insertable partitioner. Alternatively, soil blocks can be bulked for each forward position (row). The white sticks (bottom left) were inserted in line with and at known distances from the outer widths of the line of beads to mark the position before cultivation.

The framework was positioned in line with the direction of ploughing and such that the steel groove was in line with the original position of the beads. The framework was then hammered in the soil until the excavation quadrat was level with the soil and the first layer could be excavated.

Due to logistic and methodological problems no plots of T1 could be sampled in Kirton and only one plot at each plough depth in Wellesbourne. In Kirton sampling was initiated on the T2 plots first. It became clear that the soil strip cultivated by the power harrow only partly overlapped with the area where the beads were. The extra pass of the plough (see Figure 3-5), the soil settlement over time and sticks that had accidentally been removed, meant that the position of the beads could not be accurately recovered. Since T2 could be regarded as a complete seedbed preparation regime, for pragmatic reasons it was decided to focus on this treatment and ignore T1.

This meant that in Kirton the plots of T1, where sampling had not yet started, were power harrowed to replace the failed power harrowing of T2 plots.

For the single ‘T1, pd=16’ plot sampled in Wellesbourne, each 10x10 cm soil block in a diagonal sampling pattern was collected separately and surrounding soil samples were bulked according to distance to surface (see Figure 3-6 left). Contrary to the results in the pilot experiment, substantial numbers of beads were observed during sampling beyond 70 cm from the original position of beads in this plot. To assess what proportion of beads had moved beyond this distance and if certain depths were over-represented, soil from all depths was bulked over the furthest three rows (‘Bulked’ in Figure 3-7 left).

For the single ‘T1, pd=24’ plot sampled in Wellesbourne, each 10x10 cm position in the excavation quadrat where the scoop contained at least some soil was marked on a grid-map with a ‘1’ and when the excavation quadrat was lowered these positions were marked ‘2’ to highlight the increased distance to the soil surface. Soil samples from positions with the same mark were bulked.

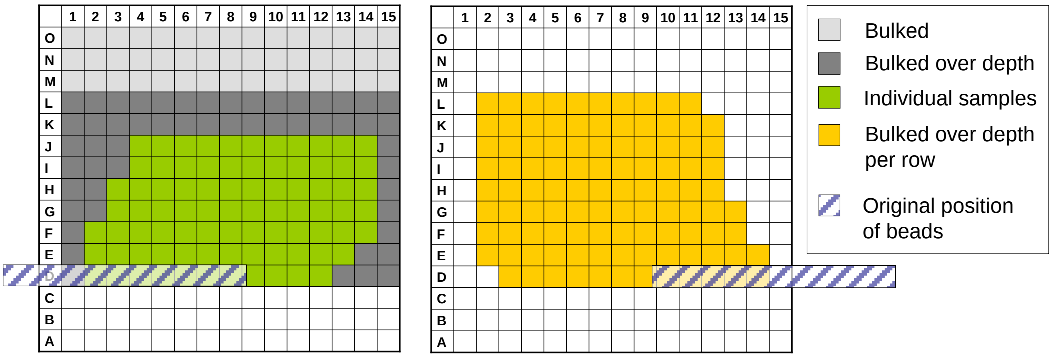


**Figure 3-7** Position of excavation framework and layout of sampled area relative to the original position of the beads before ploughing; left: T1, plough depth = 16 cm; right: T1, plough depth = 24 cm. The ‘original position of beads’ overlaps exactly with the trajectory of the three central (of five) plough bottoms. Diagonally opposite sampling areas are a reflection of the use of a reversible plough with one side set up for plough depth 16 cm and the other for plough depth 24 cm.

After sampling the two plots it was realised that this particular way of soil sampling was much more time consuming than estimated. Since the T1 plots in Kirton had been lost anyway the priority was shifted towards sampling the T2 plots. After sampling the plots of T2, insufficient time was left to sample the remaining plots of T1 in Wellesbourne.

Because the power harrow is equipped with a crumbling roll at the back, it leaves a flat soil surface which considerably simplified soil sampling for the T2 plots compared to the T1 plots. Sampling occurred within 48 hrs. after power harrowing. The soil outside the framework was excavated to allow the framework to be lowered. This meant the outer rows (A and O) and columns (1 and 15) sometimes collapsed and were not sampled. The decision on how many rows to sample was made on an ad hoc basis (based on observation of beads in soil) for individual replicates due to the variable response in forward movement of beads. The deepest layers often required fewer rows. This procedure was repeated until a depth in the soil was reached where no more beads were observed. Sampling characteristics for the T2 plots are summarised in Table 3-2.

**Table 3-2** Sampling characteristics for ‘T2’ plots.

| *Location* | *Plough depth* | *Replicate* | *Row of impact* (1) | *Sampling date* | *Rows sampled* (2) | *Layers sampled* |
|---|---|---|---|---|---|---|
| **Kirton** | 16 cm | 1 | D | 10-14 April 2006 | (C)D-H(I-M) | 7 |
| | | 2 | D | | E-L | 7 |
| | | 3 | D | | E-L | 8 |
| | 24 cm | 1 | D | | E-K(L) | 10 |
| | | 2 | D | | E-L | 10 |
| | | 3 | D | | E-K | 10 |
| **Wellesbourne** | 16 cm | 1 | D | 17-21 April 2006 | D-K | 7 |
| | | 2 | D | | E-K | 7 |
| | | 3 | D | | E-L | 7 |
| | 24 cm | 1 | D | | (D)E-K | 9 |
| | | 2 | B | | B-M | 9 |
| | | 3 | D | | (CD)E-L | 9 |

(1) The row that overlaps with the position of the beads prior to cultivation

(2) Letters in brackets indicate the rows that have been sampled for some but not all layers

### Bead counting

A power drill with a plaster mixer type device attached was used to disperse soil samples in water after which the beads were skimmed off the surface and counted per colour. For the two T1 plots, the surface was uneven and so the soil collected in Layer 1 and 2 actually did not consist of enough soil to make up the 3 cm layers, required for the transition matrices. The 10x10 cm soil samples were weighed and the average weight per sample was calculated for each soil layer. Beyond soil layer three, weight increased linearly only because of higher soil moisture. The average weight for Layers 2 and 1 had they been fully sampled was extrapolated from a linear regression of the average weight of a soil sample against (depth of) soil layers three to eight (see Figure 3-8). The depth of Layer 1 and 2 was obtained by multiplying the ratio of observed to predicted (extrapolated) weight with the default depth of sampled soil layers, i.e. 3 cm. The original transition matrix was then modified to correct for the reduced depths of Layers 1 and 2 in the following way. To create 3 cm soil layers and assuming beads are distributed homogenously within a soil layer, new probabilities were established by virtually transferring the required amount of soil from Layer 2 to Layer 1, then from Layer 3 to Layer 2, then from Layer 4 to Layer 3 etc. For example, if Layer 1 and 2 are 1.8 cm and 2.5 cm deep respectively and all deeper layers are 3.0 cm, then the modified probability of moving from a depth X to Layer 1 is the original probability plus 3 minus 1.8 divided by the depth of the second soil layer, i.e. 1.2/2.5, times the probability of moving to Layer 2. The modified probability for Layer 2 would be the remaining soil depth after subtraction of soil to Layer 1, divided by the original soil depth of Layer 2, i.e. 1.3/2.5, multiplied by the original probability of moving to Layer 2, plus the required soil depth from Layer 3 to make up a 3.0 cm soil layer, i.e. 1.7/3.0 multiplied by the probability of moving to Layer 3, etc.

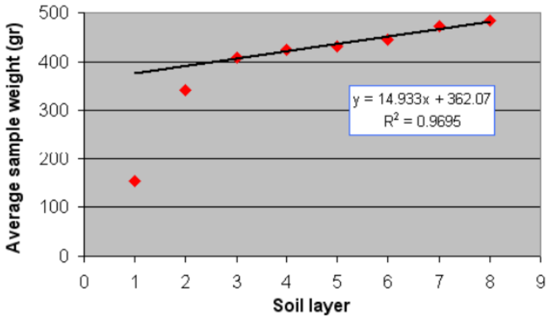


**Figure 3-8** Average weight of an individual sample over sampled soil layers (1 = 0-3 cm, 2 = 3-6 cm, etc) from T1, pd=16. Linear regression excludes Soil layer 1 and 2 for which the average 'theoretical' sample weight was extrapolated.

For each plot the following characteristics were determined: % recovery per starting depth and colour, average % recovery per treatment. The probability of moving from depth X to soil layer Y was calculated by dividing the number of recovered beads of colour (depth) X in layer Y, by the total number of recovered beads of colour X. To analyse if bead recovery was affected by plough depth, location, depth before cultivation and bead colour, arcsine transformed percentage recovery data were analysed using ANOVA. Depth before cultivation was nested within plough depth for each plough depth separately. Effect of bead colour was assessed in a separate ANOVA.

### 3.2.3.2 Results

The percentage recovery of beads in T1 using the excavation framework was 60-70% (see Table 3-3), which is ten times higher than the percentage recovery achieved by the auger in the preliminary treatment.

**Table 3-3** Percentage recovery of beads buried at different depths prior to cultivation (T1).

| *Location* | *Plough depth* | *Average recovery* | *Depth of beads prior to ploughing (cm)* | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Treatment 1:* | | | ***0*** | ***1.5*** | ***4.5*** | ***7.5*** | ***10.5*** | ***13.5*** | ***16.5*** | ***19.5*** | ***22.5*** | ***25.5*** | |
| W'bourne | 16 cm | *61* | 62 | 62 | 58 | 71 | 64 | 65 | 46 | | | | *Individual samples*[1] |
| | | *5* | 8 | 12 | 6 | 4 | 1 | 1 | 2 | | | | *Bulked over depth* |
| | | *12* | 8 | 2 | 7 | 14 | 21 | 13 | 17 | | | | *Bulked* |
| | | *77* | 78 | 76 | 71 | 89 | 85 | 78 | 65 | | | | Total |
| | 24 cm | 72 | 83 | 88 | 74 | 72 | 69 | 80 | 76 | 70 | 72 | 39 | |

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[1] See Figure 3-6 for overview of sampling lay-out. Beads from 'Individual samples' and 'Bulked over depth' were used to obtain transition matrix in Figure 3-10.

The single 'T1, pd=24' replicate in Wellesbourne revealed that, unlike in the pilot experiment, if deep beads are ploughed up, they are moved forward further than beads initially closer to the surface (see Figure 3-9).

Similarly, for the shallow ploughed plot, the number of beads recovered in the furthest section, 'Bulked' (see Figure 3-7 left), is higher for the beads buried at 10.5, 13.5 and 16.5 cm than for the beads buried at the Surface, 1.5 and 4.5 cm (see Table 3-3).

The visualized transition matrices from the two T1 plots clearly show the soil inversion plough-effect (see Figure 3-10), but a bimodal distribution over depth for the deepest beads can be observed as well indicating the plough only lifted these beads up partly. It is remarkable that whilst surface and 1.5 cm beads were deposited in the 18-

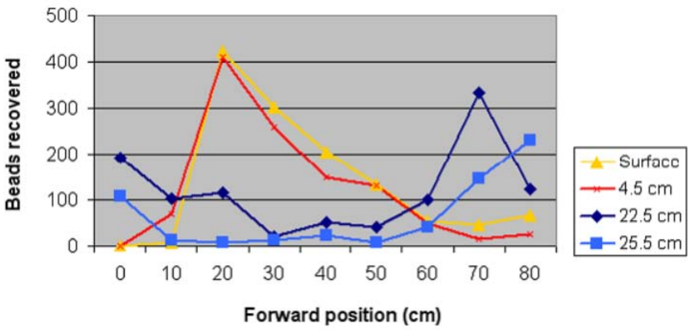
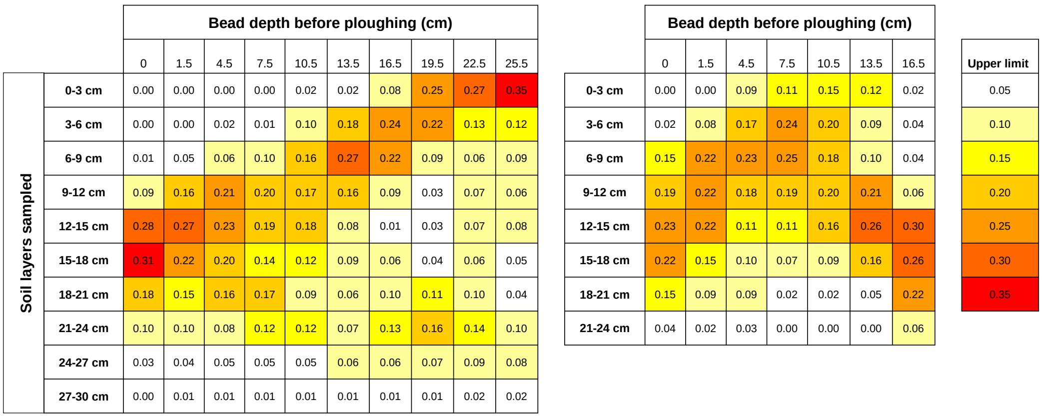


**Figure 3-9** Forward movement of beads due to ploughing as a function of depth in the soil before ploughing (T1, pd=24, Wellesbourne). Results only show two shallow and deep starting depths for contrast.

21 cm soil layer, the plough did not bring the 16.5 cm beads up to the surface in the plot ploughed at 16 cm. It suggests the 13.5 and 16.5 cm beads were pushed forward rather then lifted upwards. This would also explain the greater distance over which beads were moved forward compared to the preliminary experiment.



| Soil layers sampled | Bead depth before ploughing (cm) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 0 | 1.5 | 4.5 | 7.5 | 10.5 | 13.5 | 16.5 | 19.5 | 22.5 | 25.5 |
| **0-3 cm** | 0.00 | 0.00 | 0.00 | 0.00 | 0.02 | 0.02 | 0.08 | 0.25 | 0.27 | 0.35 |
| **3-6 cm** | 0.00 | 0.00 | 0.02 | 0.01 | 0.10 | 0.18 | 0.24 | 0.22 | 0.13 | 0.12 |
| **6-9 cm** | 0.01 | 0.05 | 0.06 | 0.10 | 0.16 | 0.27 | 0.22 | 0.09 | 0.06 | 0.09 |
| **9-12 cm** | 0.09 | 0.16 | 0.21 | 0.20 | 0.17 | 0.16 | 0.09 | 0.03 | 0.07 | 0.06 |
| **12-15 cm** | 0.28 | 0.27 | 0.23 | 0.19 | 0.18 | 0.08 | 0.01 | 0.03 | 0.07 | 0.08 |
| **15-18 cm** | 0.31 | 0.22 | 0.20 | 0.14 | 0.12 | 0.09 | 0.06 | 0.04 | 0.06 | 0.05 |
| **18-21 cm** | 0.18 | 0.15 | 0.16 | 0.17 | 0.09 | 0.06 | 0.10 | 0.11 | 0.10 | 0.04 |
| **21-24 cm** | 0.10 | 0.10 | 0.08 | 0.12 | 0.12 | 0.07 | 0.13 | 0.16 | 0.14 | 0.10 |
| **24-27 cm** | 0.03 | 0.04 | 0.05 | 0.05 | 0.05 | 0.06 | 0.06 | 0.07 | 0.09 | 0.08 |
| **27-30 cm** | 0.00 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.02 | 0.02 |

| | Bead depth before ploughing (cm) | | | | | | |
|---|---|---|---|---|---|---|---|
| | 0 | 1.5 | 4.5 | 7.5 | 10.5 | 13.5 | 16.5 |
| **0-3 cm** | 0.00 | 0.00 | 0.09 | 0.11 | 0.15 | 0.12 | 0.02 |
| **3-6 cm** | 0.02 | 0.08 | 0.17 | 0.24 | 0.20 | 0.09 | 0.04 |
| **6-9 cm** | 0.15 | 0.22 | 0.23 | 0.25 | 0.18 | 0.10 | 0.04 |
| **9-12 cm** | 0.19 | 0.22 | 0.18 | 0.19 | 0.20 | 0.21 | 0.06 |
| **12-15 cm** | 0.23 | 0.22 | 0.11 | 0.11 | 0.16 | 0.26 | 0.30 |
| **15-18 cm** | 0.22 | 0.15 | 0.10 | 0.07 | 0.09 | 0.16 | 0.26 |
| **18-21 cm** | 0.15 | 0.09 | 0.09 | 0.02 | 0.02 | 0.05 | 0.22 |
| **21-24 cm** | 0.04 | 0.02 | 0.03 | 0.00 | 0.00 | 0.00 | 0.06 |

| **Upper limit** |
|---|
| 0.05 |
| 0.10 |
| 0.15 |
| 0.20 |
| 0.25 |
| 0.30 |
| 0.35 |

**Figure 3-10** Transition matrices for T1; target plough depth was 24 cm for left transition matrix and 16 cm for transition matrix on the right. Colours are added to illustrate movement pattern, the 'hotter' the colour, the higher the probability of moving from a given depth before, to a given soil layer after ploughing.

Percentage recovery of beads in T2 was similar to the two T1 plots but beads that were buried deeper tended to have a lower recovery than beads closer to the surface, especially in Wellesbourne (see Table 3-4). It is unlikely that not sampling the original position was the sole factor responsible for this, since recovery was poor whether the original position was included in the sampling area (Wellesbourne) or not (Kirton) (data not shown). The most likely reason is that, since (a proportion of) the deeply buried beads end up in the 0-3 and 3-6 cm layers after ploughing, these beads were more prone to dispersal out of the sampling area during subsequent power harrowing.

**Table 3-4** Percentage recovery of beads buried at different depths prior to cultivation (T2).

| *Location* | *Plough depth* | *Average recovery* | *Depth of beads prior to ploughing (cm)* | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Treatment 2:* | | | ***0*** | ***1.5*** | ***4.5*** | ***7.5*** | ***10.5*** | ***13.5*** | ***16.5*** | ***19.5*** | ***22.5*** | ***25.5*** |
| Kirton | 16 cm | 64 | 62 | 69 | 66 | 63 | 71 | 62 | 56 | n/a | | |
| | 24 cm | 65 | 70 | 76 | 78 | 76 | 71 | 68 | 71 | 64 | 62 | 9 |
| W'bourne | 16 cm | 64 | 78 | 67 | 70 | 60 | 60 | 60 | 54 | n/a | | |
| | 24 cm | 61 | 78 | 75 | 76 | 64 | 61 | 63 | 54 | 58 | 48 | 32 |

Colour of beads, plough depth and location did not significantly affect recovery (see Table 3-5), but if only those bead layers that were present in both plots (Surface to 16.5 cm) were compared, bead recovery tended to be higher in plots ploughed at 24 cm.

**Table 3-5** Analysis of variance on arcsine transformed percentage recovery of beads (T2).

| ***Source of variation*** | ***df*** | ***s.s.*** | ***m.s.*** | ***v.r.*** | ***F probability*** |
|---|---|---|---|---|---|
| Location | 1 | 117.45 | 117.45 | 3.47 | 0.067 |
| Plough depth | 1 | 107.66 | 107.66 | 3.18 | 0.079 |
| Location * Plough depth | 1 | 97.06 | 97.06 | 2.87 | 0.095 |
| Plough depth * Starting depth_1 | 6 | 376.92 | 62.82 | 1.86 | 0.102 |
| Plough depth * Starting depth_2 | 8 | 1064.94 | 133.12 | 3.94 | <.001 |
| Location * Plough depth * Starting depth_1 | 6 | 251.98 | 42.00 | 1.24 | 0.297 |
| Location * Plough depth * Starting depth_2 | 8 | 278.11 | 34.76 | 1.03 | 0.425 |
| Residual | 64 | 2164.56 | 33.82 | | |
| **Total** | 95 | 4458.69 | | | |
| | | | | | |
| Location | 1 | 117.45 | 117.45 | 2.63 | 0.109 |
| Colour | 9 | 766.24 | 85.14 | 1.91 | 0.063 |
| Location * Colour | 9 | 183.58 | 20.40 | 0.46 | 0.899 |
| Residual | 64 | 3391.42 | 44.62 | | |
| Total | 95 | 4458.69 | | | |

Location = Kirton / Wellesbourne, Plough depth = 16 / 24 cm, Starting depth_1 and Starting depth_2 are the bead starting depths associated with Plough depth =16 and Plough depth = 24 cm respectively.
*df* = degrees of freedom; s.s. = sum of squares; m.s. = mean square; v.r. = variance ratio

The negative trend in percentage recovery for beads buried at increasing depths was significant for soil ploughed at 24 cm (P<0.001) but not at 16 cm (P=0.102) despite a similar negative trend in Wellesbourne. Average recovery per bead colour varied since some colours happened to be allocated more to shallow than deep depths but it was not significant (P=0.063).

Comparing the resulting transition matrices of Kirton and Wellesbourne graphically (Figure 3-11) shows that ploughing at a depth of 16 cm resulted in fairly similar distribution profiles except for the beads scattered at the ‘Surface’ and buried at 1.5 cm deep. Here the profiles reveal that ploughing was slightly deeper in Kirton than in Wellesbourne. Plough depth was quite variable between replicates (large error bars) and also within plots (data not shown). In each plot ploughed at 16 cm, beads buried at 16.5 cm were recovered over the entire forward range, both in Kirton and Wellesbourne (see Figure 3-11). The deepest soil layer in which beads were recovered was 18-21 cm, indicating that plough depth was likely somewhat deeper than 16 cm.

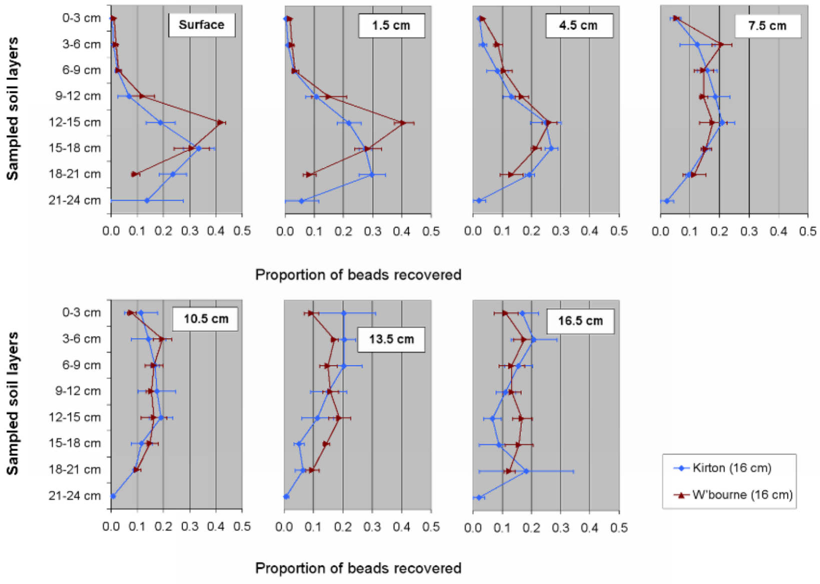


**Figure 3-11** Distribution of recovered beads over soil depth (average of three replicates) after T2: [Plough (16 cm) – Soil settling – Power harrow], for beads buried at different depths (surface, 1.5 cm, etc.) prior to ploughing in Kirton and Wellesbourne. Horizontal error bars represent plus and minus standard error of recovered beads for each sampled soil layer.

The deepest soil layer from which beads were recovered of the plots ploughed at 24 cm was 24-27 cm and 27-30 cm deep in Wellesbourne and Kirton respectively, suggesting that ploughing in Kirton occurred roughly three cm deeper. The visualised probabilities of movement for beads initially at 22.5 and 25.5 cm deep confirm this (see Figure 3-12). Beads originally at the ‘Surface’, 1.5 and 4.5 cm deep in Kirton were all buried 3 to 6 cm deeper in the soil than the beads buried at equivalent depths in Wellesbourne. It is more likely that this is due to the deeper plough setting in Kirton compared to Wellesbourne, rather than due to soil type differences. The distribution profiles also show that ploughing in Kirton resulted in a more complete inversion of the soil than in Wellesbourne; whereas the majority of beads originally at 19.5, 22.5 and 25.5 cm deep were recovered from the top 9 cm in Kirton, the majority of beads remained in the bottom 9 cm in Wellesbourne.

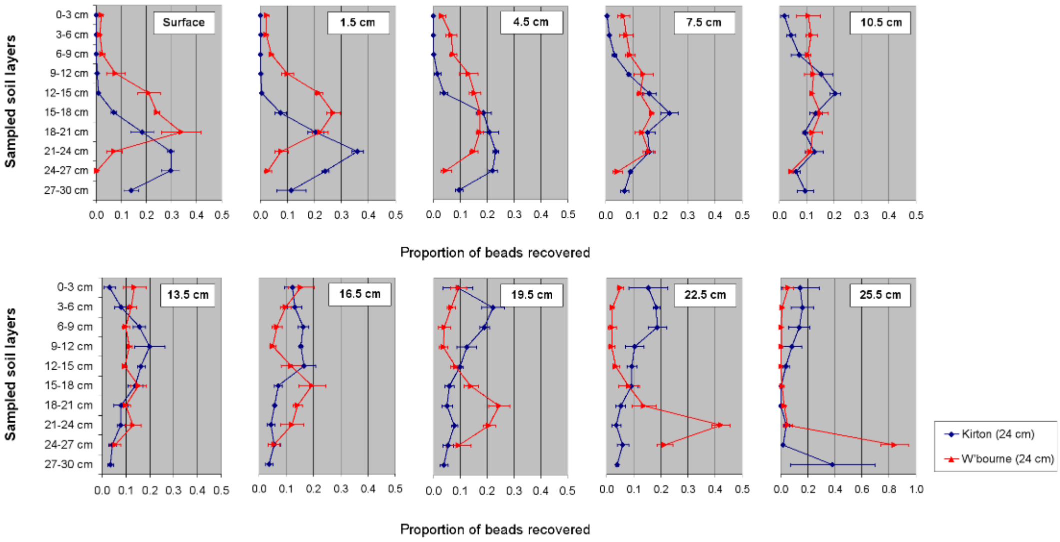


**Figure 3-12** Distribution of recovered beads over soil depth (average of three replicates) after T2: [Plough (24 cm) – Soil settling – Power harrow], for beads buried at different depths (surface, 1.5 cm, etc.) prior to ploughing. Note that scale of x-axis in graph of '25.5 cm deep beads' is different from other graphs. Horizontal error bars represent plus and minus standard error of recovered beads for each sampled soil layer.

### 3.2.4 Discussion and implementation

The problem with soil compaction in the augers in the preliminary experiment was unexpected since this phenomenon was not noticed during sampling of the previous cultivation experiments conducted at Warwick HRI (Mead *et al.*, 1998). The cultivation implements used during this experiment may not increase the volume of the soil as much as the plough does.

The original aim of the experiment, deriving the [Plough], [Soil settling after ploughing] and [Plough + Soil settling] transition matrices could not be realised. The direct implication is that there is not enough data for Treatment 1 to be implemented in the modelling framework. Fortunately only the early carrots under polythene might have required this treatment whereas for main crop carrots the plough cultivation will occur in spring.

The reformulated aim of the experiment, testing the 'multiplicativity assumption', could not be assessed either, but this is compensated for in Section 3.3. What is left is still worthwhile if only because of the increased understanding of soil and seed movement processes and the gained experience in carrying out the soil sampling.

Plough depth was not explicitly measured in the field but from the results it became clear that the realised plough depth at both locations was not equivalent. Both ploughs were set up at the required depths as accurately as possible by experienced staff of Horticultural Services. It is impossible to conclude whether the different distribution patterns can be attributed purely to the different ploughs (depth set-up, wear and tear) or to a different plough-soil interaction, although the former seems more probable. What is clear however, is that the cultivation regimes in Kirton and Wellesbourne differ substantially in their soil inversion properties. The soil inversion action of the plough dominated the distribution patterns in Kirton, even after power harrowing, with the maximum proportion recovery for beads initially close to the surface in deeper layers and vice versa. In Wellesbourne the deeper bead layers (16.5, 19.5 and 22.5 cm) were not brought up as much as would be expected. In Kirton 36% of the beads initially at the Surface and 1.5 cm deep was buried in the two deepest layers (24-30 cm) whereas in Wellesbourne only 6% of beads were recovered in the two deepest layers (21-27 cm). In Kirton, 86% of the beads in the 0-6 cm layer (from where emergence is possible) originate from the beads initially at 16.5 to 25.5 cm whereas in Wellesbourne the percentage is only 41%.

From a weed population point of view, a cultivation regime as in Kirton is best suited after a season with high seed production because it buries the weed seeds deeper. If the weed pressure in the following season is lower, deploying the cultivation regime from Wellesbourne is a better choice since it doesn’t bring as many seeds up to the surface. Unless a more rigorous approach is adopted where plough and soil type are separate factors under assessment, it will be difficult to answer questions of causality. On the other hand, the results in this study show that whatever the cause, the inherent variability requires different transition matrices for what farmers would perceive as an identical cultivation.

## *3.3 Evaluation of the transition matrix approach to modelling the effect of cultivation on soil / seed movement*

### 3.3.1 Introduction

In the previous section the ‘multiplicativity’ assumption was introduced and explained but due to experimental difficulties it could not be addressed properly. With the experience gained in the previous experiments, a new study was planned that set out to test the assumption. The cultivation sequence that was addressed was Plough - Power harrow – Spring tine. A transition matrix already exists for the Power harrow (Mead *et al.*, 1998), the preceding cultivation for which was unknown but was not the plough (personal comment Andrea Grundy).

The added condition of pre-cultivation allowed the comparison of the {Plough - **[Power harrow]**} transition matrix as derived in this experiment with the {unknown pre-cultivation **– [Power harrow]**} transition matrix from Mead *et al.* (1998)

### 3.3.2 Methodology

An experiment was set up in March 2006 at Wellesbourne containing five cultivation treatments, resulting in two sets of experimental data to test the assumption.

Treatment 1: { **[Plough]** }
Treatment 2: { **[Plough + Power harrow]** }
Treatment 3: { Plough + **[Power harrow]** }
Treatment 4: { Plough + Power harrow + **[Spring tine]** }
Treatment 5: { Plough + **[Power harrow + Spring tine]** }

Compared to the previous study design a pre-cultivation treatment was added before introducing the beads in the soil to provide similar soil conditions for the treatment in which implements would be assessed in conjunction (see Figure 3-13). This was done so that the treatments could truly assess implement effects rather than being confounded by dissimilar pre-cultivation soil conditions.

Each treatment was replicated three times and the plots were arranged in a row-column design. Plot length and the distances between plots were identical to the previous experiment. Pre-cultivation occurred in the third week of April 2006 and consisted of two parallel passes of the plough (± 24 cm deep) per plot for Treatments

3-5 and an additional pass over the centre of the ploughed strip for Treatment 4 using a 3 m. wide power harrow (Maschio Erpice DC 3000). Following cultivations were performed in opposite direction to limit bead dispersal out of the sampling area. Treatments of Set 1 were initiated before moving on to Set 2. Due to setbacks in the sampling process, there was not enough time to actually carry out Treatment 4 and 5 so Set 2 was lost from the analysis.

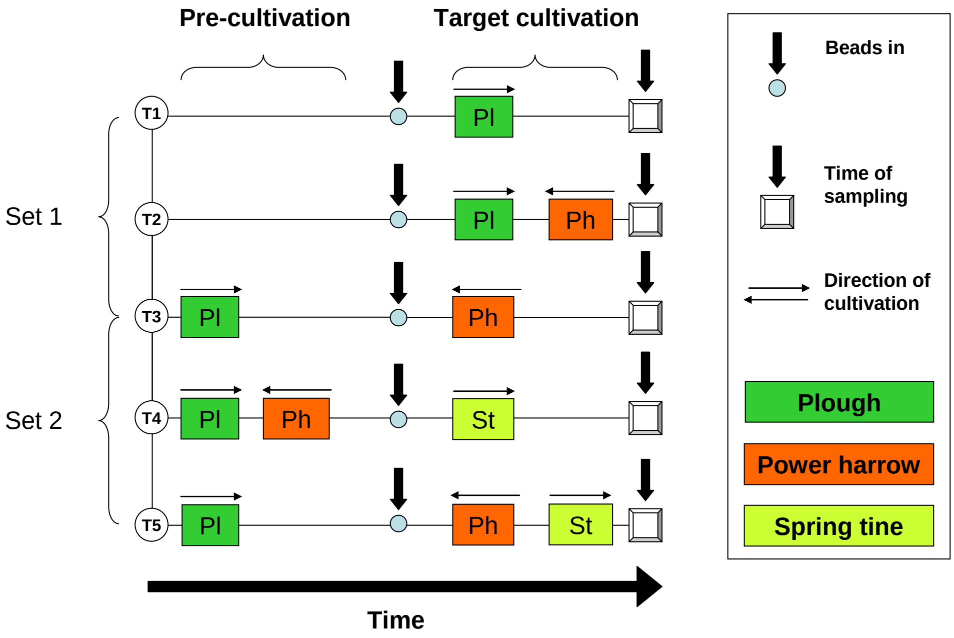


**Figure 3-13** Cultivation treatments chosen to test 'multiplicativity' assumption. Due to logistic and time constraints only Set 1 (Treatments 1-3) was carried out.

Beads were introduced at 7 depths (Surface, 1.5, 4.5, 7.5, 10.5, 13.5 and 16.5 cm) in the same way as the previous experiment with the exception of Treatment 3 where the soil was ploughed before the beads were inserted in the soil. To avoid compaction of the soil, a crawling board supported by pallets outside the plot area was used to dig the trench and insert the beads in the soil (see Figure 3-14). Due to the uneven soil surface after ploughing, the soil surface level was

**Figure 3-14** The Surface layer of beads in one of the 'Power harrow' plots in previously ploughed soil.

determined to be somewhere in between the peaks and troughs. Bulk density and gravimetric soil water content were determined prior to target cultivation. Bulk density was 1.5 ± 0.1 g/cm$^3$ and 1.3 ± 0.1 g/cm$^3$ prior to ploughing and power harrowing respectively. Water content was lower prior to power harrowing, 11 ± 1%, than prior to ploughing, 16 ± 1%. The target depth of the plough and power harrow when used as 'target cultivation' was 15 and 7.5 cm respectively. Because the 1.83 m wide power harrow was out of use at the time the area was power harrowed using the 3.0 m wide one. Time necessary to traverse a known distance through the plots was measured to obtain an estimate of implement speed. After target cultivation the soil was left for around 3-4 weeks to allow the soil to stabilise after which sampling was conducted using the excavation framework as described previously. Since the power harrow left a more or less flat soil surface, plots of Treatment 2 and 3 were bulked per row and excavation quadrat depth. Because a 3 m. rather than a 1.83 m. wide Power harrow was used, the beads in the top layers had spread out over a larger area. Therefore, power harrowed plots were sampled over a wider area to maximise the percentage recovery for beads in the top layer. Experimental details are summarised in Table 3-6.

**Table 3-6** Cultivation and sampling characteristics for experimental plots (R1 is Replicate 1)

| | ***T1-[Plough]*** | | | ***T2 -[Power harrow]*** | | | ***T3-[Plough+Power harrow]*** | | |
|---|---|---|---|---|---|---|---|---|---|
| | R1 | R2 | R3 | R1 | R2 | R3 | R1 | R2 | R3 |
| Date of cultivation (1) | 26/05 | 23/06 | 26/05 | 12/05/06 | | | 18/05/06 | | |
| Date of cultivation (2) | n/a | | | n/a | | | 15/06/06 | | |
| Tractor speed (1) - (km/hr) | 3.7 | 4.1 | 4.5 | 2.0 | 2.0 | 1.9 | 3.4 | n/m | 3.3 |
| Tractor speed (2) - (km/hr) | n/a | | | n/a | | | 3.4 | n/m | 3.4 |
| Sampling period | 22-28 June | 12-14 July | 13-15 June | 2-9 June | | | 3-8 July | | |
| Layers sampled | 8 | 8 | 8 | 4 | 4 | 6 | 7 | 7 | 7 |
| Rows sampled | E-I | E-L | D-H | Variable | | | (A-E) F-O | | |
| Line of impact | E | E | E | C/D | D | B | unknown | H | I |

Plots of Treatment 1 were sampled as described in Section 3.2.3.1 (Sampling design). Soil samples of different soil layers were mixed up during sampling in one 'Plough' replicate and a separate plot was set-up to replace this replicate. Beads were retrieved from soil samples as explained for the previous experiment. Percentage recovery of beads over depth and colour was calculated. To analyse if beads had been discovered independent of depth and colour, an ANOVA was conducted on the arcsine transformed percentage recovery data.

Prior to matrix multiplication the original transition matrices for [Power harrow] and [Plough] had the following dimensions respectively:

| | 0 | 1.5 | 4.5 | 7.5 | 10.5 | 13.5 | 16.5 |
|---|---|---|---|---|---|---|---|
| 0 – 3 | .. | .. | .. | .. | .. | .. | .. |
| 3 – 6 | .. | .. | .. | .. | .. | .. | .. |
| 6 – 9 | .. | .. | .. | .. | .. | .. | .. |
| 9 – 12 | .. | .. | .. | .. | .. | .. | .. |

| | 0 | 1.5 | 4.5 | 7.5 | 10.5 | 13.5 | 16.5 |
|---|---|---|---|---|---|---|---|
| 0 – 3 | .. | .. | .. | .. | .. | .. | .. |
| 3 – 6 | .. | .. | .. | .. | .. | .. | .. |
| 6 – 9 | .. | .. | .. | .. | .. | .. | .. |
| 9 – 12 | .. | .. | .. | .. | .. | .. | .. |
| 12 – 15 | .. | .. | .. | .. | .. | .. | .. |
| 15 – 18 | .. | .. | .. | .. | .. | .. | .. |
| 18 – 21 | .. | .. | .. | .. | .. | .. | .. |
| 21 – 24 | .. | .. | .. | .. | .. | .. | .. |

For a correct comparison of the observed and predicted [Plough + Power harrow] matrices, three conditions have to be met with regard to the matrix multiplication:

1. Each starting depth in [Power harrow] can only be multiplied with it’s corresponding soil layer [Plough], i.e. 1.5 cm and {0-3 cm}. Since the ‘Surface’ was not sampled separately in the [Plough] transition matrix, it was omitted as a starting depth from the [Power harrow] transition matrices. Note that it does not have to be omitted as a starting depth for the [Plough] transition matrices.
2. The number of columns in the [Power harrow] transition matrices has to match the number of rows in the [Plough] transition matrices. Hence, two columns were added to the [Power harrow] transition matrices (for the virtual 19.5 and 22.5 cm starting depths)
3. The dimensions of the observed and predicted [Plough + Power harrow] have to be identical, i.e. 7 rows (soil layers) and 7 columns (starting depths). Given that the number of rows and columns of the predicted [Plough + Power harrow] transition matrix is equal to the number of rows and columns of the [Power harrow] and [Plough] transition matrices respectively, the number of rows of the [Power harrow] matrix ought to be 7 so that an extra row (18-21 cm) is added. No change of the [Plough] transition matrix is required.

Hence, the transition matrix of the [Power harrow] prior to matrix multiplication was represented by:

|  | 1.5 | 4.5 | 7.5 | 10.5 | 13.5 | 16.5 | 19.5 | 22.5 |
|---|---|---|---|---|---|---|---|---|
| 0 – 3 | .. | .. | .. | .. | .. | .. | .. | .. |
| 3 – 6 | .. | .. | .. | .. | .. | .. | .. | .. |
| 6 – 9 | .. | .. | .. | .. | .. | .. | .. | .. |
| 9 – 12 | .. | .. | .. | .. | .. | .. | .. | .. |
| 12 – 15 | .. | .. | .. | .. | .. | .. | .. | .. |
| 15 – 18 | .. | .. | .. | .. | .. | .. | .. | .. |
| 18 – 21 | .. | .. | .. | .. | .. | .. | .. | .. |

From the results it could be deduced that, had there been beads introduced in the [Power harrow] plots deeper than 16.5 cm, they would not have moved in any of the plots. Given that beads from these plots were only recovered from the first four or five layers, it would appear a 4-layered [Power harrow] transition matrix should be represented as:

|  | 1.5 | 4.5 | 7.5 | 10.5 | 13.5 | 16.5 | 19.5 | 22.5 |
|---|---|---|---|---|---|---|---|---|
| 0 – 3 | ... | ... | ... | ... | ... | ... | 0.00 | 0.00 |
| 3 – 6 | ... | ... | ... | ... | ... | ... | 0.00 | 0.00 |
| 6 – 9 | ... | ... | ... | ... | ... | ... | 0.00 | 0.00 |
| 9 – 12 | ... | ... | ... | ... | ... | ... | 0.00 | 0.00 |
| 12 – 15 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.00 | 0.00 |
| 15 – 18 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.00 |
| 18 – 21 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |

with the experimentally derived probabilities taking the place of the dots. For the 5-layered [Power harrow] transition matrix, the beads initially at 19.5 and 22.5 cm were assumed to be staying in the 15-18 cm and 18-21 cm layer respectively.

The result of this matrix multiplication clearly showed an incorrect upward shift of the distribution over depth (see red curves in Figure 3-18). Therefore, a second approach was tested based on the fact that power harrowing effectively compressed the six soil layers containing the bead layers into four (R1 and R2) or five soil layers (R3). For the matrix multiplication what is relevant is not the number of soil layers *after* but *before* cultivation. For each starting depth the probabilities of the four or five soil layers were therefore ‘diluted’ over six layers using the following assumptions (stated prior to the analysis):

- All six layers have been compressed during power harrowing into either exactly 4 (R1 and R2) or 5 layers (R3).
- The rate of compression is unequal for each of the six layers; from having no compression at all in the 7th layer and a little in the 6th layer, it increases linearly over the six layers with most compression of the top soil layer. This can be intuitively comprehended for a power harrow with crumbling roll attached cultivating previously ploughed soil.

Using a spreadsheet model it can be inferred that the **only** solution that results in a linear rate of compression over the first six layers and a total compression into 4 or 5 layers, is a compression ratio where the denominator is (a multiple of) 21. For R1 and R2 the numerator increases per soil layer in steps of 2 and for R3 the numerator increases in steps of 1 (see Table 3-7).

For example if the denominator is set at 20 (D=20), then given that Layer 7 is uncompressed, Layer 7 can be represented by 20/20. Assuming a linear increase of compression from Layer 6 to Layer 1 with the numerator decreasing at 1 unit for each layer ($\Delta N\,\mathrm{layer}^{-1} = -1$) would result in: Layer 6: 19/20, Layer 5: 18/20, Layer 4: 17/20, Layer 3: 16/20, Layer 2: 15/20, Layer 1: 14/20. Adding the ratios would give a total of 4.95 soil layers exceeding the required number of 4 soil layers.

**Table 3-7** Resulting number of 3.0 cm layers for different compression rates

|  | D = 20 | D = 21 | D = 22 |
|---|---|---|---|
| $\Delta N\,\mathrm{layer}^{-1} = -1$ | 4.95 | 5.00 | 5.05 |
| $\Delta N\,\mathrm{layer}^{-1} = -2$ | 3.90 | 4.00 | 4.09 |
| $\Delta N\,\mathrm{layer}^{-1} = -3$ | 2.85 | 3.00 | 3.14 |

Using this information the observed probabilities of the 4 soil layers are expanded over 6 soil layers (see Table 3-8).

**Table 3-8** Modification of probabilities to reflect the expanded soil before [Power harrow] cultivation. Soil was expanded from 4 to 6 soil layers for Replicate 1 & 2 and from 5 to 6 soil layers in Replicate 3.

|  | ***[Power harrow] Replicate 1 & 2*** | ***[Power harrow] Replicate 3*** |
|---|---|---|
| $p_{1,\mathrm{new}} =$ | $p_{1,\mathrm{old}}$ * 9/21 | $p_{1,\mathrm{old}}$ * 15/21 |
| $p_{2,\mathrm{new}} =$ | $p_{1,\mathrm{old}}$ * 11/21 | $p_{1,\mathrm{old}}$ * 6/21 + $p_{2,\mathrm{old}}$ * 10/21 |
| $p_{3,\mathrm{new}} =$ | $p_{1,\mathrm{old}}$ * 1/21 + $p_{2,\mathrm{old}}$ * 12/21 | $p_{2,\mathrm{old}}$ * 11/21 + $p_{3,\mathrm{old}}$ * 6/21 |
| $p_{4,\mathrm{new}} =$ | $p_{2,\mathrm{old}}$ * 9/21 + $p_{3,\mathrm{old}}$ * 6/21 | $p_{3,\mathrm{old}}$ * 15/21 + $p_{4,\mathrm{old}}$ * 3/21 |
| $p_{5,\mathrm{new}} =$ | $p_{3,\mathrm{old}}$ * 15/21 + $p_{4,\mathrm{old}}$ * 2/21 | $p_{4,\mathrm{old}}$ * 18/21 + $p_{5,\mathrm{old}}$ * 1/21 |
| $p_{6,\mathrm{new}} =$ | $p_{4,\mathrm{old}}$ * 19/21 | $p_{5,\mathrm{old}}$ * 20/21 |

It was further assumed that all the beads initially at 19.5 and 22.5 cm would have remained at the 15-18 and 18-21 cm soil layers respectively ($p$ = 1). Each [Power harrow] plot was treated this way and then an average matrix created. This average matrix was then used to premultiply the average transition matrix from the three [Plough] replicates. This resulted in a predicted [Plough + Power harrow] transition matrix.

Predicted values for the distribution of beads over depth for [plough + power harrow] based on the multiplication of the transition matrices for [plough] and [power harrow] were compared to observed values in the field (see Figure 3-3) using the Pearson correlation coefficient (r).

### 3.3.3 Results

The average percentage recovery was generally high for all treatments and plots (see Table 3-9). Recovery of beads was affected by burial depth before cultivation only for the [Power harrow] treatment where significantly more beads were recovered from beads that were initially at deeper depths (P<0.001). The use of the 3 m wide power harrow undoubtedly contributed to the dispersal of shallow beads out of the sampling area. There were not enough replicates for each bead colour to be introduced at each depth, but in the current experiment design, bead colour did not appear to affect recovery probability (P = 0.323).

**Table 3-9** Percentage recovery of beads per burial depth for the three treatments.

| | | | ***Depth of beads prior to cultivation (cm)*** | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | **Repl.** | **Average** | ***0*** | ***1.5*** | ***4.5*** | ***7.5*** | ***10.5*** | ***13.5*** | ***16.5*** |
| **T1 - [Plough]** | R1 | 76 | 66 | 66 | 65 | 75 | 90 | 93 | 77 |
| | R2 | 76 | 86 | 69 | 69 | 74 | 83 | 73 | 76 |
| | R3 | 84 | 82 | 68 | 89 | 87 | 82 | 92 | 91 |
| **T2 - [Power harrow]** | R1 | 82 | 50 | 72 | 81 | 92 | 87 | 94 | 95 |
| | R2 | 82 | 47 | 76 | 75 | 92 | 93 | 93 | 99 |
| | R3 | 72 | 52 | 61 | 67 | 69 | 76 | 86 | 92 |
| **T3 - [Plough + Power harrow]** | R1 | 85 | 86 | 95 | 87 | 84 | 88 | 83 | 73 |
| | R2 | 87 | 89 | 79 | 87 | 88 | 89 | 86 | 88 |
| | R3 | 77 | 82 | 84 | 70 | 81 | 74 | 76 | 73 |

By graphically visualising the columns of the transition matrix the importance of subtle differences in plough depth become apparent. The distribution of beads over depth in the [Plough] plots shows very similar patterns for the first and second replicates (see Figure 3-15). Plough depth in the third replicate was less deep than in the other replicates as most beads buried at 16.5 cm did not move upwards. Consequently, the beads initially at 13.5 cm deep in R3 show a similar distribution to the beads initially at 16.5 cm deep for R1 and R2.

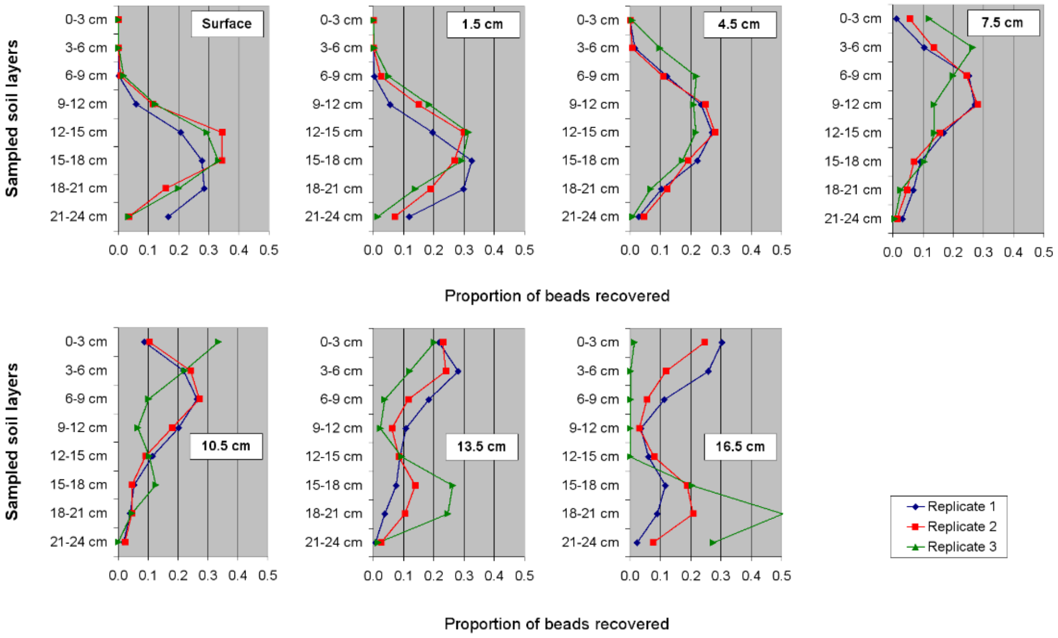


**Figure 3-15** Distribution of recovered beads over soil depth after [Plough] cultivation for beads at different depths (surface, 1.5 cm, etc.) prior to cultivation. Target depth for plough and skim coulter were 16 and 5 cm respectively.

The action of the power harrow to soil and bead distribution is very different to the plough (see Figure 3-16). Beads in Replicate 1 and 2 of the [Power harrow] plots show almost identical patterns of bead distribution over depth, whereas Replicate 3 shows a different pattern, with the 13.5 cm and 16.5 cm beads remaining in deeper soil layers. At the time of power harrowing Replicate 3, the front and rear tyres of one side of the tractor compressed the outer section of the line of beads which can be seen from the graphs for the 16.5 cm beads that had not been moved by the power harrow; 91% of beads were recovered from the 12-15 cm layer but 8% were compressed into the 15-18 cm layer.

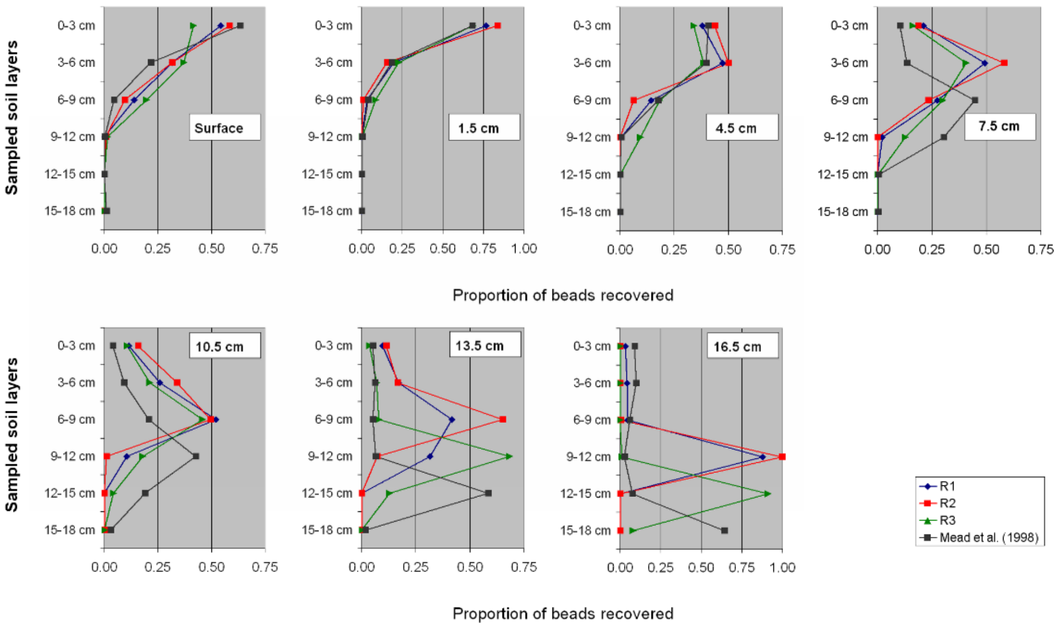


**Figure 3-16** Distribution of recovered beads over soil depth after Power harrow cultivation for beads at different depths (surface, 1.5 cm, etc.) prior to cultivation. Target depth for power harrow was 15 cm. Note that scale of X-axis varies among graphs.

Comparing the obtained transition matrix for {Plough - **[Power harrow]**} with the transition matrix for {unknown pre-cultivation - **[Power harrow]**} as derived by (Mead *et al.*, 1998), shows clear differences for deeper beads. Whereas in this experiment the plough preceded the power harrow cultivation this was not the case in the previous experiment. This indicates that the transition matrix of a certain cultivation implement is not only a function of the depth of the implement, but also of the pre-cultivation or lack thereof that the soil has received prior to the target cultivation.

The distribution of beads over depth in the [Plough + Power harrow] plots is similar to the [Plough] plots except for the fact that the soil has been compressed by power harrowing and counts seven instead of eight layers. The second replicate (R2) reveals that even after power harrowing, the soil is still more expanded than before ploughing (see Figure 3-17); the majority of the beads at 16.5 cm were not moved by the plough, yet they were recovered from the 18-21 cm layer.

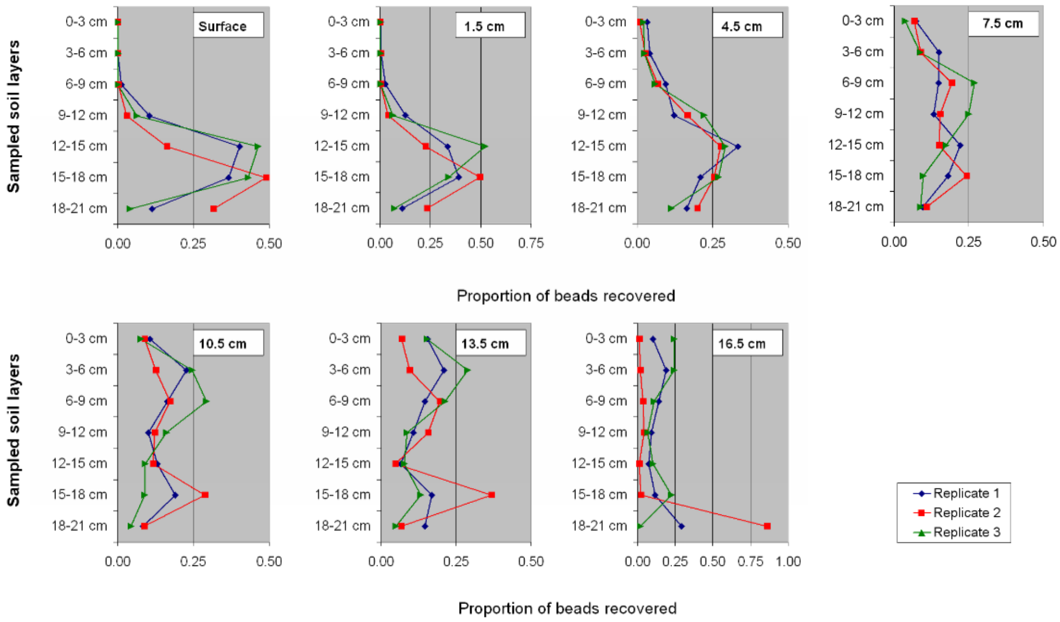


**Figure 3-17** Distribution of recovered beads over soil depth after [Plough + Power harrow] cultivation for beads at different depths (surface, 1.5 cm, etc.) prior to cultivation. Note that scale of X-axis varies.

For all three treatments, the distribution pattern over depth for beads initially at 16.5 cm deep showed the greatest variation over the three replicates compared with beads at other starting depths (data not shown). This is caused by variable working depth and emphasizes that small changes in working depth of a cultivation implement can have the largest effects on deeply buried seeds.

Without expanding the soil layers, the predicted probabilities compare very poorly with the observed results (see Figure 3-18) and the correlation coefficient was close to zero (r = 0.03). After extrapolating the probabilities over the working depth, the predicted transition matrices generally corresponded well with the observed patterns in the field except for beads initially at 16.5 cm in the deepest layers. The correlation coefficient (r) between predicted and observed probability values increased to 0.73 for the mean response and 0.68, 0.52 and 0.69 for Replicates 1, 2 and 3 respectively.

The mean correlation coefficient for the three pair-wise comparisons of the [Plough + Power harrow] replicates was 0.60, indicating that there is as much or more variability within the observed transition matrices as between the observed and predicted transition matrices.

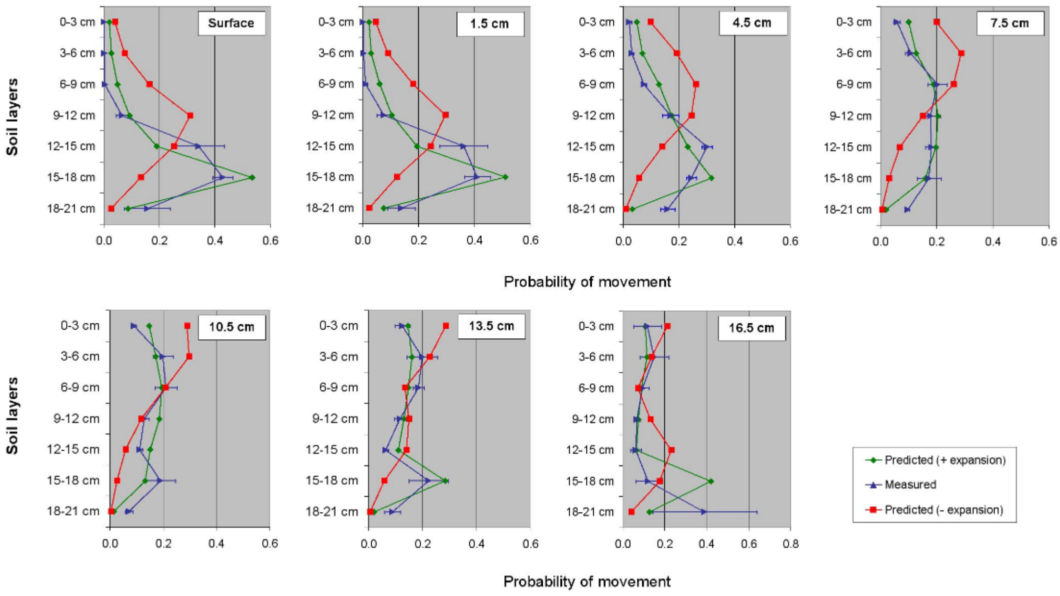


**Figure 3-18** Probabilities of movement for a bead or seed at a certain depth prior [Plough + Power harrow] cultivation to a certain soil layer after [Plough + Power harrow] cultivation. Measured values are compared with two predicted models (with and without expanding the probabilities). Horizontal bars on the 'Measured' blue line represent standard error over three replicates.

### 3.3.4 Implementation and discussion

The work done in this study verified the use of transition matrices for predicting seed movement. A new element was introduced, the effect of soil expansion and compression, which is essential to be considered. The 'raw' transition matrix, resulting from sampling the soil after an implement that compresses the soil, can not be used to pre-multiply the transition matrix of the preceding cultivation implement. Instead the probabilities have to be expanded over the depth over which the implement compressed the soil.

By carefully examining the individual replicates it is clear that apparently random changes in working depth whilst the implement is pulled through the soil can result in quite different transition matrices. When the working depth of an implement is set, the realised working depth will follow a probability density function (e.g. normal distribution) around the anticipated working depth with transition matrices varying accordingly.

In addition, it was found that transition matrices are not only implement-specific but also dependent on the preceding cultivation. This does not necessarily mean that a myriad of transition matrices have to be created for each implement, as most implements will have a fixed place in the cultivation sequence anyway. For those implements that can be used at various positions in the cultivation sequence it may be worth considering whether the bulk density of the soil varies between times of cultivation. If it does, this may well result in a different transition matrix as evidenced for the Power harrow in this and the previous study (Mead *et al.*, 1998).

Notwithstanding these relative successes, by scrutinizing the processes of soil and seed movement it was realised that there appears to be a fundamental inconsistency for most of the empirically derived transition matrices beyond the assumption of multiplicativity. Due to the lack of time this could not be addressed experimentally. A theoretic example will illustrate the idea: imagine a soil profile, 20 cm deep, and with a perfectly uniform seed distribution of 2500 seeds in each 5 cm layer. The soil is ploughed as in Cousens and Moss (1990) and can thus be modelled using the transition matrix they derived experimentally:

**Equation 3-3:**

$$\begin{bmatrix} 0.02 & 0.21 & 0.37 & 0.29 \\ 0.12 & 0.28 & 0.26 & 0.11 \\ 0.40 & 0.30 & 0.19 & 0.12 \\ 0.46 & 0.21 & 0.18 & 0.48 \end{bmatrix} * \begin{bmatrix} 2500 \\ 2500 \\ 2500 \\ 2500 \end{bmatrix} = \begin{bmatrix} 2225 \\ 1925 \\ 2525 \\ 3325 \end{bmatrix}$$

The remarkable result is that the plough, apart from *moving the soil* is also *filtering the beads out of some soil layers and depositing them in other layers.* For this effect not to be an experimental anomaly it has to be accepted that seeds embedded in soil can move independent from soil, which seems unrealistic. Algebraically this behaviour is caused by the fact that the row sums of the transition matrix do not add up to 1.

$$\begin{bmatrix} 0.02 & 0.21 & 0.37 & 0.29 \\ 0.12 & 0.28 & 0.26 & 0.11 \\ 0.40 & 0.30 & 0.19 & 0.12 \\ 0.46 & 0.21 & 0.18 & 0.48 \end{bmatrix} -- > \begin{matrix} 0.89 \\ 0.76 \\ 1.01 \\ 1.33 \end{matrix}$$

If this additional constraint is added to the transition matrix (see a modified transition matrix where this condition is satisfied in Equation 3-4) then the numbers of seeds over depth would not have changed which is what intuitively can be comprehended.

**Equation 3-4:** $$\begin{bmatrix} 0.03 & 0.22 & 0.37 & 0.38 \\ 0.15 & 0.37 & 0.37 & 0.11 \\ 0.39 & 0.30 & 0.19 & 0.12 \\ 0.43 & 0.11 & 0.07 & 0.39 \end{bmatrix} * \begin{bmatrix} 2500 \\ 2500 \\ 2500 \\ 2500 \end{bmatrix} = \begin{bmatrix} 2500 \\ 2500 \\ 2500 \\ 2500 \end{bmatrix}$$

The stable depth distribution is the vertical distribution of seeds in the soil after x cultivations and after which an additional cultivation would no longer change the distribution of seeds in the respective soil layers. The stable depth distributions of the transition matrices with and without these additional constraints are

$$\begin{bmatrix} 0.25 \\ 0.25 \\ 0.25 \\ 0.25 \end{bmatrix} \text{ and } \begin{bmatrix} 0.23 \\ 0.18 \\ 0.23 \\ 0.36 \end{bmatrix} \text{ respectively.}$$

Hence, the second transition matrix is suggesting that seeds are behaving unlike other soil particles as otherwise the bottom layer would have increased in volume, violating the notion that the layers are each 5 cm. If it is accepted that seeds behave just like soil particles the only logical conclusion is a ‘complete mixing’ as predicted by the stable depth distribution of a transition matrix where the row sums add up to one.

So what causes this anomaly? Most of the transition matrices are the result of experimental work using some form of artificial seeds. Studies that have compared the vertical redistribution of artificial beads and seeds over soil depth during cultivation found no difference (Moss, 1988; Staricka *et al.*, 1990) so it is not likely that beads behave fundamentally different from seeds.

It could be related to the way in which beads have been introduced in the soil. Researchers have either applied beads in a narrow layer in the centre of the target soil layer or mixed with soil and then introduced as a layer at the required depth. With regards to the latter, it is vital to ensure a homogenous distribution of beads over the complete soil layer, and if realised this approach delivers a ‘rough-and-ready’ matrix.

The former is less laborious but relies on the assumption that the probability of movement for beads applied in the centre of a soil layer is representative of the average probability for the entire layer. If row sums are consistently higher (compared over replicates) than 1 after elimination of the ‘Surface’ layer probabilities, then the conclusion has to be that this assumption is incorrect. As observed in the pilot experiment, applying a high number of beads in a narrow layer instead of mixing them with soil before cultivation could lead to lower aggregation into soil clods. Perhaps the enrichment of the fourth soil layer in the Cousens and Moss model is caused by beads not incorporated in soil clods and trickling down the pore spaces to the bottom layer. On the other hand, the transition matrices derived by van Melick (1996) also suffer from row sums being unequal to 1, despite introducing beads that had been completely mixed through a volume of soil in the field using an auger.

Another explanation is that the assumption that the distribution of the recovered beads over depth is representative of all moved beads does not hold true. If the beads in the bottom soil layer are recovered to a higher extent than the beads in the top layer, this will be reflected by a higher row sum for the bottom layer. Interestingly, the studies where transition matrices for the plough are derived from soil rather than seed movement (i.e. the Colbach and Roger-Estrade models) suffer less from this problem although it is still somewhat present judging from the stable depth distribution in the Colbach model (1) but it is virtually absent in the Roger-Estrade model (2).

$$(1) = \begin{bmatrix} 0.23 \\ 0.28 \\ 0.29 \\ 0.20 \end{bmatrix} \quad (2) = \begin{bmatrix} 0.25 \\ 0.23 \\ 0.27 \\ 0.25 \end{bmatrix}$$

Using an excavation framework results in recoveries six times higher than using soil cores but it can not sample as wide an area which may be required to get a representative area. The disadvantage of using soil cores is that the recovery per starting depth is low and can vary by a factor five (see Table 3-1) so that depth distribution patterns are likely to vary more between replicates.

Transition matrices are derived by normalising over columns. The question is if the raw data (recovered bead numbers) can be somehow manipulated or interpreted to derive transition matrices that are normalised over both columns and rows. Unless this can be accomplished, the predictions of modelling seed movement using the current transition matrices are as biased as the sampling scheme that was used to create the models in the first place. In the Cousens and Moss transition matrix, the row sums of the upper two layers, from where weed emergence is possible, is less than one. Any transition matrix with an even number of rows and columns and where the row sums are less than one will result in an underestimation of emergence and an overestimation of seed mortality.

Despite this deficiency, seed movement transition matrix models for cultivation implements are still the best available way to predict vertical weed seed redistribution and should therefore not be dismissed. Rather, more effort should be taken, to extend the work in a correct fashion to specific cultivation implements used outside the arable sector. For example the cultivation applied to the soil where carrots are grown includes implements such as the ridger and stone and clod separator (see section 3.6.1 and Figure 3-33) for which no transition matrices exist. Because of the enormous soil moving capacity of these implements this should not be addressed by introducing beads to the soil, a better option might be using steel tracers that can be recovered with a metal detector such as in the study by Montgomery *et al.* (1999). To save time and finances, cultivation implements that are (almost always) used in conjunction, such as the ridger and the stone and clod separator, can be addressed together rather than as separate implements.

## *3.4 Evaluation of the Colbach and Roger-Estrade models for seed movement during ploughing*

### 3.4.1 Introduction

The models developed by Colbach *et al.* (2000) and Roger-Estrade *et al.* (2001) will be referred to in this section as the Colbach model and the Roger-Estrade model respectively. Both are mechanistic models in that they postulate an explicit theory by which the soil is moved during ploughing and how this is dependent on plough characteristics (width and depth, skim coulter) and soil characteristics (fragmentation). Once the mouldboard shares hit the soil, the furrow is rotated until it is settled on the previously rotated furrow. The angle over which the furrow is rotated depends only on ploughing width and depth, i.e. the sine of the inclination angle of the rotated furrow with the plough pan equates to the ratio of tillage depth to width (see Figure 3-19A). During this movement the furrow breaks up and this phenomenon is modelled by separating the furrow into slivers which slide downwards until they reach the plough pan (see Figure 3-19B). The number of slivers depends on the condition of the soil: it is low in the case of poor fragmentation when the ploughed soil is dry or compacted; and it increases with the fragmentation of the soil, when ploughing occurs in good moisture conditions and/or when the soil to be ploughed

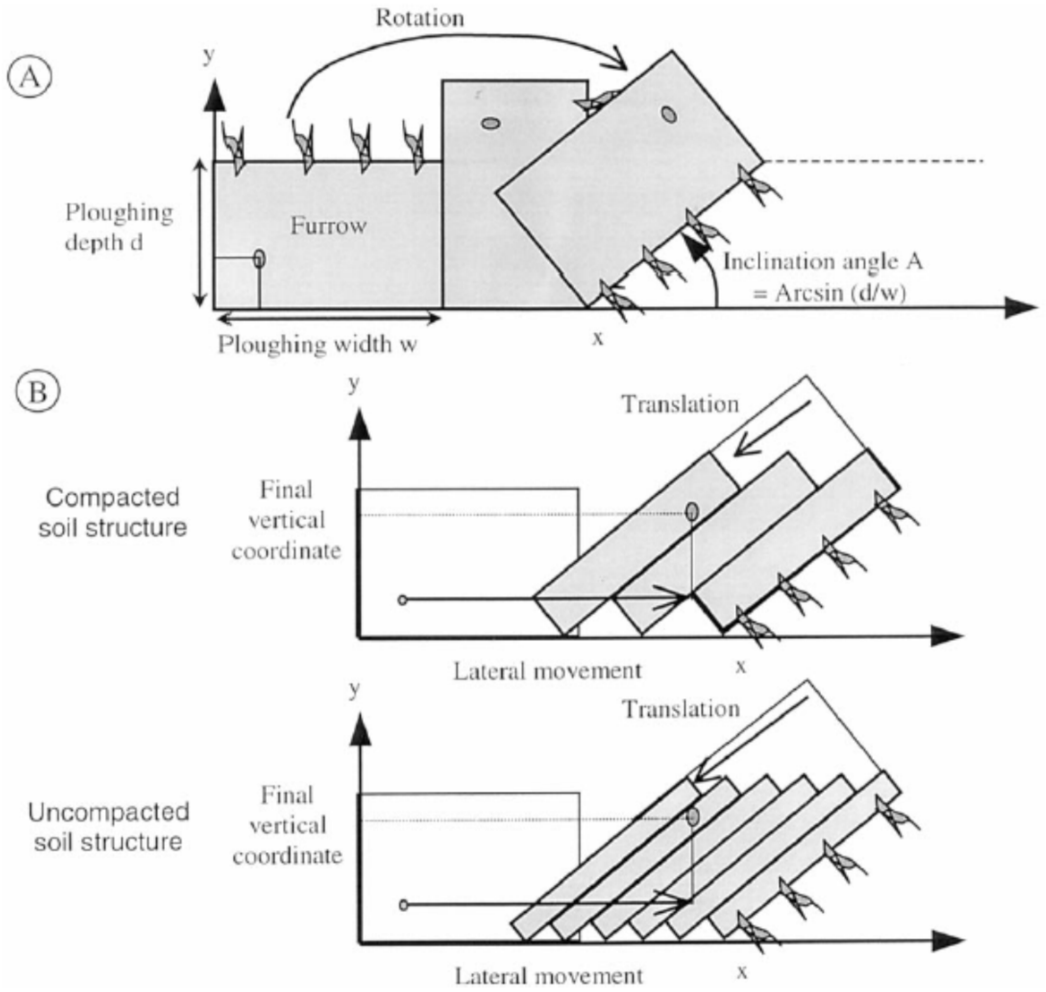


**Figure 3-19** Soil movement during ploughing explained as a succession of a rotation of the whole furrow (A), followed by a breakup into slides and their translation, with the number of slides decreasing with soil compaction (B) (after Colbach *et al.*, 2000).

is uncompacted. This representation allows the calculation of the final vertical and lateral co-ordinates of any point of the furrow as a function of, its coordinates before ploughing, ploughing depth and width, and finally soil structure.

The difference between the two models is that the Roger-Estrade model addresses the effect of a plough with a skim-coulter (see Figure 3-20) in contrast to the Colbach model where the plough contains no skim-coulter.

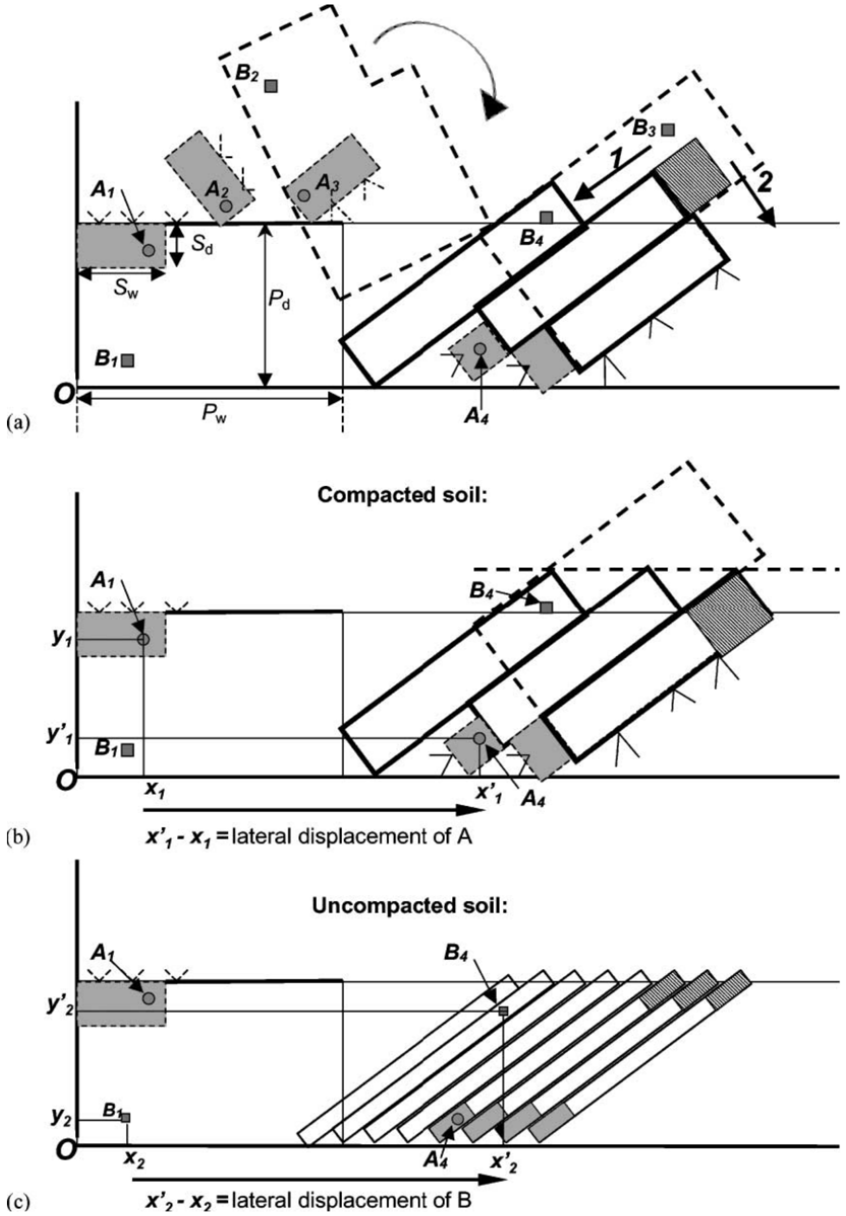


**Figure 3-20** Representation of the movement of the soil during ploughing with a skim-coulter. $A_1$, $A_2$, $A_3$, $A_4$ and $B_1$, $B_2$, $B_3$, $B_4$ are the successive positions of points A and B during the furrow slice movement: rotation (a), then translation of the slivers in case of a compacted (b) or an uncompacted soil (c) before ploughing. $S_\mathrm{d}$ and $S_\mathrm{w}$ are the depth and width of the skim-coulter, respectively. $P_\mathrm{d}$ and $P_\mathrm{w}$ are the depth and width of the plough, respectively. ■ part of the furrow slice cut by the skim-coulter; ▨ part of the furrow slice replaced in the void created by the skim-coulter (after Roger-Estrade *et al.*, 2001).

The skim-coulter is a device sometimes described as a mini-plough that scrapes off part of the surface, where straw and weed seeds have accumulated at the end of the season, and deposits this at the bottom of the previously rotated furrow just prior to the rest of the furrow so that it is effectively buried deeper than it would have been otherwise (see Figure 3-20). It is important to emphasise that the height of the soil profile and the number of slivers after ploughing are the same in the Colbach and Roger-Estrade model for a given set of soil and plough set-up characteristics.

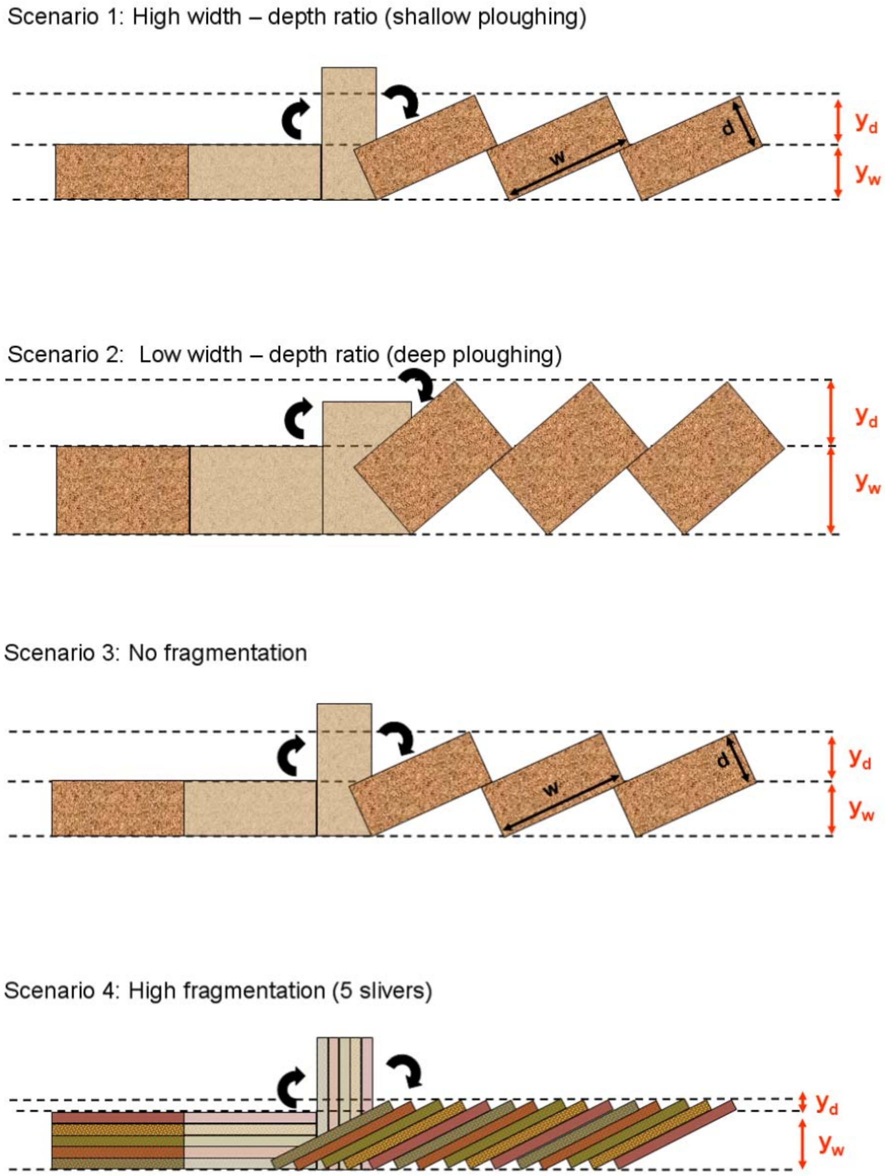
The benefit of these mechanistic models is that they can cope with different plough and soil characteristics. A critical examination of the evaluation of both models, however, reveals that the models predict soil movement reasonably well only for a limited range of conditions. Evaluation of the Colbach model by the authors showed that the modelling efficiency (Mayer and Butler, 1993) of the final vertical coordinate was high ($r^2$ = 0.85) and that there was no systematic over- or underestimation. However, including 'imperfectly' rotated furrows (constituting more than half of all data points) in the analysis reduced the modelling efficiency ($r^2$ = 0.63). From the point of evaluating a mechanistic model describing perfectly rotated furrows it makes sense to remove those data points. However, it questions the applicability of the model in 'real life' as no reason is given to assume that in reality most furrows will follow the ideal rotation pattern. Roger-Estrade *et al.* (2001) evaluated their proposed model and reported that in uncompacted soil the modelling efficiency reached 0.66 and 0.73 for two different locations with no over- or underestimation being detected. However, if the soil was compacted by driving a heavy tractor over the clay soil in wet conditions, the modelling efficiency of the final vertical coordinate in the Roger-Estrade model was considerably lower ($r^2$ = 0.55). Given that the primary reason of ploughing is to undo the soil compaction imposed by tillage, spraying and harvesting equipment deployed in the previous season (Guul-Simonsen *et al.*, 2002), the question is which scenario, compacted or uncompacted, is more representative of soil conditions at the time of ploughing.

A close look at a mouldboard plough in action and drawing from personal observation and photos found through the Google Image search engine of ploughed fields in England, France and the Netherlands, highlighted two further weaknesses of the models. The first one relates to the number of slivers. For an excessively compacted soil the authors assigned either two (Colbach model) or three slivers (Roger-Estrade model). With two or more slivers, the pattern of individual furrows becomes undetectable. Yet, many observations of ploughed soil (see example in Figure 3-21) show a clear pattern of the rotated furrows, which would indicate only one sliver.

**Figure 3-21** Ploughed land at Warwick HRI (top) a sandy loam soil and ploughed land in Groningen, the Netherlands a clay soil (bottom – courtesy of Jan Dijkstra). Individual rotated furrows can be distinguished, suggesting one 'sliver' as in the terminology of Colbach *et al.* (2000).

The other criticism, which is acknowledged by the authors, relates to the lack of soil expansion during ploughing, resulting in the underestimation of the final vertical coordinate. Close observations of a sandy soil after ploughing showed that even when no clear furrows were visible (i.e. multiple slivers), the soil level was raised considerably, relative to adjacent non-ploughed land, which is in contrast to what the

Colbach and Roger-Estrade models predict. Since the Colbach model is conceptually the simpler of the two, the geometric principles of this model can be used to predict soil height after ploughing for both the Colbach model and the Roger-Estrade model. The maximum soil height ($y_d$) is determined by the depth of ploughing and the number of slivers but not through additional soil expansion, as is illustrated in Figure 3-22a and b. In Scenario 1 and 2 it is shown that deep ploughing results in less complete rotation and therefore higher $y_d$ than in shallow ploughing.



Scenario 1: High width – depth ratio (shallow ploughing)

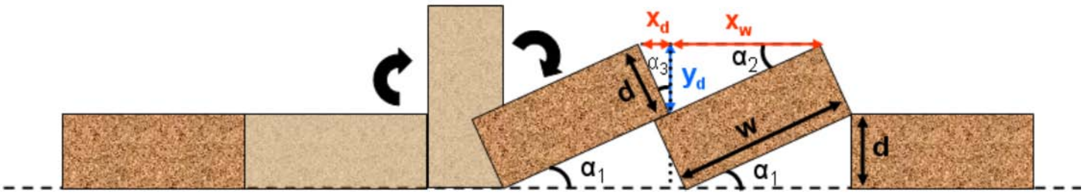
Scenario 2: Low width – depth ratio (deep ploughing)

Scenario 3: No fragmentation

Scenario 4: High fragmentation (5 slivers)

**Figure 3-22** Schematical diagram of soil movement during ploughing based on the geometric principles of the Colbach model, aiming to show that maximum soil height after ploughing ($y_d$) is (only) a function of plough depth (Scenario 1 vs. Scenario 2) and degree of soil fragmentation (Scenario 3 vs. Scenario 4).

From Scenario 3 and 4 it can be deduced that $y_d$ is inversely proportional to the number of slivers: $y_{d(5\text{ slivers})} = \frac{y_{d(1\text{ sliver})}}{5}$. Using simple trigonometry (see Figure 3-23)



1. $\alpha_1 = \alpha_2 = \alpha_3$
2. d = plough depth, w = plough width, z = # of slivers

3. $\cos \alpha_3 = y_d/(d/z)$
4. $y_d = \cos \alpha_3 {}^*(d/z)$

**Figure 3-23** Trigonometry used to calculate maximum soil height, $y_d$, as a function of plough depth (d) and number of slivers (z).

and a spreadsheet model in Excel, $y_d$, as predicted by the Colbach and Roger-Estrade models, can be plotted as a function of the number of slivers and the plough depth (see Figure 3-24).

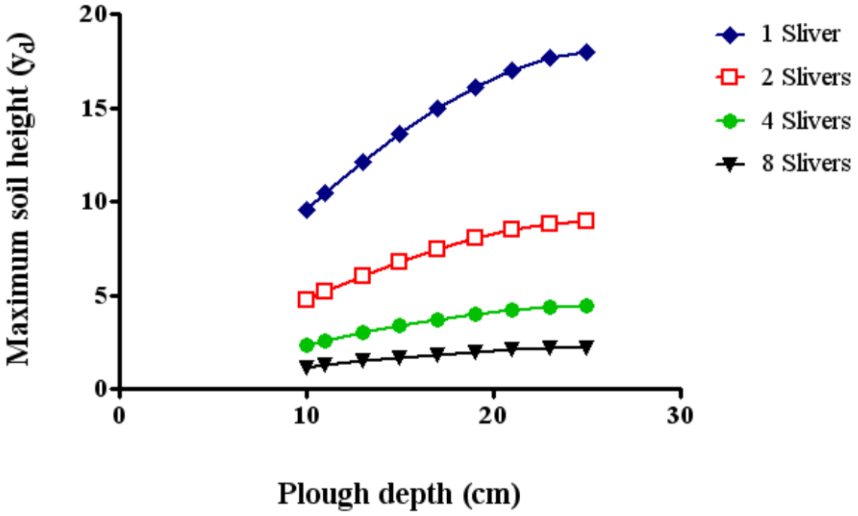


**Figure 3-24** Maximum soil height ($y_d$) as a function of plough depth and the number of slivers according to the models of Colbach and Roger-Estrade.

Neither model addresses the settling of the soil under influence of weather conditions like rain, freezing and thawing if no further cultivation takes place after ploughing and

Roger-Estrade *et al.* (2001) argued that this effect could possibly neutralize the lack of soil expansion in their model, especially for compacted soils. To come to a decision on how seed movement be modelled in the overall modelling framework a field experiment was conducted with two specific aims:

- to examine if and how much the Colbach and Roger-Estrade models underestimate soil expansion just after ploughing
- to examine how the profile of ploughed soil changes over time

## 3.4.2 Methodology

### 3.4.2.1 Experimental design

This experiment was conducted alongside the main experiment and using the experimental plots as discussed in Section 3.2 and a more detailed description of the experimental design is given there. The experiment design was a factorial treatment set with location (soil type) and plough setting as factors in two replicates. The Warwick HRI research stations (Wellesbourne and Kirton) were chosen as they provide different soil types (a sandy loam at Wellesbourne and a silty loam in Kirton) and both stations had the facilities and land available for the cultivation experiments to be conducted. Since the mouldboard ploughs at both locations were of the same brand (Dowdeswell) and the shares had the same shape and width (36 cm) it was not thought necessary to use the same plough. Plough depth was set at 16 and 24 cm and the skim coulter was nominally set at about 5 cm.

### 3.4.2.2 Measurements

Due to weather and time constraints the experiments could not be initiated on the same date; in Kirton all experimental plots were ploughed on the 12th of January 2006, in Wellesbourne both replicates with plough depth set at 16 cm plus one replicate with plough depth at 24 cm were ploughed the 12th of December 2005 the remaining replicate with plough depth 24 cm was ploughed on the 6th of January 2006. As documented in Section 3.2, the depth of cultivation was found to be around 18 cm for the treatment with plough depth set up at 16 cm. In the Results section the treatment will be referred to further as the ‘18 cm’ treatment.

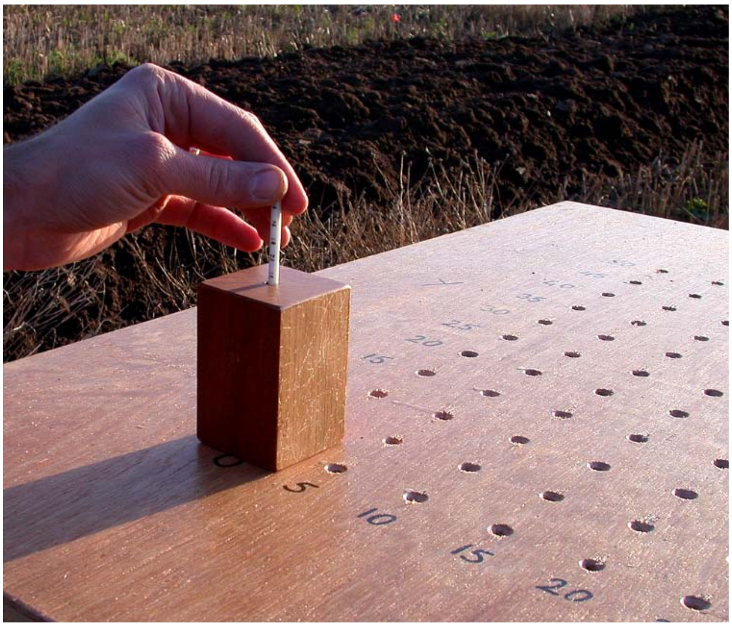


**Figure 3-25** Wooden board, block and stick with ruler used to measure relief after ploughing and change in relief over time due to weather conditions.

Just before ploughing, a random location was chosen in the strip to be ploughed. Four wooden pegs were hammered into the soil in a square shape, 80 cm distance from each other and in line with the direction of cultivation. Just outside the strip of soil to be ploughed and parallel to the four pegs, two ‘reference’ pegs were hammered in the soil. The top of the two reference pegs was made level with the four permanent pegs. A wooden board (90 x 90 cm) with 121 holes in the central 50 x 50 cm (11 x 11 holes at 5 cm from each other) was then gently placed on top of the pegs. To obtain a measure of soil height, a stick with ruler was then slid through a wooden block with empty core - to ensure a vertical projection of the stick – and the wooden board until it reached the soil level (see Figure 3-25). ‘Stick length’ measurements, defined as the length from the top of the wooden block until the soil, were taken at 5 mm precision. This was repeated so that each 10x10 cm position (36 points) of the 50x50 cm grid was sampled. The four ‘permanent’ pegs were removed just before tillage and hammered in again immediately after tillage in the same height and position using the unmoved ‘reference pegs’ as a guide. Care was taken not to compact the soil within the four pegs. To assess expansion of soil volume immediately after ploughing and soil settling afterwards, measurements were taken just after ploughing and then repeated once every two weeks for three months (see Table 3-10). Daily volume of rainfall was recorded by weather stations at both locations. After ploughing, sampling was carried out at a 5x5 cm grid (121 points), except for the first two series of measurements at Wellesbourne that were taken on a 10x10 cm grid.

**Table 3-10** Soil height sampling dates after ploughing at two depths (18 & 24 cm) and the total rainfall (mm) over the previous sampling period. R1, R2 represent replicate 1 and 2 respectively.

| *Location* | *Timing* | *Sampling dates* | *Total rainfall* | | |
|---|---|---|---|---|---|
| **Kirton** | Pre | 12/01/2006 | | | |
| | Post (1) | 12/01/2006 | | | |
| | Post (2) | 23/01/2006 | 7.5 mm | | |
| | Post (3) | 06/02/2006 | 1.2 mm | | |
| | Post (4) | 20/02/2006 | 20.7 mm | | |
| | Post (5) | 06/03/2006 | 13.0 mm | | |
| | Post (6) | 20/03/2006 | 22.8 mm | | |
| | Post (7) | 03/04/2006 | 18.4 mm | | |
| | | **Sampling dates (18&24 cm R1)** | **Total rainfall** | **Sampling dates (24 cm R2)** | **Total rainfall** |
| **Wellesbourne** | Pre | 12/12/2005 | | 06/01/2006 | |
| | Post (1) | 14/12/2005 | | 09/01/2006 | |
| | Post (2) | 09/01/2006 | 23.3 mm | 26/01/2006 | 8.5 mm |
| | Post (3) | 26/01/2006 | 8.5 mm | 09/02/2006 | 2.4 mm |
| | Post (4) | 09/02/2006 | 2.4 mm | 23/02/2006 | 16.7 mm |
| | Post (5) | 23/02/2006 | 16.7 mm | 09/03/2006 | 20.0 mm |
| | Post (6) | 09/03/2006 | 20.0 mm | 23/03/2006 | 2.3 mm |

### 3.4.2.3 Data analysis

The variation in soil level before ploughing was determined by subtracting the median ‘stick length’ from the stick length at each of the 36 points at the grid. The soil expansion and variation in soil height just after ploughing was calculated for each x,y-position by subtracting the stick length after ploughing from the median stick length before ploughing.

This allowed a comparison with the predictions by Colbach and Roger-Estrade models for two characteristics just after ploughing; soil surface roughness along the x and y-axis and soil expansion.

**Soil surface roughness**

During measurements in the field, the y-axis of the plots were kept parallel to the direction of ploughing to check for a regular pattern across the plot (along x-axis) as predicted by the Colbach and Roger-Estrade models. Since the width of the sampled area (50 cm) was wider than the plough width there was a potential caveat; if the soil would rotate as regular as predicted according to the Colbach and Roger-Estrade models and if the number of slivers is low, it would mean the distribution of soil heights in the sampling area gave a biased estimate of median soil height. If so, only the data from the 0-40, 5-45 or the 10-50 cm sections of the x-axis should be used.

Two-sample T-tests were conducted to check whether there were significant differences between ‘random roughness’ across (x-axis) and along the direction of ploughing (y-axis). Random roughness (Currence and Lovely, 1970) was calculated for each row and column:

**Equation 3-5** $$RR = \sqrt{\frac{\sum_{i=1}^{k}\left(Z_i - \overline{Z}\right)^2}{k-1}}$$

where Zi = soil height in a row or column at location i; k = number of height readings per row / column, i.e. either 11 (Kirton) or 6 (Wellesbourne). This decision process was graphically presented by contour plots of median soil height just after ploughing.

### Soil expansion

With regard to soil expansion, a spreadsheet model was used to generate soil height profiles according to the soil rotation principles as in Figure 3-20, and implemented for the experimental plough characteristics and one, two or four slivers. Given that plough width was 36 cm and the width of the sampling stick was 0.5 mm, to obtain a distribution of predicted soil height, sampling 72 positions should give the complete distribution of ploughed soil heights, regardless of the number of slivers.

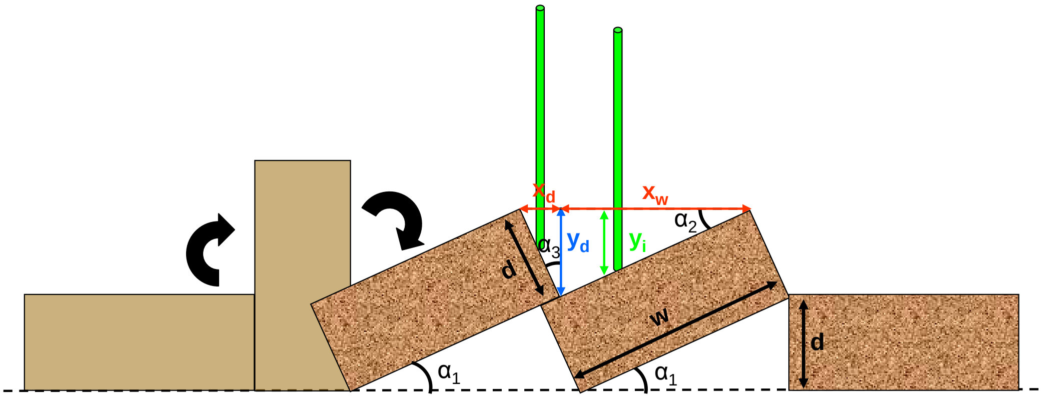


**Figure 3-26** Schematical illustration to Equations 3-6 to 3-10 that were used in a spreadsheet model in Microsoft Excel to calculate soil height.

Using simple trigonometry as illustrated in Figure 3-26, the sine functions of the angles $\alpha_1$, $\alpha_2$ and $\alpha_3$ were expressed below in A, B and C respectively.

$d = \text{plough depth}, w = \text{plough width}, z = \text{number of slivers}$

$\alpha_1 = \alpha_2 = \alpha_3$

A) $\quad \operatorname{Sin}\alpha_1 = \frac{d}{w}$

B) $\quad \operatorname{Sin}\alpha_2 = \frac{d}{X_d + X_w}(\text{for } z = 1), \operatorname{Sin}\alpha_2 = \frac{d}{z*(X_d + X_w)}\ (\text{in general})$

C) $\quad \operatorname{Sin}\alpha_3 = \frac{X_d}{d}(\text{for } z = 1), \operatorname{Sin}\alpha_3 = \frac{X_d * z}{d}\ (\text{in general})$

Given that the three angles are all the same, $X_d$ and $X_w$ can be expressed as functions of plough depth (d), plough width (w) and the number of slivers (z) using substitution. By equating the right hand sides of A and C, $X_d$ can be expressed as a function of d, w and z as in Equation 3-6.

**Equation 3-6** $\quad \frac{d}{w} = \frac{X_d * z}{d} \Rightarrow X_d = \frac{d^2}{w*z}$

By equating the (denominator of the) right hand sides of A and C, $X_d$ can be expressed as a function of x, w and $X_w$ as in Equation 3-7.

**Equation 3-7** $\quad w = z*(X_d + X_w) \Rightarrow X_d = \frac{w - (z*X_w)}{z}$

Now the right hand sides of Equations 3-6 and 3-7 can be equated to express $X_w$ as a function of d, w and z.

**Equation 3-8** $\quad \frac{d^2}{w*z} = \frac{w - (z*X_w)}{z} \Rightarrow X_w = \frac{w^2 - d^2}{w*z}$

Given the width of the sampling stick is known (0.5 cm) and the length of $X_d$ and $X_w$ can be calculated, for each stick position (i.e. 0.25, 0.75, 1.25 etc.) it can be easily determined whether it falls into the $X_d$ or $X_w$ range (see Figure 3-26) and $y_i$ can then be calculated according to Equation 3-3.

**Equation 3-9**

$$\begin{cases} \text{if stick position in } X_d : y_i = \dfrac{\text{stick position}}{\tan\alpha_3} \\ \text{if stick position in } X_w : y_i = \tan\alpha_2 * (X_d + X_w - \text{stick position}) \end{cases}$$

Finally then, given a stick position, soil height ($y_{sh}$) can be determined simply by deducting $y_i$ from $y_d$ (see Figure 3-26).

**Equation 3-10** $\quad y_{sh} = y_d - y_i$

**Soil settling**

For each plough depth and location combination, data were pooled over the two replicates and a time-series of the median soil height over all x,y-coordinates was then created for consecutive sampling dates to compare soil settling. Rainfall data was summed over sampling periods and considered in relation to the changes in soil height at both locations. Unlike in Wellesbourne, the length of sampling period (11-14 days) and the sampling scale (5x5 cm) was consistent in Kirton, which allowed a more in depth look at the changes in soil height by comparing the frequency distributions of change in soil height over different time intervals

The Colbach and Roger-Estrade models do not make exact predictions related to how the soil settles under influence of weather. In the AlomySys model (Colbach *et al.*, 2006) this feature was implemented in the model, presumably by increasing the soil fragmentation (i.e. number of slivers), and therefore decreasing soil height, over time. Even without additional fragmentation due to weather influences, the Colbach model assigns up to 12 slivers immediately after ploughing. For each plough depth and location the observed distribution of soil height at 81 (Kirton) or 87 days (Wellesbourne) after ploughing was therefore compared with model predictions using 3, 6 and 12 slivers in the Microsoft Excel spreadsheet model.

## 3.4.3 Results

### 3.4.3.1 Soil surface roughness

Contour plots of the soil surface in the experimental plots just after ploughing do not reveal a clear pattern of rotated furrows (i.e. one sliver) although in some plots linear elements of low and/or high soil can be observed (see Figure 3-27). The two-sample T-test of the Random Roughness (standard deviation) of soil heights along the x-axis and y-axis confirmed that for none of the plots except Kirton 18-R1 ($P<0.048$), was the standard deviation along the y-axis significantly lower than along the x-axis. It should be emphasized that the scale of the measurements (50 x 50 cm) is much smaller than the scale at which the eye perceives a ploughed landscape in general (see Figure 3-21).

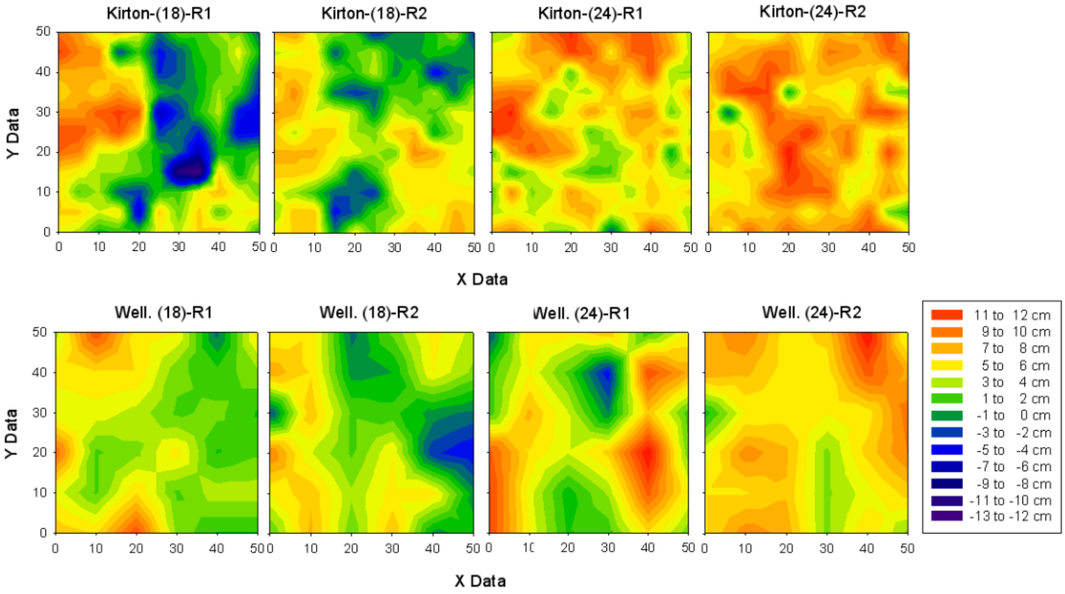


**Figure 3-27** Contour plots of soil surface just after ploughing at two depths (18 and 24 cm) in Kirton and Wellesbourne. The 'hotter' the colour, the more the soil has expanded relative to soil height just prior to ploughing. Sampling in Kirton and Wellesbourne occurred on a 5x5 and a 10x10 cm grid respectively. Abbreviations: Well.=Wellesbourne; R1, R2 represent replicate 1 and 2 respectively.

Higher frequency of the colours 'blue' and 'green' in the contour plots for soils ploughed at 18 cm shows that the soil height after ploughing was generally lower than the soil height after ploughing at 24 cm at both locations.

### 3.4.3.2 Soil expansion

The variation in soil heights before ploughing was larger in Kirton than in Wellesbourne but that is unlikely to have affected soil height after ploughing. According to expectations, the maximum, the median and the variation in soil height (interquartile range) after ploughing were higher than before ploughing (see Figure 3-28). Although the soil height distributions for the different plough depths overlap greatly, the distribution of soil ploughed at 24 cm is clearly higher than for soil ploughed at 18 cm. This effect was more pronounced in Kirton than in Wellesbourne.

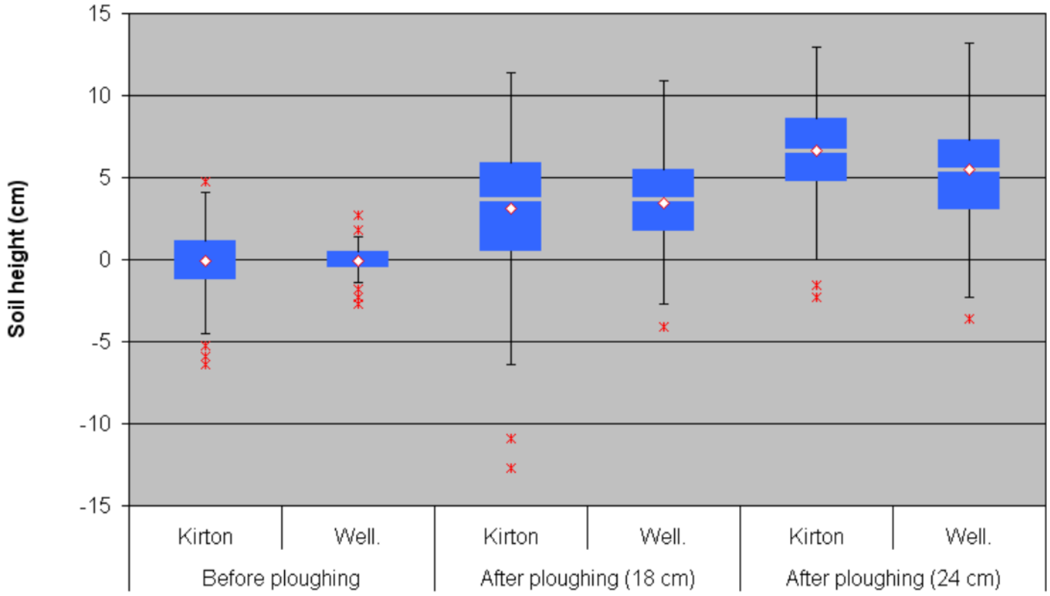


**Figure 3-28** Box plots of soil height before (pooled data of 4 replicates) and just after ploughing for two plough depths and two locations (pooled data of 2 replicates, Well. = Wellesbourne). Outliers are represented by red asterixes and are defined as those datapoints within the range 1.5-3.0 times the interquartile range, below or above the 1st or 3rd quartile respectively.

The median soil height after ploughing was higher in Kirton than in Wellesbourne for soil ploughed 24 cm but not for soil ploughed at 18 cm. From the boxplot it can be concluded that although there is considerable overlap in the distributions of soil height for soils ploughed at 18 and 24 cm, the effect of plough depth on soil expansion is more pronounced than the effect of location/soil type. This is confirmed by comparing the distribution of the pooled data over plough depth with the distribution of the pooled data over location / soil type (data not shown).

### Comparison with model predictions

Judging from the result of the T-tests and the contour plots (see Figure 3-27) it was felt that the distribution of peaks and troughs was irregular enough to use the full dataset rather than curtailing the X-data. The data from the two locations were then pooled for each plough depth to create two datasets for which the distributions could be compared with the distribution of predicted soil heights for models with various numbers of slivers. For soil ploughed at 18 cm deep the observed median was slightly lower than the predicted median for the 2 slivers model and the maximum soil height was between that for 1 and 2 slivers (see Figure 3-29). For soil ploughed 24 cm deep, both the median and the maximum soil height were between the respective values for models with between 1 and 2 slivers. The minimum soil height for all observed experimental plots was lower than the predicted values because the Colbach and Roger-Estrade models consider the slivers as ending up contiguous to each other, ignoring cracks in the ploughed soil. It is important to notice that the observed distributions of soil height for soils ploughed at 18 and 24 cm depth are more dissimilar from each other than the predicted distributions for these depths for each of the number of slivers. This suggests that the effect of plough depth could be more pronounced than is currently implemented in the Colbach and Roger-Estrade models.

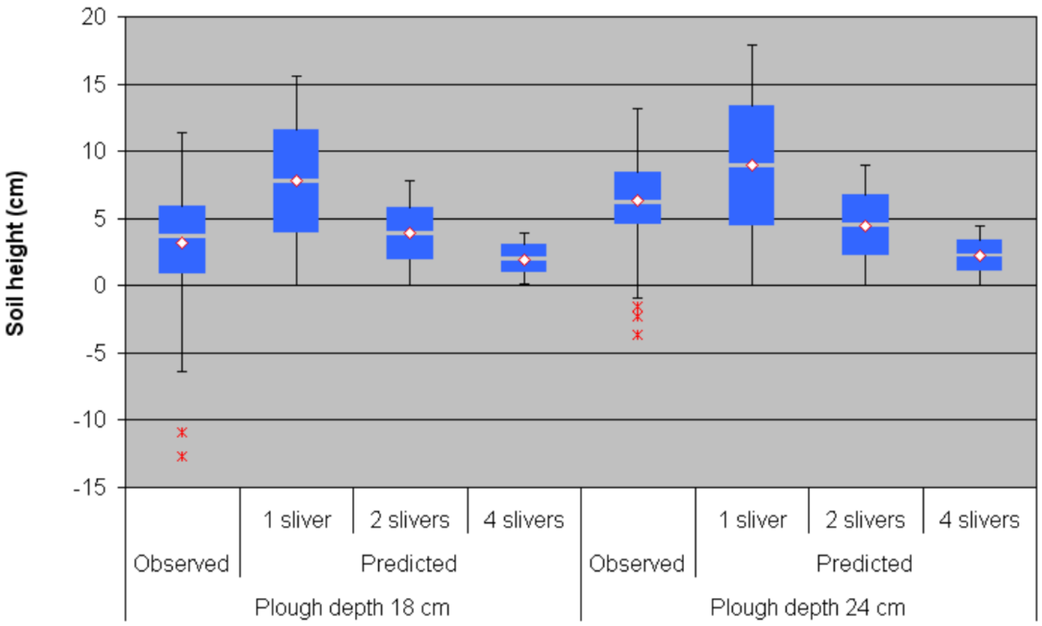


**Figure 3-29** Comparison between observed and predicted distributions of soil height just after ploughing at two different plough depths. Predicted distributions are based on the trigonometric relations that underlie the Colbach and Roger-Estrade models (see Figure 3-23). Observed values of soil height were pooled over location. Outliers are represented by red asterixes and are defined as in Figure 3-11.

#### 3.4.3.3 Soil settling

The pattern of soil settling over time was distinct for the two locations (soil types); median soil height declined fast over the first 11 days and slowly thereafter in Kirton (see Figure 3-30). In Wellesbourne soil height declined in a more constant way and only half as much as in Kirton. Interestingly, the amount of rainfall over the first 27 days in Wellesbourne was much higher than over the first 25 days in Kirton (see Table 3-8), suggesting the pattern of soil decline is more inherent to soil characteristics than amount of rainfall per se. In both locations, the pattern of decline appeared similar regardless of plough depth. In fact, the difference in median height between soils ploughed at 18 and 24 cm that existed just after ploughing remained intact until the end of the sampling period (i.e 81 and 99 days after ploughing (DAP) for Kirton and Wellesbourne respectively).

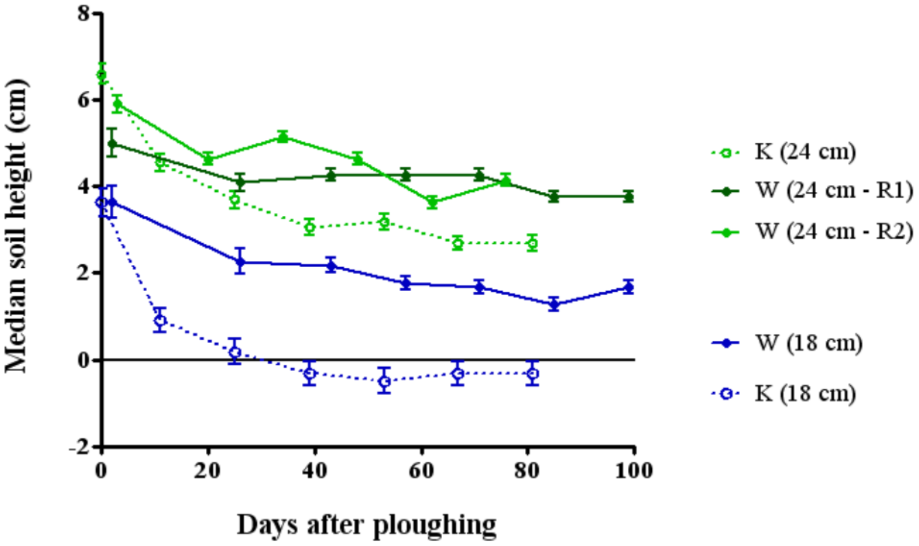


**Figure 3-30** Change of median soil height over a three month period after ploughing; data from replicates ploughed at 24 cm in Wellesbourne was not pooled because date of ploughing was different. Standard error is calculated as $SE_{median} = 1.253\sigma / \sqrt{N}$

From the frequency distributions of changes in soil height over different time intervals it is clear that the average decline in soil height at Kirton is not constant over time but most pronounced in the first 11 days, lower in the next 28 days and even less in the last 42 days (see Figure 3-31).

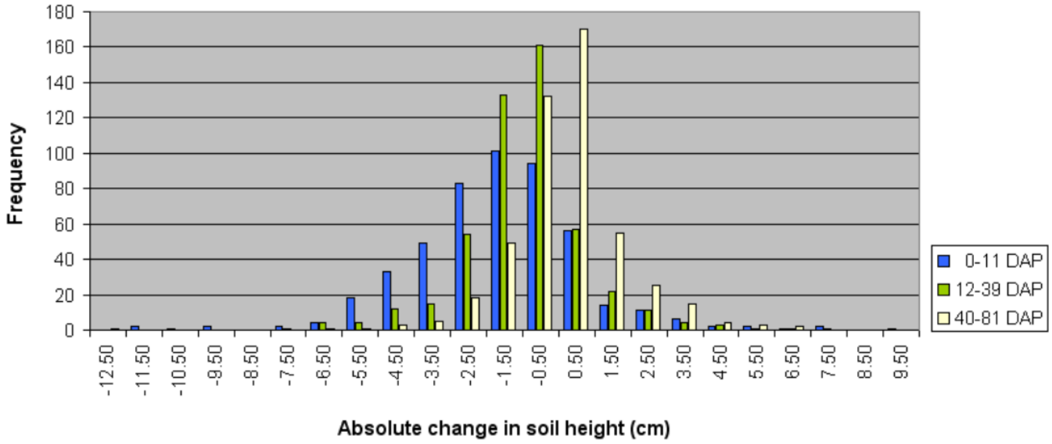


**Figure 3-31** Frequency distribution of changes in soil height at Kirton, compared for consecutive time intervals after ploughing (DAP = days after ploughing). Data from two replicates and both plough depths were pooled (N=484) since no differences were detected between their individual frequency distributions.

Furthermore, the sample variance ($s^2$) of the data over the first 11 days was larger than the sample variance over the next two intervals, in other words, absolute changes in soil height are larger over the first 11 days than thereafter.

### Comparison with model predictions

Due to different decline rates in median soil height at Kirton and Wellesbourne, it was not justified to pool the data of both locations for each plough depth at the end of the sampling period. Whereas immediately after ploughing the observed median soil height for ploughing at 18 cm seemed to agree most with the predicted median soil height given 2 slivers, this had increased to 6 slivers (Wellesbourne) or to more than 12 slivers (Kirton) at the end of the sampling period (see Figure 3-32). For soils ploughed at 24 cm the median soil height immediately after ploughing was reflected best by a value in between that predicted by models with 1 and 2 slivers and median soil height at Wellesbourne was a little higher and at Kirton a little lower than the median soil height for 3 slivers at the end of the sampling period. Because at each location the absolute change in soil height was the same for both plough depths and the decrease in absolute soil height from one sliver to the next is much greater for a lower number of slivers (see Figure 3-24), more slivers were needed to explain median soil height after 81 / 87 DAP for 18 cm than for 24 cm. This highlights the fact that the number of slivers in the model should not only be a function of the degree of soil compaction but also of plough depth.

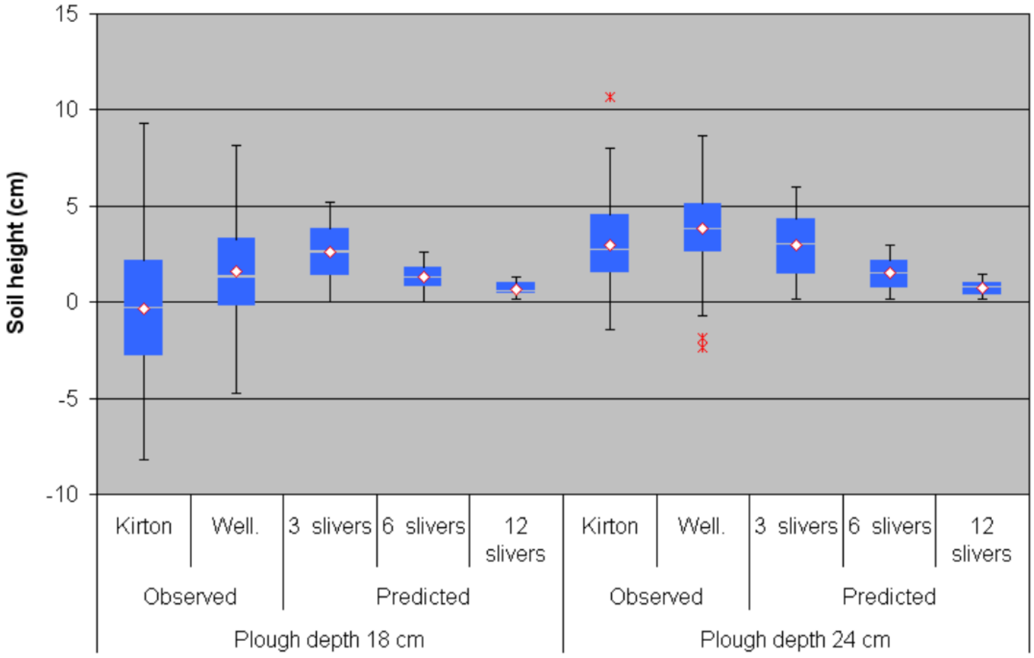


**Figure 3-32** Comparison between observed and predicted distributions of soil height, 81 (Kirton) or 87 days (Wellesbourne) after ploughing, for soils ploughed at 18 and 24 cm. Outliers are represented by red asterixes and are defined as in Figure 3-28.

## 3.4.4 Discussion and model implementation

Had soil height readings been taken over a larger area, it is possible that lower variation along compared to across the direction of ploughing would have been detected as was observed by Zhixiong *et al.* (2005). The relief aspect is less crucial however than the systematic underestimation of soil expansion after ploughing and the way soil settling over time is addressed. From this experiment it is clear that soil expansion occurs not only because of the voids created by the diagonal panning of the slivers but because soil volume *itself* expands, i.e. macro pores are created over the entire depth of the plough profile. Since germination probability is strongly influenced by a seed’s vertical position in the soil, in a model that underestimates the thickness of the soil layer, seeds will be incorrectly assigned to the zone from where emergence can be successful, thus overestimating the numbers of emerging seedlings. Obviously, this affects only the scenario in which soil is ploughed in autumn and left over winter.

In addition, this experiment showed that soil settling is more simply modelled as a natural compaction of the soil profile independent of plough depth, rather than as an increase in soil slivers over time which *is* dependent on plough depth. The Colbach and Roger-Estrade models require an estimate of the number of slivers, both for modelling seed movement and as soil settling over time. This would add a further component to ECOSEDYN and given the more straightforward use and interpretation of transition matrices and the problems identified with the Colbach and Roger-Estrade models in this study it was decided this added complexity was not warranted.

The scenario of plough cultivation in autumn and then leaving the field over winter will not be implemented because of the failed experiment (Section 3.2). Although the information on slumping has contributed to deciding which model to choose, it bears no further use in the modelling framework.

## *3.5 Summary of research findings*

At the outset two major aims were formulated. The extent to which the aims have been met and some secondary results are summarised in this section.

1. **To obtain a model for the plough, compatible with the previous models developed at Warwick HRI.**

   In Wellesbourne a transition matrix for [Plough + Soil settling] was derived for each plough depth based on 1 replicate. No [Plough] transition matrices could be derived in either Kirton or Wellesbourne but the additional work done to evaluate the ‘multiplicativity hypothesis’ in Section 3.3 delivered a transition matrix for [Plough] helping to fulfill this aim.

2. **To critically evaluate the generic and specific approach to modelling seed movement**

   **a. transition matrices; more specifically the ‘multiplicativity’ assumption**

   Until now, modelling seed movement using transition matrices has been subject to an unnoticed flaw, the fact that seeds are assumed to move independent of soil. Unless transition matrices can be constructed to have column and row sums of one, seed movement is predicted incorrectly. For the assessed cultivation sequence the ‘multiplicativity’ assumption was found to be valid, albeit, only after a modification of the ‘raw’ [Power harrow] transition matrix to account for the soil compression that occurred during power harrowing of previously expanded soil due to ploughing. It was further found that:

   - Even for a given cultivation implement, the transition matrix may vary depending on the preceding cultivation
   - The actual working depth of an implement has a major impact on the re-distribution of beads

   **b. mechanistic models of ploughing with and without skim-coulter**

   The expectation prior to carrying out the experiment that the models underestimate soil height immediately after ploughing was verified. This could overestimate seedling emergence in the case of a ploughed field left over winter. It was further found that:

- The pattern and extent of soil settling was independent of plough depth but dependent on soil type
- Soil settling should be modelled as an absolute decrease of soil height rather than an increase in soil slivers over time.

The verification of the ‘multiplicativity’ assumption justified the use of transition matrices in ECOSEDYN. Because the mechanistic soil movement models for the plough are less easy to implement than transition matrices they will not be implemented in ECOSEDYN. The exact implementation of the cultivation transition matrices in the context of the system modeled (crop rotation with carrot and winter wheat) is dealt with in Chapter 5.

## *3.6 Implementation in ECOSEDYN*

Weed seeds are vertically (and horizontally) redistributed in the soil during seedbed preparation and for root crops during the harvest operation as well. As the specialized cultivation and harvest implements used by growers are not available at Warwick HRI there was no opportunity to test vertical seed (bead) redistribution caused by these implements. As ECOSEDYN aimed to represent commercial practices as accurately as possible, transition matrices were proposed for the vertical seed redistribution during seedbed preparation and crop harvest.

### 3.6.1 Seedbed preparation

The feedback from the questionnaires (see Appendix 1) suggested that cultivation regimes varied depending on personal preferences of the growers and/or soil type. The aim was to identify the most common cultivation regime for each crop. On light mineral soils carrot growers don’t use a plough; instead the land will be disced and deep cultivated (sub-soiled) in autumn. Heavier soils may be ploughed. Both options will be followed by ridging, de-stoning, (Jones) bedforming and drilling in spring. Cultivation regimes from 6 conventional carrot growers are presented in Table 3-11. The use of a destoner (stone-and-clod separator) can be considered standard practice for moderate to large commercial growers. Destoners come in various designs (star vs webbed separators) and from various manufacturers (e.g. Reekie, Grimme, Standen).

**Table 3-11** Cultivation regimes applied by six conventional carrot growers

| | *Carrot growers* | | | | | |
|---|---|---|---|---|---|---|
| **Cultivation** | [1] | [2] | [3] | [4] | [5] | [6] |
| Subsoiler (16”) | | X | X | X | X | X |
| Plough (10-12”) | X | X | | some | | some |
| Plough + furrowpress | | | X | | | |
| Discing (5”) | | | | some | | some |
| Ridger/Bedformer (12”) | X | X | | X | X | |
| Destoner (10”) | X | X | X | X | X | X |
| Jones Bedformer (10”) | X | X | X | X | X | X |
| Drilling | X | X | X | X | X | X |

Their purpose in (carrot) seedbed preparation is to rid the seedbed of stones and soil clods and deposit these in between the beds (see Figure 3.33, (Grimme, 2003) and

**Figure 3-33** Seedbed preparation of a carrot field. Top: Ridging with a bedformer / ridger. Middle: Destoning the ridges with a stone-and-clod separator (Reekie Reliance 500); soil is taken up by a series of rotating devices that sieve the soil and deposit stones and clods in the tramlines. Bottom: Rototilled beds with Jones Engineering Triple Bedformer, now ready for carrot drilling. Images taken at Elveden Estate (Norfolk, UK) and with courtesy of Andrew Francis.

video footage of a destoner in action (SUFFOLKRB, 2008)). Destoners have been used to incorporate granular nematicide prior to planting potatoes. A spiked rotavator (Dowdeswell Powavator) incorporated granules evenly to a depth of 20 cm (Woods *et al.*, 1999) and if this treatment was followed by a destoner, the granules were distributed uniformly down to a depth of 35 cm. Incorporation using only the destoner resulted in a more or less even distribution over the first 15 cm only. For surface seeds the study by Woods *et al.* (1999) suggests total mixing but seeds already in the soil will be incorporated in smaller or larger soil clods (Reuss *et al.*, 2001) which may affect their distribution chances when going through the stone-and-clod separator. So, it is unknown if seeds initially in the deepest layer are as likely to end up in the top layer as they are to stay in the deepest layer.

From the questionnaires with the carrot growers it became clear that if a destoner is used it will be followed by a (Jones) Bedformer (see Table 3-11). When asked about the degree of mixing of the soil, growers and agronomists suggested that the combination of ridging, destoning and a Jones Bedformer (adapted rotavator) would cause total mixing of the soil over the depth profile (ca. 30 cm.). For the sake of simplicity it was assumed that the combination of these two implements leads to total mixing of the soil. For a four layer soil column this is expressed in matrix terms as:

**Equation 3-11:**

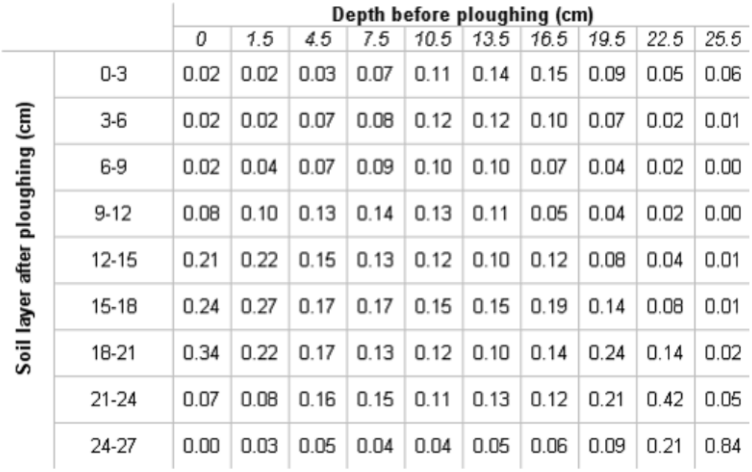
$$\underbrace{\begin{pmatrix} 0.25 & 0.25 & 0.25 & 0.25 \\ 0.25 & 0.25 & 0.25 & 0.25 \\ 0.25 & 0.25 & 0.25 & 0.25 \\ 0.25 & 0.25 & 0.25 & 0.25 \end{pmatrix}}_{\textbf{Destoner + Jones Bedformer}} * \begin{pmatrix} n_{1,t} \\ n_{2,t} \\ n_{3,t} \\ n_{4,t} \end{pmatrix} = \begin{pmatrix} n_{1,t+1} \\ n_{2,t+1} \\ n_{3,t+1} \\ n_{4,t+1} \end{pmatrix}$$

The benefit of this assumption is that it removes the need to design experiments to establish the transition matrices of the cultivation implements that precede these two implements. The working depth, the number of layers distinguished in the transition matrix and an estimate of the total number of seeds in the soil is the only information needed.

Since the working depth is 30 cm and the transition matrices operate on a 3 cm soil layer basis a rough approach would be to divide the soil into 10 layers. However, the probability to germinate and emerge is highly sensitive to depth within the first 3 cm. Therefore the two shallowest soil layers, 0-3 and 3-6 cm were further divided into six sub-layers of 5 mm each. The values of the original transition probabilities of the 3 cm layer were divided into six to give individual probabilities for the 5 mm layers. For the crop rotation where carrot constitutes the vegetable crop, the transition matrix therefore contains the surface layer, twelve 5 mm layers (0-6 cm) and eight 3 cm layers (6-30).

For onions, if the soil is considered too stony, then the seedbed preparation regime is similar to (though somewhat shallower than) that of carrots, otherwise it comprises ploughing to 20 cm. followed by power harrow cultivation (Questionnaire Carl Sharp). In the former case the seed movement is modelled exactly as for carrots but over a shallower working depth (24 cm), whereas in the latter case the transition matrices for [Plough + Power harrow] as obtained in Section 3.3 can be used.

Winter wheat growers use various cultivation regimes from zero-tillage to a plough operation followed by a one-pass drill-powerharrow combination. Working depth during seedbed preparation is around 24 cm and therefore the ‘raw’ transition matrix for plough in winter (24 cm deep) followed by power harrow in spring in Wellesbourne, as obtained in Section 3.2 was used (see Figure 3-34). Note that for convenience, the 0-3 cm layer is indicated as ‘whole’ but in ECOSEDYN this soil layer is divided into six sublayers of 5 mm each and therefore the probability needs to be divided into 6 even portions. In ECOSEDYN, the raw transition matrix is therefore modified to account for that.



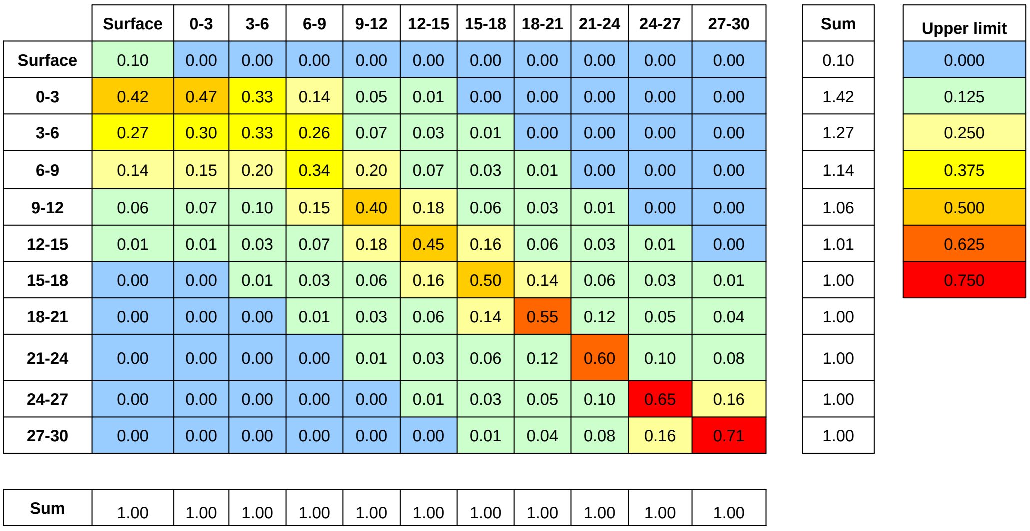
|  |  | Depth before ploughing (cm) |  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  | *0* | *1.5* | *4.5* | *7.5* | *10.5* | *13.5* | *16.5* | *19.5* | *22.5* | *25.5* |
| **Soil layer after ploughing (cm)** | 0-3 | 0.02 | 0.02 | 0.03 | 0.07 | 0.11 | 0.14 | 0.15 | 0.09 | 0.05 | 0.06 |
|  | 3-6 | 0.02 | 0.02 | 0.07 | 0.08 | 0.12 | 0.12 | 0.10 | 0.07 | 0.02 | 0.01 |
|  | 6-9 | 0.02 | 0.04 | 0.07 | 0.09 | 0.10 | 0.10 | 0.07 | 0.04 | 0.02 | 0.00 |
|  | 9-12 | 0.08 | 0.10 | 0.13 | 0.14 | 0.13 | 0.11 | 0.05 | 0.04 | 0.02 | 0.00 |
|  | 12-15 | 0.21 | 0.22 | 0.15 | 0.13 | 0.12 | 0.10 | 0.12 | 0.08 | 0.04 | 0.01 |
|  | 15-18 | 0.24 | 0.27 | 0.17 | 0.17 | 0.15 | 0.15 | 0.19 | 0.14 | 0.08 | 0.01 |
|  | 18-21 | 0.34 | 0.22 | 0.17 | 0.13 | 0.12 | 0.10 | 0.14 | 0.24 | 0.14 | 0.02 |
|  | 21-24 | 0.07 | 0.08 | 0.16 | 0.15 | 0.11 | 0.13 | 0.12 | 0.21 | 0.42 | 0.05 |
|  | 24-27 | 0.00 | 0.03 | 0.05 | 0.04 | 0.04 | 0.05 | 0.06 | 0.09 | 0.21 | 0.84 |

**Figure 3-34** ‘Raw’ transition matrix used to model weed seed redistribution in the soil during seedbed preparation for winter wheat

## 3.6.2 Harvest

Winter wheat is harvested by a combine harvester around August time without an appreciable soil disturbance so no seed redistribution is modeled in ECOSEDYN.

For carrot, two different harvesting systems are used depending on the timing of harvest. Top lifters that lift the carrots from the soil by their foliage are used until September when the foliage is still strong and the carrots prone to fractures (for video footage see: Univercoman, 2008a). From early October until next spring (April/May) carrots that are left in the ground are harvested using share harvesters, a method that causes more disturbance of the soil. In this model the latter harvesting protocol can be ignored as carrots are harvested before the end of the simulation year (September). A transition matrix was proposed that represents the actions during top-lifting of carrots (see Figure 3-35). The underlying assumption of the transition matrix is that close to the soil surface there is appreciable mixing of soil but this decreases over depth. Like with the transition matrix shown in Figure 3-34, the top 0-3 cm layer is divided into six sublayers of 5 mm each. The insights gained in Chapter 3 (row sums have to be 1) were applied in the matrix, i.e. 90% of the seeds initially on the surface were distributed over the 0-15 cm layer but otherwise no net loss occurred in any other layer.



| | Surface | 0-3 | 3-6 | 6-9 | 9-12 | 12-15 | 15-18 | 18-21 | 21-24 | 24-27 | 27-30 | Sum |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Surface** | 0.10 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.10 |
| **0-3** | 0.42 | 0.47 | 0.33 | 0.14 | 0.05 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.42 |
| **3-6** | 0.27 | 0.30 | 0.33 | 0.26 | 0.07 | 0.03 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 | 1.27 |
| **6-9** | 0.14 | 0.15 | 0.20 | 0.34 | 0.20 | 0.07 | 0.03 | 0.01 | 0.00 | 0.00 | 0.00 | 1.14 |
| **9-12** | 0.06 | 0.07 | 0.10 | 0.15 | 0.40 | 0.18 | 0.06 | 0.03 | 0.01 | 0.00 | 0.00 | 1.06 |
| **12-15** | 0.01 | 0.01 | 0.03 | 0.07 | 0.18 | 0.45 | 0.16 | 0.06 | 0.03 | 0.01 | 0.00 | 1.01 |
| **15-18** | 0.00 | 0.00 | 0.01 | 0.03 | 0.06 | 0.16 | 0.50 | 0.14 | 0.06 | 0.03 | 0.01 | 1.00 |
| **18-21** | 0.00 | 0.00 | 0.00 | 0.01 | 0.03 | 0.06 | 0.14 | 0.55 | 0.12 | 0.05 | 0.04 | 1.00 |
| **21-24** | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.03 | 0.06 | 0.12 | 0.60 | 0.10 | 0.08 | 1.00 |
| **24-27** | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.03 | 0.05 | 0.10 | 0.65 | 0.16 | 1.00 |
| **27-30** | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.04 | 0.08 | 0.16 | 0.71 | 1.00 |
| **Sum** | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | |

| Upper limit |
|---|
| 0.000 |
| 0.125 |
| 0.250 |
| 0.375 |
| 0.500 |
| 0.625 |
| 0.750 |

**Figure 3-35** Hypothetical transition matrix for soil and seed movement during carrot harvest using top-lifters. Colours are added to illustrate (lack of) movement, the 'hotter' the colour the higher the probability of moving from a soil layer before harvest to another after harvest.

Onions are harvested around August – September time using so-called windrowers. During this procedure the bulbs are lifted from the bed and left to dry on the soil surface for a number of days before being finally picked up to be stored indoors. The procedure for onions can be assumed to cause complete mixture of seeds throughout the top 15 cm of soil (for video footage see: Univercoman, 2008b). The transition matrix would therefore follow the same principles as applied for the seedbed preparation transition matrix for carrot (see Equation 3-11), only over a narrower soil depth.

# 4 Plant growth and reproduction in a dynamic environment: experimental work and model implementation

## *4.1 Introduction*

It was concluded that there was a need to develop a comprehensive dynamic model capable of linking the dynamic processes of plant growth, flowering and seed shedding (see Section 2.6.2).

Dynamic models are better suited to model the development of the target organism than static models provided that the mechanisms that cause the variability in onset and rate can be sufficiently captured. In that sense they become mechanistic models. Static models often have a limited validity. For example a linear regression model for seed production against weed biomass collected at crop harvest of a long-maturing crop may not be valid for a short-maturing crop. With ‘crop cultivar’ (time to maturity) set as one of the cultural control components of the weed management scenarios it is imperative that the number of viable weed seeds at the time of crop harvest can be predicted accurately. Even though events in the life of a weed need to be simplified in a model, the timing and relationship between dynamic processes such as plant growth, flowering and seed shedding are intricately linked both quantitatively and temporally. It would be unrealistic to model these events separately from each other as it would jeopardise the accuracy of the long-term predictions made by ECOSEDYN.

The overall aim of the research described in this chapter was therefore to define a simplified yet sound way of dynamically modelling plant growth and reproduction. More specifically the following objectives were identified and addressed through experimental work:

- To establish the appropriate environmental conditions that drive (early) growth and to quantify the amount of this environmental variable to reach defined growth stages (1st, 2nd, 4th and 6th true leaf stages). By including this in ECOSEDYN the effect of different timing of weed control could be assessed since seedling mortality is size-dependent and most weed control is focused at these early stages. The results of this work are presented in Section 4.2 and an explanation of the implementation in ECOSEDYN follows in Section 4.7 after the model component for ‘Biomass increase’ has been presented.
- To establish how the onset and development of flowering over time is related to biomass increase. This objective is dealt with in an innovative way combining successional destructive harvests with image analysis as described in Section 4.3.

- To establish how plant age at crop harvest affects the static biomass – seed production relationship. Section 4.4 starts with a comprehensive overview on modelling seed production and then the experiment conducted to answer the above research question is presented.

The experiment described in Section 4.4 raised a number of additional questions on flowering phenology that were explored in more depth in another experiment described in Section 4.5. The main objective of this experiment was:

- To explore how much the timing and duration of flowering is regulated by plant biomass.

The results of the experiments relating to growth and reproduction as described in Sections 4.3-4.5 are closely related and therefore the implementation in ECOSEDYN of these results is not dealt with separately but holistically in Section 4.7. Before proceeding with the construction of the model components a summary of the research findings from which the model components follow is given in Section 4.6

Then in Section 4.7 the model components for ‘Biomass increase’, ‘Flowering’ and ‘Seed shedding’ are presented and parameterized.

# 4.2 *Effective day-degrees during early growth*

## 4.2.1 Introduction

Most weed control applications are timed when both crop and weed are still small. At these early stages of weed growth, efficacy of both mechanical weed control (Ascard, 1995) and herbicide applications (Schuster *et al.*, 2007) are often dependent on the developmental stage of the seedling. Age or size-dependent mortality is thus important in regulating plant population dynamics (e.g. Roach and Gampe, 2004). Since seed production and therefore likely future population dynamics is dependent on the number and size of the weeds that survive weed control operations, information should be gathered on the relative growth rate during these early growth stages.

An estimate of day degrees can be obtained from maximum and minimum temperature as well as an estimate of the base temperature, $T_b$:

**Equation 4-1**

$$\mathrm{DD}(\mathrm{d}) = \frac{\mathrm{T}_{\mathrm{max}}(\mathrm{d}) + \mathrm{T}_{\mathrm{min}}(\mathrm{d})}{2} - \mathrm{T}_{\mathrm{b}}$$

The effective day-degrees method was proposed by Scaife *et al.* (1987) and embraces the idea that growth can be limited by both light and temperature. The form of the effective day-degrees function includes day-degrees as well as solar radiation as reciprocals, in the same way conductors can be positioned in series in an electrical circuit. The Conductance model (Benjamin and Park, 2007) which is the plant competition model that was developed based on Scaife and Aikman’s ideas, derives its name from this principle. The *f* parameter was introduced to scale the relative importance of temperature and solar radiation (DD $m^2$ $MJ^{-1}$) .

**Equation 4-2**

$$\frac{1}{\mathrm{EDD}(\mathrm{d})} = \frac{1}{\mathrm{DD}(\mathrm{d})} + f * \frac{1}{\mathrm{PAR}(\mathrm{d})}$$

This introduces an extra variable that can perhaps be avoided if the effect of solar radiation is not large. Storkey (2004) showed that a model of growth against effective day-degrees (EDD) was superior in describing weed growth compared to a day-degrees (DD) model especially for species that are limited by reduced radiation values in autumn.

Based on the data collected in his study, Storkey (2004) quantified the f parameter as being 0.12 and 0.13 for *S. media* and *T. inodorum* respectively. This indicates a moderate sensitivity to solar radiation as compared to crops that are insensitive (*Brassica napus*, f = 0.08; *Triticum aestivum*, f = 0.06) and compared to weeds that are relatively sensitive (e.g. *Chenopodium album*, f = 0.51).

The aims of this experiment were firstly to confirm that effective day-degrees (EDD) rather than day-degrees (DD) should be used to model biomass increase during early growth for the two weed species and secondly to quantify the amount of EDD to reach defined growth stages (1st, 2nd, 4th and 6th true leaf stages) for which weed control efficacy (mortality) figures are available from the Danish site 'Pl@nteInfo - Crop protection online' (Faculty of Agricultural Sciences (Aarhus University Denmark), 2001).

## 4.2.2 Methodology

Seeds of *S. media* and *T. inodorum* were incubated at 20 ºC for 3 and 5 days respectively. For each species, four sets of one hundred and fifty seeds for which the radicle had emerged were then chosen and sown at a fixed depth of 1.0 cm on the 19th and 21st of April 2007 respectively, in 150-hole seed trays filled with Levington F2S compost.

Trays were placed outside in a coldframe with a wide-meshed plastic cover on top to prevent birds from entry and were watered carefully when required. A few seedlings that were infested by aphids/cutworm were removed from the tray.

The trays were inspected daily for emergence and the day of emergence noted for each tray-position. From this 'baseline' date the number of days required to reach the 1st true leaf stage and subsequently the 2nd and 4th true leaf stage were determined. For *S. media* the proportion emergence was very high and seedling growth-rate turned out to be very regular. Therefore, seedlings in only one of the 4 trays were followed throughout whereas for *T. inodorum* proportion emergence was low and seedlings in all 4 trays were followed up to the 4th true-leaf stage.

The true-leaf stages were defined as the first day when the true leaves had properly extended and on which the initiation of the following true-leaf pair could be observed (see Figure 4-1). In each replicate, 20 positions were randomly allocated in which the seedling was to be harvested at the 'cotyledon-' or any of the three other stages (i.e. 5 individuals per growth stage). Soil was carefully washed off the roots of seedlings and the seedlings were then dried in an oven for 24 hrs. at 70˚C and the dry weights noted. It was assumed that only the absolute time to reach a certain growth stage could differ over the season but not the average weight at each seedling growth stage. Therefore no further weight measurements were taken in the other sowings. However, some of the seedlings at the first sowing were accidentally taken out of the oven after only 12 hrs and these data were removed and replaced by seedling weights of the appropriate growth stage at sowing 2.

**Figure 4-1** *S. media* seedlings between 1st and 2nd true leaf stage in seed tray.

The harvested individuals meant that fewer observations could be made for the later stages but the large number of seedlings made up for that. It was observed that leaves of neighbours started overlapping and roots started protruding from the bottom of the tray around the 4th true leaf stage and it was suspected this could limit plant growth-rate. Therefore no measurements were made for the 6th true leaf stage. The experiment was repeated four times over the summer season (see Table 4-1), to check if thermal time to the defined growth stages was constant. For the later sowings, fewer seeds were sown and the cotyledon stage was included. Seedlings of *T. inodorum* were not followed through to the 4th true-leaf stage in Sowing 3 and only 7 seedlings were followed to the 4th true-leaf stage at Sowing 4 because the seedlings were required for transplanting in another experiment (see Section 4.5).

**Table 4-1** Sowing dates of seeds and number of tracked individual seedlings to determine thermal time to defined growth stages

| **Sowing** | ***Stellaria media*** | **Seedlings followed** | ***Tripleurospermum inodorum*** | **Seedlings followed** |
|---|---|---|---|---|
| 1 | 19/04/2007 | 143 (until 4th true-leaf) | 21/04/2007 | 133 (until 4th true-leaf ) |
| 2 | 18/05/2007 | 142 (until 4th true-leaf ) | 25/05/2007 | 125 (until 4th true-leaf ) |
| 3 | 01/06/2007 | 143 (until 4th true-leaf ) | 31/05/2007 | 81 (until 2nd true-leaf) |
| 4 | 04/07/2007 | 117 (until 4th true-leaf ) | 02/07/2007 | 7 (until 4th true-leaf) |

Maximum and minimum daily temperature and solar radiation were retrieved from the on-site weather station. Daily values of day-degrees and effective day-degrees were then calculated as in Equation 4-1 and 4-2 respectively. It was assumed the mesh would not significantly reduce daily solar radiation received. The values for f and

Tbase for each of the two weed species were taken from Storkey (2004). The cumulative number of DD and EDD required to grow from growth-stage N to growth-stage N+1 was summed over the interval from the first census day at which the seedling reached growth-stage N until the day prior to the census day at which the seedling reached growth-stage N+1. It was assumed that the environmental variable that accounts for most of the variability in plant growth would lead to the least amount of variability in the time from one growth stage to the next between the different sowings. For each species and inter-growth stage interval (e.g. from 1st to 2nd true leaf stage) ANOVA tests were carried out to test whether cumulative DD and EDD required for growth from one plant growth stage to the next were significantly different for the four sowing times. The variance ratios (F) were used to determine which environmental variable (DD or EDD) explained plant growth best; high variance ratios indicate more variability between than within sowing times for the quantity of the environmental variable required for growth from one growth stage to the next. If EDD is a more accurate desciptor of biomass accumulation than DD, then the values of the variance ratios of EDD for the growth interval – species combinations should be consistently lower than those of DD.

To test whether plant growth was limited at or before the 4th true leaf stage a second experiment was initiated. Ten seedlings of each species were sown in individual P11 pots (volume 1 liter) on the 31st of July, harvested when the 4th true leaf stage was reached, then dry weight determined in the way it was done for the other seedlings. One-tailed T-tests were performed to check whether the weight at the 4th true leaf stage was larger for seedlings grown in pots than for seedlings grown in trays.

Relative growth rate from the cotyledon to the 4th true leaf stage was calculated as the slope of the linear regression of ln-transformed biomass values at each seedling growth stage against the chosen variable for environmental time (DD or EDD). In addition, residual plots of the linear regression line were produced to see if relative growth rate was constant (exponential growth) or if, and at which growth stage, growth was restricted for the seedlings growing in the seedling trays.

The values for the chosen variable for environmental time (DD or EDD) to be used in the model were derived by pooling the results of the 4 sowing times and fitting Gaussian distribution functions to the data to determine the best fitted values for Mean and Standard deviation (SD).

### 4.2.3 Results

Average daily temperature increased over the experimental period (April-August 2007) but average solar radiation was constant (see Table 4-2) due to more hours of sunshine than usual in April and fewer than usual over the following months. April and July were both exceptional in that they were (one of) the driest and wettest months respectively on record whereas May and June also received more rainfall than average.

**Table 4-2** Average daily solar radiation and temperature over the experimental period in 2007

| | ***April*** | ***May*** | ***June*** | ***July*** | ***August*** |
|---|---|---|---|---|---|
| Total rainfall (mm) | 6.5 | 91.6 | 111.8 | 161.5 | 26.2 |
| Solar radiation (MJ/m$^{-2}$) | 16.7 | 15.8 | 16.8 | 15.6 | 15.8 |
| Temperature (˚ C) | 11.7 | 12.4 | 15.8 | 16.0 | 16.2 |

Individual plant weight at the 4th true leaf stage was significantly higher for both *T. inodorum* (one-tailed $P<0.01$) and *S. media* (one-tailed $P<0.05$) grown in pots in August as compared to plants that had been grown in a 150-hole seedling tray in April.

Because the experiment did not include measurements in autumn, the differences between DD and EDD were relatively small. On average *S. media* plants reached each of the growth stages earlier than *T. inodorum* plants (see Figure 4-2 and Table 4-4).

Except from emergence to the 1st true leaf stage, there was a tendency to require more DD and EDD for growth from one growth stage to the next at later sowings for both species (see Figure 4-2). In April, which was exceptionally dry, the least amount of EDD was required from emergence to the 4th true leaf stage. It was observed that seed trays were waterlogged during some periods with much rainfall, especially in July, and perhaps this excessive moisture had an adverse effect on growth. The high values of the variance ratio for *S. media* over the 2nd – 4th true leaf growth interval (see Table 4-3) appear to indicate that *Stellaria media* seedlings were particularly affected during this growth stage.

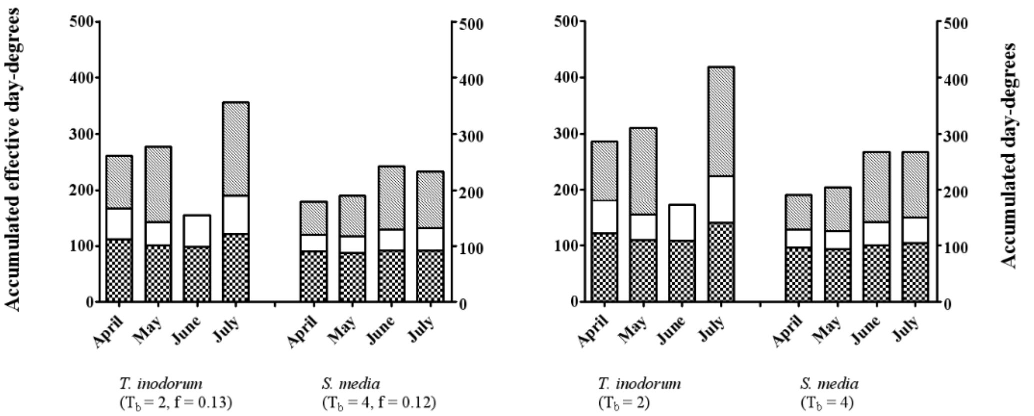


**Figure 4-2** Effective day-degrees (left) and day-degrees (right) accumulated over three growth intervals: the bottom (blocked), middle (open) and top (shaded) stacks represent the 'time' required to grow from emergence to the 1st true leaf-stage, from the 1st to the 2nd and from the 2nd to the 4th true leaf stage respectively. In June *T. inodorum* plants were only assessed until 2nd true leaf stage. Species-specific parameters to determine DD and EDD were taken from Storkey (2004).

The variance ratio of DD required for growth from emergence to the 4th true leaf stage was higher than the variance ratio of EDD for both species (see Table 4-3, row 1). This was the case as well for each separate growth interval for both species. Hence, the variation in the 'time' required for growth from one growth stage to the next between sowings relative to the variation within each sowing was lower for EDD. This indicates that using effective day-degrees as environmental variable is more consistent and will give a more accurate estimate of biomass increase as a function of environmental conditions.

**Table 4-3** Variance ratio (F) values for ANOVA tests on the DD and EDD sums required for growth over various growth intervals

| | ***S. media*** | | | | ***T. inodorum*** | | | |
|---|---|---|---|---|---|---|---|---|
| | *d.f.(b)* [1] | *d.f.(w)* | DD | EDD | *d.f.(b)* | *d.f.(w)* | DD | EDD |
| Em – 4th true leaf | *3* | *449* | **1082.00** | **782.30** | *2* | *261* | **73.74** | **45.10** |
| | | | | | | | | |
| Em – 1st true leaf | *3* | *478* | **38.49** | **8.16** | *3* | *738* | **77.38** | **64.95** |
| 1st – 2nd true leaf | *3* | *466* | **98.04** | **61.75** | *3* | *672* | **122.80** | **97.93** |
| 2nd – 4th true leaf | *3* | *449* | **611.60** | **467.60** | *2* | *261* | **182.20** | **142.70** |

[1] d.f.(b) and d.f.(w) indicate the degrees of freedom between and within each sowing respectively

The RGR of biomass during the month for the April sowing of *T. inodorum* was 0.023 (see Figure 4-3 left), very similar to the value found by Storkey (2004) for the RGR of green area (0.024). Similarly, the RGR of biomass for the April sowing of *S. media* was 0.028 (data not shown), almost equal to the value found by Storkey (2004) for the

RGR of green area (0.029). The close agreement between both $RGR_{Biomass}$ and $RGR_{Green}$ confirms that during early growth all plant biomass is invested in green area.

The residual plot of the linear regression line showed that the growth rate of biomass was reduced between the 2nd and 4th true leaf stage for both *S. media* (data not shown) and *T. inodorum* (see Figure 4-3, right).

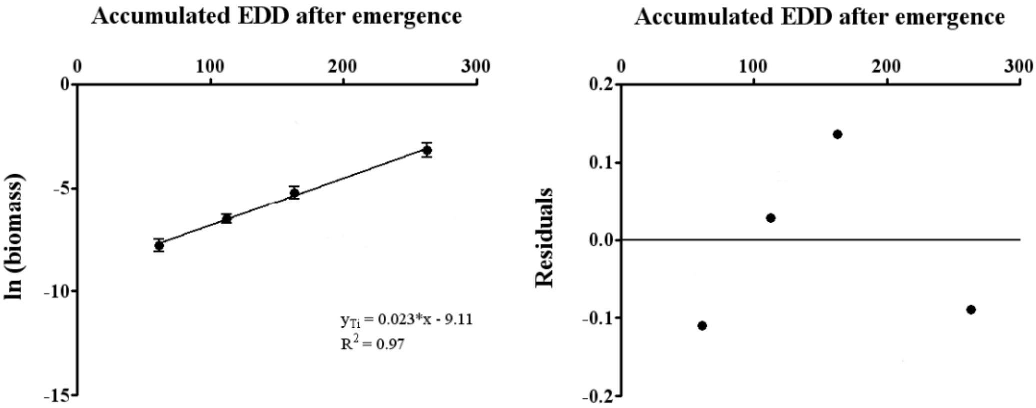


**Figure 4-3** **Left:** Relative growth rate for *T. inodorum* seedlings growing in seedling trays (April). Datapoints represent average biomass at the cotyledon, 1st, 2nd and 4th true leaf stage respectively, bars represent SD. **Right:** Residuals of linear regression line indicating limitation of growth rate between 2nd and 4th true leaf stage.

If the 4th true leaf values were removed from the linear regression analysis then the RGR of biomass (slope value) for *T. inodorum* and *S. media* increased to 0.025 and 0.030 respectively. In that case the regression lines for 'ideal growth' would be $y_{Ti} = 0.025x - 9.36$ and $y_{Sm} = 0.030x - 8.30$.

Assuming biomass at the 4th true leaf stage is constant and only the environmental day degrees required to reach the 4th true leaf stage varies, then, using the regression lines for 'ideal growth' (i.e. April data without 4th true leaf data) the 4th true leaf stages of *S. media* and *T. inodorum* could be reached after 173 EDD and 244 EDD respectively.

### 4.2.4 Discussion

From the results it was clear that solar radiation in the early stages of growth contributes to biomass accumulation in *S. media* and *T. inodorum* and that accumulated EDD is a better descriptor for growth of these two species than accumulated DD.

Baerveldt and Ascard (2002) mentioned that it took *T. inodorum* seedlings 13, 20 and 27 days from seeding to 2nd , 4th and 6th true-leaf stage. This is faster than in this study where the 2nd and 4th true-leaf stage in the least constrained timing (April) took 16 and 27 days. In that study, temperature appeared to be in the same range as those of the sowing in April of this experiment but possibly daily solar radiation was higher due to longer day lengths. Although seed trays were chosen with the largest seedling soil space, it did not prevent plants competing prior to the 6th true-leaf stage. In hindsight seedlings should have been grown in solitary P11 pots. It took 78% and 39% more effective day-degrees for *S. media* and *T. inodorum* respectively to grow from the 2nd to the 4th true leaf stage when averaging data of all sowings (see 'Constr. growth' in Table 4-4) and including the 4th true leaf stage data, compared to the data for April only with the 4th true leaf data removed (see 'Ideal growth' in Table 4-4).

**Table 4-4** Summary of parameters (biomass values are untransformed data)

| | *S. media* | | | | *T. inodorum* | | | |
|---|---|---|---|---|---|---|---|---|
| | 'Ideal growth' | | 'Constr. growth' | | 'Ideal growth' | | 'Constr. growth' | |
| **EDD required** | Mean | SD | Mean | SD | Mean | SD | Mean | SD |
| Emerg. – 2nd true leaf stage | 121.0 | 4.13 | 131.0 | 9.1 | 163.0 | 14.5 | 162.7 | 14.6 |
| 2nd - 4th true leaf stage | 52.3 | -- | 93.1 | 36.9 | 84.4 | 21.4 | 117.6 | 29.8 |
| 4th – 6th true leaf stage | 52.3 [2] | -- | -- | -- | 84.4 [1] | -- | -- | -- |
| **Biomass (gr)** | Mean | | SD | | Mean | | SD | |
| Cotyledon | 0.0014 | | 0.0002 | | 0.0004 | | 0.00015 | |
| 2nd true leaf | 0.0094 | | 0.0016 | | 0.0055 | | 0.00157 | |
| 4th true leaf | 0.0440 | | 0.0054 | | 0.0440 | | 0.01478 | |

[1] Extrapolated from Baerveldt and Ascard (2002)

[2] Assuming time from 4th to 6th true leaf stage is equal to time from 2nd to 4th true leaf stage

In the study by Baerveldt and Ascard (2002) the time from the 2nd to 4th is equally long as the time from the 4th to 6th true-leaf stage. Using this information, the accumulated EDD required to grow from the 4th to the 6th true-leaf stage under 'Ideal growth' conditions is 84.4 (see Table 4-4). No information about the time from 4th to 6th true leaf stage could be found for *S. media* so it was assumed this principle was valid for *S. media* too.

# 4.3 The phenology of flowering

## 4.3.1 Introduction

From empirical data it is possible to forecast the onset of flowering for photoperiodic plants such as *Tripleurospermum inodorum* (Roberts and Feast, 1974). Many studies have shown that the shift to the reproductive phase in annuals is timed so as to maximise reproductive yield (Cohen, 1976; Sugiyama and Hirose, 1991). Photosynthate produced by the vegetative parts is partitioned over the vegetative and reproductive parts according to a control function that determines the fraction of photosynthate that is allocated to reproductive structures. Rather than being instantaneous, the shift from the vegetative to the reproductive phase occurs according to a 'graded pattern' (King and Roughgarden, 1983). The number of produced flowers over time is thus closely associated with the increase of biomass over time and it would be unrealistic to model the onset and duration of flowering as a completely independent process from biomass accumulation over time.

Several studies have noted that plant growth is (close to) exponential up until flower initiation (Heath, 1937; Gregorczyk, 1998; Shitaka and Hirose, 1998). Given that reproductive structures are invariably less efficient than leaves in their photosynthesis (Aschan and Pfanz, 2003), it is intuitive that biomass does not increase exponentially from the onset of flowering onwards. Gregorczyk (1998) analysed the biomass increase of buckwheat (*Fagopyrum esculentum* Moench) using the Richards function (Richards, 1959), which is one of a family of sigmoid growth curves.

**Equation 4-3** $$y = y_{max}\left(1 + b * e^{-k*t}\right)^{\frac{1}{1-m}}$$

where y = plant biomass (dry weight), t = time, $y_{max}$ is the maximum plant biomass and the asymptote to which the function increases when $t \to \infty$, m, k and b are fixed parameters that determine the symmetry, steepness of the slope and horizontal shift on the t-axis respectively.

Gregorczyk (1998) characterised three ‘critical moments’ during plant growth: $P_1$, $P_2$, $P_3$

- $P_1$ represents the point where ‘acceleration’ of growth is maximal
- $P_2$ represents the point where growth rate is maximal
- $P_3$ represents the point where the ‘deceleration’ of growth is maximal

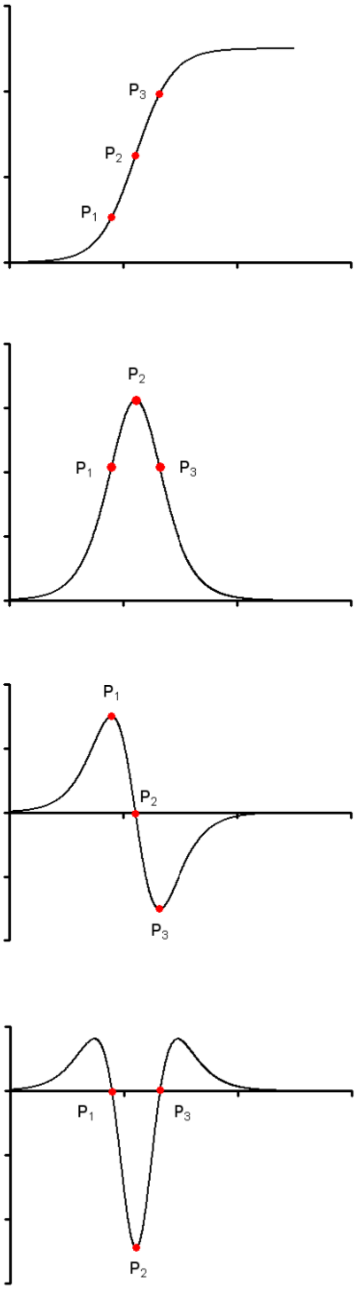


**Figure 4-4** From the top down: the Richards function as defined in Equation 4-3 (with m=2) and the first, second and third derivatives.

Between $P_1$ and $P_3$, growth is near linear. $P_2$ is the maximum of the first derivative (growth rate curve) of the Richards function and $P_1$ and $P_3$ are the maximum and minimum respectively of the second derivative of the Richards function. The X-coordinates of the points $P_1$, $P_2$ and $P_3$ can be calculated by finding the intersections with the X-axis in the second and third derivatives (see Figure 4-4).

If it is assumed that biomass increases exponentially until the onset of flowering then the initiation of flowering occurs at or close to the point $P_1$. If this is the case then the empirically determined dates of the onset of flowering can be used to scale the growth curves of plants established at any time of the year in ECOSEDYN.

An experiment was conducted with the aim to find parameters for the Conductance model (Benjamin and Park, 2007). With insight in modelling and understanding of the biology increasing it was, however, decided not to implement the Conductance model as part of the dynamic model. The reason for this was that the Conductance model only models biomass increase but not flower initiation and development. The Conductance model is parameterised based on destructive harvests of individual plants at several stages during the development. The data collected therefore comprised:

- Ground cover
- Crown zone area; the area of the smallest circle to encompass all the leaves of a plant when viewed from above
- Total plant leaf area
- Plant dry weight

Using image analysis software (Corel PSP and MatLab), the area of ground cover was determined from photos taken in the field just prior to each harvest. Even though this information was no longer needed for parameterising the Conductance model after rejecting that model, the data allowed assessing how the onset and development of flowering is timed relative to the points $P_1$ and $P_2$; the area occupied by flowers and leaves over time could be expressed as a function of accumulated time.

### 4.3.2 Methodology

**Field**

The methodology and results of this experiment will only include the aspects that relate to the image analysis of whole plants in the field, leading to a measure of ground cover.

This experiment was carried out at Warwick HRI (Wellesbourne) in the summer of 2005. 144 pre-germinated seeds of *S. media* and *T. inodorum* were sown in hassy trays on the 6th of June and 120 young plants were transplanted in the field on the 28th of June. Twenty individuals were dried for 48 hrs. at 80°C weighed to determine dry weight at transplanting. The 120 remaining individuals were planted as a single line in the centre of a 1.83m bed. The beds were prepared six weeks before transplanting to encourage weed seed germination and emergence. Emerged weeds were controlled with a non-selective herbicide and fertiliser was added to the beds according to normal horticultural practice. Six harvests were anticipated and therefore 20 blocks of 6 individuals were arranged as illustrated in Figure 4-5.

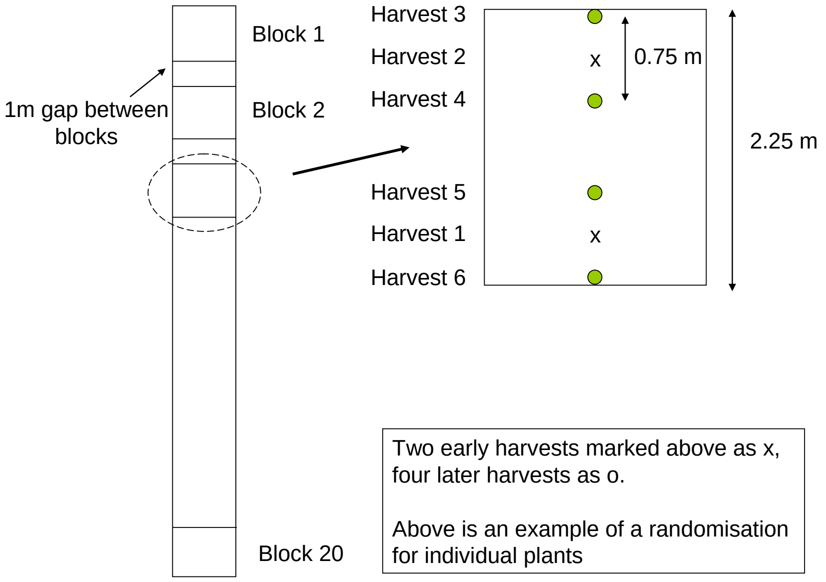


**Figure 4-5** Experimental design of the experiment initially aimed at obtaining parameters for the 'Conductance' model (Benjamin and Park, 2007).

For each block an initial randomisation determined which of the centre plants (marked x in Figure 4-5) were harvested first and second. A second randomisation determined the order in which the remaining four plants were harvested. Due to the large size of the *T. inodorum* plants at harvest 4, the randomisation was ignored and plants were harvested that would have otherwise started competing. Since the processing of leaf area took progressively longer with later harvests, the time between two harvests was more than the anticipated 14 days (see Table 4-5). It was noticed that two to three weeks after the last harvest on 29 September some leaves had been shed and many were turning brown. For that reason the 6th harvest was not carried out.

**Table 4-5** Harvest dates, age of plants (days after sowing / transplantation) and number of processed plants.

| Harvest | Harvest dates (2005) | DAS / DAT | plants harvested and processed |
|---|---|---|---|
| 1 | 19 July | 43 / 21 | 19 |
| 2 | 1 August | 57 / 35 | 20 |
| 3 | 23 August | 79 / 57 | 10 |
| 4 | 12 September | 99 / 77 | 10 |
| 5 | 29 September | 116 / 94 | 8 |

Images from which groundcover and crown zone area were to be determined, were captured immediately before harvest using a Nikon Coolpix 995 camera held vertically above the plants. A label of known size identifying the plant was included in the image. Prior to taking the image, branches of neighbouring plants were gently pushed aside and newly emerged weeds were removed. If necessary, overexposure of the label and strong shading due to sunlight was prevented by blocking the sunlight using a white cotton sheet.

### Image analysis

In Corel PaintShop Pro the images were analysed and the following characteristics determined: image length and height (pixels), length of the label in pixels. Given that the actual length of the additional object in the image was known, the actual total area of the image could be simply deduced and was included in the name of the image. Crown zone area (in pixels) was calculated by determining the radius of the smallest possible circle that covered the plant in the image in Corel PSP. To determine plant ground cover, first the background was homogenised with the ‘Clone’ tool in Corel PSP. Then the image was split into its Red, Green and Blue channels and the Red Channel selected for further analysis. The Red rather than the Blue or Green channel is chosen since this allows the best segmentation of the whole flower, i.e. white rays and yellow centres against both the green leaves and the soil back ground. By manually shifting the threshold level and observing the resulting black and white image, a ‘flower threshold’ level was chosen for each image. For each harvest the threshold values were saved as an input-file to MatLab.

The next step was to read the images into MatLab and apply specific functions pertaining to the Image Analysis Toolbox from the same program. The original code was written by and obtained from Preben Klarskov Hansen (Flakkebjerg, Denmark) and was adapted to account for and calculate the area that was covered by flowers.

To determine ‘plant ground cover’, ‘flower area’ and ‘leaf area’ in MatLab, the image analysis procedure took the following steps (see Appendix 2):

1. In MatLab, after splitting the image into its Red, Green and Blue channels, the ‘Red Channel’ image was converted to BW based on a threshold level that was determined in Corel PSP. Experience showed that this threshold level was too variable to be calculated automatically in MatLab as was done later on to segment leaves from background. This results in images with white flowers (white petals + yellow centres) and black background (leaves + soil)
2. The number of white pixels is calculated and expressed as a proportion of the total number of pixels. From the actual total area calculated earlier the actual flower area is determined using this proportion.
3. A new image is created from the RGB channels according to the excessive green parameter: ExcessiveGreen = 2 * Green – Red – Blue (Woebbecke *et al.*, 1995); this colour index is computationally simple and gives good results in distinguishing (green) plants from a non-plant background.
4. For the newly created image a threshold level is calculated using Otsu’s method (Otsu, 1979), this threshold level is used to separate foreground and background pixels and thus create a binary black-and-white image. Comparison of the resulting BW images with the originals showed that the calculated threshold levels systematically underestimated leaf area; therefore the threshold level was multiplied with a scaler, the value of which was empirically determined. The white pixels comprise all leave parts but also the yellow centres of the flowers; this image is referred to as ‘incomplete plant groundcover’.
5. To obtain ‘total plant ground cover’, the images containing ‘floral area’ and ‘incomplete plant groundcover’ were combined (i.e. in the resulting image a pixel was white if it was white in either one, or both images).
6. To obtain ‘leaf area’, the BW ‘flower area’ image is subtracted from the BW ‘total plant ground cover’ image; in a BW image, white pixels have the value 1 and black pixels 0, therefore subtracting the flower area from the total plant area results in white pixels constituting flower area becoming black (1-1), white pixels constituting leaf area remaining white (1-0) and black pixels (background) remaining black (0-0).

The image analysis process as described above is visualised in the 4 graphs in Figure 4-6.

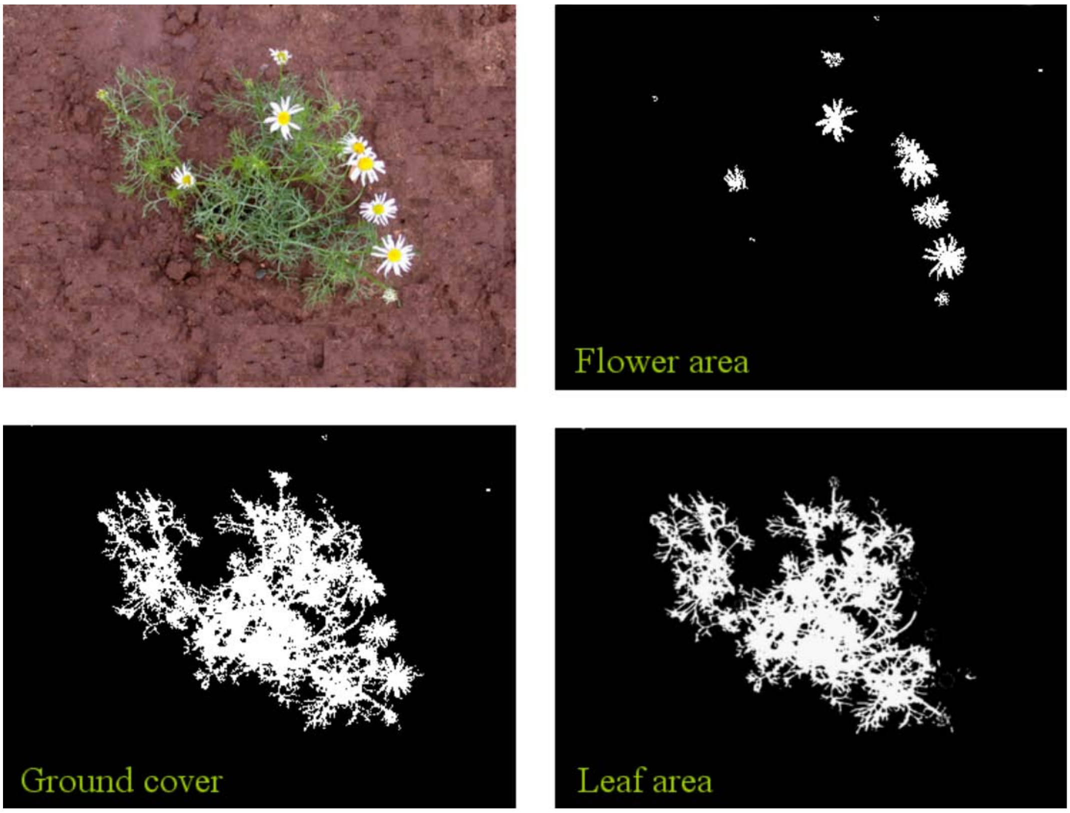


**Figure 4-6** Resulting BW images after manipulation of the original RGB image of a *T. inodorum* plant at Harvest 2 (top left) in MatLab using the Image Analysis Toolbox. The ‘Leaf area’ picture (bottom right) is produced by subtracting the ‘Flower area’ (top right) from the ‘Ground cover’ image (bottom left).

## Data analysis

The Beta distribution function was suggested by Yin *et al.* (2003) as an alternative sigmoid growth curve to other sigmoid functions such as the Richards, Weibull and Gompertz functions. The simplicity of this function, the lack of asymptotes and the biological meaning of the parameters makes this a more appealing function than the Richards function and other sigmoid growth functions. Assuming growth, W, is simulated from the start of growth (W = 0 and t = 0) the Beta distribution is written as:

**Equation 4-4**

$$W = W_{max}\left(1+\frac{t_e - t}{t_e - t_m}\right)\left(\frac{t}{t_e}\right)^{\frac{t_e}{t_e - t_m}} \text{ with } 0 \le t_m < t_e$$

where $w_{max}$ is the maximum biomass that is reached at $t_e$. The maximum growth rate occurs at $t_m$, which is equivalent to the X-coordinate of point $P_2$ in the Richards function. Like other sigmoid growth functions, the Beta distribution can take on different shapes determined by the position of $t_m$ relative to $t_e$. However, in the form proposed by Yin *et al.* (2003) it does not have the same properties as ‘true’ sigmoid curves such as the Richards function. If the Beta distribution is right-skewed ($t_m$<0.5*$t_s$) then the growth acceleration curve (second derivative) has just one maximum ($P_1$) which mathematically speaking is located prior to emergence (see Figure 4-7), which is unrealistic. If the Beta distribution is symmetric ($t_m$=0.5*$t_s$) then the growth acceleration curve (second derivative) is a linearly declining line and contains neither a minimum nor maximum. Only if biomass growth is left-skewed ($t_m$>0.5*$t_s$) can point $P_1$ be defined (see Figure 4-7). Regardless of the location of $t_m$, the second derivative always lacks a minimum over the sigmoid growth part and the Beta distribution as proposed by Yin *et al.* (2003) therefore does not define $P_3$. For the purpose of this analysis it is just point $P_1$ and point $P_2$ that are of interest. The Beta distribution was fitted to the biomass data as a function of effective day-degrees (EDD) from transplanting using the species-specific parameters specified by Storkey (2004) to check the position of $t_m$ relative to $t_e$. If $t_m \leq 0.5*t_e$, then a Beta distribution was not capable of defining point $P_1$ and a Richards growth curve should be fitted to the data. Point $P_1$ and $P_2$ can be calculated by finding the intersection with the X-axis of the second and third derivatives respectively using the formulas given by Yin *et al.* (2003) for the Beta distribution and by Gregorczyk (1998) for the Richards function.

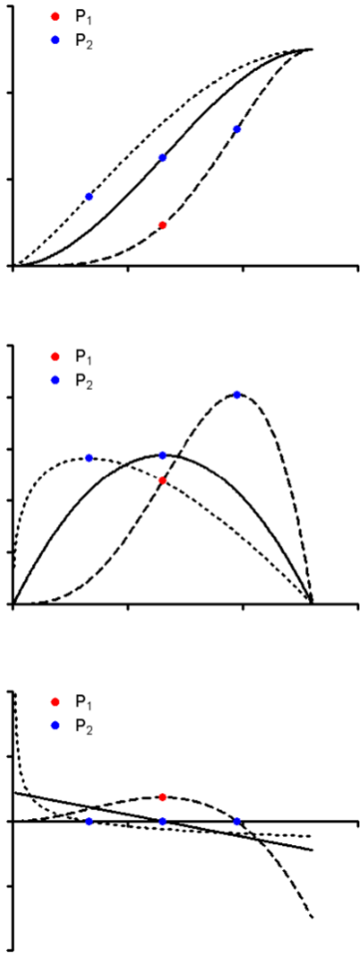


**Figure 4-7** From the top down: Beta distributions and their 1st and 2nd derivatives. Dotted, solid and dashed lines represent Beta distributions (see Equation 4-4) with $T_m$=0.25*$T_e$, $T_m$=0.50*$T_e$ and $T_m$=0.75*$T_e$ respectively. Points $P_1$ and $P_2$ represent maximum growth acceleration and maximum growth rate respectively.

Flowering did not start immediately after transplanting ($t_s \neq 0$) and to model flowering area as a function of EDD, the $t_s$ parameter has to be included in the Beta distribution. With the starting parameter, $t_s$, the Beta distribution for flower area is now written as:

**Equation 4-5** $$Fa = a - Fa_{max}\left(1+\frac{t_e - t}{t_e - t_m}\right)\left(\frac{t - t_s}{t_e - t_s}\right)^{\frac{t_e - t_s}{t_e - t_m}} \text{ with } 0 \leq t_m < t_e$$

where Fa is the area covered by flowers as calculated in MatLab. Without constraining any parameters, the Beta distribution predicted that onset of flowering ($t_s$) occurred prior to the first harvest whereas in fact no plants were flowering and only at the time of the second harvest 14 out of 20 of the sampled plants had started flowering. From the images it was estimated that the day on which 50% of the population had initiated flowering was one to two days prior to the second harvest and therefore, $t_s$ was constrained as (not being allowed to go below) the effective day-degrees accumulated until two days before the 2nd harvest. Points $P_1$ and $P_2$ were calculated as for the Beta distribution fitted to biomass increase. To compare the shape of the fitted Beta distributions for biomass and flowering area, the symmetry of both functions was calculated as:

**Equation 4-6** $$s_{Beta} = \frac{t_m - t_s}{t_e - t_s}$$

with $t_s$ being zero for the Beta distribution for biomass increase.

### 4.3.3 Results

Unfortunately the stock population of *S. media* that was used in this study had an atypical reproductive strategy compared to individuals of the natural population that were observed in the trial area. For no apparent reason the majority of the *S. media* plants grown in this trial did not flower at all which was in stark contrast with ‘background’ weeds that flowered within 5 weeks after emergence. Therefore only data for *T. inodorum* is presented here.

The parameter values for the Beta distribution that gave the best fit ($R^2 = 0.88$) to biomass as a function of accumulated effective day-degrees (EDD) were:

$W_{max} = 416.5$, $t_e = 1314$ and $t_m = (P_2) = 1003$.

The estimated (average) maximimum weight for plants was only 8% higher than the average weight at harvest 5 and would have been reached exactly two weeks after harvest 5. This seems plausible given that around two weeks after harvest 5 the plants had started senescing which was the primary reason why the 6th harvest was not carried out. The symmetry of the Beta distribution for growth was 0.76 and this allowed point $P_1$ to be defined using the Beta distribution. For the above written combination of parameter values, point $P_{1,}$ the time when growth acceleration was maximal, was at 692 EDD after transplanting (see orange diamond in Figure 4-8).

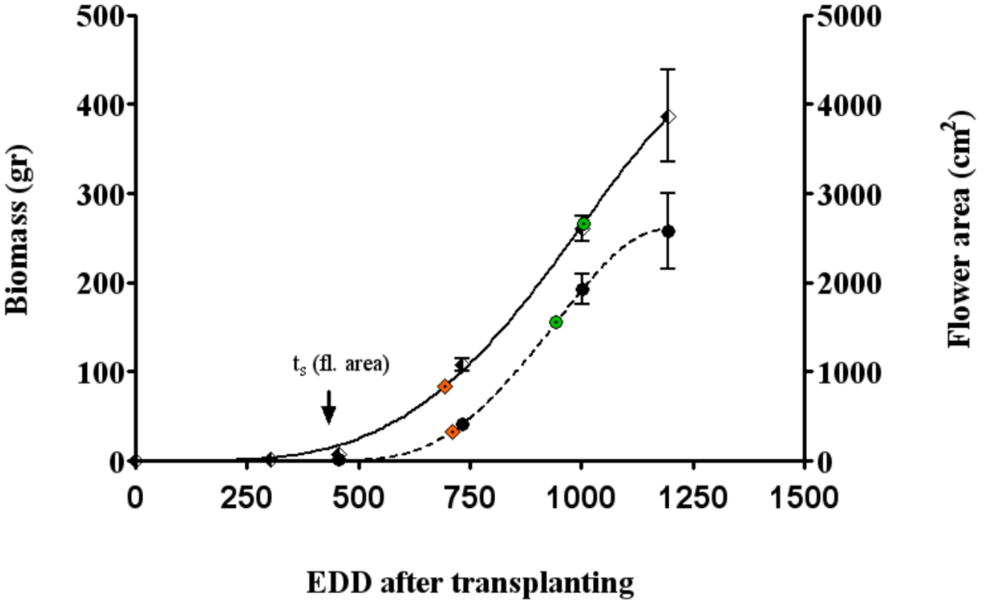


**Figure 4-8** Biomass (solid line and semi-filled diamonds, plotted on left Y-axis) and 'Flower area' (dashed line and filled circles, plotted on right Y-axis) of *T. inodorum* after transplanting to the field on the 28th of June. Fitted lines are Beta distributions. The black arrow indicates the estimated time with 50% of plants flowering. The orange filled diamonds indicate the timing of acceleration ($P_1$) and the green circles indicate maximum growth ($P_2$). Error bars represent SEM.

The estimated time of 50% flowering was at 432.5 EDD after transplanting. At the third harvest all harvested plants had produced flowers. Inspection of the images showed that flowering continued until the 5th harvest and beyond. The parameter values (with $t_s$ constrained at 432.5) for the Beta distribution that gave the best fit ($R^2 = 0.80$) to flower area as a function of accumulated effective day-degrees (EDD) were: $Fa_{max} = 2586$, $t_e = 1178$ and $t_m = (P_2) = 943.3$,

giving an $s_{Beta}$ of 0.69. For the above written combination of parameter values, point $P_{1,}$ the time when the acceleration of flower area was maximal, was at 709 EDD after transplanting (see orange diamond in Figure 4-8). Hence, first flowering occurred well before (21 days) maximum acceleration of growth. The growth rate of flowering area peaked ($P_2$) earlier than that of biomass. In contrast, there was a close agreement (1 day difference) between the estimated timing of maximal acceleration of growth ($P_1$) of biomass and flowering area.

### 4.3.4 Discussion

Fitting a Beta distribution to the experimental data for *T. inodorum* does not confirm Gregorczyk's (1998) observation that first flowering occurs at the time of maximal acceleration of biomass. The acceleration of biomass reached a maximum 21 days after the initiation of flowering and this was unexpected since flowers are thought to contribute less to photosynthesis than leaves and over time the flowers bar the light from reaching the leaf layer underneath. Investing in reproductive structures therefore 'should' reduce growth rate. In contrast, it appeared that maximal acceleration of biomass coincided with maximal acceleration of flowering.

It should be noted that these plants grew isolated and reached gigantic proportions; by the time of the 5th harvest the total ground cover of the largest individual exceeded 1.6 $m^2$ (dry weight = 619 gr.). As will be shown in Section 4.4 and 4.5, in general larger plants flower longer than smaller plants and as a consequence of that reach their maximal reproductive output later. For smaller plants the absolute amount of time between flowering and reaching the maximum acceleration of growth is therefore limited.

The temporal distribution of flowering can result in symmetrical, left-skewed or right-skewed flowering curves (Thomson, 1980; Malo, 2002) but inevitably the number of newly produced flowers levels off to zero after a peak. Estimates of flower area are not cumulative unlike cumulative frequency distribution of flowers over time. The flower area consists for a large part of the white petals that shrivel up and fall off before all seeds on the seed head have matured. The flower area of a plant therefore decreases before plants cease accumulating biomass. Overlapping flowers and the less-than-horizontal position of flowers at the time of image capture are other factors that contribute to flower area being only a relative estimate of reproductive potential. This probably accounts for the fact that the maximum growth rate ($P_2$) of flower area occurred earlier than the maximum growth rate ($P_2$) of biomass.

Ideally measurements on plant biomass and flower area would have been carried out more frequently to obtain a more precise estimate of the parameters. The symmetry values reported in this study should be regarded with caution as they are dependent on the fitted values of a non-ideal dataset. Perhaps values higher than 0.5 may have been caused by a delay in plant growth after transplanting.

# 4.4 *Towards a dynamic biomass - seed production relationship (Part I)*

## 4.4.1 Introduction

Most of the early approaches to weed population dynamics models kept track of the population density in units of individuals rather than, or as well as, plant biomass (Cousens and Mortimer, 1995; Holst *et al.*, 2007). To estimate the seed return to the seed bank the average number of produced viable seeds / plant is then multiplied with the number of surviving plants.

The problem is that, without taking into consideration plant size (biomass), estimates of seed production can be out by a large factor. Different times of emergence lead to large size differences that are reflected by large differences in seed potential as has been observed in many studies (Fernandez Quintanilla *et al.*, 1986; Sattin *et al.*, 1992; Bello *et al.*, 2000). Average weed seed production per plant varied between five and fifteen-fold for different crops, reflecting the differences in crop competitiveness (Lutman, 2002; Steinmaus and Norris, 2002).

Seed production of an individual plant may vary hugely within the same crop, site and year; for *Chenopodium album* in cabbage, seed production varied by a factor 35 (Grundy *et al.*, 2004), for *Sinapis arvensis* in wheat it varied by a factor 300 (Lutman, 2002) and for *Tripleurospermum inodorum* in wheat it varied by a factor 1000 (Lutman, 2002). This variation may be attributed to (local) variation in the crop and/or weed density, patches of high nutrient availability or genetic make-up.

The variation in reproductive output is largely a reflection of the underlying variation in plant biomass. Hence, accurate prediction of seed production requires accurate prediction of plant biomass.

Most attempts to relate biomass to seed production follow the function $Y = aX^b + c$, where X is plant weight, Y is reproductive structures, and a, b and c are parameters;

- ‘a’ represents the number of seeds per unit biomass (steepness of slope)
- ‘b’ determines if reproductive output is size-dependent (linearity of function), values lower than 1 indicate that large plants produce relatively fewer seeds per unit biomass than small plants
- ‘c’ indicates presence of a minimum size for reproduction

The function can be simplified to Y = aX by assuming there is no minimum size for reproduction (c=0) which was argued for by Rees and Crawley (1989) and that reproductive output is size-dependent in an approximate linear fashion (b=1) as was suggested previously (Samson and Werk, 1986; Weiner, 1988). A large body of studies (Debaeke, 1988b; Wilson *et al.*, 1988; Thompson *et al.*, 1991; Wright, 1993; Lintell Smith *et al.*, 1999; Schnieders, 1999; Baumann *et al.*, 2001; Lutman, 2002; Mertens and Jansen, 2002; Grundy *et al.*, 2004) supports the latter notion.

However, there are two factors that make it likely that the parameter a, the number of mature seed(head)s per unit biomass, is not constant but a function of plant age:

1. initially all photosynthate is allocated to vegetative structures and the proportional allocation of photosynthate to reproductive structures only maximises at the end of a plant’s life cycle
2. a lag phase exists between flower production and seed maturation

The current static [biomass – seed number] relationships that are derived from long-maturing crops may therefore result in a considerable overestimation of seeds for later emerged weeds or in the case of earlier maturing crops / varieties. Since the currently built model is dynamic it requires a seed production component that accounts for the age of the plant.

Within the DEFRA project of which this Phd is a part, a joint experiment was set up with Paul Neve to explore the effect of variation in the emergence times of crop and weed on size hierarchy and crop yield. The design of this experiment allowed establishment of the biomass – seed production relationship of plants that had accumulated different amounts of thermal time as it included early established weeds versus late established weeds that were to be harvested at the same time. The specific aim of the experiment was to find a meaningful way of accounting for seed production per unit biomass over time rather than just at crop harvest.

### 4.4.2 Methodology

The experiment was conducted in the spring-summer season of 2005. Prior to establishment, soil was regularly cultivated to stimulate weed emergence and emerged seedlings were controlled with herbicide to reduce weed emergence from the natural seed bank over the course of the experiment. Prior to seedbed preparation, the area was fertilised at a rate identical to that used for field beds. Irrigation lines were put in place and irrigiation was supplied when required.

#### Experimental design

The experiment was conducted on a 5.5 x 20m plot of land as a randomised block design with the following treatments:

| | |
|---|---|
| 1 x crop monoculture | Carrot |
| 2 x Interactions: | Carrot vs S.media<br>Carrot vs T. inodorum |
| 4 x Relative establishment times: | Early weed (single weed cohort)<br>Early weed (5 weed cohorts)<br>Early carrot (single weed cohort)<br>Early carrot (5 weed cohort) |
| 4 x Harvest intervals | |
| 3 x Replicates | |

96 PLOTS (crop-weed competition) + 12 PLOTS (crop monoculture)

Individual plots were 50 x 50 cm. and each of the 96 crop-weed competition plots consisted of alternating rows of crop and weed spaced 5 cm. from each other (see Figure 4-9).

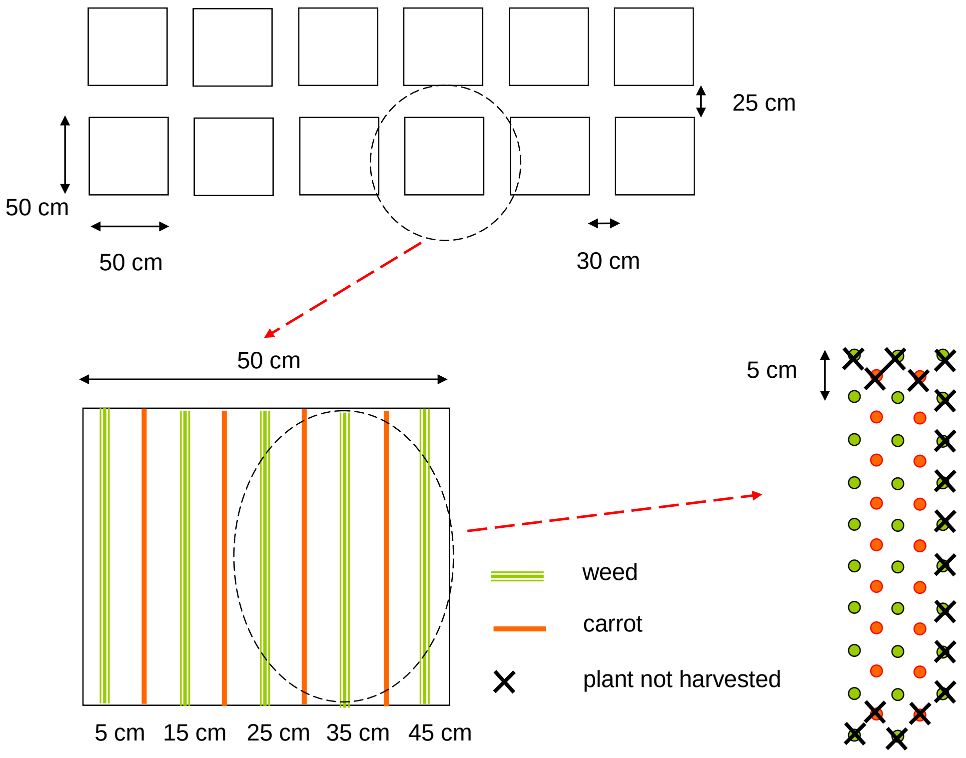


**Figure 4-9** Plot size of carrot-weed competition experiment and transplanting pattern of carrot and weed plants within plots. In multi-cohort plots the position of different-aged weeds was randomly allocated.

All crop (carrot cv. Nerac) and weed (*S. media / T. inodorum*) individuals were established as transplants previously raised under glass and hardened off for a period prior to field transplanting. The four relative emergence time treatments were simulated by sowing appropriate mixtures of even-aged individuals or of mixtures of cohorts of various ages (see Table 4-6). In all plots the carrot crop was the same age/size and was transplanted to the field 21 days after sowing (DAS) pre-germinated seed into Hassy trays. Weeds of each cohort were sown at appropriate times to acquire the right age at the time of transplanting to the field (28th of June) (see Table 4-6). Plots and surrounding area were weeded frequently to avoid background weeds competing with either or both of the target weeds and/or carrot.

**Table 4-6** Treatments, age at transplanting and relative density of weeds in multi-cohort plots

| Plants | Cohort | Age at transplanting (28th of June) | Relative density |
|---|---|---|---|
| Carrot | -- | 21 | -- |
| | | | |
| Early – single cohort | E3 | 28 | -- |
| Early – multi-cohort | E1 | 35 | 1.5 |
| | E2 | 31 | 2.5 |
| | E3 | 28 | 4 |
| | E4 | 25 | 2.5 |
| | E5 | 21 | 1.5 |
| Late – single cohort | L3 | 14 | -- |
| Late – multi-cohort | L1 | 21 | 1.5 |
| | L2 | 18 | 2.5 |
| | L3 | 14 | 4 |
| | L4 | 12 | 2.5 |
| | L5 | 10 | 1.5 |

## Harvest and measurements

The four harvests took place on 13 July, the 5 August, the 31 August and the 21 September. Plants from the earliest cohorts just initiated flowering at the 3rd harvest but mature seeds had not yet been produced. Therefore, measurements on biomass and seed production were only taken for plants harvested on the last harvest day.

The outer rows of weed plants were not harvested, nor were the plants at each end of crop and weed rows (see Figure 4-9). Hence a total of 28 crop plants and 24 weed plants / plot were harvested.

Since most weeds will be either unrooted or cut off at crop harvest, the number of buds and flowers is irrelevant since they do not contribute to seed production. Therefore, only the number of seed capsules or mature seed heads was counted for each of the 24 weed plants in a plot. In the case of *T. inodorum* a seed head was counted

**Figure 4-10** The earliest stage of a seed head of *T. inodorum* to be counted as 'mature seed head'.

as ‘mature’ if (at least) the white ray-flowers had shrivelled up (see Figure 4-10), indicating that a proportion of the seeds were viable (Kucewicz and Hodynski, 2003).

To estimate the number of seeds / seedhead, five intact seed heads were collected from 12 randomly assigned plants in the one-cohort plots. In the multi-cohort plots, 5 seedheads were taken from 2, 3 and 5 plants of the cohorts with relative density 1.5, 2.5 and 4 respectively.

Seedheads were put individually in small paper envelopes and stored together with the plant to which they belonged. After being dried in the oven at 80 ˚C for 24 hrs., plant weight, including reproductive structures (buds, flowers and seedheads) added with the weight of the 5 seedheads that were taken off, was recorded. At a later stage the seed heads were gently broken up and a subsample selected from which the seeds were counted.

### Statistical analysis

Although the assumption of homoscedasticity (standard deviation of *y* constant for all *x*) is not met in the data, regression analysis was performed on untransformed data to provide a more intuitive representation of the effects of plant size and age on reproductive output. Regression analysis of the number of mature seedheads against biomass was performed for each of the four datasets using the extra-sum-of-squares F-test (Motulsky and Christopoulos, 2004) comparing different regression models. In these comparisons, the null-hypothesis always was that the simpler model (model with one parameter less) is correct vs the alternative hypothesis that the model with the extra parameter is correct. The analysis was performed in two runs to evaluate the effect of the b (Analysis 1) and c (Analysis 2) parameters separately, resulting in four possible regression models (see Figure 4-11). The focus in this analysis was not to define the precise values of the a, b and c parameters (see Section 4.4.1) but rather to focus on the mechanisms involved in biomass – seed production relationships.

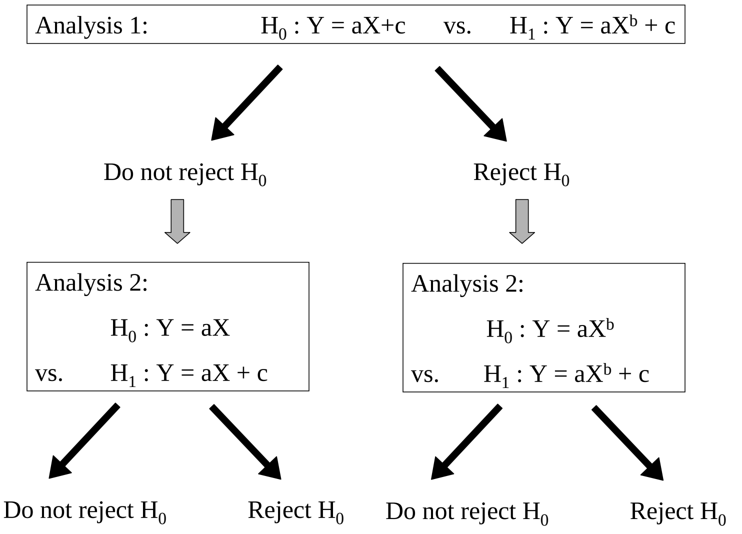


**Figure 4-11** Decision rules used to determine which regression model fitted best to each of the 4 biomass – seed production datasets.

Reproductive effort was determined for all plants (Early and Late) and expressed as a function of plant size to reveal age x size interactions in allocation patterns. It has to be noted that 'reproductive effort' has been interpreted in two different ways in biomass allocation studies (Karlsson and Méndez, 2005). One definition regards the proportion of resources invested in reproduction whereas the other definition focuses on the cost involved for the organism. Klinkhamer *et al.* (1992) argued that reproductive effort is best defined and analysed as the total biomass of seeds, R, divided by the total biomass of vegetative plant material, V. In most of the weed ecological studies an approximation of this concept is used, i.e. the total number of reproductive structures (e.g. flowers, capsules, mature seedheads or seeds) per unit total plant biomass and this approach will be adopted here as well.

### 4.4.3 Results

Unlike *T. inodorum* which is an erect species, *S. media* is prostrate and produces roots at the internodes. At the time of the 3rd harvest, *S. media* plants had become tangled into each other so much (see Figure 4-12) that it was impossible to distinguish the original plants. Trying to do so resulted in loss of branches, leaves and reproductive structures. Since the measurements had to be taken on individual plants, the decision was taken to omit *S. media* from the analysis.

**Figure 4-12** Plot with carrot and *Stellaria media;* image taken on the 10th of August.

After the seed heads of *T. inodorum* were dried in the oven, inspection showed that many of the immature seeds had shriveled up and clumped together. As a result, counting the seeds became very time-consuming and was subsequently abandoned. Rather than presenting the [biomass – seed production] results, the data will be restricted to the [biomass – # of mature seed heads] relationship. When presenting the data in this way it should be noted that some distinction is lost because the criterion ‘mature seed head’ imposed in this study, includes seed heads where all the seeds are still on the cone (viability in these seed heads is only 10-20% from fully matured seeds) up to seed heads where all the seeds had been shed. In other words, the ‘mature seed heads’ criterion tends to overestimate the reproductive output of ‘Late’ weed cohorts compared to ‘Early’ weed cohorts.

On the other hand, the onset of senescence and the concomitant shedding of leaves and reproductive structures led to a reduction in biomass at the 4th harvest (compared to 3rd harvest) for the early established cohorts. Since the weight of reproductive structures was not excluded from total plant weight, the shedding of seeds for the early cohorts will tend to overestimate the reproductive effort (# of mature seed heads / unit biomass) for ‘Early’ compared to ‘Late’ weed cohorts.

### Reproductive output in relation to plant age and plant size

Plants of the two ‘Early’ treatments had produced more mature seed heads than plants of the ‘Late’ treatments at crop harvest and this effect was disproportionally larger for larger plants (see Figure 4-13).

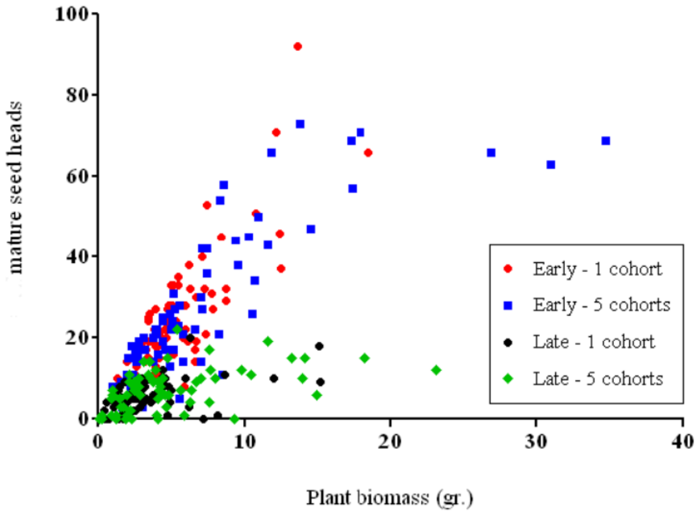


**Figure 4-13** Plant biomass – seed production relationship for *T. inodorum* plants at crop harvest; on average (‘Early’) and (‘Late’) weeds were 7 days older and younger than carrots respectively. Weed and crop plants were all transplanted and harvested on the same day.

The four datasets could not be modeled using just one regression model (see Table 4-7). The values of the parameters a, b and c are not given since they can not be compared to each other given different regression models.

If the three large plants with relatively few mature seed heads in the ‘Early – 5 cohorts’ were considered outliers (see Figure 4-12), then the simplest regression model, Y=aX is sufficient for the ‘Early’ treatments whereas the regression model with the b parameter, $Y=aX^b$ is required for the data of the ‘Late’ treatments. If the best regression model included the b parameter then the value of b was always lower than 1 indicating that in these datasets large plants at the time of sampling had produced fewer mature seed heads per unit biomass than small plants.

**Table 4-7** Results of extra sum-of-squares F-test for regression models of the biomass – mature seed heads datasets.

| | **Run 1: Reject $H_0$ ?** | **Run 2: Reject $H_0$ ?** | **Regression model** |
|---|---|---|---|
| Early (1 cohort) | No (P=0.802) | No (P=0.091) | Y=aX |
| Early (5 cohorts) | Yes (P<0.0001) | Yes (P<0.05) | $Y=aX^b+c$ |
| Early (5 cohorts, minus 3 outliers) | No (P=0.695) | No (P=0.077) | Y=aX |
| Late (1 cohort) | Yes (P<0.05) | No (P=0.277) | $Y=aX^b$ |
| Late (5 cohorts) | Yes (P<0.01) | No (P=0.333) | $Y=aX^b$ |

## Reproductive effort in relation to plant size and plant age

Plotting reproductive effort as a function of plant biomass at harvest confirms the results found above: small plants tend to have a higher reproductive effort than large plants and this effect was more pronounced for the late cohorts than for the early cohorts (see Figure 4-14). Hence reproductive effort is both size- and age dependent.

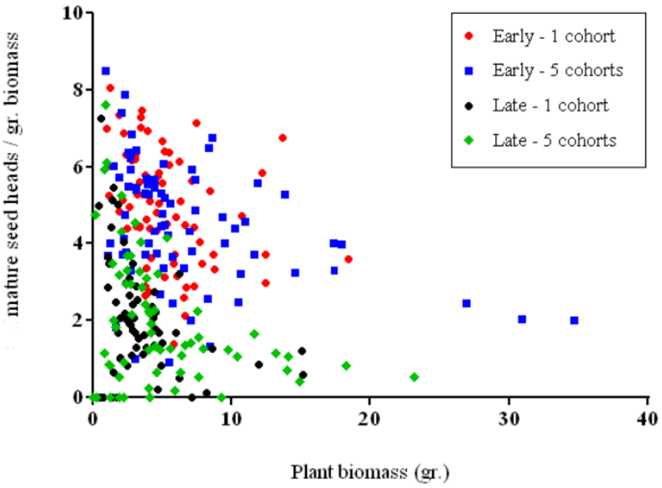


**Figure 4-14** Relationship between realized reproductive effort for 'Early' and 'Late' cohorts of *T. inodorum* and plant biomass at harvest.

### 4.4.4 Discussion and implementation

The data presented in this section suggests that small *T. inodorum* plants either start flowering earlier than late plants or that they finish flowering sooner than larger plants, i.e. have a reduced life-span. The latter option seems most plausible since plants that can acquire more resources relative to their neighbours also produce photosynthates longer and will end up larger. Either way, since the proportional allocation to reproductive structures only maximizes towards the second half of a plant's life span, it follows that the reproductive effort in large plants is lower than that of small plants unless the timing of sampling is after all plants have senesced. Indeed, during harvesting it was commonly observed that larger plants had more buds and flowers than smaller plants, regardless of age-cohort. The higher the number of weed individuals per unit area, the smaller individual plant size becomes and the faster the maximum reproductive effort is reached. For heavily infested fields, the best strategy would therefore be to shift to early maturing crop varieties.

Samson and Werk (1986) illustrated that reproductive effort is size-independent only when the y-intercept of the linear regression line of reproductive biomass as a function of vegetative biomass is zero. From a biological point of view, negative y-intercepts are obvious but positive y-intercepts are counter-intuitive since they indicate that a plant of zero weight produces seed. Positive Y-intercepts are most likely artifacts due to the incorrect assumption that the b parameter is 1 whereas in fact the b parameter in the function $Y=aX^b + c$, is lower than 1; it takes only a few scattered data points of disproportionally large plants that are still flowering to cause positive Y-intercepts.

If the data of the 'Early' treatments truly followed the model Y=aX, then the reproductive effort should be constant regardless of plant size. However, the shape of the data-cloud in Figure 4-14 reveals that reproductive effort is larger for small plants. This is characteristic of a linear biomass seed production relationship with a positive Y-intercept (c>0), i.e. plants of zero weight produce seeds (Samson and Werk, 1986). As mentioned in the methodology section, reproductive effort of 'Early' plant biomass was overestimated in that plant weight included the weight of reproductive structures but at the time of harvest many plants had already shed seeds and lost leaves due to a dry summer. Whether or not seeds had been shed, a mature seedhead was still counted as such. In reality therefore the datapoints should be shifted horizontally to the right in Figure 4-13. If small plants have lost more biomass, in absolute terms, than large plants then the Y-intercept could become negative.

The results of this experiment clearly showed that prior to full maturation, biomass – seed relationships are curvilinear and the relationship becomes linear only once the plants approached the end of the life-cycle. Over the course of flowering duration, the b parameter increases from 0 to 1. At the same time the ‘a’ parameter (slope) increases to its maximum as well. Both parameters are positively related to the age of plants after induction of flowering, but both are affected by the size-distribution of the population as well. By assuming the linearity parameter (b) is less important than the slope parameter (a), conceptually a simpler model remains (Y=aX+c) where the static biomass – seed production relationship can be made dynamic in a more simplistic way.  The minimum biomass a plant should acquire to produce one flower (or the equivalent number of seeds) is defined as the ‘hinge’ point, around which a linear regression line ‘hinges’ with the slope of the line being a function of time (see Figure 4-15).

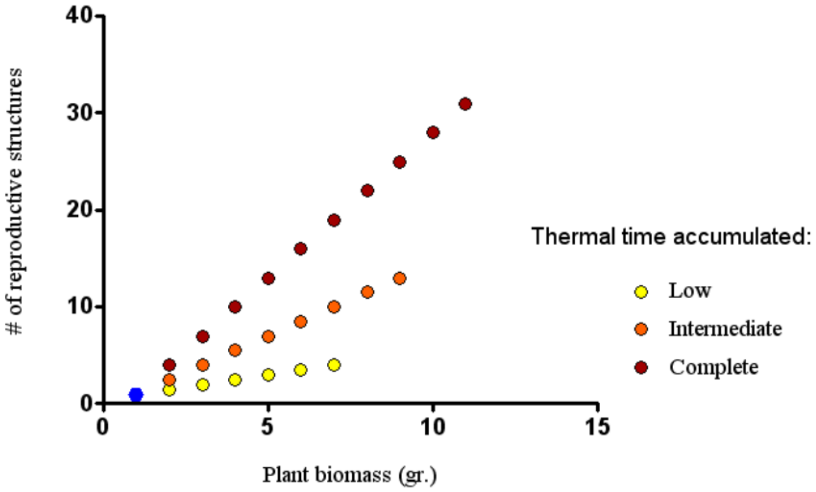


**Figure 4-15** Conceptual representation of how the biomass-seed production relationship can be made dynamic. The slope of the line is a function of accumulated thermal time, with the amount of thermal time required being a function of plant size at the initation of flowering. The blue point represents the ‘hinge’ point, that is, the minimum plant size that can support 1 flower. After producing the flower the plant does not produce any more biomass and therefore remains in the same position.

This would be an indirect way of modelling seed production over time in that flower production itself is not accounted for. However, what is still required for this ‘model’ to be implemented, is data and/or assumptions about:

- the minimum size of flowering
- the onset and end of flowering

- the rate at which the slope parameter increases from 0 to its maximum value

For a single plant, reproductive effort increases according to the ratio of the cumulative distribution of produced flowers over time vs the weight increase over the same interval. If flower production in annuals follows approximately a Gaussian distribution, then the slope parameter is a function of (thermal) time in a logistic way. Hence, the pace with which the slope parameter increases for a population of plants depends on the size-distribution within the population; if the population consists of many small plants (that are assumed to have short flower duration) then the slope parameter increases more rapidly than for a population with a few large individuals. This was indeed observed by van Acker *et al.* (1997) for *S. media* planted at two densities (see Figure 4-16). Their data also suggests that small plants have an inherently higher reproductive effort than large plants which would lead to a non-linear biomass – seed production relationship. The drop in the number of capsules per g DW for *S. media* planted at high density (in contrast with those planted at low density) also suggests that small plants finish the life-cycle earlier than large plants and therefore flower over a shorter time span.

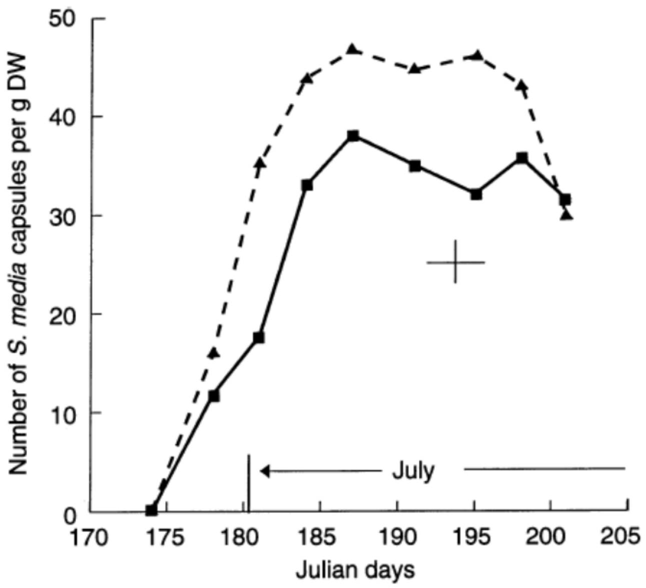


**Figure 4-16** Temporal changes of the number of *S. media* capsules per g dry weight (DW). ▲ ---▲= high density (average density = 600 plants m-2), ■ ---■ = low density (average density = 50 plants m-2). Cross hairs represent SED (figure and data after van Acker *et al.*, 1997). Note: the drop in the 'high density' data after 198 Julian days respresents the loss of capsules through abscission.

The temporal change in reproductive effort of weeds is much like the increase in harvest index (HI) in crops (Lecoeur and Sinclair, 2001) and the increase in HI can be modelled in a simple way as was shown by Soltani *et al.* (2004).

From a mechanistic modelling point of view, adopting 'empirical shortcuts' is a somewhat unsatisfactory approach. On the other hand such 'shortcuts' can be accepted in parsimonious models if their predictive potential matches the actual situation over a range of environmental conditions. However, phenological characteristics such as onset and duration of the reproductive phase are much less uniform in weeds than in crops. It is therefore better to define simple rules for processes such as biomass increase, onset and duration of flowering and how they are related. Even though these rules or assumptions may be too simplistic it is more likely to increase understanding and from an academic point of view that is of greater worth.

## *4.5 Towards a dynamic biomass - seed production relationship (Part 2)*

### 4.5.1 Introduction

The results of the experiment described in Section 4.4 led to the decision to model flowering itself rather than reproductive effort. Section 4.3 showed that the number of flowers that a plant produces during its lifetime is closely, in fact linearly, related to its final size. However, small plants seemed to realise their maximum reproductive output before large plants did. This could mean that small plants tend to flower over a shorter period or that plants that are large at the time of harvest started flowering later. The latter could be explained as that those plants exploited their relative superior competitive position by prolonging the vegetative state. The larger the physical support network (branches), the more numerous the 'photosynthesis factories' (green leaves) and the bigger the reproductive potential. On the other hand, delaying flowering is risking precocious mortality and hence unrealised reproductive output.

Cumulative flowering curves of individual plants generally follow a sigmoid shape (Hof *et al.*, 1999; Meagher and Delph, 2001) which provides the opportunity to use the Beta distribution with four parameters as applied in Equation 4-6. Since $t_{max}$ refers to the point in time where the growth rate of the relevant variable is maximal, it could be regarded as the parameter reflecting the skewness of flowering. One of the main aims of the work done in this section is to examine how $t_{max}$ can be expressed relative to $t_s$ and $t_e$. Thomson (1980) successfully showed that the skewness of flowering curves was related to the timing of flowering which is basically a mechanism to facilitate flower pollination. If skewness of the cumulative distribution of flowers in *T. inodorum* is related to plant size or to phenological characteristics such as the onset and/or duration of flowering, then $t_{max}$ ought to be made a function of this / these characteristic(s). If this is not the case then $t_{max}$ can be represented by a fixed value with the null assumption being that flowering is symmetric.

Using Equation 4-6, $t_{max}$ can be expressed as:

**Equation 4-7:** $t_{max}=s_{Beta}*(t_e-t_s)+t_s \Rightarrow t_{max}= s_{Beta}*t_e+(1-s_{Beta})*t_s$

For symmetric flowering ($s_{Beta}$=0.5), $t_m$ can be expressed as:

**Equation 4-8:** $t_{max}=0.5*(t_e-t_s)+t_s \Rightarrow t_{max}=0.5*(t_e+t_s)$

Unless emergence of weed seedlings from species that have a wide periodicity of emergence such as *S. media* and *T. inodorum* (Roberts, 1964; Chancellor, 1986) is (assumed to be) prevented by the presence of a crop, small flushes of weeds may emerge when the crop has already established. The longer the interval between crop establishment and weed emergence, the more final biomass, and therefore seed return to the seedbank, will be impaired. Baumann *et al.* (2001) showed that 90 days after crop establishment, average plant biomass / $m^2$ of *Senecio vulgaris* was reduced by 51%, 83%, 96% and 99% if *Senecio vulgaris* emerged 10, 20, 30 or 40 days after crop (leak / celery intercrop) establishment compared to simultaneous emergence of *S. vulgaris* with crop establishment. Those weeds that emerge 30 or 40 days later may not produce viable seeds if they do not reach the minimum size for reproduction or if crop harvest precedes the time required to produce viable seeds. Hence estimates of the minimum size for flowering, the onset of flowering and the interval between flowering and seed dispersal are required.

In conclusion the following research questions were proposed:

1. What is the probability of and minimum weight for flowering?
2. How is the onset of flowering distributed in the population and is it correlated with plant weight?
3. Is the duration of flowering related to plant weight?
4. Is the time to flowering dependent on the timing of establishment?
5. Can flower production over time be modelled using a symmetrical Beta distribution ($t_{max} = 0.5*(t_e+t_s)$) ?
6. Is the skewness of flowering related to plant size or to onset and/or duration of flowering?
7. How many accumulated day(-degree)s are required from first flowering to first seed shedding?

### 4.5.2 Methodology

The experiment was conducted in the spring-summer season of 2007 and was conducted as a randomised block design with the following treatments:

| | |
|---|---|
| 2 x Interactions: | Carrot vs *S. media* |
| | Carrot vs *T. inodorum* |
| 2 x Establishment times | May, June |
| 3 x Replicates | |

12 PLOTS

To answer the research questions this experiment aimed at generating a population of weeds over a range of sizes representative of a commercial vegetable field, for which phenological characteristics can be collected over the season.

Two establishment times were included: one simulataneous with and the second several weeks after crop establishment.

Prior to sowing soil was prepared as a stale seedbed in March and sprayed off with glyphosate approximately two weeks before crop sowing. The soil was irrigated because of excessive drought and then power harrowed a few days before crop sowing. Carrots cv *Nerac* were sown on the 20th of April as four triple row bands on a standard bed width (1.83 m), at an average of 75 seeds / meter giving approximately 600.000 seeds/acre. Due to drought crop emergence was irregular and occurred over a time span of 15-35 days after sowing. The plots were handweeded regularly over the course of the experiment.

Since the aim of this experiment was to generate weeds of different sizes and not to explicitly measure plant competition, individual plots comprised 1.75 m. long sections of the bed without additional space between the plots. Weed seedlings used for transplanting were acquired from and grown as described in section 4.2.2. Plots were divided in two sections: in the first 1.0 m, weeds were transplanted within the three carrot rows whereas in the remaining 0.75 m weeds were transplanted between the rows (see Figure 4-17). Weeds were transplanted at different densities both within and between the rows, to generate plants at a range of sizes within each establishment treatment. At the time of transplanting in May the seedlings were at the 4th true leaf stage, but seedlings were transplanted between the 2nd and 3rd true leaf stage in June.

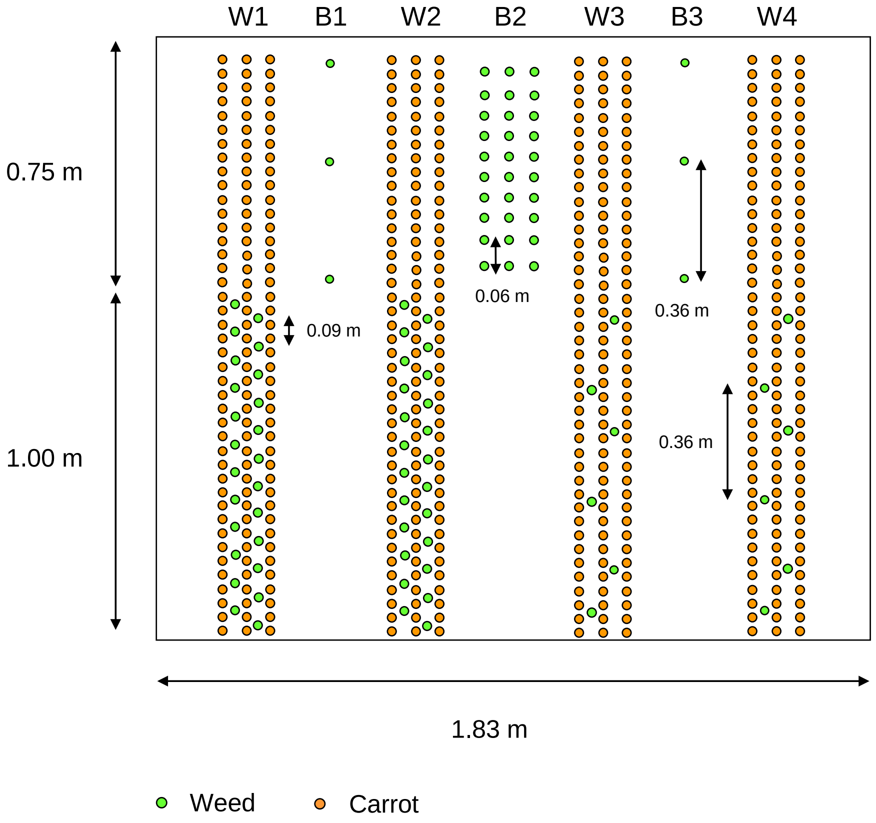


**Figure 4-17** Position and planting distance in a plot of weed seedlings transplanted in May. Carrot positions within an individual row were less regular than indicated due to irregular sowing and failed emergence. Not on scale. Letter codes indicate from left to right the various ‘Within-row’ (W) and ‘Between-row’ (B) sections of the bed in which the weed seedlings were transplanted (see Table 4-8 and 4-9).

Due to poor emergence not enough weed seedlings were available at the 2nd establishment time to create an identical transplanting pattern, therefore no weeds were transplanted within the two outer carrot triplet rows (June) (see Table 4-8) but the distance between individual plants remained the same.

**Table 4-8** The number of transplanted seedlings per experimental plot for different sections within the carrot crop (see also Figure 4-17)

| | Position on bed (B=between row, W=within row) | | | | | | |
|---|---|---|---|---|---|---|---|
| **Transplant date** | **W1** | **B1** | **W2** | **B2** | **W3** | **B3** | **W4** |
| 18 & 25 May 2007 [1] | 24 | 3 | 24 | 30 | 6 | 3 | 6 |
| 15 June 2007 | 0 | 3 | 24 | 24 | 6 | 0 | 0 |

[1] *T. inodorum* was transplanted a week later than *S. media* because of slower growth

For each of the transplanted weeds, the date of first flowering and first seed shedding was determined. The latter is easy for *T. inodorum* since the seed are attached to the receptacle in a honeycomb kind of way, so as soon as one or more seeds get dislodged and fall off the receptacle a space becomes visible. In each plot nine weeds from the within- or between-row sections were randomly allocated and labelled and the number of flowers over time was followed until no more flowers were produced (see Table 4-9). In addition, at the second establishment time, 10 weed seedlings were transplanted in the field at sufficient distance to avoid competition of each other of which two plants were selected to count the cumulative numbers of flowers over time. Plots were harvested from the 9th to the 12th of September, 142-145 days after sowing which is slightly later than the recommendation (130 days) for this carrot variety from Elsoms. For the weed seedlings transplanted in May, the number of flower buds, open flowers and seed heads was counted for 36-50 plants per replicate, including the plants within the carrot rows for which flowering over time was followed (see Table 4-9). At harvest the buds, flowers and mature seed heads were counted and then cut off the plant to avoid the overestimation of biomass for plants that had shed few seeds relative to plants of which most seeds had been shed. Four batches of in total 80 seed heads were taken to the lab to count viable number of seeds per seed head. Seed heads were gently crushed per batch and the seeds then thoroughly mixed to avoid seed samples of unrepresentative seeds. 3 batches of 100 seeds were counted and weighed and the total viable seeds determined. Seeds were counted as viable if they looked plump rather than shriveled which proved to be a good descriptor in germination experiments.

**Table 4-9** Number of transplanted weeds in May per experimental plot for different sections within the carrot crop (see also Figure 4-17) for which flowering over time was followed and for which biomass – reproduction relationship at harvest was established (numbers varied per replicate).

| | Position on bed (B=between row, W=within row) | | | | | | |
|---|---|---|---|---|---|---|---|
| | **W1** | **B1** | **W2** | **B2** | **W3** | **B3** | **W4** |
| **Flowering over time** | 1 | 1 | 1 | 3 | 1 | 1 | 1 |
| **Biomass – reproduction** | 8-12 | 2-3 | 8-12 | 9-15 | 2-4 | 2-3 | 2-3 |

Due to time constraints, duration of flowering and time from first flowering to seed shedding was only measured for the weed seedlings transplanted in May. The biomass of the seedlings transplanted in June was reduced to a great extent compared to the seedlings transplanted in May so much so that a proportion did not meet the minimum requirement for flowering. This allowed expressing the proportion of plants flowering as a logistic function (Verhulst) of plant biomass (W), to determine the minimum weight for flowering ($pr_{fl}$ = 0.99).

**Equation 4-9:** $$pr_{fl} = \frac{1}{1+e^{-k\left(W-W_{50(fl)}\right)}}$$

Where k is the slope of the logistic equation and $W_{50(fl)}$ is the weight of plants at which 50% is able to initiate flowering.

For the various analyses, dates were converted to Julian days. Data of flowering over time was expressed against accumulated effective day-degrees after the first plant that started flowering. Prior to fitting a Beta distribution, the data were modified in the following way:

- when no additional flowers were produced at the following census-day(s) the median value for accumulated effective day-degrees replaced the two or more values
- flowering was set as zero on the census-day preceding the census-day with first flowering

To test whether the distribution of flowering is symmetrical, i.e. whether plants reach $t_{max}$ halfway between $t_s$ and $t_e$, for each of the 27 plants for which flowering over time was followed, two versions of the Beta distribution were fitted to the data. In the null hypothesis model, $t_{max}$ was explicitly made a function of $t_s$ and $t_e$: $t_{max} = 0.5*(t_e+t_s)$ whereas in the alternative hypothesis model $t_{max}$ was allowed to vary. Significance was tested with the extra sum of squares F-test.

- $t_s$ was set at zero on the census-day preceding the census-day with first flowering
- $t_e$ was set as the number of accumulated effective day-degrees from $T_b$ until the last census-day for which new flowers were produced

For each plant the degree of symmetry of the fitted Beta distribution, expressed as $s_{beta}$, was then expressed as in Equation 4-6. Values for $s_{Beta}$ were tested for normality using the D'Agostino-Pearson K2 omnibus test. $s_{Beta}$ was then correlated with plant biomass, day of first flowering and duration of flowering to examine if $t_{max}$ should be made a function of other factors.

## 4.5.3 Results

As in the image-analysis trial only a few (<1%) of the transplanted *S. media* seedlings started to flower before harvesting in September and therefore only results for *T. inodorum* could be obtained.

**Probability of and minimum size for flowering**

All weed seedlings transplanted into the carrot crop in May survived and 99% of the plants produced flowers before harvest on the 8th of September. In contrast, six percent of the weed seedlings transplanted in June died and only 74% of the remaining weed seedlings flowered and before harvest in September. All of the plants that did not flower (26%), weighed less than 0.14 gram dry weight.

The absolute minimum requirement for flowering was at 0.04 gram (see Figure 4-18). The parameters of the fitted logistic equation (see Equation 4-9) were: K = 156.3, $W_{50(fl)}$ = 0.046. Hence, out of a sample of weed seedlings weighing 0.046 gram (dry weight) at harvest, half of the seedlings will flower. The dry weight at which 99% of the seedlings will flower is 0.075 gram.

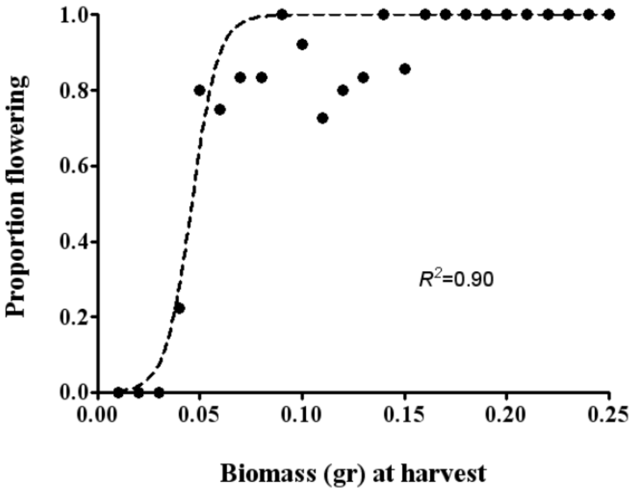


**Figure 4-18** Size-dependency of the probability of flowering for *T. inodorum* seedlings transplanted in a carrot crop in June. Line is fitted logistic function (Verhulst).

### First flowering date: distribution and relationship to plant size

The onset of flowering approximately followed a normal distribution pattern and was more right-skewed in May than in June (see Figure 4-19). The median first flowering date for *T. inodorum* plants transplanted in the carrot crop on the 25th of May and 18th of June was on Julian day 198 (17th of July) and 226 (14th of August) respectively. The time from emergence in the seedling trays until median date of flowering was 83 and 84 days respectively for the May and June transplants.

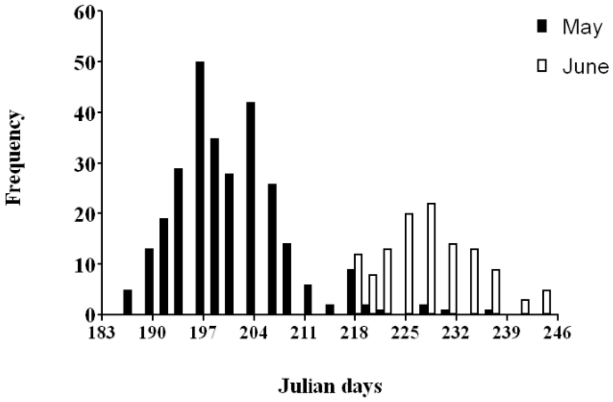


**Figure 4-19** Distribution of first flowering date for *T. inodorum* plants transplanted in a crop in May and June. In June fewer plants were transplanted in the carrot crop but the proportion of plants flowering was lower as well.

Regardless of whether plants were transplanted in the crop in May or June, no relationship was found between weed biomass at harvest and the first day of flowering; the slope of the linear regression line of biomass against Julian day was not significantly different from zero (P=0.08, May and P=0.08, June; see Figure 4-20). However, whereas each of the ten seedlings transplanted to a non-competitive environment in June had started flowering by the 13th of August, only 45% of the original number of weeds transplanted in the crop at the same time had started flowering by that day. The plants growing in isolation were considerably larger than those transplanted in the crop. Hence, both the probability and onset of

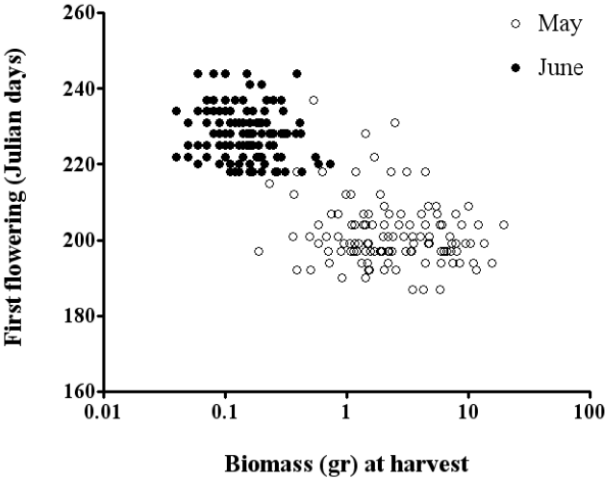


**Figure 4-20** Relationship between plant biomass at harvest (8 September) and the date of first flowering for *T. inodorum* seedlings transplanted in a carrot crop in either May or June. Note that X-axis is on log scale.

flowering are affected by the intensity of competition for resources but the effect of biomass on the onset of flowering is masked by the large individual variation independent of size.

### Duration of flowering and plant weight

The duration of flowering in *T. inodorum* was positively correlated with plant size at harvest and the correlation between the two variables was significant (P<0.005). However, only 29% of the variability in duration of flowering could be explained by plant size (Pearson r = 0.54).

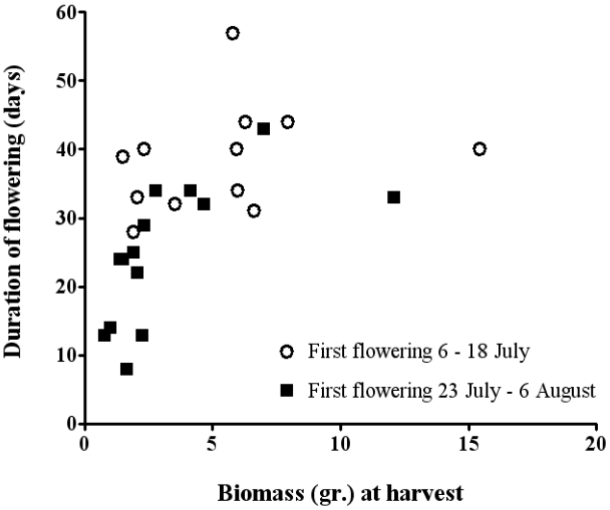


**Figure 4-21** Correlation of plant biomass at harvest, when all plants had stopped flowering, and duration of flowering for *T. inodorum* seedlings transplanted in a carrot crop around May and harvested in September.

After dividing the data into two groups based on first day of flowering there was no significant correlation for early flowering plants (n=12, P=0.38) though the correlation was significant for late flowering plants (n=14, P<0.01) – see Figure 4-21. The segmentation of the data did not consistently improve the percentage of explained variation ($r^2$ = 0.077 for early flowering plans and $r^2$ = 0.39 for late flowering plants). With such high plant to plant variability a larger number of plants would have to be monitored to get a clearer picture of the effect of first flowering date.

Unfortunately the two plants for which flowering over time was followed were accidentally removed by Horticultural Services staff in October, so information on dry weight of these plants is not available. By that time, the two plants had accumulated 621 and 581 flowers and flower duration was 79 and 95 days respectively. Including that data in Figure 4-21 would suggest a positive (non-linear) relationship between plant biomass or total flowers and flower duration is evident.

### Can flower production over time be modelled by a symmetrical Beta distribution?

Flower production over time followed a sigmoid pattern in most of the monitored plants which was more apparent for larger plants (many flowers) as compared to small plants (few flowers) (see Figure 4-22). However the duration of flowering in plants of the same size varied greatly.

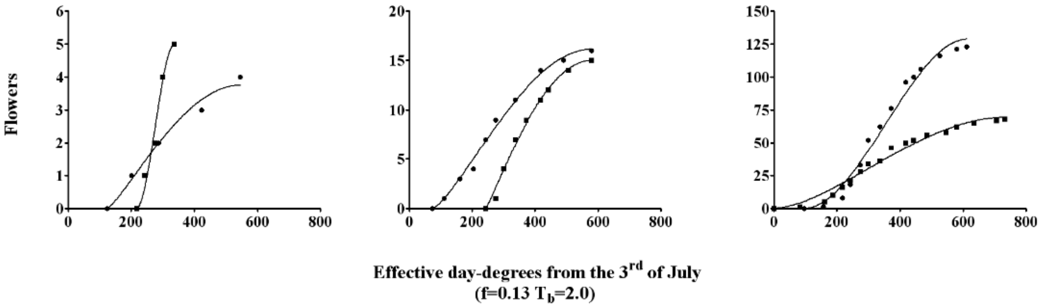


**Figure 4-22** Flowering curves, fitted with the Beta distribution, for 6 individuals of *T. inodorum*. Note that X-axis is on the same scale but Y-axis is not. Although flowering duration generally increases with plant size, large plant phenotypic variability exists in plant growth rates and consequently flower duration.

In general the Beta distribution fitted the cumulative flower counts rather well; the $R^2$ ranged from 0.926 to 0.997 with a median of 0.985.

$s_{Beta}$ varied between 0.11 and 0.65 with the mean being 0.43. Despite the frequency distribution of $s_{Beta}$ values being left-skewed, the $s_{Beta}$ values did not significantly deviate from normality (D’Agostino-Pearson Omnibus K2 = 2.17, P=0.338). No single value for $s_{Beta}$ exists that fitted all of the flowering curves. For 18 out of the 27 plants for which a Beta distribution was fitted to the flowering data over time, the null hypothesis (Beta model with $t_m = 0.5*(t_e+t_s)$) was rejected. When the null hypothesis was formulised as $t_{max} = 0.43*t_e+(1-0.43)*t_s$ (see Equation 4-7), it was rejected for 14 out of the 27 plants, indicating the high plant to plant variability and that even the best fitted value is not suitable for more than half of the population.

### Relationship between skewness of flowering and phenological characteristics

Based on the data collected in this experiment, the position of $t_m$ relative to $t_s$ and $t_e$ is not associated with final biomass or with phenological characteristics; neither the correlation between plant biomass at harvest and curve-symmetry ($S_{Beta}$) (Pearson r = 0.29; P=0.153, two-tailed), between flower duration and curve symmetry (Pearson r = 0.05; P=0.823, two-tailed) nor the correlation between first flowering date and curve-symmetry (Pearson r = -0.22; P=0.272, two-tailed) were significant. Hence, regardless of other growth characteristics $t_{max}$ can be defined as $t_{max} = 0.43*t_e+(1-0.43)*t_s$.

### Time from first flowering to first seed shedding

The time from flowering to first seed shedding was recorded for 261 plants that started flowering over the period from 6 to 31 July and started seed shedding from the 8th of August until the 4th of September. The median time from first flowering until seed shedding was about 34 days / 556 degree-days (see Figure 4-23). This is similar to the findings by Leguizamon and Roberts (1982) who found that it took between 25 and 40 days from first anthesis to dispersal of the first ripe seeds regardless of when the seedlings emerged.

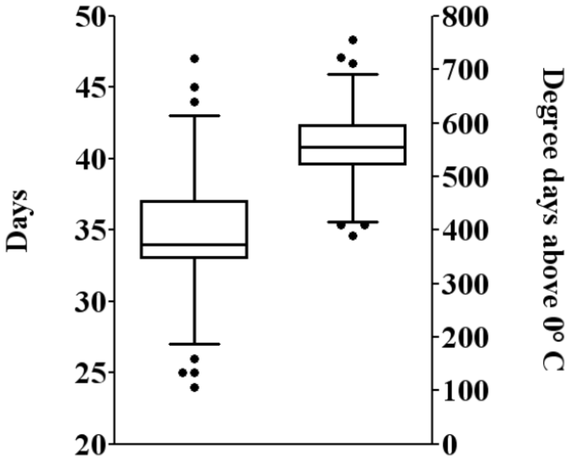


**Figure 4-23** Box-plots of number of days (left) and day-degrees (right) from first flowering until seed shedding of *T. inodorum* plants transplanted in carrot in May. Whiskers represent 1.5 times interquartile distance. Outliers are represented by black dots and are defined as those datapoints within the range 1.5-3.0 times the interquartile range, below or above the 1st or 3rd quartile respectively.

The ratio of the standard deviation relative to the median was 0.10 both if measured on a daily basis and on a degree-day basis. There was no relationship between the time of first flowering and the time from first flowering to first seed shedding (data not shown). After acquiring enough degree days to complete maturation on the plant, chance events play some part in dislodging seeds from capitula and it was observed that seeds were being retained on the capitula of some seed heads much longer than on others. Consequently, the number of days / day degrees from first flowering to seed shedding was variable as well.

## 4.5.4 Discussion

The identification of a minimum size for flowering as discussed in Section 4.4 was confirmed in this study. This emphasizes the notion that the delayed fulfillment of maximum reproductive effort by large plants relative to small plants increases the value of the Y-intercept of the linear regression of the non-transformed biomass – seed numbers data, and thus obscures the presence of a minimum weight for flowering.

The equivalent time to flowering for plants in May and June was not expected given the observations by Roberts and Feast (1974) that the vegetative period of plants that emerge later is shortened. Transplanting conditions for May and June were different (4th vs 2nd true leaf stage & 35 vs 50 days after crop sowing respectively) and perhaps this affected the switch to the reproductive phase. Blackshaw and Harker (1997) also provided evidence that the photoperiodic response to day-length is an essential feature for *T. inodorum.*

Small plants at harvest did not start flowering earlier as suggested in Section 4.4.4 as one possible explanation for small plants reaching the maximum reproductive effort earlier. Although biomass at the time of flowering could not be assessed, there is no reason to suggest that if plants had been harvested at the time of flowering, an effect of biomass on the timing of flowering would have been present. Interestingly, isolated plants transplanted to the field in June did start flowering earlier than their equivalent aged siblings transplanted in the carrot crop. Since these plants were not restricted by competition for light with the crop they had accumulated much more biomass at the time of flowering. Hence, if anything, there is a negative relationship between plant size and first flowering date rather than positive.

A positive effect was found between the duration of flowering and plant weight at harvest, the other explanation suggested in Section 4.4.4 for small plants reaching the maximum reproductive effort earlier. Similarly, Asumadu *et al.* (1998) showed a positive linear relationship between the duration from first flowering to harvest maturity and plant dry weight at harvest for soyabean cultivars. When dividing the data into two groups based on first day of flowering the effect disappeared for the early-flowering plants but not for the late-flowering plants. Perhaps the biomass range over which this was assessed was not large enough compared to the high plant-to-plant variability.

The question is if the biomass at the onset of flowering determines the duration of flowering (causation) or if both are the outcomes of the quality of the habitat (correlation). If the concept of habitat is understood as “the sum of the factors at a point in space that may affect a plant’s ability to survive and to contribute offspring to the next generation” (Cousens and Mortimer, 1995), then biomass accumulation of a weed plant is a function of the quality of a habitat. Habitats can be qualitatively poor because of low-nutrient soil conditions or because of intense competition for resources (as in crop-weed competition). Flowering stops in annual plants because resource acquisition has come to a halt and plants start to senesce. The duration of flowering is therefore most likely a reflection of the quality of the habitat.

When plants compete for resources without subsequent disturbance of the plant canopy, initial size-differences are magnified over time (Obeid *et al.*, 1967; Weiner and Solbrig, 1984). Given that only 29% of the variability in the duration of flowering could be explained by plant size it is likely that plant weight at the time of flowering is even less significant in explaining the duration of flowering. The best way therefore seems to distinguish habitats with different quality that can explain both flowering duration and final biomass.

The pattern of flowering was not symmetrical but the flowering pattern of more than half of the plants was better modeled with a different value for $s_{Beta}$ than the mean value for all plants. At the same time none of the variation of $s_{Beta}$ could be attributed to onset or duration of flowering or plant weight at harvest. This suggests that the allocation of biomass to flowers is an intrinsic trait that is regulated by the plant’s genotype.

If day-degrees is a more accurate descriptor of the time to seed shedding than days, then the standard deviation of the time measured in days should be higher than the standard deviation of the day-degrees to seed shedding. This was not the case, suggesting that either seed shedding is not so much affected by temperature but by other conditions like wind speed or that temperature within the experimental period was rather constant. Inspection of the temperature data revealed that this was indeed the case.

## 4.6 Summary of research findings

The experiments described in this chapter addressed a number of research questions that had to be clarified in order to define a holistic modelling approach for biomass increase, flowering and seed shedding. This section briefly recapitulates the objectives and the obtained results

1. **To establish the appropriate environmental conditions that drive (early) growth and to quantify the amount of this environmental variable to reach defined growth stages (1st, 2nd, 4th and 6th true leaf stages).**

   The experiments showed that the biomass increase of both weed species, *S. media* and *T. inodorum*, is better described as a response to effective day degrees, a combined estimator of temperature and solar radiation, rather than temperature alone, as was suggested by an earlier study (Storkey, 2004). Seeding weights for the 1st to 4th true leaf stage were determined from experimental results and seedling weight for 6th true leaf stage was extrapolated from data and from information in the literature.

2. **To establish how the onset and development of flowering over time is related to biomass increase.**

   Prior to the data analysis it was hypothesized that the onset of flowering would coincide with the acceleration of biomass increase. Using a novel approach to image analysis this was found not to be the case. Instead, the acceleration of growth occurred 21 days after the initiation of flowering, suggesting that shortly after flowering, the time being dependent on plant size, the allocation to reproductive biomass is not reducing the overall rate of biosynthate produced during photosynthesis.

3. **To establish how plant age at crop harvest affects the static biomass – seed production relationship.**

   A clear effect of plant age on the biomass – seed relationship was found for *T. inodorum*, confirming the findings by van Acker *et al*. (1997) for *S. media*. The results also showed a non-linear relationship between biomass and mature seedheads for the ‘young’ but not for ‘old’ plants, in other words, small plants reached maximum reproductive effort earlier than large plants. This suggested that either small plants started flowering earlier or small plants had a shorter flower duration.

### 4. To explore the onset, pattern and duration of flowering and the potential role of biomass in these phenomena

- A minimum plant weight to initiate flowering was found for *T. inodorum* suggesting that the lack of a minimum size as found in many studies is the result of a combination of the low minimum size in many annual plants and the delayed fulfillment of maximum reproductive effort of large plants.
- The onset of flowering was approximately normally distributed in the plants. There was no effect between plant size at harvest and the onset of flowering, for either the seedlings transplanted in the carrot crop in May or June. However, isolated (larger) plants transplanted to the field at the same time as the seedlings transplanted in the crop in June started flowering earlier.
- A positive effect between plant weight and the duration of flowering was found but this effect was weaker for plants that started flowering later.
- There was no difference in the time to flowering for the May and June transplanted seedlings which is contrary to what was expected according to a previous study (Roberts and Feast, 1974).
- The pattern of flowering of individual plants was not symmetrical, with the peak in flowering occurring slightly before the halfway point (0.43 instead of 0.5)
- The (a)symmetry of produced flowers over time is neither related to plant size, onset of flowering or duration of flowering but appears to be a function of plant genotype
- The time from first flowering to first shedding of seeds was 34 days and day-degrees was not a better estimator than days.

## *4.7 Implementation in ECOSEDYN*

In the concluding section of this chapter the research findings are integrated and model components presented for Biomass increase, Flowering and Seed shedding respectively. Both the mathematical representation and the parameterisation are given in this section.

Despite its shortcomings, the Beta growth function is attractive in terms of modelling plant growth and flower production. Using the Beta growth function it is easier to allow models for biomass increase, flower production and seed shedding to match in a meaningful way than using other sigmoid growth curves, due to the straightforward biological interpretation of the parameters. For example, the timing parameters can be used to implement a simple delay of seed shedding relative to flowering. The maximum value of the dependent variable of each of the three Beta distributions can also easily be related to each other since the number of seeds shed on the surface is dependent on the average number of seeds produced per flower and the number of flowers is dependent on plant size. Note that whereas in the previous sections of this chapter the notation for start, end and the timing of maximum increase of the Beta growth function were indicated by $t_s$, $t_e$ and $t_{max}$, following the original notation by Yin *et al.* (2003), in this section and in ECOSEDYN they are represented by $d_s$, $d_e$ and $d_{max}$ respectively.

## 4.7.1 Biomass increase

### 4.7.1.1 Mathematical representation

For each weed cohort of a maximum of 12 that emerge over consecutive 5 day intervals, biomass increase of a single plant within that cohort is modelled by a Beta growth function:

**Equation 4-10:**

$$W_{cum}(c,h) = W_{d_{Ws}} + W_{max-r}(c,h) * \left(1 + \frac{d_{We}(c) - d_{sim}}{d_{We}(c) - d_{W\max}(c)}\right)\left(\frac{d_{sim} - d_{Ws}(c)}{d_{We}(c) - d_{Ws}(c)}\right)^{\left(\frac{d_{We}(c) - d_{Ws}(c)}{d_{We}(c) - d_{W\max}(c)}\right)}$$

Here the parameters $d_{Ws}$, $d_{We}$, $d_{Wmax}$ reflect the start time, end time and time of maximum rate of growth of biomass relative to the simulation day, $d_{sim}$. $W_{cum}$ is the accumulated biomass as a function of the simulation day, the weed cohort (time of emergence) and the crop habitat (more or less competitive). It will be equal to $W_{max-r}(c,h)$ when $d_{sim}$ is equal to $d_{We}(c)$, i.e. when a plant of a given cohort has stopped accumulating biomass.

The start date of biomass increase for a given weed cohort, $d_{Ws}(c)$, follows from the way in which the emerged seedlings, as forecast by the autonomous 'Germination and Emergence' model, have been separated into weed cohorts (see Section 2.5.2.2 and Equation 4-28).

For summer annuals the end of biomass increase for a given weed cohort, $d_{We}(c)$, generally occurs in late autumn whereas for winter annuals it occurs in late spring. Because of their wide periodicity of emergence *S. media* and *T. inodorum* can not be identified as strict summer or winter annuals and are therefore sometimes referred to as facultative winter annuals (Håkansson, 2003). *T. inodorum* seedlings that emerge in August or later, survive as rosettes over winter with no appreciable growth until spring. It is assumed that in annual plants, the start of senescence, $d_{We}$, coincides with the end of flowering, $d_{Fe}$:

**Equation 4-11:** $d_{We}(c) = d_{Fe}(c)$

where the end of flowering is defined explicitly in the next section (see Equation 4-32). The timing of maximum rate of biomass growth for a given weed cohort is a function of $s_{Beta\_W}$ (see Equation 4-7):

**Equation 4-12:** $d_{W\max}(c) = s_{Beta\_W} * (d_{We}(c) - d_{Ws}(c)) + d_{Ws}(c)$

The final, or maximum, size that a plant can realise, $W_{max-r}$, is a function of various intrinsic and extrinsic factors. Isolated individuals of each plant species have an intrinsic maximum size above which no biomass can be accumulated, $W_{max-t}$. In photoperiodic species this intrinsic maximum size can be reduced by late emergence (e.g. Blackshaw and Harker, 1997). Extrinsic factors that regulate plant size comprise the number, size and proximity of surrounding crop and weed plants at the time of emergence and/or later stages, soil heterogeneity, weather and genotype (relative growth rate).

Since climate scenarios are included in the simulations it is relevant to incorporate the effect of environmental conditions on biomass increase / seed production. Several studies have observed the drought-sensitivity of *S. media* (van der Vegte, 1978; Sobey, 1981; Leguizamon and Roberts, 1982) and often dry summer conditions end the life-cycle. Moist conditions also favour growth of *T. inodorum* (Blackshaw and Harker, 1997) and higher yield losses have been reported in wet years as compared to dry years (Douglas *et al.*, 1991). Final plant biomass of winter emerged *T. inodorum* in a winter wheat crop in a dry year was only a third of the final plant biomass in a wet year and biomass reduction in summer annuals was reduced even more. The geographic distribution of *T. inodorum* is largely confined to the northern part of Europe (Kay, 1994; Radics *et al.*, 2004) as it is not able to maintain itself in conditions of high summer temperatures combined with low rainfall. Lutman (2002) found that a dry year resulted in a reduction of over 50% of the number of seeds / gram plant dry matter in both *S. media* and *T. inodorum*.

It is hypothesised here that there is a theoretical absolute maximum size, $W_{max-t}$, for any weed that can be reached only under ideal conditions. The ideal conditions in order of importance are:

- no competition with other plants
- ideal weather
- no reduction in the length of the vegetative growth period

More specifically in ECOSEDYN it was assumed that the realized final plant size, $W_{max-r}$, is determined by the intrinsic maximum weight, $W_{max-t}$, modified by three factors:

- the number, size, proximity and relative timing of emergence of surrounding crop and weed plants, altogether referred to as ‘habitat quality’. Habitat quality is a function of crop competitivity and crop density. Hence, for crops that are grown in rows on beds different habitats need to be distinguished. Habitat quality is also a function of crop development (weed cohort): the later a weed seedling emerges relative to the crop, the more plant growth will be restricted

- rainfall and temperature over the growing season. This varies depending on the day of crop sowing, the timing of weed emergence (weed cohort) and the weather year.
- the time of emergence

It is proposed here that suboptimal conditions in each of the three categories can diminish the maximum weight that can be attained by weed plants, $W_{max-t}$. Hence ‘biodiversity conservation coefficients’, bcc, are proposed for each of these three categories (see Table 4-10), that should represent what proportion of the maximum biomass is maintained as a function of the relevant factors.

**Table 4-10** The three ‘biodiversity conservation coefficients’ proposed to modify the maximum weight that can be obtained by weed plants, $W_{max-t}$

| **Plant size determining factors** | **Notation of biodiversity conservation coefficients** [1] |
|---|---|
| Habitat quality | $bcc_{hq}$ (c,h) |
| Rainfall and temperature | $bcc_{rf+t}$ (c,$d_{sowing}$,wy) |
| Time of emergence | $bcc_{em}$ (c,$d_{sowing}$) |

[1] Acronyms in brackets: ‘c’=cohort, ‘h’=crop habitat, ‘$d_{sowing}$’=day of crop sowing, ‘wy’=weather year

In reality (and therefore in ECOSEDYN) these constraints operate at the same time. The realized maximum plant weight, $W_{max-r}$, is therefore a function of the theoretical plant weight, $W_{max-t}$, in the following way:

**Equation 4-13:**

$$W_{max-r}\left(c, d_{sowing}, h, wy\right) = W_{max-t} * \left(bcc_{hq}\left(c, h\right) * bcc_{rf+t}\left(c, d_{sowing}, wy\right) * bcc_{em}\left(c, d_{sowing}\right)\right)$$

The fact that genotype is ignored means that no size-hierarchies can develop within weed cohorts that emerged in the same interval, i.e. all plants have the same initial growth rate and all plants are equally limited by competing plants. Although this is not exactly true, seedlings within a cohort would be spread out spatially so that competition for resources would be both within and between cohorts. It was therefore assumed that, provided the interval over which seedlings were grouped was not too large, larger size differences would develop between age-cohorts than within.

Separate sections address how the three biodiversity conservation coefficients are defined.

#### 4.7.1.1.1 Habitat quality - $\mathbf{bcc_{hq}}$

The objective is for $bcc_{hq}(c,h)$ to be able to account for differences in the relative timing of emergence of crop and weed, and for weed density. Cousens *et al.* (1987) proposed a regression model for relative crop yield loss as a function of weed density and the period between crop and weed emergence. This was formulated by Kropff and van Laar (1993) as:

**Equation 4-14:** $$RYL_c = \frac{xN_w}{\exp(yT_{cw}) + \left(\frac{x}{z}\right)N_w}$$

Here $RYL_c$ is the relative yield loss of the crop, $N_w$ is the weed density (plants $m^{-2}$), $T_{cw}$ is the relative time of emergence of crop and weed and ‘x’, ‘y’ and ‘z’ are non-linear regression coefficients. This regression model considers the relative yield loss of total crop yield for a given (fixed) crop density due to weed density and relative time of emergence of crop and weed. This principle was thought to apply to per plant weed weight as well: for a given (fixed) crop density, the relative yield loss of per plant weight of weeds is a function of weed density and time of weed emergence relative to the crop.

An Excel chart was created where the behavior of the $RYL_c$ function was examined for different combinations of parameter values. Assuming a constant plant weight, it was found that the $RYL_c$ function produces results that are fundamentally counter-intuitive for per plant weed weight as a function of weed density and relative time of emergence. This is illustrated in Figure 4-24 (left) for the Cousens function with $T_{cw} = 0$ and $T_{cw} = 15$ where the coefficients ‘x’, ‘y’ and ‘z’ had values 0.05, -0.05 and 1 respectively.

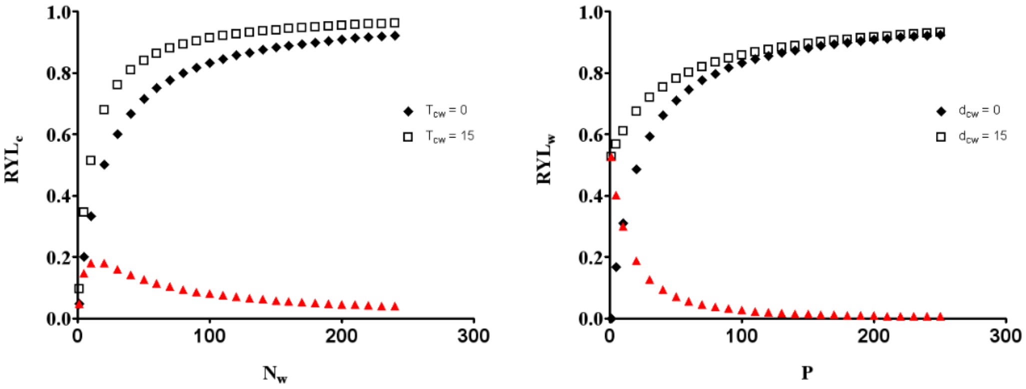


**Figure 4-24** Relative yield loss (% reduction) of per plant weight as a function of plants per m$^2$, N$_w$ / P with weed emergence at T$_{cw}$ / d$_{cw}$ = 0 (open squares) and T$_{cw}$ / d$_{cw}$ = 15 (filled diamonds). Red lines represent the difference in relative yield loss between the two curves. Left figure is result of Equation 4-14 as proposed by Cousens *et al.* (1987). Right figure is result of Equation 4-15, as proposed in this Phd research.

It is common sense to expect that a delay of weed emergence relative to the crop (T$_{cw}$=15) would result in a higher relative yield loss of per plant weight and the RYL$_c$ model confirms this. However, the RYL$_c$ model predicts that the difference between the proportion relative yield loss of per plant weight initially increases and then decreases (see red triangles in Figure 4-24) which is counter-intuitive. Each additional weed plant beyond a certain threshold density (1 m$^{-2}$ for *T. inodorum*), should be causing the average per plant weight to decrease more in a crop that establishes prior to a weed cohort than in a crop that establishes together with, or later than a weed cohort, because of reduced intraspecific competition in the latter. Therefore, one would expect to find that the density at which the difference between the relative yield loss of per plant weight for T$_{cw}$=0 and T$_{cw}$=15 is largest, is at a density of one plant and is monotonically declining towards zero beyond this density.

Given the inadequacy of the RYL$_c$ function, it was therefore used as a template to create a new function that was representative of the relative yield loss of per plant weed weight, RYL$_w$ as a function of weed density and relative timing of emergence of crop and weed:

**Equation 4-15:**

$$\mathrm{RYL} = 1 - \frac{1}{\exp(y * d_{cw}) + x * (P - P_{opt})} = \frac{\exp(y * d_{cw}) + x * (P - P_{opt}) - 1}{\exp(y * d_{cw}) + x * (P - P_{opt})}$$

where the notations of N$_w$ and T$_{cw}$ have been replaced by P and d$_{cw}$ respectively. The new RYL$_w$ equation was used to create the right chart in Figure 4-24 in which the per plant weight loss due to later emergence of the weed relative to the crop monotonously declined with weed density. With regard to the biological meaning of the parameters:

- $P_{opt}$ is the maximum plant density in the absence of plants of other species at which there is no per plant yield loss due to intraspecific competition for resources. The ‘x’ parameter is a measure of the strength of intraspecific competition; the higher the value for ‘x’, the more final plant weight is reduced with increasing weed density.
- The ‘y’ parameter indicates the sensitivity of final per plant weight due to delayed emergence of weed cohorts relative to the crop; the higher the value for ‘y’, the more final plant weight is reduced for a cohort emerging a given amount of time after the crop. This parameter is a function of the competitiveness of the crop habitat, h, since the more competitive a crop, the more impact a delay of weed emergence relative to crop emergence will have on per plant biomass.
- The ‘z’ parameter, the maximum relative yield loss per weed plant, is not included as it is assumed to be 1. It is plausible that the maximum relative yield loss for a crop is lower than one, since no grower would apply weed control to such low standards that it would result in complete crop yield loss. For weeds however, biomass reductions of up to 99% have been observed. In one year, biomass of *S. media* plants emerging 10 and 20 days after an oilseed rape crop were reduced by 86 and 98% respectively compared to those emerging with the crop (Klostermyer, 1989).
- The $d_{cw}$ parameter is not equivalent to the $T_{cw}$ in the Cousens function since in the newly proposed function, negative values for $d_{cw}$, i.e. weeds emerging prior to crop, would result in relative yield losses higher than one. The scenario with $d_{cw}$=0 therefore represents the situation in which weeds emerged so much earlier than the crop that, regardless of the weed density, final per plant weight is not further reduced by crop competition. To retain the time of emergence of the crop relative to various weed cohorts, $d_{cw}$ can be written as:

  **Equation 4-16:** $d_{cw}(c) = \mathrm{delta}_{C_s \to W_s(c)}(c) + c_{cw}$

  and

  **Equation 4-17:** $\mathrm{delta}_{C_s \to W_s(c)}(c) = d_{W_s}(c) - d_{C_s}$

i.e. if a weed cohort emerges earlier than the crop, $\text{delta}_{C_s \to W_s(c)}(c)$ becomes negative. The values for $\text{delta}_{C_s \to W_s(c)}(c)$ can be easily calculated from the day of 50% crop emergence, $d_{Cs}$ (see Section 2.5.2.2) and the median day of emergence of each crop cohort, $d_{Ws}(c)$.

$c_{cw}$ is the maximum number of days required for a weed to emerge prior to the crop without suffering additional weight loss during growth. It is likely that $c_{cw}$ is a function of the competitiveness of the crop. Since crop competitiveness is already addressed by the 'y' parameter, this additional complexity was omitted and instead it was assumed that $c_{cw}$ would be constant in both winter wheat and carrot.

It should be noted that the concepts of relative yield loss of per plant weed weight, $RYL_w$, and $bcc_{hq}$ are complimentary:

**Equation 4-18:** $$RYL_w + bcc_{hq} = 1$$

Hence, from the $RYL_w$ function, the biodiversity conservation coefficient relating to habitat quality, $bcc_{hq}$, is easily derived.

### Weed cohorts

With regard to plant density, P, in Equation 4-15, different weed cohorts should be distinguished as the size differences between plants in early and late weed cohorts can be so large that it would be incorrect to count individuals of such cohorts as equal. Hence, a weighted plant density is calculated for each habitat, $P_{wt}(h)$: for each weed cohort the average per plant weight, $W_{cum}(c)$, is divided by the average per plant weight of the weeds in the first weed cohort to emerge after crop sowing, $W_{cum}(1)$ and then multiplied with the plant density in the cohort, $P(c)$. The weighted cohort densities are then summed to obtain the overall plant density in a given crop habitat, $P_{wt}(h)$:

**Equation 4-19:** $$P_{wt}(h) = \sum_{c=1}^{c_{max}} \frac{W_{cum}(c,h)}{W_{cum}(c=1)} * P(c,h)$$

By substituting unweighted plant density, P, in Equation 4-15 for the weighted plant density in a given (crop) habitat, $P_{wt}(h)$, the function is written as:

**Equation 4-20:**
$$RYL_w(c,h) = 1 - \frac{1}{\exp(y(h) * d_{cw}(c)) + x * (P_w(h) - P_{opt})}$$

**Density dependent competition for resources**

An assumption of the newly proposed relative yield loss function of per plant biomass is that density-dependent resource competition effects operate on the weed population even at low densities, which is incorrect (see Figure 4-25).

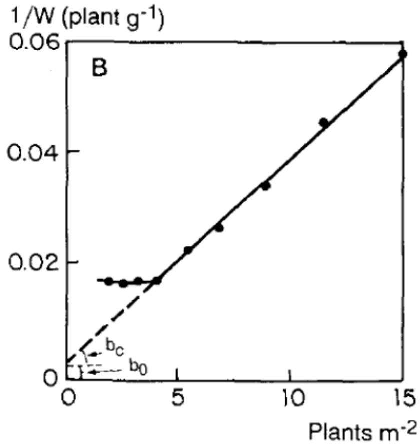


**Figure 4-25** The reciprocal per plant weight versus plant density in maize. Below five plants $m^{-2}$ the zones of influence of plants did not overlap and the maximum plant weight is density independent. Data from Spitters (1983) and figure from Kropff and van Laar (1993).

In fact, the more maximum plant (weed) weight is restricted by crop competition, the higher the minimum density is below which there are no density-dependent competition effects. The reason for this is that the zone of resource exploitation of a plant is a function of plant size. The higher the inter-specific competition with the crop the more (weed) plant size is restricted so that the so-called zones of influence of different weeds do not start to overlap whereas that would have happened in the absence of the crop. Equation 4-20 was therefore modified to include $P_{dd\text{-}th}$, the relative threshold weed density below which no density-dependent size regulation occurs:

**Equation 4-21:**
$$\text{if } P_{wt}(h) \le (P_{opt} + P_{dd-th}): RYL_w(c,h) = 1 - \frac{1}{\exp(y(h) * d_{cw}(c))}$$
$$\text{if } P_{wt}(h) > (P_{opt} + P_{dd-th}): RYL_w(c,h) = 1 - \frac{1}{\exp(y(h) * d_{cw}(c)) + x * (P_w(h) - (P_{opt} + P_{dd-th}))}$$

It should be noted that $P_{dd\text{-}th}$ is not absolute but relative to $P_{opt}$; for example, a hypothetical plant species might have a $P_{opt}$ of 5 plants $m^{-2}$ and, given a certain crop at a certain density, a $P_{dd\text{-}th}$ of 2 plants $m^{-2}$, so that in reality the absolute threshold weed density at which no density dependent size regulation occurs is 7 plants m$^{-2}$ for that particular scenario.

Arguably $P_{dd\text{-}th}$ is a reflection of the balance between intra- and interspecific competition. The more competitive the crop, the higher $P_{dd\text{-}th}$, the more competitive the weeds, the lower $P_{dd\text{-}th}$. It is therefore positively influenced by y(h) and $d_{cw}$(c) but negatively by 'x'. The threshold value would be higher if all weeds emerged in one late cohort relative to the crop, as compared to one early cohort relative to the crop. The reason is that late emergence results in weeds facing more competition from the crop, their growth rates and zones of influence being reduced and therefore the weed density at which no intraspecific plant competition occurs becoming higher. In reality, weeds are most likely to emerge as multiple cohorts and the actual threshold, assuming homogenous distribution of weed cohorts and individual plants over space, is a function of the number of weeds in each cohort.

### Scale

Since the weighted plant density, $P_{wt}$(h), expresses total plant density in terms of the number of weeds in the first weed cohort, $P_{dd\text{-}th}$ was therefore also expressed relative to the first weed cohort by using the value of $d_{cw}$ for the first cohort to emerge, $d_{cw}$(c=1):

**Equation 4-22:** $$P_{dd-th}(h) = \text{scaler} * \left( y(h) * d_{cw}(c=1) + \frac{\text{beta}}{x} \right)$$

The additional 'scaler' parameter needs to be included since the actual threshold density is completely dependent on the scale at which weed population dynamics are considered. Following Equations 4-18 and 4-21, the biomass conservation coefficient, $bcc_{hq}$(c), can then be formulated as:

**Equation 4-23:**

$$\text{if } P_w(h) \le \left(P_{opt} + P_{dd-th}(h)\right)\text{: } bcc_{hq}(c,h) = \frac{1}{\exp\left(y(h) * d_{cw}(c)\right)}$$

$$\text{if } P_w(h) > \left(P_{opt} + P_{dd-th}(h)\right)\text{: } bcc_{hq}(c,h) = \frac{1}{\exp\left(y(h) * d_{cw}(c)\right) + x * \left(P_w(h) - \left(P_{opt} + P_{dd-th}(h)\right)\right)}$$

#### 4.7.1.1.2 Rainfall and temperature – $\mathrm{bcc}_{rf+t}$

It was shown in Section 4.7.1.1 that growth for both *S. media* and *T. inodorum* is limited under hot and dry weather conditions. It is assumed that higher temperature favours growth but only if moisture conditions are sufficient, otherwise high temperature actually negatively affects growth. A simple function was sought that reflected that the higher the accumulated (effective) day-degrees over the interval over which plants grow, the larger the difference between final biomass under dry and moist conditions. The third biomass reduction coefficient, $\mathrm{bcc}_{rf+t}$, is a linear function of rainfall and temperature:

**Equation 4-24:** $$\mathrm{bcc}_{rf+t}\left(c, d_{sowing}, wy\right) = rf\left(c, d_{sowing}, wy\right) * a * X\left(c, d_{sowing}, wy\right) + b$$

where 'a' is the slope of the linear relationship, $rf\left(c, d_{sowing}, wy\right)$ represents a coefficient of rainfall for a certain weed cohort over the growth interval, varies between -1 and 1 and therefore basically modifies the slope value, 'a', to be positive, zero or negative. $X\left(c, d_{sowing}, wy\right)$ represents the accumulated effective day degrees (EDD) for a certain weed cohort over the growth interval. *b* represents the intercept with the Y-axis of the linear lines: $-a * X\left(c, d_{sowing}, wy\right) + b(rf=-1)$ and : $a * X\left(c, d_{sowing}, wy\right) + b\ (rf = 1)$. If these two lines intersect at X = 0, then the intercept with the Y-axis, *b*, is a constant, independent of rainfall. For an intersection at any point other than at X = 0, *b* is different for both lines and therefore both the slope, *a*, and intercept, *b*, would be a function of rainfall. It is assumed that if moisture is optimal (*rf*-coefficient is 1) and the number of accumulated effective day-degrees is maximal, then there is no weight reduction, i.e. $\mathrm{bcc}_{rf+t}(c) = 1$. It was further assumed that weight could be reduced by 50% in an unusually dry year compared to a year with optimum rain. Since the *rf*-coefficient ranges between -1 and 1 it can be shown that the y-coordinate ($\mathrm{bcc}_{rf+t}(c)$) of the intersection of the two lines is at 0.75 by expressing the equation as a function of the *a* parameter:

**Equation 4-25:** $$\begin{cases} \text{if } rf = -1 \quad 0.5 = -a * X\left(c, d_{sowing}, wy\right) + b \rightarrow a = \dfrac{b - 0.5}{X\left(c, d_{sowing}, wy\right)} \\ \text{if } rf = +1 \quad 1.0 = a * X\left(c, d_{sowing}, wy\right) + b \rightarrow a = \dfrac{1 - b}{X\left(c, d_{sowing}, wy\right)} \end{cases}$$

By equating the right-hand sides it follows that b=0.75. Suppose $X\left(c, d_{sowing}, wy\right)$ is expressed as the cumulative effective day-degrees over the interval from April to

September using the weather data of 17 different years. Now the potential gain (and loss) of biomass is more affected by soil moisture than by effective day-degrees (see Figure 4-26, left). If on the other hand $X(c, d_{sowing}, wy)$ is expressed as the cumulative effective day-degrees above the minimum cumulative effective day-degrees in any one year over the same period, then the sensitivity to temperature has increased but the sensitivity to moisture is zero for the year with the least accumulated day-degrees (see Figure 4-26: right).

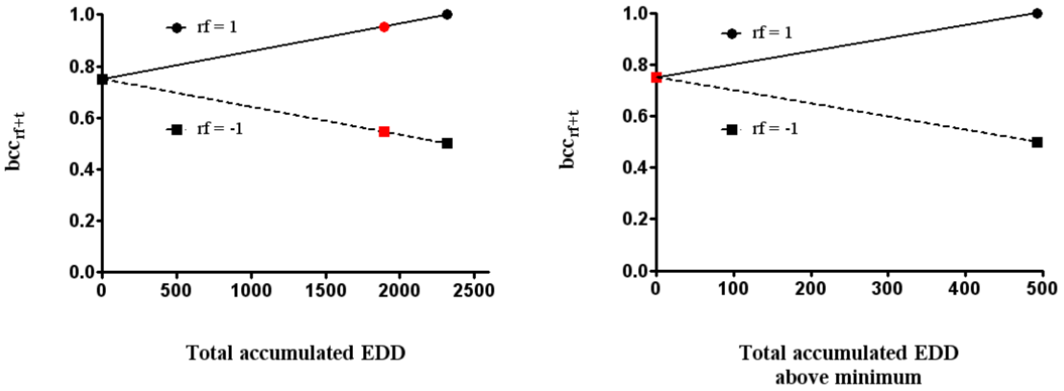


**Figure 4-26** Illustration of how the definition of $X(c,d_{sowing},wy)$ affects the sensitivity of $bcc_{rf+t}$ to temperature and soil moisture. It is assumed that the worst combination of temperature and soil moisture can reduce per plant weight by up to 50%. In the left graph $X(c,d_{sowing},wy)$ is defined as the total accumulated EDD from 1 April to 30 September. In the right graph $X(c)$ is defined as the accumulated EDD above the minimum accumulated EDD. The red points reflect the maximum and minimum value for $bcc_{rf+t}$ in the year with the least accumulated day-degrees.

Between these two alternatives the left scenario seems the most plausible and the scenario with $X(c, d_{sowing}, wy)$ expressed as effective day-degrees from the median date of emergence of a given weed cohort until harvest and a maximum reduction of biomass of 0.50 due to drought ($rf$ = -1) was therefore applied in ECOSEDYN.

#### 4.7.1.1.3 Timing of emergence - bcc$_{em}$

What is required to decide on the mathematical representation of bcc$_{em}$ is empirical data of final plant biomass of *T. inodorum* plants sown at different times of the year. In the experiment described in Section 4.4, only one planting date of *T. inodorum* was examined whereas Park *et al.* (2001) applied three planting dates. The latter study showed a trend of decreasing biomass for later sowings but data were not collected over a wide enough time frame to be able to show detailed pattern. Blackshaw and Harker (1997) measured final plant biomass for isolated individuals of *T. inodorum* sown at five different planting dates. Their data show a clear reversed sigmoid pattern (see Figure 4-27). This lead to the assumption that seedlings emerging early in spring experience no reduction in final biomass, but seedlings emerging from early May onwards experience a sigmoidal decline in the final biomass. In the absence of weed control or cultivation, the late emerging seedlings would remain as rosettes over winter and start to increase biomass again in spring. However, in ECOSEDYN all plants were set to be killed at crop harvest and final biomass is therefore an appropriate concept. Hence final biomass due to date of emergence can be described by modified logistic equations (Verhulst, 1838):

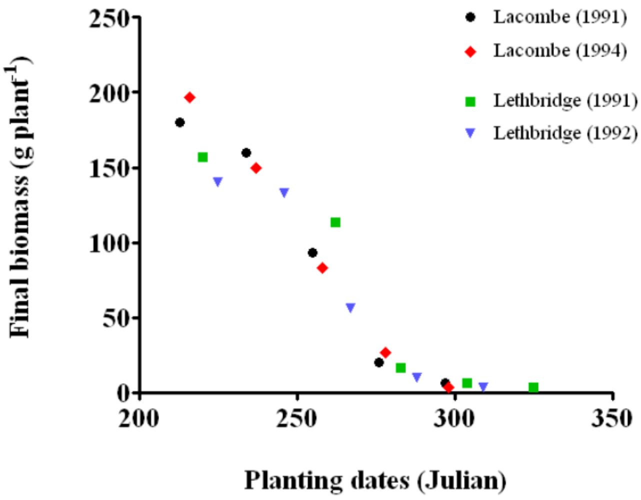


**Figure 4-27** Relationship between planting date and final biomass for *T. inodorum* plants sown between May and August at two different locations in Canada. Data from Blackshaw and Harker (1997).

**Equation 4-26:** $$W_f = W_{f-max} - \frac{W_{f\text{-}max} - W_{f-min}}{1 + e^{-k*(d_{Ws} - d_{Ws\text{-}max})}}$$

where W$_f$ is final per plant biomass and is a function of the start of biomass increase, d$_{Ws}$, i.e. the day of emergence. W$_{f\text{-}max}$ is the maximum amount of biomass that plants can possibly accumulate (upper asymptote), if emerging prior to last half of May. W$_{f\text{-}min}$ is the minimum amount of biomass that plants will accumulate (lower asymptote), k, is the slope of the downward curve and $d_{Ws\text{-}max}$ is the timing at which $W_f$ is half the value of $W_{f\text{-}max}$.

To create a function for $bcc_{em}$, the plant weight data needs to be transformed to proportional data, i.e. as a proportion of the maximum final biomass, $W_{f\text{-}max}$, where $W_{f\text{-}max} = 1$ over the interval for which day length is not limiting final biomass of plants. It was assumed that the minimum amount of biomass that plants would invest to survive winter as a rosette, $W_{f\text{-}min}$, is 1% of the maximum final biomass $W_{f\text{-}max}$. $W_{f\text{-}max}$ and $W_{f\text{-}min}$ can then be represented as 1 and 0.01 respectively. The logistic equation that is used to calculate $bcc_{em}$ for a given weed cohort in ECOSEDYN can therefore be written as:

**Equation 4-27:** $$bcc_{em}(c) = 1 - \frac{0.99}{1 + e^{-k*\left(d_{Ws}(c) - d_{Ws-max}\right)}}$$

#### 4.7.1.1.4 Early growth

So far weed cohorts are explicitly distinguished based on age, but not on size. Since post-emergence weed control success is modeled only as a function of seedling size, size categories need to be created. Given that the experimentally derived 2nd, 4th and 6th true-leaf weights of the seedlings are available (Section 4.2) for each age cohort the Beta distribution for biomass increase appears to be a suitable tool to classify the weed seedlings of a given age cohort into a true-leaf size class.

### 4.7.1.2 Parameterisation and implementation

The parameters for which a value must be found are plant starting weight, $W_{d_{W_s}}$ (Equation 4-10), starting time of biomass accumulation, $d_{Ws}$ (Equation 4-10), the Beta symmetry parameter, $s_{Beta\_W}$ (Equation 4-12), the intrinsic maximum weight, $W_{max-t}$ (Equation 4-13) and the parameters relating to the three 'biomass conservation coefficients', $bcc_{hq}$, $bcc_{rf+t}$, $bcc_{em}$, In addition the way in which seedlings were classified into 'true-leaf' stages during early growth needs to be specified.

**Plant starting weight**

The seed weight, $W_{d_{W_s}}$, was taken as the starting weight for the seedling. The value for seed weight of *S. media* (5.1 x $10^{-4}$ gr.) was taken from the Ecological Flora of the British Isles (Fitter and Peat, 1994) and that for *T. inodorum* (4.26 x $10^{-4}$ gr.) from an Oxfordshire population (Kay, 1994).

**Starting time of biomass accumulation**

For each weed cohort the Beta function was set to start accumulating biomass on the median day of the 5 day interval over which seedlings are grouped into a cohort (see Section 2.5.2.2). For the earliest possible weed cohort (c=1), the Beta function starts accumulating biomass two days after crop sowing, one of the cultural control components (see Table 2-1). For the second and following cohorts, the Beta function start accumulating biomass five days after the previous weed cohort:

**Equation 4-28:**
$$\begin{cases} \text{if } c = 1 & d_{Ws}(1) = d_{sowing} + 2 \\ \text{if } c \neq 1 & d_{Ws}(c) = d_{Ws}(c-1) + 5 \end{cases}$$

**Symmetry of Beta function**

It was assumed that the maximum rate of weed biomass growth occurs halfway ($s_{Beta\_W}$ = 0.5) during a carrot year, but three-quarters ($s_{Beta\_W}$ = 0.75) during a winter wheat year since plant growth is delayed during winter.

**Intrinsic maximum weight**

Lutman (2002) found that *T. inodorum* plants that emerged in autumn in uncropped land and did not face further plant competition reached on average 407 grams in biomass by the following summer and this value was therefore used in ECOSEDYN for $W_{max-t}$ in Equation 4-14.

#### 4.7.1.2.1 Habitat quality - $bbc_{hq}$

Because carrot and onion crops are grown in rows on 1.83 m centered beds different habitats exist. For carrots three different habitats can be identified: 'between beds (bb)', 'within bed, between rows (wb-br)' and 'within bed, within rows (wb-wr)'. The canopy closes first within the carrot rows (wb-wr), then between the rows (wb-br) but the plant canopy does not develop sufficiently to close between the beds (bb). Proximity not only affects competition for light but also competition for water and nutrients. Ranking the habitats in order of the most competitive environment gives: wb-wr > wb-br > bb.

Given that the centres of the beds are 1.83 meters from each other and the width of the tramlines between the beds is approximately 0.30 m, then on the field scale the percentage of the total habitat that is constituted by tramlines (bb) is approximately 16%. Within a carrot crop the ratio of a between-row: within-row section is about 1.0, with 4 within-row sections and 3 between-row sections (see Figure 4-28). Hence the remaining 84% was split into 36% for the between-row area and 48% for the within-row. Over time the carrots planted in rows will overgrow the between-row area and the distinction in the habitat quality is reduced.

**Figure 4-28** Carrot seed drilling using a Stanhay Singulaire 785. Seeds are drilled as triple rows in the compressed strips. Image courtesy of Paul Neve.

Onions were assumed to be sown as five equidistant rows per bed, 25 cm apart (Grundy *et al.*, 2004). Hence for onions there are two habitats, within-bed and between-bed. Winter wheat is sown in rows approximately 10 cm apart and over time a uniform crop-canopy will develop and this was therefore regarded in ECOSEDYN as one uniform habitat. The values for the parameters $P_{opt}$, x, y, $c_{cw}$ are listed below:

- Observations from the field experiment as described in Section 4.3.2 suggest that the value for $P_{opt}$ is 1 plant $m^{-2}$ for *T. inodorum*.
- The value for the 'x' parameter could be found by fitting a curve through data derived from a simple weed density experiment in which the total area is kept constant but plant density is increased. In absence of this data, the way in which the 'x' parameter can be determined is from the fact that regardless of weed density total weed biomass per square meter should remain more or less constant. The only two parameters that affect how total biomass changes over time are 'x' and $P_{opt}$. Hence, by implementing Equation 4-23 in an Excel spreadsheet model and setting $P_{opt} = 1$, the value for 'x' was determined that results in a constant total weed biomass: 'x' = 0.99. Values for 'x' below 0.99 would result in ever increasing total biomass whereas values higher than 0.99 would result in a peak at 2 plants $m^{-2}$ and a decrease thereafter.
- The larger the value for 'y', the larger the relative weight loss for the first weed plant and the lower the additional relative yield loss for each additional weed plant added to the weed density beyond $P_{dd\text{-}th}$, the threshold density for density dependent biomass regulation. Van Heemst (1985) classified carrots and onions as the least competitive of 25 crops and wheat as one of the most competitive crops. Data on the yield losses from volunteer potato, one of the most competitive weeds in both vegetable crops, suggest that onion is a less competitive crop than carrot (Williams and Boydston, 2006). The ranking for the y parameter therefore was set: winter wheat > carrot (wb-wr) > onion. Within carrot the ranking is 'between-bed' > 'within-bed, between-row' > 'within-bed, within-row'. Although the rate of crop development is dependent on the weather, the intrinsic differences of growth rate between the crops are likely to remain and for this reason the effects of weather on crop growth were not included. In addition, fast and slow maturing crop varieties were assumed to be equally competitive. There was no time available to properly parameterize 'y' for all the crops and therefore 'guestimates' had to be made based on the

reduction of weight of *T. inodorum* plants as recorded in the field experiment presented in Section 4.5. After correction for biomass reduction due to late seasonal emergence the Excel spreadsheet model was used to find the 'y' value that gave the reduction in per plant biomass that corresponded with what was observed in the June vs May transplants. The values for 'y' for the various crops / crop habitat are stored in Table 4-11.

**Table 4-11** Parameter values for the 'y(h)' parameter for the different crops and habitats; bb= between beds; wb-br = within bed, between rows; wb-wr = within bed, within rows.

| Crop | Habitat | *T. inodorum* |
|---|---|---|
| Carrot | bb | 0.028 |
| | wb-br | 0.052 |
| | wb-wr | 0.067 |
| Onion | bb | 0.028 |
| | wb | 0.043 |
| Winter wheat | wb | 0.067 |

The 'y(h)' parameter for *S. media* was set at 80% of the value of the 'y(h)' parameter for *T. inodorum* since *S. media* is known to be shade tolerant and would therefore be less sensitive to a delayed emergence relative to the crop than *T. inodorum.*

- It was assumed that the minimum number of days that weed seedlings have to emerge prior to the crop for final per plant weight of weeds not to be reduced, is 75 days (i.e. $c_{cw}$=75 in Equation 4-16).
- Since in ECOSEDYN weed population dynamics was modeled assuming a field size of 25 ha, the value for the 'scaler' in Equation 4-22 was set at 250000.

#### 4.7.1.2.2 Rainfall and temperature – $\mathbf{bcc_{rf+t}}$

Prior to a simulation run in ECOSEDYN, raw rainfall scores, rf(c,$d_{sowing}$,wy), are calculated for each of the combinations of twelve weed cohorts, eight sowing dates (carrot + winter wheat) and seventeen weather years to determine the maximum and minimum rainfall scores. The rainfall score for a certain weed cohort constitutes the average of the rainfall scores given to seven consecutive 10-day intervals. Although a weed's lifecycle is expected to stretch beyond 70 days, it was assumed that after 70 days the plant would have extended its root system to deeper soil layers, the moisture degree of which would not be affected so much by rainfall. The rainfall score for a 10-day interval is based on total accumulated rainfall over that period and, assuming that any rain beyond a cumulative of 30 mm rainfall would not deliver the plant any additional gain, is then scored as in Table 4-12.

**Table 4-12** Scores given according to the cumulative rainfall over a 10-day interval

| **Amount of cumulative rainfall** | **Score** |
|---|---|
| Cumulative rain $\leq$ 5 mm | -1.00 |
| 5 $\leq$ Cumulative rain < 10 mm | -0.66 |
| 10 $\leq$ Cumulative rain < 15 mm | -0.33 |
| 15 $\leq$ Cumulative rain < 20 mm | 0.00 |
| 20 $\leq$ Cumulative rain < 25 mm | 0.33 |
| 25 $\leq$ Cumulative rain < 30 mm | 0.66 |
| Cumulative rain $\geq$ 30 mm | 1.00 |

The first 10-day interval for which a rainfall score is calculated starts two days prior to the median day of emergence of each cohort. First the maximum and minimum rainfall score were determined over all weather years and sowing dates for carrot and winter wheat separately. Because arbitrary rainfall scores were given, the maximum and minimum rainfall scores were then shifted so that these scores were evenly balanced around zero. In other words, it is assumed that compared to an average weather year that would have a rainfall score of zero, the driest weather year is about as far from the average as the wettest weather year would have been. Raw rainfall scores in ECOSEDYN for any particular [crop-sowing date] combination were calculated as above and then scaled against the modified rainfall score for maximum rainfall. For example: suppose a weed management scenario where sowing date of carrot is the 1st of March and the assigned weather year is 1989 (i.e. actual date is 1st of March 1990). The calculated raw rainfall score for the first weed cohort is -0.6667. The maximum and minimum rainfall scores over all carrot sowing times, weather years and weed cohorts that are calculated at the start of the simulation are +0.7143 and -0.9048 respectively. The maximum range of rainfall scores is therefore 1.6190 and this can be evenly balanced around zero so that the maximum and minimum are now 0.8095 and -0.8095 respectively. The calculated raw rainfall score of -0.6667 now needs to have 0.0952 added to it (0.8095 – 0.7143) so that it becomes -0.5715. The final rainfall score for the first weed cohort (rf(1) in Equation 4-24) is now calculated by dividing the modified rainfall score by 0.8095 so that rf(1) becomes: -0.5715 / 0. 8095 = -0.7059.

To calculate the amount of thermal time that a weed plant accumulates during its life time it is necessary to estimate the harvest date first. To generate a realistic harvest date, the prevailing weather conditions both prior to and after 50% crop emergence were considered. This required a pre-modelling re-calculation of the maturity time from days to thermal time (DD or EDD). For carrot, first the day to 50% crop emergence was calculated for each of the 85 weather year – sowing time combinations using the output from the germination and emergence model (see Section 2.5.2.2). The values ranged from 8 to 54 days and the time to 50% crop emergence between years with higher than average temperatures from April to September (‘Heating up’, see Section 2.3.3) and years with lower than average temperatures were not different. Similarly there was no trend for later sowing dates to result in shorter times to 50% crop emergence although there was a trend for more variability in the time to 50% crop emergence for later sowing dates.

Commercial growers would normally make sure that the soil is irrigated to ensure rapid germination and this option is currently not implemented in the germination and emergence model. It was assumed that the maturity times (time from crop sowing to harvest) as given in Table 2-2 represent optimal conditions of germination and emergence, and that this constituted 14 days regardless of sowing time. Hence, the 14 days were subtracted from the total time from crop sowing to harvest to obtain 84, 98 and 116 days from 50% crop emergence to harvest. For each of the 17 weather years the minimum and maximum temperature and solar radiation values were used to calculate the daily effective day-degrees (EDD) from 14 days after the median sowing date (29 March) until the appropriate number of days had passed in each of the three ‘maturity times’.

Effective day-degrees were calculated as shown in Equations 4-1 and 4-2 following Scaife *et al.* (1987). The value of the parameters $T_b$ and $f$ that are required to calculate EDD were derived from Tei *et al.* (1996) for onion and from Thorup-Kristensen and van den Boogaard (1999) for the base temperature in carrot (see Table 4-13).

**Table 4-13** Parameter values to calculate the average number of effective day-degrees (EDD) required for biomass increase from 50% emergence to the harvest date.

| | Carrot | Onion | | | Carrot | Onion |
|---|---|---|---|---|---|---|
| $T_b$ | 0 ˚C | 5.9 ˚C | | f | 0.136 | 0.136 |

No data could be found for the value of the *f* parameter of carrot. Research conducted by Storkey (2004) showed that crops that can be both sown in spring and autumn (wheat, oilseed rape) have a low *f* value. Carrot is predominantly spring-sown and the value of the *f* parameter of onion was therefore assumed to be a suitable proxy. The daily values for EDD were summed over the interval for each of the 17 complete weather datasets collected on site (Warwick HRI, Wellesbourne) between 1989 and 2006 and an average value was then calculated. The average amount of EDD required from 50% crop emergence to harvest was 950, 1159 and 1438 for the early, intermediate and late maturing variety respectively.

In ECOSEDYN the harvest date of the carrot crop in any particular year and weed management scenario is determined as follows: first the day to 50% crop emergence is calculated from the output of the germination and emergence model and then using the weather data of the particular weather year assigned, the harvest date is determined by calculating on which day the required total EDD was reached, starting from the day of 50% crop emergence.

For winter wheat day degrees rather than effective day degrees were used since data of the timing of the critical period of weed competition, which is required to calculate the timing of post-emergence weed control, was only available in day degrees. First each of the maturity times (313, 320 and 327 days) was recalculated from days to day degrees (DD) from the median sowing date (19 October) for each of the 17 weather years and then averaged. The average amount of DD accumulated was 2666, 2767 and 2865 for the early, intermediate and late maturing variety respectively.

In ECOSEDYN the harvest date of winter wheat in any particular year and weed management scenario is determined by subtracting the amount of DD required to 50% crop emergence under standard conditions (150 DD) from the total. As for carrot, the weather data of the particular weather year assigned was used to determine the harvest date by calculating on which day the required total DD was reached, starting from the day of 50% crop emergence. For 6 of the 135 scenarios the harvest date of winter wheat would have exceeded the end of the simulation year (i.e. 30th of September), which the model does not allow for. In these circumstances the harvest date was set to the 30th of September.

At the start of the simulation, the value for $X_{max}$ is obtained in the following way:

1. Calculate the date with 50% crop emergence for each of the 17 weather year / sowing time combinations
2. Using the EDD values of the weed (f, $T_b$), calculate the total EDD for the earliest cohort that could possibly emerge, i.e. taking the median date of the first five days after seedbed preparation / crop sowing until 50% crop emergence
3. Calculate the harvest date of the crop with the longest crop maturity time (A_MT = 3 / V_MT = 3) for each of the 17 weather years / sowing time combinations
4. Calculate the accumulated EDD for the weed from the date of 50% crop emergence until harvest date
5. Sum the EDD values that are found in step 2 and 4 and find the maximum value for the 17 weather year / sowing time combinations. This value is referred to '$X_{max}$'.

The *a* parameter is calculated by filling in the value for $X_{max}$ in Equation 4-25: $a = 0.25/X_{max}$. For each weed management scenario, X ($c, d_{sowing}, wy$) is determined for each of the 12 weed cohorts in the way as described above for $X_{max}$.

#### 4.7.1.2.3 Timing of emergence - $\mathbf{bcc_{em}}$

Only the study in Canada by Blackshaw and Harper (1997) provided a complete dataset. The latitude at which the data from Lacombe was collected, (52°30’N), is similar to the latitude of the East Anglia region (52°N - 53°14’N) where most vegetables in the UK are grown. Hence, the Lacombe data (final plant biomass data for 1991 and 1994) were taken as a reference.

First, logistic equations (Equation 4-26) were fitted to the separate year data in GraphPad Prism to obtain the fitted value for $W_{f\text{-}max}$ (Lacombe, 1991: $R^2=0.9994$, SS=14.09; Lacombe, 1994: $R^2=0.9976$, SS=6292). During fitting $W_{f\text{-}min}$ was constrained to 1% of the average plant weight at the first sowing date but none of the other parameters were constrained. The time was expressed as a function of day number from the first of October to match simulation time in ECOSEDYN. Then the experimental data for each year were transformed to proportional data by dividing the year data by the respective fitted values for $W_{f\text{-}max}$.

The logistic equation for $bcc_{em}$ (Equation 4-27) was then fitted to the proportional data, where $W_{f\text{-}max}$ and $W_{f\text{-}min}$ were constrained as 1.0 and 0.01 respectively. The fitted parameters were: $k = 0.08198$, $d_{Ws\text{-}max} = 253$ (10th June). Given the dates at which weeds in a given cohort emerge and start accumulating biomass, $d_{Ws}(c)$, follow from the sowing date (see Equation 4-11) the $bcc_{em}$ (c) can be easily determined in ECOSEDYN. For *S. media* there is no documented effect of day-length on the maximum size of plants and thus for *S. media*: $bcc_{em}(c) = 1$.

#### 4.7.1.2.4 Early growth

For each of the three crop habitats in carrot or for the single crop habitat in winter wheat a matrix was created with 12 rows (weed age cohorts) and 5 columns (growth stages). The growth stages distinguished were:

- Cotyledon – 2nd true leaf stage ($P_1$)
- 2nd – 4th true leaf stage ($P_2$)
- 4th – 6th true leaf stage ($P_3$)
- 6th true leaf stage – flowering ($P_4$)
- flowering – senescence ($P_5$)

Initially biomass was chosen as the basis on which seedlings in the first three growth stages would be distinguished as this would be easy given the implemented Beta distribution function for ‘Biomass increase’. Prior to the real simulations, test-runs were performed to check how many days the seedlings would remain in each ‘true-leaf’ class compared to the experimental observations. It was found that the seedlings remained in each seedling stage far longer than was realistic. This implies that although the Beta distribution function is a great tool for modeling biomass increase over a season, the $s_{beta}$ value chosen may not have been accurate and therefore early growth rate was underestimated. Since there was not enough time to find a more appropriate value for $s_{beta}$, it was decided to model early growth, i.e. progression from one true-leaf stage to the next, based on the experimentally determined threshold values for EDD rather than biomass. It was decided to take the ‘Ideal growth’ EDD values as they represent the scenario in which seedling growth is least likely to be underestimated. An underestimation of growth rate would lead to seedlings remaining longer in growth stages where the weed control efficacy is higher and therefore overestimating overall seedling mortality due to weed control. Hence the values required to reach the 2nd, 4th and 6th true leaf stage of *T. inodorum* were 163.0, 247.4 and 331.8 respectively. In ECOSEDYN the daily EDD after emergence was calculated and seedlings were transferred in the matrix from one column to the next if the cumulative EDD had exceeded the relevant threshold value.

## 4.7.2 Flowering

### 4.7.2.1 Mathematical representation

The Beta function for cumulative flower production for one plant within a given weed cohort can be written as:

**Equation 4-29:** $$F_{cum} = F_{max}\left(1+\frac{d_{Fe}-d_{sim}}{d_{Fe}-d_{F\max}}\right)\left(\frac{d_{sim}-d_{Fs}}{d_{Fe}-d_{Fs}}\right)^{\left(\frac{d_{Fe}-d_{Fs}}{d_{Fe}-d_{F\max}}\right)}$$

where $F_{cum}$ is the accumulated number of flowers at a certain simulation day, $d_{sim}$ , $F_{max}$ the final number of flowers, $d_{Fs}$, $d_{Fe}$ and $d_{Fmax}$ are the parameters that define the start, end and the timing of maximum rate of flower production respectively. The Beta function for all plants in a given weed cohort and crop habitat, P(c,h) is:

**Equation 4-30:**

$$F_{cum}(c,h) = \left(P(c,h) * F_{max}(c,h)\right)\left(1+\frac{d_{Fe}(c)-d_{sim}}{d_{Fe}(c)-d_{F\max}(c)}\right)\left(\frac{d_{sim}-d_{Fs}(c)}{d_{Fe}(c)-d_{Fs}(c)}\right)^{\left(\frac{d_{Fe}(c)-d_{Fs}(c)}{d_{Fe}(c)-d_{F\max}(c)}\right)}$$

The start of flowering is independent of biomass and determined by the day of emergence plus $\mathrm{delta}_{Ws\to Fs}$ (c), the time from emergence to flowering:

**Equation 4-31:** $$d_{Fs}(c) = d_{Ws}(c) + \mathrm{delta}_{Ws\to Fs}(c)$$

$\mathrm{delta}_{Ws\to Fs}$ is either constant over the season (*S. media*) or otherwise a function of $d_{Ws}$ (*T. inodorum*) and needs to be parameterised.

Investment in reproduction is the last activity in the plant's life, therefore the end of flowering coincides with the end of biomass increase:

**Equation 4-32:** $$d_{Fe}(c) = d_{Fs}(c) + \mathrm{delta}_{Fs\to Sen}$$

Following Equation 4-7 the timing of maximum rate of flower production can be expressed as:

**Equation 4-33:** $$d_{F\max}(c) = s_{Beta\_F} * \left(d_{Fe}(c) - d_{Fs}(c)\right) + d_{Fs}(c)$$

The final number of flowers produced by all plants in a cohort, $F_{max}$(c), is a function of final plant size, $W_{max\text{-}r}$(c), which is dependent on the crop habitat. The log-log relationship between plant biomass and the number of produced flowers is represented by the linear function:

**Equation 4-34:** $\log(F_{max}(c,h)) = a_{W-F} * \log(W_{max-r}(c,h)) + b_{W-F}$

Hence, if for individual plants over a range of plant sizes data is available that includes biomass and total number of flowers produced at senescence, then from that the final number of flowers per plant can be obtained:

**Equation 4-35:** $F_{max}(c,h) = 10^{\log(F_{max}(c,h))}$

If the raw data is not available then the number of reproductive structures (flowers or seed capsules) per gram plant dry weight should be obtained. This is simply the slope parameter ‘a’ of the simplest linear regression model

**Equation 4-36:** $Y = aX$

with reproductive structures against plant dry weight (see Section 4.4.3).

#### 4.7.2.2 Parameterisation and implementation

The parameters for which a value need to be found are the time from emergence to flowering, delta$_{Ws\rightarrow F}$ (Equation 4-31), the duration of flowering, delta$_{Fs\rightarrow Sen}$ (Equation 4-32), the measure of symmetry of the Beta distribution function for flowering, s$_{beta}$ (Equation 4-33) and the slope and intercept of the log-log relationship between biomass and flower production, a$_{W-F}$ and b$_{W-F}$ (Equation 4-34).

**Time from emergence to flowering**

*T. inodorum* is a long-day plant and seedlings emerging later than the second half of July (Blackshaw and Harker, 1997) or the beginning of August (Roberts and Feast, 1974) do not flower in that year but overwinter as a rosette. Since weed germination and emergence are only assumed to happen as a consequence of seedbed preparation, the time from sowing to flowering has to be defined for the period (60 days) after carrot and winter weed seedbed preparation. However, implementing the datapoints shown in Figure 4-29 resulted in the first and last cohort of weeds to emerge after sowing on the 1st of March, to start to flower on the 12th and 24th of July respectively, which is (at least) a month later than observed in the field (during seed movement work). The literature suggests that flowering of overwintered rosettes starts in May and for seedlings emerged in spring in June at the earliest (Woo *et al.*, 1991; Kay, 1994). A modification of the Roberts and Feast (1974) data was therefore applied to prevent late flowering. Equation 4-40 represents that seedlings emerging from the 21st of April (day 203) until the end of June (day 273) will start to flower after 55 days but any seedlings emerging prior to this interval take a longer time from emergence to anthesis:

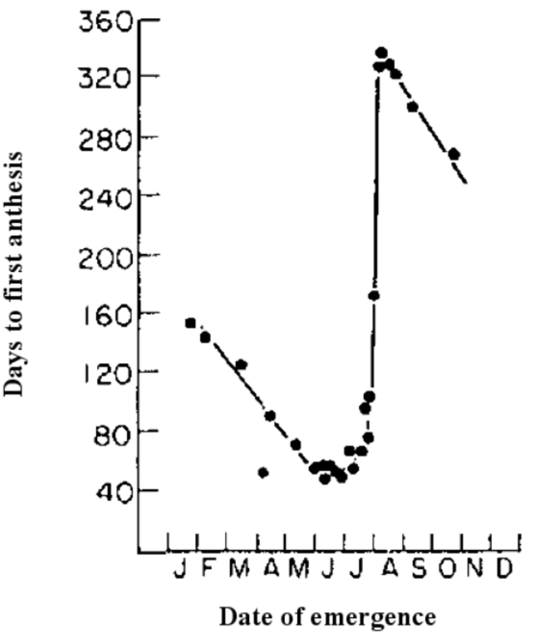


**Figure 4-29** Relationship between induction of flowering and time of emergence of *T. inodorum*. Data and figure after Roberts and Feast (1974).

**Equation 4-37:** $$\begin{cases} \text{if } d_{Ws} \le 202 & \text{delta}_{Ws\to Fs} = -0.847 * d_{Ws} + 227.0 \\ \text{if } 203 \le d_{Ws} \le 273 & \text{delta}_{Ws\to Fs} = 55 \end{cases}$$

For *S. media* flowering usually takes place from early spring until late autumn although it can be found flowering throughout the year (van den Brand, 1987). From the literature the variability in time from emergence to flowering becomes apparent. Van Delden *et al.* (2002) mention that without competing crop, *S. media* flowered 30 days after emergence but in a wheat crop plants started flowering seven days later. Leguizamon and Roberts (1982) recorded that seed rain from plants emerged in April commenced in July. Briggs *et al.* (1991) showed that there is wide variability between populations of different habitats but also between populations of the same habitat with the time from sowing to 50% flowering between 100 and 132 days. Finally, Barnwell and Cobb (1989) showed that mecoprop resistant plants of *S. media* took longer to start flowering than susceptible plants: 33 and 57 days from sowing respectively.

In the experiment described in section 4.2 it was observed that individuals from the natural population of *S. media* flowered much earlier (>2 months) than the individuals of the experimental population. Given the time from sowing to harvest (‘maturity time’) was a cultural control option in the weed management scenarios, this variability is guaranteed to have a large impact on the predictions in ECOSEDYN. It appears that model conclusions are valid only for the population from which the parameters were derived. Experimental research is needed to quantify the variability within natural populations in agricultural fields (experimental seeds were obtained from a commercial supplier). The $\text{delta}_{Ws\to F}$ parameter for *S. media* could then be made stochastic and multiple model runs with values drawn from a distribution applied. As a default value, 60 days was proposed, an arbitrary figure within the range as reported in the literature.

### Duration of flowering

The correlation between duration of flowering (days), $\text{delta}_{Fs\to Sen}$ (Equation 4-32) and plant biomass at harvest explained only little of the variation (see Section 4.5.3). Moreover, over the limited range of plant sizes that can be expected to occur in a carrot or winter wheat crop, there was no effect of plant size on duration of flowering for early flowering plants, which comprises all the plants in winter wheat and the majority in carrot. Duration of flowering, $\text{delta}_{Fs \rightarrow Sen}$, is therefore represented as a constant value of 35 days.

### Symmetry of Beta function

The experimental results in Section 4.5 indicated a value of 0.43 for $s_{Beta\_F}$ of the Beta function of the area covered by flowers. It is possible that the value for $s_{Beta\_F}$ for the Beta function of flower production is different, in particular when assessed for plants emerged at a different time, but until that information becomes available the best information is the current value of 0.43.

### $a_{W\text{-}F}$ and $b_{W\text{-}F}$

The parameters $a_{W\text{-}F}$ and $b_{W\text{-}F}$ can not be derived from the data presented in Section 4.4 (see Figure 4-13) since only mature seed heads were counted and included in the plant weight. The data are available however from the experiment presented in Section 4.5 where harvest was delayed until plants had matured sufficiently. It was noted that 87% of the plants harvested contained only flowers and mature seed heads and no flower buds, an indication of the advanced stage of maturity of the population. To meet the condition of homoscedasticity, the vegetative plant weight and total reproductive structures (buds, flowers and seed heads) were log-transformed before linear regression. The values of the parameters $a_{W\text{-}F}$ and $b_{W\text{-}F}$ for *T. inodorum* are derived from this regression (see Figure 4-30 and Table 4-14) and are 0.93 and 0.95 respectively. For *S. media* no raw data were available but the value of the slope parameter ‘a’ in Equation 4-36, the number of seed capsules per gram plant dry weight, 33.9, as established by van Acker *et al.* (1997) can be used.

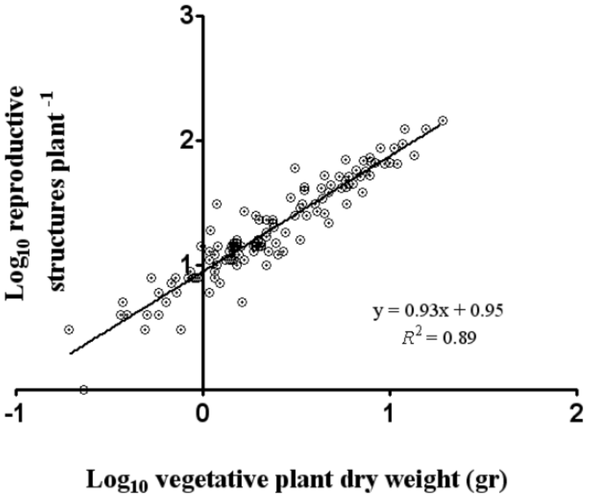


**Figure 4-30** Relationship between $\log_{10}$ vegetative plant dry weight and the $\log_{10}$ transformed value of the cumulative number of buds, flowers and seed heads per plant for *T. inodorum* individuals transplanted in a carrot crop in May (see Section 4.5).

### 4.7.3 Seed shedding

Apart from the Beta distribution for seed shedding, the Beta distribution for viable seed production needs to be determined to calculate viable seeds added to the seedbank during the harvest operation. Omitting this would result in underestimating seed production since only shed viable seeds would be counted as seeds added to the seedbank. It was assumed that the two Beta distribution functions had the same shape but that the ‘start’ and ‘end’ points of the Beta distribution for viable seed production precede the Beta distribution function for seed shedding by a constant number of days.

#### 4.7.3.1 Mathematical representation

Until the day of harvest, seed shedding for a single plant in a given cohort is defined by the Beta distribution for seed shedding, which is represented as:

**Equation 4-38:** $$S_{cum} = S_{max}\left(1+\frac{d_{Se}-d_{sim}}{d_{Se}-d_{S\max}}\right)\left(\frac{d_{sim}-d_{Ss}}{d_{Se}-d_{Ss}}\right)^{\left(\frac{d_{Se}-d_{Ss}}{d_{Se}-d_{S\max}}\right)}$$

It is basically a staggered and slightly stretched version of the Beta distribution for flower production in that the start, end and max point are defined relative to the Beta distribution for flower production. The Beta distribution initiates if sufficient time, $\mathrm{delta}_{F\to S}$, has accumulated from the time of first flowering ($d_{Fs}$) onwards.

**Equation 4-39:** $$d_{Ss} = d_{Fs} + \mathrm{delta}_{F\to S}$$

The end of seed-shedding occurs at:

**Equation 4-40:** $$d_{Se} = d_{Fe} + \mathrm{delta}_{F\to S} + x_{ss}$$

i.e. a plant finishes seed shedding at the time the last flower is produced plus the interval required from opening the flower to first seeding, $\mathrm{delta}_{F\to S}$, and an unknown period, $x_{ss}$, over which seed shedding continues before all seeds are shed from the plant. The point in time where the rate of seed shedding on the surface is maximal, $d_{Smax}$, is expressed as:

**Equation 4-41:** $$d_{S\max} = s_{Beta\_S} * (d_{Se} - d_{Ss}) + d_{Ss}$$

Finally $S_{max}$ is related to $F_{max}$ in the following simple way:

**Equation 4-42:** $S_{max} = S_f * F_{max}$

where $S_f$ is the average viable number of seeds produced per flower. To calculate the maximum number of seeds shed for a complete weed cohort, the number of plants in that cohort is included:

**Equation 4-43:** $S_{max}(c) = S_f * F_{max}(c) * P(c)$

The Beta function for the total number of shed seeds for a given cohort and crop habitat can thus be written as:

**Equation 4-44:**

$$S_{cum}(c,h) = S_{max}(c,h) * \left(1 + \frac{d_{Se}(c) - d_{sim}}{d_{Se}(c) - d_{S\max}(c)}\right)\left(\frac{d_{sim} - d_{Ss}(c)}{d_{Se}(c) - d_{Ss}(c)}\right)^{\left(\frac{d_{Se}(c) - d_{Ss}(c)}{d_{Se}(c) - d_{S\max}(c)}\right)}$$

The daily number of seeds shed then becomes:

**Equation 4-45:** $S_s = S_{cum}(d_{sim}) - S_{cum}(d_{sim} - 1)$

On the day of harvest, seed production is defined by the cumulative number of seeds shed until the day of harvest, added to the number of mature seeds that were still on the plant but are incorporated into the soil during crop harvest and/or further cultivation practices (i.e. discing). Experimental work not presented in this thesis showed that viable seed production starts between 14 and 21 days after flower opening. Since seed shedding is set to start 34 days after flower opening, the maximum duration of the interval between seed production and seed shedding is 20 days. The number of viable seeds that are produced on day = T is therefore equal to the number of seeds that would have been shed on day = T+20. Given that all weeds were set to be killed on the day of harvest ($d_{har}$) the cumulative number of viable produced seeds on the day of harvest is calculated as in Equation 4-46.

**Equation 4-46:**

if $d_{har}+20 \leq d_{Ss}(c)$: $\quad S_{cum} = 0$

if $d_{har}+20 > d_{Ss}(c)$ and $d_{har}+20 \leq d_{Se}(c)$:

$$S_{cum}(c,h) = S_{max}(c,h) * \left(1 + \frac{d_{Se}(c) - (d_{har}+20)}{d_{Se}(c) - d_{S\max}}\right)\left(\frac{(d_{har}+20) - d_{Ss}(c)}{d_{Se}(c) - d_{Ss}(c)}\right)^{\left(\frac{d_{Se}(c)-d_{Ss}(c)}{d_{Se}(c)-d_{S\max}(c)}\right)}$$

if $d_{har}+20 > d_{Ss}(c)$ and $d_{har}+20 > d_{Se}(c)$:

$$S_{cum}(c,h) = S_{max}(c,h) * \left(1 + \frac{d_{Se}(c) - d_{Se}(c)}{d_{Se}(c) - d_{S\max}(c)}\right)\left(\frac{(d_{har}+20) - d_{Ss}(c)}{d_{Se}(c) - d_{Ss}(c)}\right)^{\left(\frac{d_{Se}(c)-d_{Ss}(c)}{d_{Se}(c)-d_{S\max}(c)}\right)} =$$

$$S_{cum}(c,h) = S_{max}(c,h) * \left(\frac{(d_{har}+20) - d_{Ss}(c)}{d_{Se}(c) - d_{Ss}(c)}\right)^{\left(\frac{d_{Se}(c)-d_{Ss}(c)}{d_{Se}(c)-d_{S\max}(c)}\right)}$$

The number of seeds added to the seedbank on the harvest day can be calculated as in Equation 4-45, where $d_{sim} = d_{har}$.

#### 4.7.3.2 Parameterisation and implementation

The parameters for which a value need to be found are the duration from flowering to first seed shedding, $\text{delta}_{F\rightarrow S}$ (Equation 4-39, 4-40), the duration of seed shedding, $x_{ss}$ (Equation 4-40), the measure of symmetry of the Beta function, $s_{Beta\_S}$ (Equation 4-41) and the number of viable seeds per flower, $S_f$ (Equation 4-42, 4-43), need to be defined for both weed species. In addition, from the Beta distribution for seed shedding the Beta distribution of viable seed production needs to be determined on the day of harvest. Omitting this would mean that on the day of harvest only the shed seeds are counted as seeds added to the seedbank whereas in fact seeds that have not yet been shed but are mature and viable are added to the seedbank if mature plants are killed during the harvest operation.

**Duration from flowering to first seed shedding**

From the data there was no indication that day-degrees was a far superior estimator of time from first flowering to first seeding and therefore the data based on days was implemented in ECOSEDYN. For *T. inodorum* the experimentally derived value for

$\mathrm{delta}_{F \to S}$ was 34 days (see Figure 4-23). For *S. media* no specific value could be found, although the review by Sobey (1981) suggested two weeks. From experience in the field a value closer to 3 weeks seems appropriate for the $\mathrm{delta}_{F \to S}$ of *S. media*.

### Duration of seed shedding

No literature or experimental data are available for either species for the $x_{ss}$ parameter. For *T. inodorum* it probably depends largely on the weather, with dry weather promoting rapid seed shedding compared to seeds sticking on the capitula in wet conditions. *S. media* seemed less affected by the weather. It was 'guestimated' that the $x_{ss}$ parameter was equally as long as $\mathrm{delta}_{F \to S}$ (i.e. $x_{ss}$=34) for *T. inodorum* and half as long as $\mathrm{delta}_{F \to S}$ for *S. media*, i.e. $x_{ss}$=17.

### Symmetry of Beta function

The measure of symmetry for seed shedding, $s_{Beta\_S}$, was set in accordance with the value for $s_{Beta\_F}$, i.e. $s_{Beta\_S}$=0.43.

### Number of seeds per flower

The number of apparently viable seeds for *T. inodorum* ranged from 222 to 330 with an average of 263 seeds per flower. This is in congruence with Kay (1994) but lower than Blackshaw and Harker (1997) and Woo *et al.* (1991) who estimated between 345 and 533 seeds per capitulum. However, even when using an average of 250 seeds per capitulum, a plant weighing 10 gram would produce 18,941 seeds, three times as many as Lutman (2002) projected.

For *S. media* the number of seeds per flower or capsule is also highly variable, for example, on average 12.81 seeds per capsule were found in a linseed crop and only 6.57 in a field bean crop (van Acker *et al.*, 1997). From the references mentioned by Sobey (1981) an average of 9 seeds / capsule seems a reasonable value. The chosen parameter values are summarised in Table 4-14.

**Table 4-14** Parameter values for the Beta function for 'Seed shedding'

| Parameter | Units | *Stellaria media* | *Tripleurospermum inodorum* |
|---|---|---|---|
| $\mathrm{delta}_{F \to S}$ | days | 21 | 34 |
| $x_{ss}$ | days | 11 | 34 |
| $S_f$ | days | 9 | 263 |

# 5 Modelling – Part 2: Results

# 5.1 Introduction

In Chapters 2, 3 and 4 all the required model components have been presented and parameterized and a complete conceptual representation of the weed biological cycle as implemented within ECOSEDYN is given in Figure 5-1. With the implementation of ECOSEDYN complete it is time to focus again (see Section 2.3) on the aim of this modeling study. From the outset the aim of this Phd project was to identify those weed management scenarios, based on cultural control, that are intrinsically best suited to counteract the loss of herbicides. The methodology chosen was to build a model framework, able to rapidly simulate the impacts of a wide range of weed management scenarios over a long-term period. The agricultural system that is represented in ECOSEDYN comprises a 6 year crop rotation with carrot in the first year and winter wheat in the remaining 5 years. This crop rotation is repeated four times to create a timeframe long enough to filter out weather effects. The cultural control methods under investigation and to be applied in the two crops were:

- Crop sowing time
- Crop variety (maturity time)

The cultural components were to be assigned different levels, then combined in a factorial manner to create a range of weed management scenarios which would be run against two possible future weather projections. It was anticipated to simulate the combinations of two weed species (*S. media* and *T. inodorum*) and two vegetable crops (carrot and onion). However, the complexity of the model meant that model building took considerably longer. To demonstrate the potential of ECOSEDYN, one of the four anticipated simulation sets was carried out. Since more accurate data were available for *T. inodorum* and carrot, that crop-weed combination was chosen for the simulations. Three questions were addressed through the simulation study:

1. Which cultural control practice, sowing time or crop variety (maturity time), and applied in which crop, has most potential in alleviating long term weed seedbank levels?
2. Can cultural control practices applied in one crop (carrot or winter wheat) maintain sufficient low weed seedbank levels or is the application in both crops required?
3. Are the answers given for questions 1-2 different under the two climate scenarios?

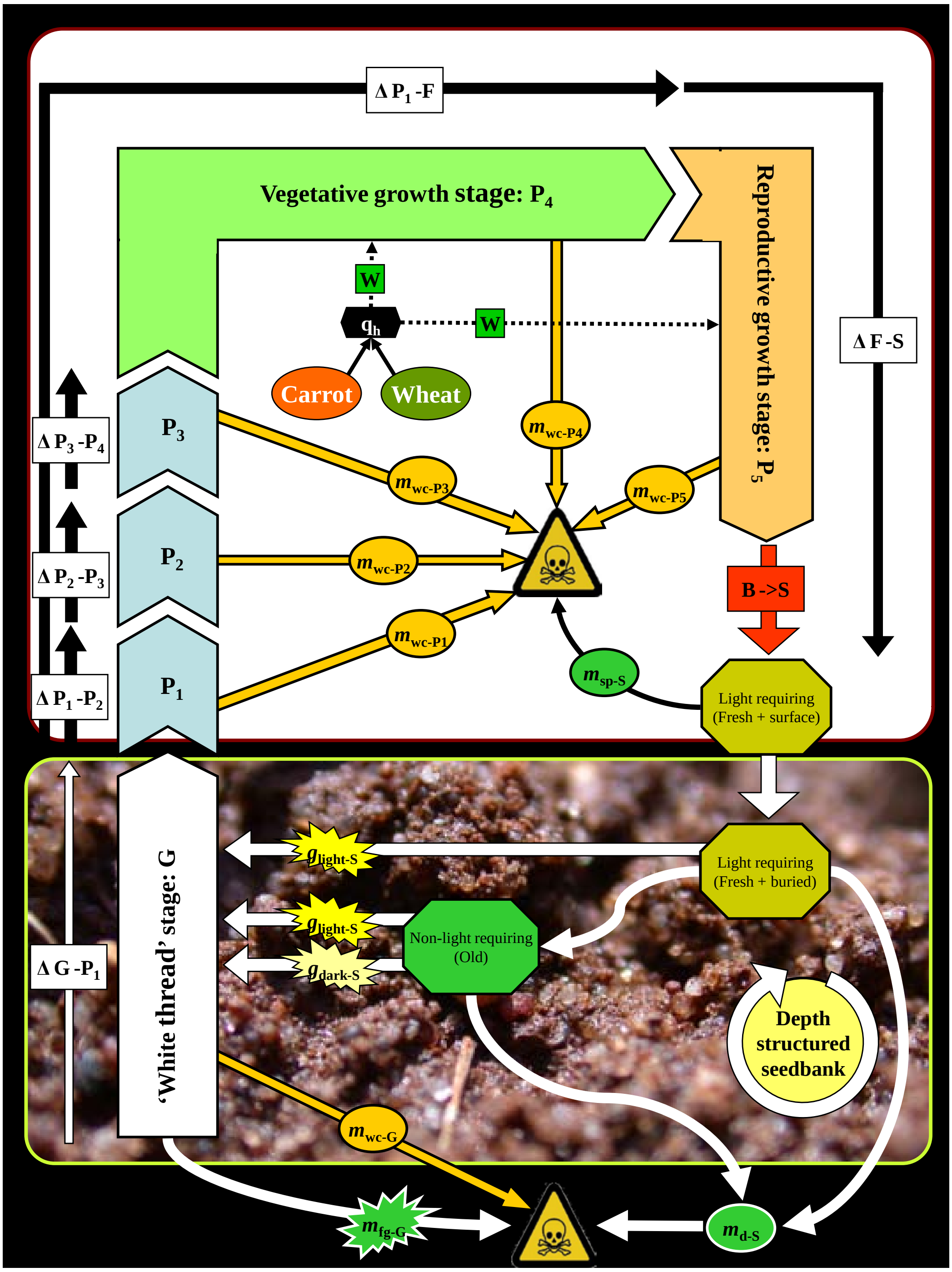


**Figure 5-1** Graphical representation of weed biology processes and regulating factors as implemented in ECOSEDYN.

Regarding the 135 weed management scenarios (see Section 2.3.2) a specific hypothesis was proposed:

The three weed management scenarios (orange shaded in Table 5-1) that are best suited to reduce the level of the weed seedbank after 24 years, regardless of climate, have a late weed sowing time in carrot (reduction of weed biomass through day length effect) and fast maturing carrot and winter wheat varieties.

**Table 5-1** Factorial of cultural control components (sowing time and maturity time) to create 135 weed management scenarios. A_MT and A_ST represent sowing and maturity time in winter wheat whereas V_MT and V_ST represent sowing time and maturity time in carrot respectively. The orange shaded scenarios are hypothesized to result in the lowest levels of the weed seedbank after 24 years compared to other weed management scenarios.

|  | A_MT | 1 |  |  | 2 |  |  | 3 |  |  |
|---|---|---|---|---|---|---|---|---|---|---|
|  | A_ST | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 | 3 |
| V_MT | V_ST |  |  |  |  |  |  |  |  |  |
| 1 | 1 | X | X | X | X | X | X | X | X | X |
|  | 2 | X | X | X | X | X | X | X | X | X |
|  | 3 | X | X | X | X | X | X | X | X | X |
|  | 4 | X | X | X | X | X | X | X | X | X |
|  | 5 | X | X | X | X | X | X | X | X | X |
| 2 | 1 | X | X | X | X | X | X | X | X | X |
|  | 2 | X | X | X | X | X | X | X | X | X |
|  | 3 | X | X | X | X | X | X | X | X | X |
|  | 4 | X | X | X | X | X | X | X | X | X |
|  | 5 | X | X | X | X | X | X | X | X | X |
| 3 | 1 | X | X | X | X | X | X | X | X | X |
|  | 2 | X | X | X | X | X | X | X | X | X |
|  | 3 | X | X | X | X | X | X | X | X | X |
|  | 4 | X | X | X | X | X | X | X | X | X |
|  | 5 | X | X | X | X | X | X | X | X | X |

Considering the two climate scenarios, it is hypothesized that the ‘Heating up’ Scenario will lead to higher levels of the weed seedbank after 24 years than the ‘No change’ Scenario. The reason is that on average the 8 chosen years are warmer but not drier which should, according to the principles proposed in Section 4.7.1.1.2, work in favour of *T. inodorum* biomass and seed production.

In Section 5.2 the modelling methodology and analysis of the results is given, then in the following section the simulation results are presented and the chapter finishes with the conclusions and discussion in Section 5.4.

## *5.2 Methodology*

### 5.2.1 Software

At the start of the project MatLab was suggested as the preferred software package as it provides a number of advantages over other packages. It is a numerical computing environment based on matrix algebra which is ideal for structuring the state variables of the weed population into matrices and vectors. Another advantage is that MatLab is an interpreted language which means that, contrary to a compiled language such as C++ or Visual Basic, one can write scripts and functions, examine the result of individual commands quickly and tweak where necessary. Functions exist to integrate MATLAB based algorithms with external applications and languages, such as C, C++, Fortran, Java, COM, and Microsoft Excel (2007). Early in the project two alternatives to Matlab were explored; Simulink (The MathWorks) and Stella (isee Systems). Both packages differ from MatLab in that they offer a graphical block diagramming tool. Some modelling was done in these programs but it was soon realised that the possibilities, especially with regard to matrix manipulations, were severely limited and that it was therefore much easier to proceed using MatLab. The simulations were run on a PC with Intel(R) Core(TM)2 Duo CPU processor (E8400 @ 3.00GHz) and 1.95 GB of RAM. The time required to run the two sets of 135 simulations under those parameters was approximately an hour.

### 5.2.2 Code structure

The complete Matlab code exists of (see Figure 5-2), or uses:

- two Matlab function files (crop files) in which the model components described in Chapter 2, 3 and 4 are implemented in relation to the farming practices occurring in the carrot and winter wheat year respectively. The simulation runs from 1 October to 30 September and the files contain a counter (‘for-loop’ in Matlab terms) from 1 to 365 to enable specific and precise dates for crop sowing and harvest and weed biology events.
- one Matlab script file (scenario file) which encodes the weed management and climate scenarios into a series of ordinal scores so that the right weather year file is selected and crop sowing and harvest in the crop files occur at the right

time. This file also stores the data that is being produced by the two crop two Matlab function files (crop files).

- auxiliary Matlab function files (calculation files) that enable certain calculations (e.g. to infer harvest date) to be made outside the crop files.
- independent data files containing parameter values (e.g. weather data, weed seed size, germination data) created prior to running ECOSEDYN and loaded into the crop files at the start of a specific year or simulation run.

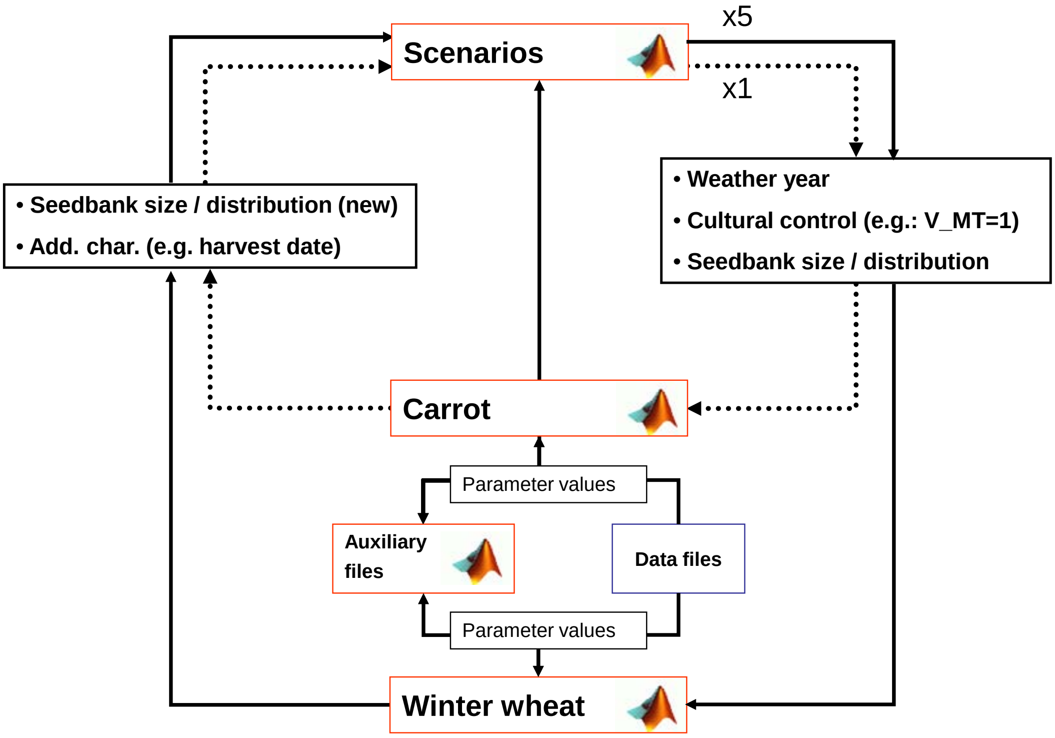


**Figure 5-2** Dataflow within ECOSEDYN during one crop rotation (one year of carrot followed by five years of winter wheat)

At the end of each simulation year (i.e. $d_{sim}$=365) the total size of the seedbank is calculated in the crop function-file, then passed on to and stored by the scenario script-file and once again passed on to either one of the crop function-files. Some other characteristics such as annual seed production, date of 50% crop emergence and crop harvest are also passed on and stored by the scenario script-file to aid explaining the rank order of the weed management scenarios. For each weed management scenario (i.e. 24 simulation years, 4 crop rotations) the average size of the seedbank over the last crop rotation is calculated and stored.

Due to weather differences, individual years varied greatly in the level of weed seed production and different weather year randomisations could therefore lead to considerable differences in the average size of the weed seedbank over the last crop rotation. Each of the two sets of 135 weed management scenarios was therefore run for 50 different weather year sequences and the average seedbank size calculated over the 50 randomisations.

Once all weed scenarios have finished, Matlab exports the output data to an Excel file. The complete Matlab code of ECOSEDYN was too long to be included as an Appendix but is available upon request (e-mail bastiaan.brak@googlemail.com or Andrew.Mead@warwick.ac.uk).

### 5.2.3 Initiation of seedbank

Prior to running the weed management scenarios a representative 'starting' seedbank density had to selected. According to recent estimates of seed banks in agricultural fields the total number of weed seeds in most fields is about 4000 m$^{-2}$ (Squire *et al.*, 2003). To initiate the seedbank for each of the scenarios it was assumed that on the 1st of October, the target species constituted 10% of that total, i.e. 400 m$^{-2}$. This number was multiplied by 250,000 to reflect a field size of 25 ha. Since the dormancy status of the seeds is a function of seed age, the seedbank was to be divided over four different age groups in the seedbank matrix in ECOSEDYN (see Section 2.5.2.3). If the first simulation year is identified as $Y_1$ then it was assumed that 50% of the initial seed bank were produced in $Y_0$, 25% of the seed bank were produced in $Y_{-1}$ and that 25% are from years before that: $Y_{\leq -2}$.

Seeds produced in $Y_0$ were stored in Array 2. The distribution of seeds followed that as described in Section 2.5.6, i.e. 57% on the soil surface, 29% in the 0-5 mm and 14% in the 5-10 mm soil layer. Seeds produced in $Y_{-1}$ would have been subject to one [Plough + power harrow] cultivation. The maximum depth of cultivation in the rotation, and hence the distribution of weed seeds, is assumed to be limited to 30 cm. These seeds, that were for convenience assumed to be all on the surface at the time of cultivation, were therefore distributed over the soil layers according to the first column ('Surface') of the transition matrix shown in Figure 3-34. These *T. inodorum* seeds would have been in Array 2 in the previous season and were therefore stored in Array 3. The seeds produced two or more years ago, $Y_{\leq -2}$, were stored in Array 4. These seeds would have received two or more [Plough + power harrow] cultivations and were evenly distributed over the 0-30 cm.

## 5.2.4 One year simulations

After the 24 year simulations had been finished, additional one-year simulations were carried out for each of the 9 or 15 maturity time x sowing time combinations within winter wheat and carrot respectively, and for each of the 17 weather years, to help understand the rank order of the weed management scenarios. The model parameter values were kept the same as during the 24 year simulations except for the $W_{max-t}$ and $S_f$ parameters. It became apparent that during the 24 year simulations different values for these two parameters had been defined in the carrot and winter wheat files. In the one year simulations the value for $W_{max-t}$ and $S_f$ listed in Section 4.7.1.2 and 4.7.3.2 respectively were used in both carrot and winter wheat. The variables assessed were:

- number of emerged weed seedlings
- total weed biomass (gram dry weight) at crop harvest
- stage of weed maturity: a single 'maturity score' was calculated from the weeds in the different cohorts (1-12) that represented the proportion realized seed production of the maximum seed production $S_{max}$. The score was calculated in the following way:

  **Equation 5-1**
  $$\mathrm{mat-score} = \sum_{h=1}^{H} \left( \frac{\sum_{c=1}^{12} S_{cum}(c,h)}{\sum_{c=1}^{12} \left( \frac{S_{cum}(c,h)}{0.95 * S_{max}(c,h)} * S_{cum}(c,h) \right)} \right) * \frac{1}{h}$$

  where 'h' represents the crop habitat and 'c' represents the (number of) cohorts. H is the total number of habitats within a crop; for carrot H=3 whereas for winter wheat H=1.
- number of viable seeds produced at crop harvest

### 5.2.5 Analysis

The Matlab output contained the day at which 50% of the crop had emerged and the day at which the crop is harvested for each of the 135 weed management scenarios x 50 randomisations and for each of the 24 years within each weed management scenario. Using this information and the sowing dates (see Table 2-1), the average duration of crop sowing to 50% crop emergence and of crop sowing to crop harvest could be determined under the two climate scenarios for each of the weed management scenarios within the two crop [MT x ST] factorials.

As an informal analysis, and for illustration purpose, scatter plots were made of the rank order of the weed management scenarios against the ordinal scores of the cultural control components. In addition, analysis of variance tests were performed on the seedbank data. Because of unequal within-group variance in the dataset, a $\log_{10}$ transformation was performed first on the seedbank numbers to meet the assumption of homoscedasticity. Then an ANOVA test was performed in GenStat for the datasets for each weather scenario and for the two datasets combined. For the separate analyses, replicates were marked as 'blocks' and the 4 different cultural control components as treatment factors. The analysis included all interactions between the four treatment factors. For the combined dataset the two climate scenarios were marked as 'blocks' and the replicates as nested within that, with the cultural components again as treatment factor and the fitted model including interactions within climate scenario.

For each weed management scenario the effect of climate was assessed in two ways:

- the mean seedbank size was determined over the 50 weather randomisations for each of the two climate scenarios and the difference between the two means was then determined from it
- 50 pairs of simulation results were formed by comparing the seedbank size under the two different climate scenarios for each of the 50 independent weather randomisations. From this data the probability of the seedbank increasing if the weather were to change from 'No change' to 'Heating up' was determined.

Means and standard errors were calculated for the variables that were obtained using the one-year crop simulations under the two climate scenarios 'No change' (n=17) and 'Heating up' (n=8).

## 5.3 *Results*

**Time to 50% crop emergence and crop harvest**

For both carrot and winter wheat, the later the crop sowing date, the less time it took from sowing to harvest for a given crop maturity time (see Table 5-2). Carrot harvest date tended to be 2-3 days earlier under ‘Heating up’ as compared to ‘No change’ climate, except for the weed management scenarios with [V_ST=3] and [V_ST=4]. In (some of) the weather years from the ‘Heating up’ climate, the soil was rather dry at these sowing dates. Since no irrigation was assumed in the germination and emergence simulation model, crop emergence was delayed relative to the average of the ‘No change’ weather years. It is noteworthy also that the standard deviation of the time to 50% carrot emergence is twice as large under ‘Heating up’ as compared to ‘No change’ climate.

**Table 5-2** Average duration from crop sowing to 50% crop emergence and crop harvest under two climate scenarios (‘No Change’ = NC and ‘Heating up’ = HU) for the factorial of crop sowing time x crop maturity time in carrot and winter wheat.

| | MT=1 | | | | MT=2 | | | | MT=3 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $d_{s\rightarrow 50\%em}$ [1] | | $d_{s\rightarrow harvest}$ [1] | | $d_{s\rightarrow 50\%em}$ [1] | | $d_{s\rightarrow harvest}$ [1] | | $d_{s\rightarrow 50\%em}$ [1] | | $d_{s\rightarrow harvest}$ [1] | |
| **V_ST** | NC | HU | NC | HU | NC | HU | NC | HU | NC | HU | NC | HU |
| 1 | 21 | 20 | 115 | 112 | 21 | 20 | 129 | 127 | 21 | 20 | 148 | 145 |
| 2 | 17 | 15 | 106 | 103 | 17 | 15 | 120 | 117 | 17 | 15 | 138 | 135 |
| 3 | 19 | 24 | 100 | 102 | 19 | 24 | 114 | 115 | 19 | 24 | 132 | 133 |
| 4 | 16 | 20 | 92 | 94 | 16 | 20 | 106 | 107 | 16 | 20 | 124 | 125 |
| 5 | 16 | 13 | 87 | 84 | 16 | 13 | 101 | 98 | 16 | 13 | 120 | 116 |
| | | | | | | | | | | | | |
| **A_ST** | NC | HU | NC | HU | NC | HU | NC | HU | NC | HU | NC | HU |
| 1 | 14 | 13 | 318 | 311 | 14 | 13 | 324 | 317 | 14 | 13 | 331 | 324 |
| 2 | 18 | 17 | 311 | 305 | 18 | 17 | 319 | 311 | 18 | 17 | 326 | 318 |
| 3 | 24 | 25 | 302 | 296 | 24 | 25 | 309 | 302 | 24 | 25 | 316 | 309 |

[1] For carrot: average of 200 values (50 weather randomisations x 4 years within weed management scenario). For winter wheat: average of 1000 values (50 weather randomisations x 20 years within weed management scenario).

Winter wheat was predicted to be harvested 6-8 days earlier under ‘Heating up’ as compared to ‘No change’ climate at each sowing date (see Table 5-2). Under the assumptions used to model winter wheat germination in ECOSEDYN (see Section 2.5.2.2), the later the sowing of winter wheat, the longer the duration from sowing to 50% crop emergence but the shorter the duration from sowing to crop harvest.

### Weed management (cultural control) scenarios

The scatter plots show that the time from sowing to harvest in carrot was by far the most important cultural control factor affecting the ranking of the weed management scenarios in both climate scenarios (see Figure 5-3) and this is confirmed by comparing the variance ratios (v.r.) in the ANOVA tables (Table 5-3 and 5-4). Under 'No change' climate, sowing time of carrot was of secondary importance followed by sowing time of winter wheat. Time from sowing to harvest in winter wheat (winter wheat variety) was the least important of all and there was no significant effect whereas for the other cultural control factors the effects were highly significant (P<0.001; see Table 5-3 and 5-4).

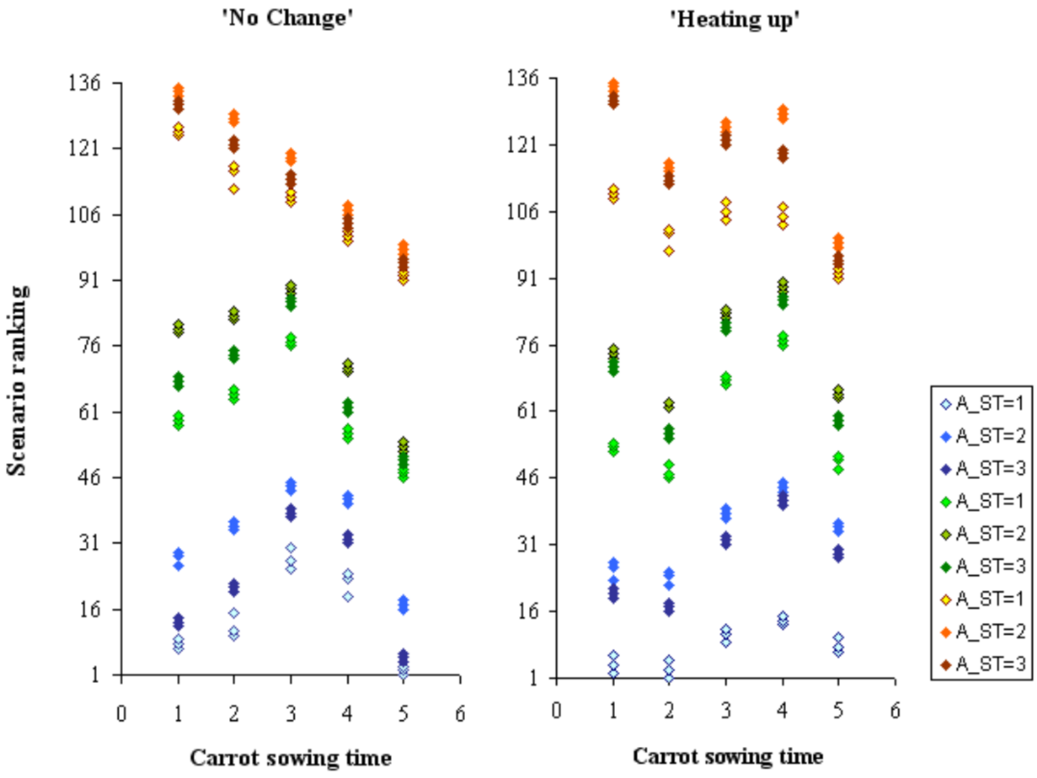


**Figure 5-3** Rank order of weed management scenarios (the higher the ranking number the higher seedbank level) under two Climate scenarios, 'No Change' (left) and 'Heating up' (right), according to the average seedbank size (50 weather replicates) over the course of the last crop rotation. Blue, green and orange points represent fast, intermediate and slow maturing carrot varieties (V_MT=1, V_MT=2, V_MT=3) respectively. Data points of the same colour represent the maturity time in winter wheat with the consistent rank order: A_MT=1< A_MT=2< A_MT=3

For each of the 45 weed management scenarios with a given V_MT score under the ‘No Change’ climate scenario, the weed management scenarios where carrot was sown on the latest date (V_ST=5) had the lowest ranking numbers (i.e. relatively low seedbank sizes) compared to the other carrot sowing times (see Figure 5-3). The carrot variety that took the longest time from sowing to harvest (V_MT=3; see orange data points in left graph of Figure 5-3) showed a trend for later sowings to end up with lower seedbanks whereas the other two carrot varieties (maturity times) did not. Hence the interaction between sowing time and maturity time in carrot was significant (P<0.001, see Table 5.3). None of the second or third order interactions were significant.

**Table 5-3** Anova table for the treatment (cultural control) and first-order effects on the log-transformed seedbank simulation data under ‘No change’ climate.

| Source of variation | d.f. | s.s. | m.s. | v.r. | F. pr. |
|---|---|---|---|---|---|
| | | | | | |
| Rep | 49 | 2.39E+02 | 4.88E+00 | 62.17 | |
| **V_ST** | 4 | 7.25E+02 | 1.81E+02 | 2311.86 | <.001 |
| **V_MT** | 2 | 9.88E+03 | 4.94E+03 | 62953.02 | <.001 |
| **A_ST** | 2 | 4.68E+01 | 2.34E+01 | 298.32 | <.001 |
| A_MT | 2 | 1.12E-01 | 5.57E-02 | 0.71 | 0.491 |
| **V_ST * V_MT** | 8 | 3.29E+02 | 4.12E+01 | 524.62 | <.001 |
| V_ST * A_ST | 8 | 1.73E-02 | 2.16E-03 | 0.03 | 1.000 |
| V_MT * A_ST | 4 | 3.49E-01 | 8.73E-02 | 1.11 | 0.348 |
| V_ST * A_MT | 8 | 1.50E-05 | 1.91E-06 | 0.00 | 1.000 |
| V_MT * A_MT | 4 | 2.20E-04 | 5.49E-05 | 0.00 | 1.000 |
| A_ST * A_MT | 4 | 1.73E-01 | 4.33E-02 | 0.55 | 0.697 |
| V_ST * V_MT*A_ST | 16 | 9.19E-03 | 5.74E-04 | 0.01 | 1.000 |
| V_ST * V_MT*A_MT | 16 | 2.04E-05 | 1.28E-06 | 0.00 | 1.000 |
| V_ST * A_ST*A_MT | 16 | 4.32E-05 | 2.70E-06 | 0.00 | 1.000 |
| V_MT * A_ST*A_MT | 8 | 3.31E-04 | 4.13E-05 | 0.00 | 1.000 |
| V_ST * V_MT*A_ST*A_MT | 32 | 3.52E-05 | 1.10E-06 | 0.00 | 1.000 |
| Residual | 6566 | 5.15E+02 | 7.84E-02 | | |
| Total | 6749 | 1.17E+04 | | | |

In contrast, under ‘Heating up’ climate, the maturity time of winter wheat had a significant effect on the seedbank levels (P=0.007, Table 5-4). Comparing the variance ratios under the two climate scenarios shows that, relative to the sowing time in carrot, the sowing time of winter wheat had more impact under ‘Heating up’(see

Table 5-3 and 5-4). In addition, the interaction between sowing time and maturity time in winter wheat was significant (P=0.003).

Contrary to 'No change' climate, a clear trend for later sowings to end up with lower seedbanks was not present under 'Heating up' for any of the carrot varieties nor was there any carrot sowing date that was consistently resulting in the lowest seedbanks (see right graph in Figure 5-3). Instead, for each carrot variety the rank order of seedbank size according to carrot sowing date was different and hence the interaction (V_ST*V_MT) was significant (P<0.001, see Table 5.4).

**Table 5-4** Anova table for the treatment (cultural control) and first-order effects on the log-transformed seedbank simulation data under 'Heating up' climate.

| Source of variation | d.f. | s.s. | m.s. | v.r. | F. pr. |
|---|---|---|---|---|---|
| | | | | | |
| Rep | 49 | 2.02E+02 | 4.13E+00 | 73.90 | |
| **V_ST** | 4 | 1.66E+02 | 4.14E+01 | 741.32 | <.001 |
| **V_MT** | 2 | 1.04E+04 | 5.18E+03 | 92774.10 | <.001 |
| **A_ST** | 2 | 1.73E+02 | 8.63E+01 | 1545.48 | <.001 |
| **A_MT** | 2 | 5.62E-01 | 2.81E-01 | 5.03 | 0.007 |
| **V_ST * V_MT** | 8 | 1.31E+02 | 1.64E+01 | 293.57 | <.001 |
| V_ST * A_ST | 8 | 6.96E-03 | 8.70E-04 | 0.02 | 1.000 |
| V_MT * A_ST | 4 | 3.60E-01 | 9.00E-02 | 1.61 | 0.168 |
| V_ST * A_MT | 8 | 1.55E-05 | 1.93E-06 | 0.00 | 1.000 |
| V_MT * A_MT | 4 | 2.25E-03 | 5.63E-04 | 0.01 | 1.000 |
| **A_ST * A_MT** | 4 | 8.84E-01 | 2.21E-01 | 3.96 | 0.003 |
| V_ST * V_MT*A_ST | 16 | 9.58E-03 | 5.99E-04 | 0.01 | 1.000 |
| V_ST * V_MT*A_MT | 16 | 1.25E-04 | 7.83E-06 | 0.00 | 1.000 |
| V_ST * A_ST*A_MT | 16 | 4.36E-05 | 2.72E-06 | 0.00 | 1.000 |
| V_MT * A_ST*A_MT | 8 | 3.84E-03 | 4.80E-04 | 0.01 | 1.000 |
| V_ST * V_MT*A_ST*A_MT | 32 | 1.93E-04 | 6.02E-06 | 0.00 | 1.000 |
| Residual | 6566 | 3.67E+02 | 5.59E-02 | | |
| Total | 6749 | 1.14E+04 | | | |

**Cultural control hypothesis: best three weed management scenarios are characterized by [V_MT=1, V_ST=5, A_MT=1]**

The three weed management scenarios with the lowest seedbank after 24 years were not precisely those as hypothesized (see Table 5-1). Under ‘No Change’ climate they had three characteristics in common: V_MT=1, V_ST=5, A_ST=1. Under ‘Heating up’ climate they had two characteristics in common: V_MT=1, A_ST=1 (see Figure 5-3). Hence, a fast maturing carrot variety and early sowing in winter wheat are the most consistent, ‘climate proof’, cultural control components that can maintain low weed seedbank levels.

### One year simulation results

The autonomous ‘Germination and Emergence’ model predicted that the later carrot is sown, the fewer *T. inodorum* seedlings would germinate and emerge (see charts in first row of Figure 5-4). At the same time, the duration from crop sowing to 50% crop emergence generally decreased for later sowing dates (see Table 5-2) which results in a decrease in the maximum per plant biomass for each cohort. Together these effects resulted in lower total weed biomass at crop harvest for later crop sowings (see charts in second row of Figure 5-4).

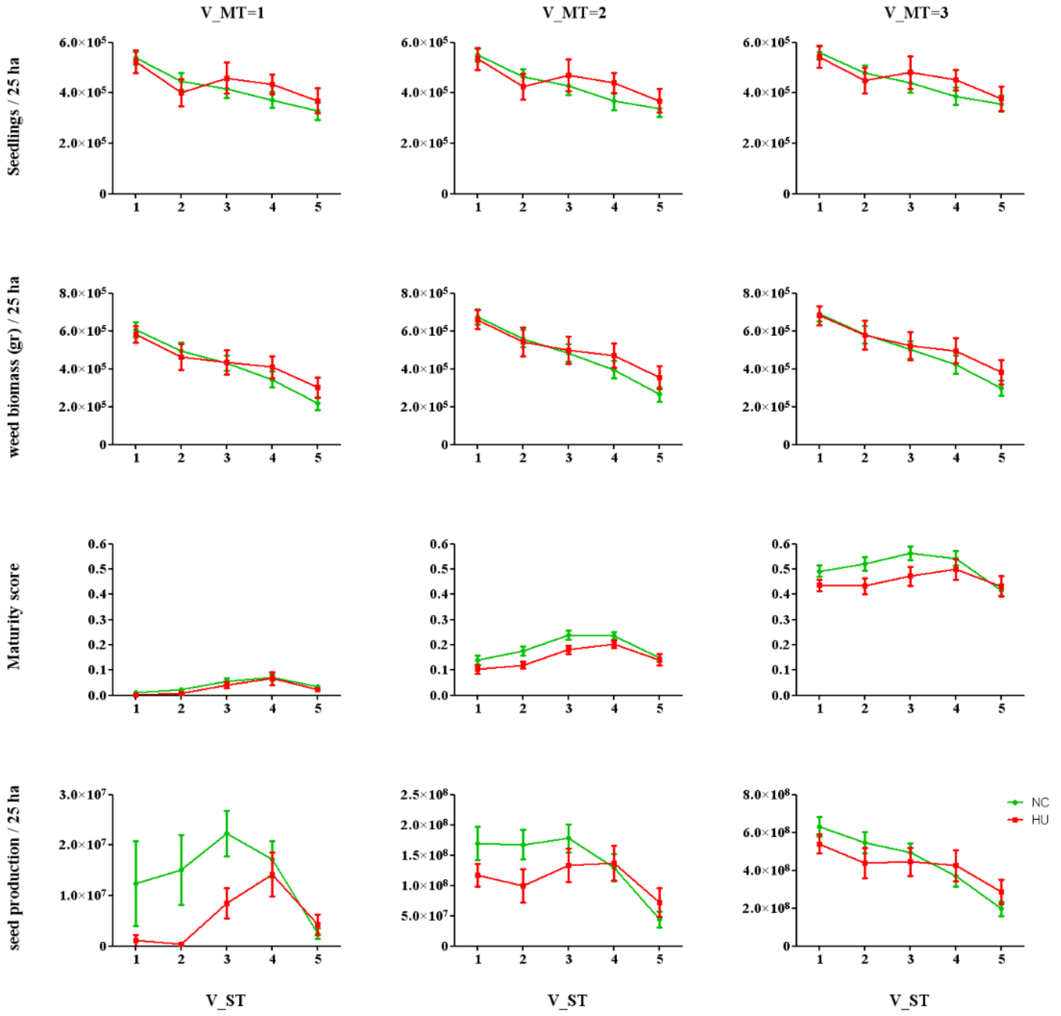


**Figure 5-4** Results of 1 year simulations in carrot. Charts in the first, second and third column represent increasing times from sowing to harvest (V_MT). X-axes of charts represent carrot sowing time (V_ST). The green lines represent the mean over 17 weather years (‘No change’ climate) and the red lines represent the mean over the 8 hottest weather years (‘Heating up’ climate) from those seventeen years. Bars represent standard error. Note that Y-axes of the charts in row 4 (seed production) have different scales.

The more time a carrot variety required from sowing to harvest, the higher the proportion of maximum seed production (maturity score) that was realised by weeds at crop harvest (see charts in third row of Figure 5-4). Maturity scores tended to be highest for the third and / or fourth sowing times. The reduction in the maturity score at the fourth but particularly the fifth sowing time is related to the way the timing of flowering is modeled in ECOSEDYN (see Equation 4-37), which is itself a reflection of the presence of photoperiodicity in *T. inodorum*. For weed cohorts that emerge after 21 April, the starting date of flowering is delayed by 5 days for each subsequent cohort whereas for each subsequent weed cohort that emerges prior to 21 April the starting date of flowering is delayed at most by one day (see Figure 5-5).

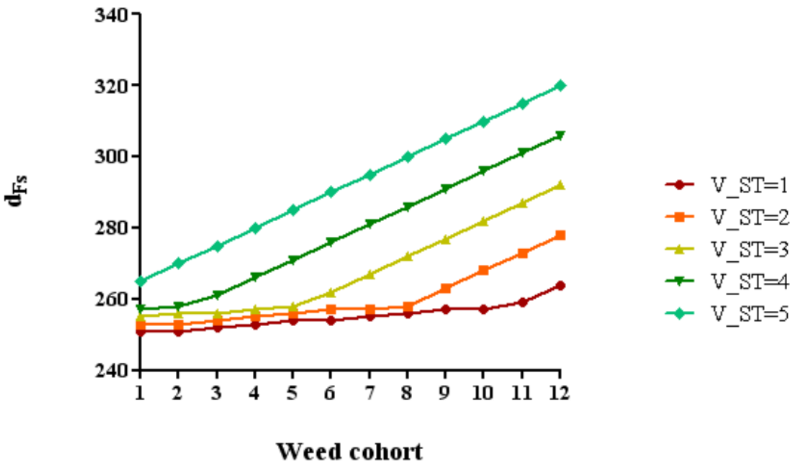


**Figure 5-5** Start of weed flowering dates ($d_{Fs}$) for each of the 12 weed cohorts at each of the five different carrot sowing times. Earliest weed flowering date is 251 (8 June).

Even though the time from sowing to harvest decreases for later sowing times (see Table 5-2), the average harvest date is still 5 to 10 days later for each consecutive sowing time. The average number of days over all cohorts by which flower initiation is delayed for consecutive sowing times is lower than the average number of days by which crop harvest is delayed for early sowing times, but higher for later sowing times. The maturity score therefore initially increases but later decreases for consecutive sowing times.

Maturity scores tended to be lower under ‘Heating up’ than ‘No change’ climate because either one of the following conditions held:

- Carrot tended to be harvested earlier under ‘Heating up’ than ‘No change’ climate (V_ST=1, V_ST=2 and V_ST=5)
- Average weed seedling emergence tended to be later under ‘Heating up’ than under ‘No change’ climate (V_ST=3, V_ST=4) (see Figure 5-6)

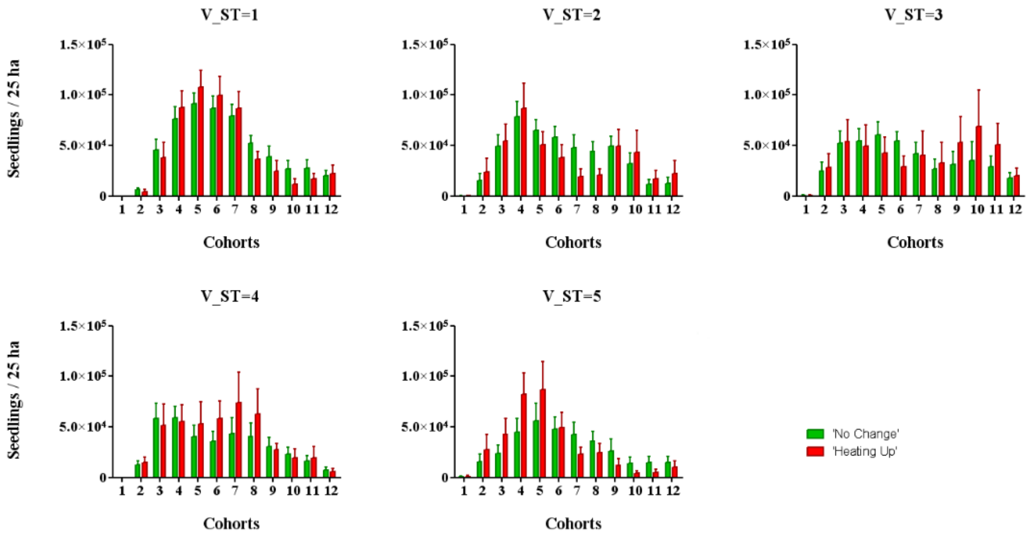


**Figure 5-6** Average distribution of weed emergence under ‘No change’ climate (17 weather years) and ‘Heating up’ climate (8 weather years) after seed bed preparation of carrot at five sowing dates. V_ST=1-5 represent carrot sowing dates as given in Table 2-1. The first weed cohort comprises all weed seedlings that emerged within 5 days from sowing / seed bed preparation, the second weed cohort represents all the weeds that emerged in the 6-10 day interval after sowing, etc.

Seed production at crop harvest is a function of both biomass production and the phenological stage of a plant; the latter factor explains most of the variation in weed seed production at various sowing times when a fast maturing carrot variety (V_MT=1) is grown, whereas weed biomass explains most variation when a slow maturing carrot variety (V_MT=3) is grown. Seed production (see charts in fourth row of Figure 5-4) correspond rather well with the rank order of the weed management scenarios as shown in Figure 5-3. Bearing in mind that each weather year is selected once in the one year simulations, any discrepancies between the graphs are most likely due to a relatively low number of weather randomizations (50) in the 24 yr weed management scenario simulations.

For winter wheat the dynamics are rather different (see Figure 5-7). Fewer *T. inodorum* seedlings emerged in winter wheat than in carrot but there was no effect of sowing time.

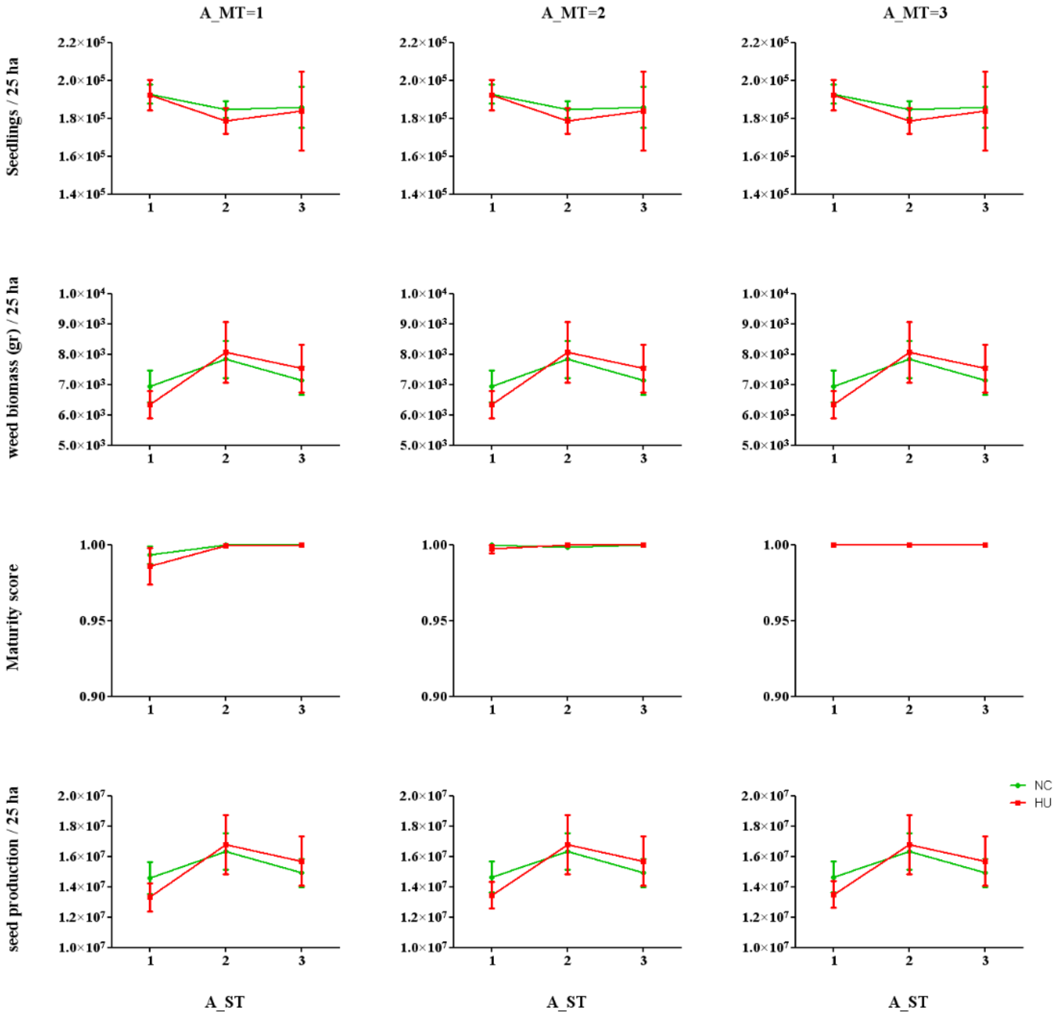


**Figure 5-7** Results of 1 year simulations in winter wheat. Charts in the first, second and third column represent increasing times from sowing to harvest (A_MT). X-axes of charts represent carrot sowing time (A_ST). The green lines represent the mean over 17 weather years (‘No change’ climate) and the red lines represent the mean over the 8 hottest weather years (‘Heating up’ climate) from those seventeen years. Bars represent standard error.

Since crop development is slow in autumn there was no dampening effect of the canopy on weed seed germination and therefore equal numbers of weeds emerged and survived until crop harvest in winter wheat varieties with different lengths from sowing to harvest. The first sowing time resulted in the lowest amount of total weed biomass at crop harvest. At first sight this may appear surprising, given that on average more seedlings were produced at the first than at the second or third sowing time. However, this total consists of twelve weed cohorts of weeds of different size. It is the relative time of emergence of crop and weed that has the largest effect on total plant biomass. The distribution of weed seedling emergence over time and the duration until 50% crop emergence are the key factors in determining final plant weed biomass. Assuming a weed seedling survives weed control, the earlier it emerges relative to the crop the higher the potential biomass $W_{max}$-r. Hence, given an equal number of seedlings, the more right-skewed a weed emergence distribution is over the twelve cohorts, the higher total weed biomass gets. At the same time, given a certain distribution of weed emergence, the longer crop emergence is delayed, the more the potential biomass for weeds in each cohort will increase. In winter wheat, two antagonistic effects were operating:

1. On the one hand, the earlier winter wheat was sown, the more right-skewed the distribution of emergence was over time (see Figure 5-8). A shift occurs in the distribution of emergence towards more seedlings emerging in later cohorts for later sowing dates. All other factors being equal this would result in a decrease in total weed biomass for later sowing dates.

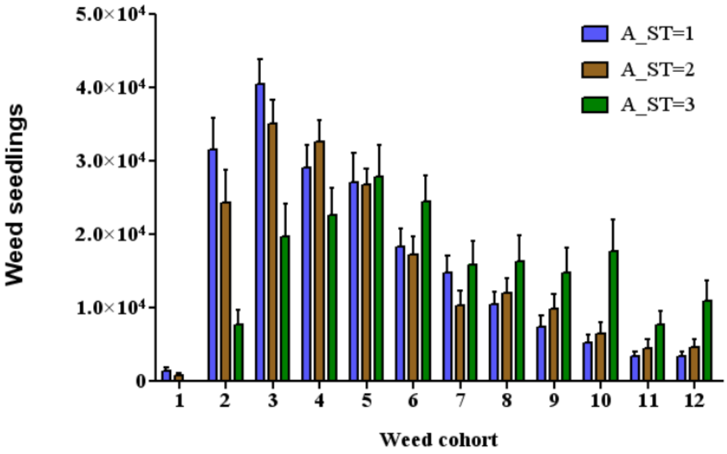


**Figure 5-8** Average distribution of weed emergence over 17 weather years after seed bed preparation of winter wheat for three sowing dates. A_ST=1-3 represent an early, intermediate and late winter wheat sowing date respectively, as given in Table 2-1. The first weed cohort comprises all weed seedlings that emerged within 5 days from sowing / seed bed preparation, the second weed cohort represents all the weeds that emerged in the 6-10 day interval after sowing, etc.

2. On the other hand, the later winter wheat was sown, the longer the duration from sowing to 50% crop emergence (see Table 5-2). This results in higher values for the parameter $bcc_{hq}$ which represents the proportion that per plant biomass is maintained relative to the maximum per plant biomass due to plant competition, (see Equation 4-23) and therefore higher values for the realized per plant biomass, $W_{max-r}$ (see Equation 4-13) for each cohort for later sowing

times. All other factors being equal this would result in an increase in total weed biomass for later sowing dates.

The net result is that the intermediate sowing time of winter wheat results in the highest total weed biomass production. Given that in winter wheat weed seed production is exclusively a function of total weed biomass, the intermediate sowing time resulted in the highest amount of seed production and therefore weed management scenarios with [A_ST=2] resulted on average in higher seedbanks than weed management scenarios with [A_ST=1] or [A_ST=3] (see Figure 5-3).

The total amount of weed biomass produced was not affected by winter wheat variety since the number of weed seedlings was constant and the harvest date exceeded the end of flowering, $d_{Fe}$, after which biomass does not increase, for all [A_MT] x [A_ST] x weather year combinations. The phenology component predicted that the latest weed cohort to emerge would finish seed shedding on day 339 (4 September), 342 or 344 for the different wheat sowing times (see Table 5-5).

**Table 5-5** Start and end dates of flowering ($d_F$) and seed shedding ($d_S$) for the last weed cohort to emerge after three different winter wheat sowing dates.

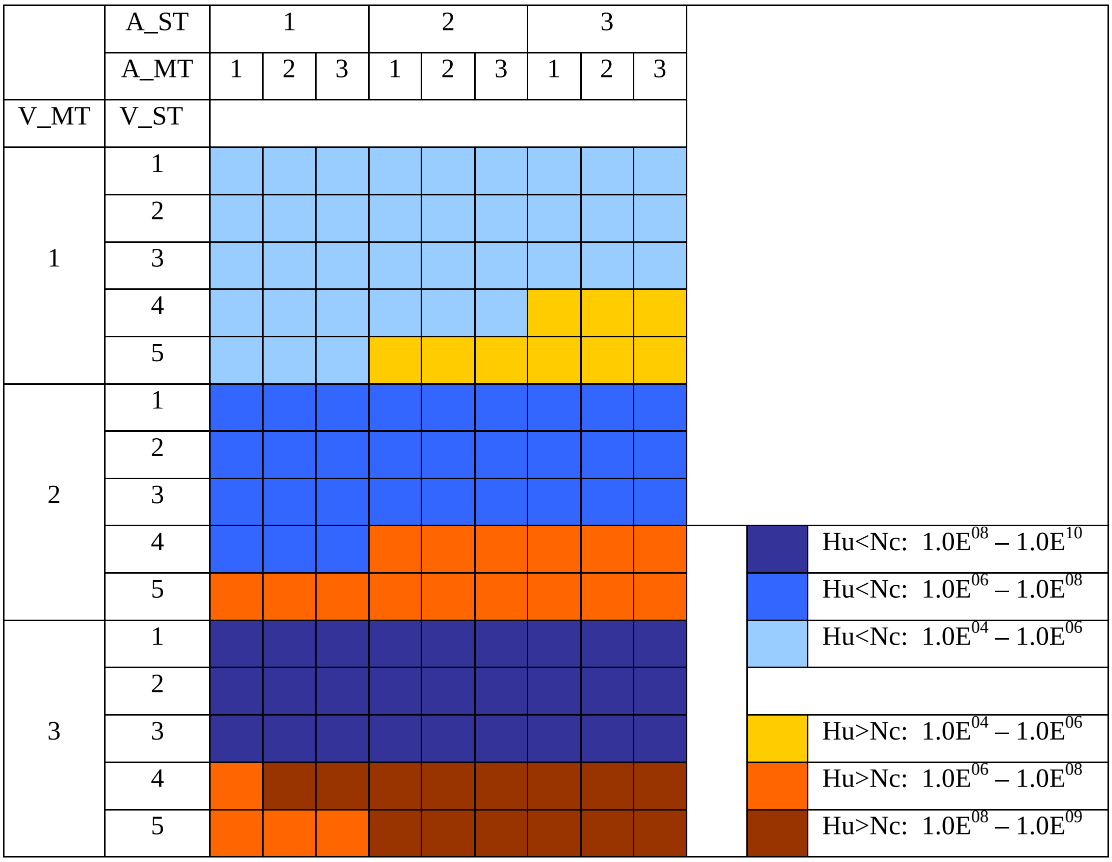
| | $d_{Fs}$ | $d_{Fe}$ | $d_{Ss}$ | $d_{Se}$ |
|---|---|---|---|---|
| 1 October (A_ST=1) | 236 | 271 | 270 | 339 |
| 19 October (A_ST=2) | 239 | 274 | 273 | 342 |
| 8 November (A_ST=3) | 241 | 276 | 275 | 344 |

This means that the point with maximum viable seed production in the population has been reached twenty days earlier than these dates (see Section 4.7.3). Given that harvest dates of winter wheat generally exceeded these ‘maximum viable seed production’ dates and that the last weed cohort generally constitutes only a very small proportion of the weed population, this resulted in maturity scores close to one in nearly all scenarios. Due to this lack of distinction in seed maturity, the variation in seed production was explained exclusively by total weed biomass at crop harvest; seed production was lowest for the first sowing date and highest for the second and this is reflected in the rank order of the weed management scenarios as well (see Figure 5-3).

### Climate hypothesis: seedbank (‘Heating up’) > seedbank (‘No change’)

For the majority of the weed management scenarios (93 out of 135), the average seedbank of a given weed management scenario under ‘Heating up’ climate was lower than its equivalent under ‘No change’ climate, unlike hypothesised. If carrot was sown in March (V_MT=1, V_MT=2 or V_MT=3) then the weed management scenarios under ‘Heating up’ climate resulted, on average, in lower seedbanks than the weed management scenarios under ‘No change’ climate (see Table 5-6). Conversely, if carrot was sown on the 4th or the 5th sowing date, then ‘Heating up’ climate was on average more likely to result in larger seedbanks than ‘No change’ climate. This effect was enhanced by increasing time from sowing to maturity in carrot (V_MT).

**Table 5-6** Relative seedbank sizes for the full factorial of weed management scenarios under two climate scenarios: Hu = ‘Heating up’ and Nc = ‘No change’. Colours indicate the order of magnitude of the difference between the seedbank size under the different climate scenarios for the model parameter values used in the 24 year scenarios. Blue shades indicate that ‘Heating up’ results in lower seedbanks than ‘No change’ whereas orange shades indicate the reverse.



|  | A_ST | 1 |  |  | 2 |  |  | 3 |  |  |
|---|---|---|---|---|---|---|---|---|---|---|
|  | A_MT | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 | 3 |
| V_MT | V_ST |  |  |  |  |  |  |  |  |  |
| 1 | 1 | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ |
|  | 2 | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ |
|  | 3 | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ |
|  | 4 | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | 🟨 | 🟨 | 🟨 |
|  | 5 | ▨ | ▨ | ▨ | 🟨 | 🟨 | 🟨 | 🟨 | 🟨 | 🟨 |
| 2 | 1 | 🟦 | 🟦 | 🟦 | 🟦 | 🟦 | 🟦 | 🟦 | 🟦 | 🟦 |
|  | 2 | 🟦 | 🟦 | 🟦 | 🟦 | 🟦 | 🟦 | 🟦 | 🟦 | 🟦 |
|  | 3 | 🟦 | 🟦 | 🟦 | 🟦 | 🟦 | 🟦 | 🟦 | 🟦 | 🟦 |
|  | 4 | 🟦 | 🟦 | 🟦 | 🟧 | 🟧 | 🟧 | 🟧 | 🟧 | 🟧 |
|  | 5 | 🟧 | 🟧 | 🟧 | 🟧 | 🟧 | 🟧 | 🟧 | 🟧 | 🟧 |
| 3 | 1 | ⬛ | ⬛ | ⬛ | ⬛ | ⬛ | ⬛ | ⬛ | ⬛ | ⬛ |
|  | 2 | ⬛ | ⬛ | ⬛ | ⬛ | ⬛ | ⬛ | ⬛ | ⬛ | ⬛ |
|  | 3 | ⬛ | ⬛ | ⬛ | ⬛ | ⬛ | ⬛ | ⬛ | ⬛ | ⬛ |
|  | 4 | 🟧 | 🟫 | 🟫 | 🟫 | 🟫 | 🟫 | 🟫 | 🟫 | 🟫 |
|  | 5 | 🟧 | 🟧 | 🟧 | 🟫 | 🟫 | 🟫 | 🟫 | 🟫 | 🟫 |

|  |  |
|---|---|
| ⬛ | Hu<Nc: 1.0E$^{08}$ – 1.0E$^{10}$ |
| 🟦 | Hu<Nc: 1.0E$^{06}$ – 1.0E$^{08}$ |
| ▨ | Hu<Nc: 1.0E$^{04}$ – 1.0E$^{06}$ |
|  |  |
| 🟨 | Hu>Nc: 1.0E$^{04}$ – 1.0E$^{06}$ |
| 🟧 | Hu>Nc: 1.0E$^{06}$ – 1.0E$^{08}$ |
| 🟫 | Hu>Nc: 1.0E$^{08}$ – 1.0E$^{09}$ |

The ANOVA of both datasets combined indicated that ‘Climate’ had a significant impact on seedbank size (P<0.001, see Table 5-7). Significant interactions were found between ‘Climate’ and all cultural control treatments except time from sowing to harvest in winter wheat (A_MT). Sowing time in carrot (V_ST) is the cultural control component that would show the largest response to a change in climate but perhaps surprisingly, sowing time in winter wheat (A_ST) was highly significant too; if the climate were to change to 'Heating up' then sowing winter wheat at the first, second or third date would reduce population size by about 45%, 20% and 9% on average compared to their equivalent sowing dates under 'No change'. The 2$^{nd}$ order interaction between 'Climate' and 'V_ST' and 'V_MT' was the only higher order interaction that was significant (P<0.001).

**Table 5-7** Anova table for the 1$^{st}$ and 2$^{nd}$ order effects on the log-transformed seedbank simulation data.

| Source of variation | d.f. | s.s. | m.s. | v.r. | F. pr. |
|---|---|---|---|---|---|
| | | | | | |
| **Scenario (Sc)** | 1 | 5.87E+01 | 5.87E+01 | 13.03 | <.001 |
| Residual | 98 | 4.41E+02 | 4.50E+00 | 67.05 | |
| | | | | | |
| **Sc * V_ST** | 4 | 2.26E+02 | 5.64E+01 | 839.98 | <.001 |
| **Sc * V_MT** | 2 | 8.04E+00 | 4.02E+00 | 59.85 | <.001 |
| **Sc * A_ST** | 2 | 2.83E+01 | 1.42E+01 | 210.74 | <.001 |
| Sc * A_MT | 2 | 8.64E-02 | 4.32E-02 | 0.64 | 0.526 |
| **Sc * V_ST * V_MT** | 8 | 4.89E+01 | 6.11E+00 | 91.06 | <.001 |
| Sc * V_ST * A_ST | 8 | 9.67E-03 | 1.21E-03 | 0.02 | 1.000 |
| Sc * V_MT * A_ST | 4 | 3.44E-02 | 8.61E-03 | 0.13 | 0.972 |
| Sc * V_ST * A_MT | 8 | 3.08E-05 | 3.84E-06 | 0.00 | 1.000 |
| Sc * V_MT * A_MT | 4 | 5.36E-04 | 1.34E-04 | 0.00 | 1.000 |
| Sc * A_ST * A_MT | 4 | 1.37E-01 | 3.43E-02 | 0.51 | 0.728 |
| ….. | | | | | |
| Residual | 13132 | 8.82E+02 | 6.71E-02 | | |
| Total | 13499 | 2.32E+04 | | | |

The high variance ratio for 'Residual' in Table 5-7 relative to that of 'Scenario' reflects that the random weather permutations have a considerable impact on seedbank dynamics within ECOSEDYN. This is largely due to the different seed production potential in the different weather years. For example, the number of viable seeds produced at the time of harvest of the carrot variety with the intermediate maturity time (V_MT=2) under 'No change' climate, varies approximately by a factor

15 in the 1st sowing time but by a factor 250 for the 5th sowing time between the least and the most beneficial weather year. Hence, cultural control scenarios in which three or four of the weather years assigned to carrot happen to be very advantageous for seed production result in far larger seedbanks than when three of the worst weather years for seed production are assigned to carrot (see Figure 5-9).

Hence, even for weed management scenarios where the average size over 50 replicates under one climate scenario is much larger than the average size under the other climate scenario, for a given weather year there is always a certain probability for a reverse effect (see Table 5-8, note that row order is different than in Table 5-6).

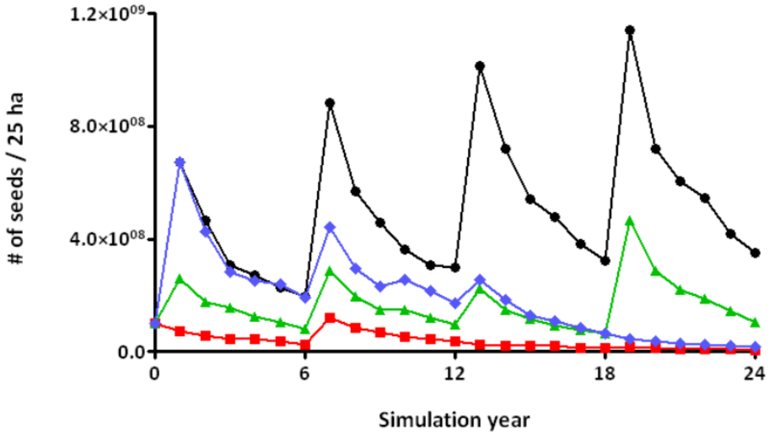
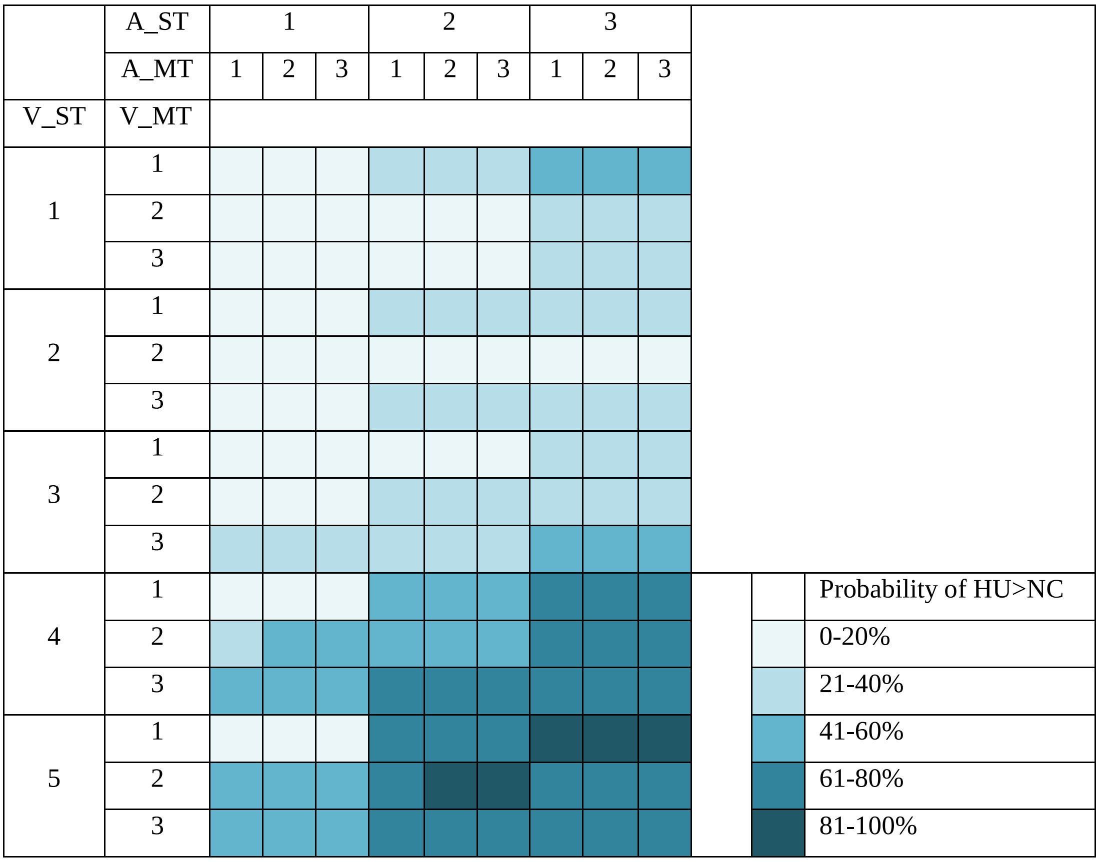


**Figure 5-9** Seed population dynamics for four different weather randomisations over the course of 4 crop rotations. The cultural control components were constant (A_ST=1, A_MT=1, V_ST=5, A_MT=3) as was the climate scenario ('No Change'). The black and the red line represent scenarios where three of the four weather years with carrot were in the top 3 and bottom 3 respectively of the seed production rank order.

For example, the average size of the seedbank of the three weed management scenarios with the characteristics [V_MT=3, V_ST=3, A_ST=3] is much larger under 'No change' than under 'Heating up' ($1.0E^{08} – 1.0E^{10}$, see Table 5-6) but there is still a 41-60% probability that a given weather year results in a higher seedbank under 'Heating up' than under 'No change' (see Table 5-8). Interestingly, whereas the maturity time in carrot (V_MT) has a large effect on the amplitude of the difference between the seedbank sizes in the two different climate scenarios (see Table 5-6), it is of minor importance regarding the probability of a given weather year resulting in a higher seedbank under one climate scenario than under another. The probability of the seedbank being higher under 'Heating up' than under 'No change' is largely a function of the time of sowing, both in carrot and winter wheat; the later the time of sowing, the higher the probability that the seedbank is larger under 'Heating up'. The weed management scenarios with the characteristics [V_ST=5, V_MT=1, A_ST=1] form a noteworthy exception to this trend. In addition, if winter wheat is sown early (A_ST=1) and a fast maturing carrot variety is chosen (V_MT=1), then, regardless of winter wheat variety (A_MT) or sowing time of carrot (V_ST), the probability that the seedbank will increase if the climate were to change to ‘Heating up’ is always less than 20%.

**Table 5-8** Probability of the seedbank being higher under ‘Heating up’ (HU) than under ‘No change’ (NC) for the full factorial of weed management scenarios. Blue shades indicate the percentage of 50 paired simulations in ECOSEDYN in which seedbanks were larger under ‘Heating up’ than under ‘No change’.



| | A_ST | 1 | | | 2 | | | 3 | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | A_MT | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 | 3 |
| V_ST | V_MT | | | | | | | | | |
| 1 | 1 | □ | □ | □ | ░ | ░ | ░ | ▒ | ▒ | ▒ |
| | 2 | □ | □ | □ | □ | □ | □ | ░ | ░ | ░ |
| | 3 | □ | □ | □ | □ | □ | □ | ░ | ░ | ░ |
| 2 | 1 | □ | □ | □ | ░ | ░ | ░ | ░ | ░ | ░ |
| | 2 | □ | □ | □ | □ | □ | □ | □ | □ | □ |
| | 3 | □ | □ | □ | ░ | ░ | ░ | ░ | ░ | ░ |
| 3 | 1 | □ | □ | □ | □ | □ | □ | ░ | ░ | ░ |
| | 2 | □ | □ | □ | ░ | ░ | ░ | ░ | ░ | ░ |
| | 3 | ░ | ░ | ░ | ░ | ░ | ░ | ▒ | ▒ | ▒ |
| 4 | 1 | □ | □ | □ | ▒ | ▒ | ▒ | ▓ | ▓ | ▓ |
| | 2 | ░ | ▒ | ▒ | ▒ | ▒ | ▒ | ▓ | ▓ | ▓ |
| | 3 | ▒ | ▒ | ▒ | ▓ | ▓ | ▓ | ▓ | ▓ | ▓ |
| 5 | 1 | □ | □ | □ | ▓ | ▓ | ▓ | █ | █ | █ |
| | 2 | ▒ | ▒ | ▒ | ▓ | █ | █ | ▓ | ▓ | ▓ |
| | 3 | ▒ | ▒ | ▒ | ▓ | ▓ | ▓ | ▓ | ▓ | ▓ |

| | Probability of HU>NC |
|---|---|
| □ | 0-20% |
| ░ | 21-40% |
| ▒ | 41-60% |
| ▓ | 61-80% |
| █ | 81-100% |

## *5.4 Conclusions and discussion*

The following research questions were postulated prior to the simulations:

1. Which cultural control practice, sowing time or crop variety, and applied in which crop, has most potential in alleviating long term weed seedbank levels?
2. Can cultural control practices applied in one crop (carrot or winter wheat) maintain sufficient low weed seedbank levels or is the application in both crops required?
3. Are the answers given for questions 1-2 different under the two climate scenarios?

Choosing a fast maturing carrot variety is the key to maintaining a low seedbank regardless of the prevailing climate. It must be emphasized that this result relies to some extent on the assumption of the carrot varieties being equally competitive, i.e. reducing the maximum per plant weed weight $W_{max-t}$ to the same extent. Bennett and Shaw (2000) found that late (i.e. slow) maturing soybean cultivars reduced weed seed production compared to intermediate maturing, most likely due to increased competitiveness. If slow maturing carrot varieties are associated with a higher reduction of maximum per plant weight $W_{max-t}$ through $bcc_{hq}$ (i.e. more competitive than fast maturing carrot varieties), then the benefits of choosing a fast maturing carrot variety may be reduced. However, the magnitude of difference of seed production between the fast (V_MT=1) and slow (V_MT=3) carrot varieties is so large (see bottom charts in Figure 5-4) that the reduction in maximum per plant weed weight $W_{max-t}$ in a slow carrot variety should be enormous to compensate for that.

The results of the ECOSEDYN simulations suggest that it is of no real benefit for carrot growers to persuade the arable farmer from whom the land is rented to select a fast maturing winter wheat variety unless varieties become available that mature considerably faster than the variety represented by [A_MT=1]. The reason for this is that each winter wheat variety is generally harvested after all or the vast majority of viable seeds have been produced whereas the harvest date of carrot either precedes or falls within the interval of viable seed production by the weed plants, depending on weather year and maturity time.

The simulations in ECOSEDYN further suggest that by consistently sowing winter wheat at the earliest date, the seedbank can be kept at a lower level than by sowing winter wheat at the second or third date. This shows that the benefit of a short time from sowing to 50% crop emergence outweighs the disadvantage of a right-skewed weed seedling emergence distribution. This effect was enhanced under ‘Heating up’.

In addition, compared to the intermediate and late sowing dates for winter wheat, sowing on the 1st of October results in the lowest probability of seedbanks increasing in size if the climate were to change to ‘Heating up’. Even though carrot maturity time is more influential in keeping the seedbank low, it is therefore still of extra benefit to select the earliest sowing date for winter wheat as an option of cultural weed control.

The simulations in ECOSEDYN suggest that, regardless of variety chosen, sowing carrot at the 5th sowing date (26 April) is the best strategy to maintain low seedbank levels if the climate does not change towards warmer spring – summer periods (i.e. remains as under ‘No change’). The fifth sowing time of carrot resulted in lower seedbank levels than other sowing times because simultaneously less biomass and fewer mature seeds per unit plant biomass were being produced.

If the climate were to change towards warmer spring – summer periods (‘Heating up’), then sowing carrot at the 5th sowing date is still best for the weed management scenarios with the longest maturity time of carrot [V_MT=3], but the 1st and 2nd sowing date result in slightly lower levels of the seedbank after 24 years than sowing at the 5th sowing date for the weed management scenarios with the short and intermediate maturity time of carrot, [V_MT=1] and [V_MT=2].

An encouraging result for growers is that this research suggests that the weed management scenarios that result in the lowest seedbank levels given ‘No Change’ climate, [V_MT=1, V_ST=5, A_ST=1], will lead to a decrease in seedbank levels of *T. inodorum* if the weather were to change towards warmer spring-summer periods (‘Heating up’) as well as a low probability for a bad year under ‘Heating up’. The weed management scenarios that are recommended based on this research are therefore characterized by short maturity time in carrot, late sowing time of carrot and early sowing time of winter wheat.

The results of the one year simulations provided explanation for the patterns observed in the 24 year simulations really well. This makes sense since the different parameter values for $S_f$ (number of seeds per flower) and $W_{max-t}$ used in carrot and winter wheat during the 24 year simulations affect only the number of seeds produced but not the ranking of the scenarios relative to each other.

For the carrot varieties with the short and intermediate maturity times, [V_MT=1] and [V_MT=2], there was no clear trend for seedbanks to be lower when sowing time was delayed (see Figure 5-4). Hence, components such as the distribution of seedling emergence, the time of 50% crop emergence and in particular the start of flowering are far more important in determining total plant biomass than the reduction in maximum per plant biomass due to late emergence in the season (see Section 4.7.1.1.3). This suggests that if the latest carrot sowing time does not exceed the 26th of April, the third biodiversity conservation coefficient for $W_{max}$, i.e. $bcc_{em}$, which relates to the proportion by which per plant biomass is maintained relative to the maximum per plant biomass when emerging early in the season, can therefore be left out of the model.

Because the germination and emergence model assumed no irrigation took place around the time of crop sowing, the distribution of seedling emergence varied widely and according to rainfall patterns. Assuming that primed carrot seeds require less moisture to germinate than weed seeds, then withholding irrigation would result in a more left-skewed distribution of weed seedling emergence, particularly in dry years. This in turn would mean that on average, weeds will remain smaller and start flowering and producing seeds later, resulting in lower seedbank levels.

# 6 Synthesis and discussion

## 6.1 Introduction

A brief overview is given of the research findings of the experimental work described in Chapters 3 and 4, with additional points for discussion. I then focus on the main priority of this PhD project, the development of ECOSEDYN, a modelling framework capable of simulating the long-term dynamics of weed populations. First I summarise the weed management guidelines based on the simulation results presented in Chapter 5. I then reflect on the model development phase of ECOSEDYN, the remaining work (sensitivity analysis and validation) and a general perspective on the future of weed science.

## 6.2 Experimental work

Although each experiment started out with a clear purpose related to the model, several experiments led to a discovery or development of techniques that were not anticipated beforehand but proved to be advantageous to the understanding of and the accuracy with which the system was represented within ECOSEDYN. These ‘accidental discoveries’ are an inherent serendipitous feature of research in all scientific disciplines (Singh, 2002). For example, the image analysis code to determine plant leaf area in MatLab had to be expanded to cope with the bright white flowers of *T. inodorum*. This enabled measuring ‘flowering area’ over time and propelled the idea to link biomass and flower production conceptually. Ultimately this led to a coherent set of model components for Biomass increase, Flowering and Seed shedding.

### 6.2.1 Seed distribution due to cultivation

The work on seed modelling revealed several issues, either directly from the experiments or afterwards from increased understanding. The experimental results showed that the ‘raw’ transition matrices of separate cultivation implements can not be directly multiplied if the effect on soil bulk density of successive cultivation events is opposite. This refers to cultivation events where the first cultivation expanded and the second cultivation compressed the soil. In practice this includes each cultivation event after the plough and possibly the spader. Given the experimental difficulties of sampling uneven loose soil and the imperative analytical modification of the transition matrix of the ‘soil compressing’ cultivation event afterwards, it is suggested from this work that for pragmatic reasons such combinations be modeled as one transition matrix. In that sense the decision to use one transition matrix for the ploughing plus the additional cultivation afterwards by Cousens and Moss (1990) was correct although at the time these analytical issues were not clarified.

A second result from the experimental work is the considerable replicate to replicate variation of transition matrices, partly a function of variation in working depth of the cultivation implement. From the experimental results it is hypothesized that the true working depth in the field follows a normal distribution around the working depth as set by the farm personnel. It follows that vertical re-distribution of seed in the soil also varies. This emphasizes the use of continuous models such as the one based on the Beta distribution used by Mohler *et al.* (2006) which assigns a probability density function for seeds at any depth prior to cultivation. To account for the variability in working depth, the parameters of the probability density function should be expressed as a function of starting depth and working depth of the cultivation implement. Combining spatially explicit models such as cellular automata, the Beta distribution function for the probability of vertical seed movement and germination and emergence models, the effects of variation in working depth could then be assessed on the variation in timing of emergence in the field.

A simple evaluation of average soil height before and after ploughing and the decrease of soil height over time indicated that the mechanistic soil movement models proposed by Colbach *et al.* (2000) and Roger-Estrade *et al.* (2001) underestimated final soil height. In reality the soil is compacted less than as suggested by these models and therefore the proportion of seeds in the active layer from where germination is not inhibited by depth-sensing mechanisms deployed by the seeds, is overestimated. On the other hand this would not necessarily have to lead to an overestimation of germination since the increase in soil compaction would result in a reduction of gas exchange in the soil with a consequent lower probability of germination (Benvenuti, 2003). The level of detail included in the germination and pre-emergence growth model used in combination with these seed movement models therefore determines the bias.

Indirectly the work on seed movement and the use of transition matrices as a tool for modelling seed movement, led to the realization that transition matrices have not considered seeds as part of the soil matrix but as independent particles. Except for seeds on the surface it is highly implausible to suggest that seeds at any depth in the soil should behave differently than the surrounding soil particles. The reason this might occur nonetheless under experimental conditions is because beads were applied at one depth in the soil rather than mixing the beads over a soil layer and/or uneven sampling. The stable depth distribution of a transition matrix with even soil layers should therefore be homogenous. In order to comply with this condition the row sums of such transition matrices should add up to one. This added constraint was implemented in ECOSEDYN for the hypothesized transition matrices of seedbed preparation and harvesting of carrots.

### 6.2.2 Plant growth and reproduction

The experimental work conducted on plant growth and reproduction was necessary to understand and represent the intricate relations that are present both temporally and quantitatively between biomass increase, flowering and seed production. The most important outcome of this work is a coherent set of component models based on the Beta growth function that was proposed by Yin *et al.* (2003) that has been described and parameterized in Chapter 4.

Mathematical descriptions were proposed for the effects of increased density of weed plants, delayed emergence relative to the crop, daylength and rainfall on the maximum size for plants, $W_{max}$. This was done based on established principles in crop and plant ecology such as the reciprocal yield law (Yoda *et al.*, 1963), empirical data found in the literature and by carefully scrutinizing the species-specific information that is available for *T. inodorum*.

Other results included the confirmation of effective day-degrees rather than day-degrees as the environmental variable to which *S. media* and *T. inodorum* responded in terms of biomass production. The relative growth rate of biomass was very similar to the relative growth rate of ‘green area’ reported by Storkey (2004).

In a paper by Gregorczyk (1998) it was hypothesized that the onset of flowering would coincide with the timing after which the increase in growth rate would start to decrease. This seemed intuitive given that reproductive structures generally contribute less than leaves to photosynthates. This was not the case however with a lag phase of 21 days in the response of biomass growth rate to the changed allocation patterns. Perhaps the cost of photosynthate allocation to reproductive plant parts consisting of less efficient photosynthetic tissues can be compensated for by the difference in specific leaf area (g $m^{-2}$) of buds as compared to leafs. Lower SLA figures imply reduced self-shading for plants in the early flowering stage when most reproductive structures are buds.

Interestingly, experiments show that large plants reach their reproductive effort later than small plants, leading to a non-linear relationship between plant biomass and reproductive structures. A correlation of the duration of flowering and plant size was hypothesized as a possible explanation for this which was confirmed in a second experiment. The non-linear relationship also provides a good explanation for the lack of a minimum size for flowering that is commonly inferred from linear regression lines. In practice a minimum size for flowering of 0.04 gr. was observed for *T. inodorum*.

## *6.3 ECOSEDYN*

I started out this project with the expectation that models were like take-away diners that just needed picking up from the right restaurant but ultimately it was back to the kitchen to create a recipe first for most of the component models. Clearly the order in which a modeling project should be carried out starts first and foremost with understanding the biology of the system, reflecting at what level it should be represented mathematically in the model and then finding plausible parameters. This was a slow process because of the sheer amount of new information at the start of the Phd.

A phenomenological approach was chosen for ECOSEDYN, i.e. including biological phenomena even if the exact relationships between the underlying mechanisms are not yet fully understood. This inevitably necessitated making assumptions. As long as it is clear when an assumption is made and on what arguments it is based there is no fundamental argument against taking assumptions. Science has to deal with reality and in reality we do not know everything, hence the need for assumptions. Providing clarity and rationale for assumptions was therefore attempted throughout the thesis. From a research point of view it is quite likely that a modelling project is one of the most successful ways of coming up with new hypotheses exactly because so many assumptions had to be made. This is one of the indirect contributions that models can make to research as argued by France and Thornley (1984). In that way from this thesis a range of further questions could be addressed over a wide range of scientific disciplines.

### 6.3.1 Weed management guidelines based on simulation results

Based on the simulations in ECOSEDYN the recommended weed management guidelines to carrot growers are in order of importance:

1. **Select a fast maturing carrot variety.** The sooner carrots are harvested the fewer viable weed seeds are produced. This study was limited to main crop carrots, i.e. those sown from April to mid-June but not the early carrots grown under polythene. However, large commercial carrot growers will grow a wide range of carrot types and varieties. According to the latest information from Elsoms (2009b), the fastest maturing carrot varieties are the Chantenay carrot (± 90 days), the varieties grown for bunching (± 88-90 days), some of the coloured varieties (e.g. Purple Haze F1, ± 85 days) and a few varieties for the pre-pack market (± 104 days). Given that crop growers aim to supply a wide variety of carrot types throughout the year they should, soil conditions permitting, try to alternate slow and fast maturing carrot varieties in the crop rotation of a given field. Fields that are known to have high weed levels could receive a higher proportion of fast maturing carrot varieties.
2. Persuade the arable farmer of whom the land is rented to **sow winter wheat early in October.** The reason for this is that the later winter wheat is sown, the longer the duration from sowing to 50% crop emergence. Since weeds do not experience an equal delay in emergence, the early winter wheat sowing is characterized by a lower total weed biomass. However, if weather conditions don’t permit sowing in early October it is better to postpone sowing until the end of, rather than halfway, October because the delay of weed seed emergence is more proportional to the delay of crop emergence.
3. **Sow carrot late in April, rather than early in March.** This is down to the combined effects that are induced by later carrot sowing times: a tendency of weed seedling emergence to decrease, a reduction of per plant weed biomass due to faster crop emergence and an increase of the proportion of weed plants in which flowering is initiated too late to achieve maximum seed production (photoperiodicity effect, see Figure 5-5). This study compared carrot sowing times over a time frame (March – April) narrower than the potential range of sowing times according to the cropping guide from Elsoms (2009a). It is most likely that

sowing carrot in May will result in even lower long-term weed seed bank levels because all of the above effects are enhanced.

The simulations also emphasise the importance of seed priming; the treatment of crop seed in such a way that minimises the level of soil moisture required to germinate. Indirect recommendations are therefore to maximize the potential of seed priming and to use irrigation only sparingly. In that way only the crop seed base water potential is fulfilled but not that of the majority of the weed seeds. Alternatively, since late sowing is recommended, irrigation may be applied some time prior to crop sowing in order to stimulate weed seed germination and emergence, followed by an application of glyphosate.

### 6.3.2 Future work

It would be unrealistic to divorce the required work on ECOSEDYN and the opportunities to address alternative research questions using ECOSEDYN from the somewhat bleak situation that weed science finds itself in at the moment.

Over the last decade, the UK, and other countries in the EU such as the Netherlands, have experienced a reduced interest from policy makers and funding bodies in traditional agronomical sciences and weed science in particular (Fernandez Quintanilla *et al.*, 2008). The current situation at Warwick HRI with just one active researcher in the Weeds group is symptomatic for many institutes and Universities in the UK that used to hold weed research groups. Has weed research become so successful that it has made itself redundant? Ask this question to the carrot growers affected by the loss of herbicides and the answer would be an unsurprising and resounding ‘No’. Ask the same question to the arable farmers that are faced with multiple resistance problems in blackgrass (*Alopecurus myosuroides*) and the answer is likely to be no again. What then causes this perceived notion of redundancy that surrounds applied agronomical sciences such as entomology, soil science and weed research?

Fernandez-Quintanilla *et al.* (2008) attribute this trend to “an increasing social and political perception of our lack of power to offer valuable services to society”. In the same paper they note that one of the major weaknesses in weed research is the relative weak knowledge of the biology and ecology of weeds. The plethora of assumptions that were required to ‘guestimate’ the value of parameters for biological model components in this project confirms this notion. According to Fernandez-Quintanilla *et al.* (2008) the “very limited human and financial resources available in the past” are to blame. Hence, weed science finds itself in a vicious circle in that without consistent research grants coming in, no consistent research programme can be set up to derive the imperative information on the biology and ecology of weed species. In turn, the lack of knowledge contributes to the high uncertainty related to yield loss predictions that has not been solved by recent modelling approaches.

Even some weed scientists remain skeptical about the role that models can play in weed research with Stephen Moss (2007) posing the question ‘Weed management: is it a case of trying to predict the unpredictable?’ at the 14th EWRS Symposium in Hamar. This notion exists most likely due to false expectations of the potential of models. Perhaps this is a result of exaggerating the potential of models in order to find the available funding from research funding bodies or stakeholders.

It would be more correct and would help avoid disappointment if the potential of models be communicated as giving projections rather than predictions. The definition of projection (from The Free Dictionary) better captivates the essence of what models are about:

> **To project:** to calculate, estimate, or predict (something in the future), based on present data or trends.
>
> **To predict:** to state, tell about, or make known in advance, especially on the basis of special knowledge.

It is difficult to meet expectations if the bar has been set too high, and in the long run, over hyping the potential of models is likely to prove counterproductive to the probability for weed research proposals aiming for a modeling approach. This idea has been reflected in the design of the modelling framework where ECOSEDYN was designed to be:

- ambitious in the range of processes included
- thorough at the level of representing the biology
- modest at the level of complexity
- realistic in the evaluation of model output

A quote epic amongst modelers is that ‘all models are wrong but some are useful’ by George Box (1979). The question whether a model is useful should be extended to include whether the assessment of model output is useful. The absolute value of the seedbank after 24 years is sensitive to a wide range of parameters but the ranking of the weed management scenarios is only sensitive to the values of the parameters in those component models that, when changed, affect some scenarios more than others. Ranking the outcome of the simulated weed management scenarios by ECOSEDYN should warrant the certificate ‘useful model’ since the uncertainty of most model parameters will equally affect each weed management scenario.

One of the most important phases of a modelling project is the evaluation phase (‘validation’) of the constructed model. Evaluating the proposed modelling framework is possible by comparing the ranking of the weed management scenarios with long-term field experiments. Though this can verify the projections of ECOSEDYN, it is not a verification of the component models themselves since it is possible that underestimation in one area is cancelled out in another. Given the scarcity of research grants available it is doubtful that such long-term evaluation studies are feasible in the current situation. A proper model evaluation therefore should attempt a validation on a component basis. Within the current timeframe this was feasible only for the model component for seed redistribution due to cultivation.

More specifically, future work on ECOSEDYN should address and focus on those model components (parameters) that have the highest impact on the ranking of the weed management scenarios.

The fact that maturity time of carrot is the dominant factor determining the ranking of the cultural control scenarios suggests that the starting time and duration of flowering are likely to be the two most sensitive components of the model. The limited data for flower duration that was available suggested that for the range of plant sizes expected within crops, flower duration is independent of starting time of flowering or plant size. In addition, the extent to which carrot varieties are equally competitive, i.e. reducing the maximum per plant weed weight, $W_{max-t}$ should be evaluated. Attempts at validating the model should therefore prioritise these three issues. A multi-year survey of the range of individual weed biomass present at harvest of both crops and crop varieties would provide some sort of validation of the chosen parameters of crop competitivity and the year-to-year variation due to weather effects on individual plant size.

It is important to note that the ranking of the scenarios is likely to be weed-specific; weed species with a more restricted period of emergence and/or weed species that are not photoperiodic are less likely to be affected as much by the maturity time in carrot and more by sowing time, either in carrot or winter wheat. This emphasizes the point that individual weed species would each be best controlled by different combinations of cultural control options. For ECOSEDYN to become of more practical value, it needs to be expanded with additional weed species, so that the optimal combination of cultural control options can be tailored to the particular weed species mixture present in the soil. However, this research has shown that to collect the required weed biology parameters for just one species already requires a substantial effort.

A potential step for ECOSEDYN is to simulate seedbank dynamics whilst alleviating the constraint of fixed cultural control factors. Suppose, for example the hypothetical situation where each of the three carrot varieties should be grown at least once over the course of 24 years. The question could be asked: what is the most beneficial order in which the varieties must be grown? ECOSEDYN could also be used to assess ideal crop rotation length (from a sustainable weed pressure perspective) for carrot varieties with intermediate to long times from sowing to harvest.

A number of significant factors are expected to change within the agricultural sector. In Europe the available number of herbicide products is expected to continue to decrease as well as the release of new products due to high investment costs (Kropff *et al.*, 2008). The current interest in biofuel crops is expected to increase over the coming decades and this could provide opportunities to get more diverse crop rotations and include highly competitive crops to compensate for reduced weed control in some years of the crop rotation (Kropff *et al.*, 2008). The reduced number of herbicides available should raise more interest in cultural control options that can be addressed by modeling frameworks such as ECOSEDYN.

# References

**van Acker, R. C., Lutman, P. J. W. and Froud-Williams, R. J.** (1997). The influence of interspecific interference on the seed production of *Stellaria media* and *Hordeum vulgare* (volunteer barley). *Weed Research*, **37** (4), 277-286.

**ADAS** (2003). Pest, Disease and Weed incidence report - Harvest year 2003. 175 p. Available at: http://www.pesticides.gov.uk/uploadedfiles/Web_Assets/PSD/pest_disease_weeds_report2003.pdf.

**ADAS** (2007). Pest, Disease and Weed incidence report - Harvest year 2006. 167 p. Available at: http://www.pesticides.gov.uk/uploadedfiles/Web_Assets/PSD/psd%20report%20harvest%20year%202006.pdf.

**Albrecht, H.** (2005). Development of arable weed seedbanks during the 6 years after the change from conventional to organic farming. *Weed Research*, **45** (5), 339-350.

**Andersson, L.** (1994). Effects of Mcpa and Tribenuron-Methyl on seed production and seed size of annual weeds. *Swedish Journal of Agricultural Research*, **24** (2), 49-56.

**Andersson, L., Milberg, P. and Noronha, A.** (1997). Germination response of weed seeds to light, light of short duration and darkness after stratification in soil. *Swedish Journal of Agricultural Research*, **27** (3), 113-120.

**Andersson, L. and Milberg, P.** (1998). Variation in seed dormancy among mother plants, populations and years of seed collection. *Seed Science Research*, **8** (1), 29-38.

**Andersson, L.** (1998). Post-dispersal seed removal in some agricultural weeds. *Aspects of Applied Biology*, **51**, 159-164.

**Anonymous** (2003). SAFETY DATA SHEET - ALPHA LINURON 50 SC. Available at: http://www.mauk.co.uk/pdfs/Alpha%20Linuron%2050SC.pdf. [Accessed 1/09/2008]

**Anonymous** (2001). Mayweeds. Herbiseed Brief Weed Guide. Herbiseed Twyford UK: 2001. 9 3.

**Anonymous** (2005). The impacts of climate change on agriculture - A vision for our rural landscape. *Proceedings of the a seminar held on Monday 7 February 2005*, London, p. 59. Available at: http://www.defra.gov.uk/farm/environment/climate-change/pdf/seminar-report.pdf.

**Ascard, J.** (1995). Effects of flame weeding on weed species at different developmental stages. *Weed Research*, **35** (5), 397-411.

**Aschan, G. and Pfanz, H.** (2003). Non-foliar photosynthesis - a strategy of additional carbon acquisition. *Flora (Jena)*, **198** (2), 81-97.

**Assured Produce** (2006). Crop specific protocol - Onions (Bulb and Shallots). 37 p. Available at: http://www.assuredproduce.co.uk/resources/000/158/236/Onions_bulb_00036_06.pdf.

**Assured Produce** (2007). Crop specific protocol - Carrots. 03/09. Available at: http://www.assuredproduce.co.uk/resources/000/237/702/carrots_2007.pdf.

**Assured Produce** (2008). Assured Produce standards. Available at: http://www.assuredproduce.co.uk/ap/scheme/standards.aspx. [Accessed 01/09/2008]

**Asumadu, H., Summerfield, R. J., Ellis, R. H. and Qi, A.** (1998). Variation in the Durations of the Photoperiod-sensitive and Photoperiod-insensitive Phases of Post-first Flowering Development in Maturity Isolines of Soyabean [Glycine max(L.) Merrill] 'Clark'. *Ann Bot*, **82** (6), 773-778.

**Azam-Ali, S. N., Crout, N. M. J. and Bradley, R. G.** (1994). Perspectives in modelling resource capture by crops. In: *Resource capture by crops*. Edited by J.L. Monteith, R.K. Scott and M.H. Unsworth. Nottingham: Nottingham University Press. pp. 125-148.

**Baerveldt, S. and Ascard, J.** (2002). Effect of cutting heigth on weed regrowth. *Proceedings of the 5th EWRS Workshop on Physical Weed Control*, Pisa, Italy, pp. 272-279.

**Balci, O.** (1994). Validation, verification, and testing techniques throughout the life cycle of a simulation study. *Annals of Operations Research*, **53**, 121-173.

**Ball, D. A.** (1992). Weed seedbank response to tillage, herbicides, and crop rotation sequence. *Weed Science*, **40** (4), 654-659.

**Ballaré, C. L., Scopel, A. L., Ghersa, C. M. and Sanchez, R. A.** (1987). The demography of *Datura ferox* (L.) in soybean crops. *Weed Research*, **27** (2), 91-102.

**Bàrberi, P. and Cascio, B. l.** (2001). Long-term tillage and crop rotation effects on weed seedbank size and composition. *Weed Research*, **41** (4), 325-340.

**Barnwell, P. and Cobb, A. H.** (1989). Physiological studies of mecoprop resistance in chickweed (*Stellaria media* L.) *Weed Research*, **29**, 135-140.

**Barralis, G., Chadoeuf, R. and Lonchamp, J. P.** (1988). Longevite des semences de mauvais herbes annuelles dans sol cultive. *Weed Research*, **28** (6), 407-418.

**Baskin, J. M. and Baskin, C. C.** (1976). High temperature requirement for afterripening in seeds of winter annuals. *New Phytologist*, **77** (3), 619-624.

**Baskin, J. M. and Baskin, C. C.** (1986). Temperature requirements for after-ripening in seeds of nine winter annuals. *Weed Research*, **26** (6), 375-380.

**Baskin, C. C. and Baskin, J. M.** (2006). The natural history of soil seed banks of arable land. *Weed Science*, **54** (3), 549-557.

**Batlla, D., Kruk, B. C. and Benech-Arnold, R. L.** (2000). Very early detection of canopy presence by seeds through perception of subtle modifications in red:far red signals. *Functional Ecology*, **14** (2), 195-202.

**Baumann, D. T., Bastiaans, L. and Kropff, M. J.** (2001). Effects of intercropping on growth and reproductive capacity of late-emerging *Senecio vulgaris* L., with special reference to competition for light. *Annals of Botany*, **87** (2), 209-217.

**Beckie, H. J. and Jana, S.** (2000). Selecting for triallate resistance in wild oat. *Canadian Journal of Plant Science*, **80** (3), 665-667.

**Beckie, H. J. and Kirkland, K. J.** (2003). Implication of reduced herbicide rates on resistance enrichment in wild oat (*Avena fatua*). *Weed Technology*, **17** (1), 138-148.

**Beckie, H. J. and Gill, G. S.** (2006). Strategies for managing herbicide-resistant weeds. In: *Handbook of sustainable weed management*. Edited by H. P. Singh, D. R. Batish and R. K. Kohli. Binghamton, USA: Food Products Press. pp. 581-625.

**Bello, I. A., Hatterman-Valenti, H. and Owen, M. D. K.** (2000). Factors affecting germination and seed production of *Eriochloa villosa*. *Weed Science*, **48** (6), 749-754.

**Ben Amar, C., Zaied, M. and Alimi, M. A.** (2005). Beta wavelets: synthesis and application to lossy image compression. *Journal of Advances in Engineering Software*, **36** (7), 459-474.

**Benech Arnold, R. L., Ghersa, C. M., Sanchez, R. A. and Insausti, P.** (1989). Temperature effects on dormancy release and germination rate in *Sorghum halepense* (L.) Pers. seeds: a quantitative analysis. *Weed Research*, **30** (2), 81-89.

**Benjamin, L. R. and Park, S. E.** (2007). The Conductance model of plant growth and competition in monoculture and species mixtures: a review. *Weed Research*, **47** (4), 284-298.

**Bennett, A. C. and Shaw, D. R.** (2000). Effect of preharvest desiccants on weed seed production and viability. *Weed Technology*, **14** (3), 530-538.

**Benvenuti, S., Macchia, M. and Miele, S.** (2001a). Quantitative analysis of emergence of seedlings from buried weed seeds with increasing soil depth. *Weed Science*, **49** (4), 528-535.

**Benvenuti, S., Macchia, M. and Miele, S.** (2001b). Light, temperature and burial depth effects on *Rumex obtusifolius* seed germination and emergence. *Weed Research*, **41** (2), 177-186.

**Benvenuti, S.** (2003). Soil texture involvement in germination and emergence of buried weed seeds. *Agronomy Journal*, **95** (1), 191-198.

**Benvenuti, S.** (2007). Natural weed seed burial: effect of soil texture, rain and seed characteristics. *Seed Science Research*, **17** (3), 211-219.

**Bierzychudek, P.** (1999). Looking backwards: Assessing the projections of a transition matrix model. *Ecological Applications*, **9** (4), 1278-1287.

**Bindi, M., Sinclair, T. R. and Harrison, J.** (1999). Analysis of seed growth by linear increase in harvest index. *Crop Science*, **39** (2), 486-493.

**Bischoff, A.** (2005). Analysis of weed dispersal to predict chances of re-colonisation. *Agriculture, Ecosystems & Environment*, **106** (4), 377-387.

**Blackshaw, R. E. and Harker, K. N.** (1997). Scentless chamomile (*Matricaria perforata*) growth, development, and seed production. *Weed Science*, **45** (5), 701-705.

**Blackshaw, R. E., O'Donovan, J. T., Harker, K. N., Clayton, G. W. and Stougaard, R. N.** (2006). Reduced herbicide doses in field crops: a review. *Weed Biology and Management*, **6** (1), 10-17.

**Blanco Moreno, J. M., Chamorro, L., Masalles, R. M., Recasens, J. and Sans, F. X.** (2004). Spatial distribution of *Lolium rigidum* seedlings following seed dispersal by combine harvesters. *Weed Research*, **44** (5), 375-387.

**Blumenthal, D. and Jordan, N.** (2001). Weeds in field margins: a spatially explicit simulation analysis of Canada thistle population dynamics. *Weed Science*, **49** (4), 509-519.

**Boatman, N. D. and Freeman, K. J.** (1988). The effects of timing and dose on the control of *Galium aparine* (cleavers) and other broadleaved weeds by fluroxypyr in cereal headlands. *Aspects of Applied Biology*, **18**, 117-128.

**Bond, W. and Turner, R. J.** (2004). Rare arable weeds. Retrieved 31/08/2007, from http://www.gardenorganic.org.uk/organicweeds/downloads/rarearableweeds.pdf.

**Booth, B. D., Murphy, S. D. and Swanton, C. J.** (2003). Weed ecology in natural and agricultural systems. Wallingford, Oxon, UK: Cabi Publishing. 303 p.

**BOPA** (2006). British Onion Producers Association (BOPA) Research and Development Committee – Research Strategy 2006/07 Season. Available at: http://www.hdc.org.uk/sectors/FV%20R&D%20Onion%20Research%20Priorities%202006.pdf. [Accessed 15/08/2006]

**Botto, J. F., Scopel, A. L. and Sanchez, R. A.** (2000). Water constraints on the photoinduction of weed seed germination during tillage. *Australian Journal of Plant Physiology*, **27** (5), 463-471.

**Bowes, G. G., Thomas, A. G. and Lefkovitch, L. P.** (1995). Changes with time in the germination of buried scentless chamomile (*Matricaria perforata* Merat) seeds. *Canadian Journal of Plant Science*, **75** (1), 277-281.

**Box, G. E. P.** (1979). Robustness in the strategy of scientific model building. In: *Robustness in statistics*. Edited by R.L. Launer and G.N. Wilkinson. New York: Academic Press. p. 296.

**Boyd, N. and van Acker, R.** (2004). Seed and microsite limitations to emergence of four annual weed species. *Weed Science*, **52** (4), 571-577.

**Bradford, K. J.** (2002). Applications of hydrothermal time to quantifying and modeling seed germination and dormancy. *Weed Science*, **50** (2), 248-260.

**Brain, P. and Cousens, R.** (1990). The effect of weed distribution on predictions of yield loss. *Journal of Applied Ecology*, **27** (2), 735-742.

**Brainard, D. C. and Bellinder, R. R.** (2004). Assessing variability in fecundity of *Amaranthus powellii* using a simulation model. *Weed Research*, **44** (3), 203-217.

**van den Brand, W. G. M.** (1987). Biologie en ecologie van vogelmuur (*Stellaria media*). Lelystad: Proefstation voor de akkerbouw en de groenteteelt in de vollegrond. 49 p.

**Briggs, D., Hodkinson, H. and Block, M.** (1991). Precociously developing individuals in populations of chickweed [*Stellaria media* (L.) Vill.] from different habitat types, with special reference to the effects of weed control measures. *New Phytologist*, **117** (1), 153-164.

**van den Broek, R. C. M. F.** (2002). Rassenbulletin zaaiuien: 2001/2002. PPO, Wageningen University. Available at: http://documents.plant.wur.nl/ppo/rassenbulletins/RB_Zaaiuien_20012002.pdf.

**Buchanan, F. S., Swanton, C. J. and Gillespie, T. J.** (1990). Postemergence control of weeds in winter rapeseed, *Brassica napus*, with DPX-A7881. *Weed Science*, **38** (4-5), 389-395.

**Buckley, Y. M., Hinz, H. L., Matthies, D. and Rees, M.** (2001). Interactions between density-dependent processes, population dynamics and control of an invasive plant species, *Tripleurospermum perforatum* (scentless chamomile). *Ecology Letters*, **4** (6), 551-558.

**Buckley, Y. M., Briese, D. T. and Rees, M.** (2003). Demography and management of the invasive plant species Hypericum perforatum. I. Using multi-level mixed-effects models for characterizing growth, survival and fecundity in a long-term data set. *Journal of Applied Ecology*, **40** (3), 481-493.

**Buhler, D. D.** (1999). Expanding the context of weed management. In: *Expanding the context of weed management*. Edited by D. D. Buhler. Binghamton, NY: Food Products Press, an imprint of The Haworth Press, Inc., pp. 1-7.

**Cappuccino, N.** (2004). Allee effect in an invasive alien plant, pale swallow-wort *Vincetoxicum rossicum* (Asclepiadaceae). *Oikos*, **106** (1), 3-8.

**Carmona, R. and Boas, H. D. d. C. V.** (2001). The dynamics of *Bidens pilosa* seeds in the soil. *Pesquisa Agropecuaria Brasileira*, **36** (3), 457-463.

**Caswell, H.** (2001). Matrix population models: construction, analysis and interpretation. 2nd Edition. Sunderland, Massachusetts: Sinauer Associates, Inc. Publishers.

**Central Science Laboratory** (2008). Pesticide Usage Statistics. Available at: http://pusstats.csl.gov.uk/mytreatindex.cfm. [Accessed 6/2/2008]

**Chambers, J. C. and MacMahon, J. A.** (1994). A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. *Annual revues ecological systems*, **25**, 263-292.

**Chancellor, R. J.** (1986). Decline of arable weed seeds during 20 years in soil under grass and the periodicity of seedling emergence after cultivation. *Journal of Applied Ecology*, **23** (2), 631-637.

**Clarke, J. H., Clark, W. S. and Hancock, M.** (1997). Strategies for the prevention of development of pesticide resistance in the UK - lessons for and from the use of herbicides, fungicides and insecticides. *Pesticide Science*, **51** (3), 391-397.

**Clarke, J.** (1998). Managing herbicide resistant weeds. Available at: http://www.hgca.com/publications/documents/cropresearch/RD_roadshow_1998_paper_6.pdf. [Accessed 2008/15/02]

**Clarke, J.** (2002). Weed management strategies for winter cereals. In: *Weed management handbook*, ninth edn. Edited by Robert E L Naylor. Oxford: Blackwell Science Ltd. for British Crop Protection Council. pp. 354-358.

**Clay, S. A. and Aguilar, I.** (1998). Weed seedbanks and corn growth following continuous corn or alfalfa. *Agronomy Journal*, **90** (6), 813-818.

**Cohen, D.** (1976). The optimal timing of reproduction. *American Naturalist*, **110**, 801-807.

**Colbach, N. and Debaeke, P.** (1998). Integrating crop management and crop rotation effects into models of weed population dynamics: a review. *Weed Science*, **46** (6), 717-728.

**Colbach, N., Roger-Estrade, J., Chauvel, B. and Caneill, J.** (2000). Modelling vertical and lateral seed bank movements during mouldboard ploughing. *European Journal of Agronomy*, **13** (2/3), 111-124.

**Colbach, N., Durr, C. and Roger-Estrade, J.** (2005). How to model the effects of farming practices on weed emergence. *Weed Research*, **45** (1), 2-17.

**Colbach, N., Durr, C., Roger-Estrade, J., Chauvel, B. and Caneill, J.** (2006). AlomySys: Modelling black-grass (*Alopecurus myosuroides* Huds.) germination and emergence, in interaction with seed characteristics, tillage and soil climate - I. Construction. *European Journal of Agronomy*, **24** (2), 95-112.

**Copping, L. G.** (2002). Herbicide discovery. In: *Weed management handbook*. Edited by R.E.L. Naylor. Oxford: Blackwell Publishing. pp. 93-113.

**Cousens, R., Brain, P., Odonovan, J. T. and Osullivan, P. A.** (1987). The use of biologically realistic equations to describe the effects of weed density and relative-time of emergence on crop yield. *Weed Science*, **35** (5), 720-725.

**Cousens, R. and Moss, S. R.** (1990). A model of the effects of cultivation on the vertical distribution of weed seeds within the soil. *Weed Research*, **30** (1), 61-70.

**Cousens, R. D. and Mortimer, A. M.** (1995). Dynamics of weed populations. Cambridge: Cambridge University Press. 332 p.

**Crawley, M. J.** (1990). The population dynamics of plants. *Philosophical Transactions of the Royal Society of London*, **330** (1257), 125-140.

**Crawley, M. J.** (1997). Plant-Herbivore Dynamics. In: *Plant Ecology*, 2nd edn. Edited by Michael J. Crawley: Blackwell Science. p. 426.

**CRC for Catchment and Hydrology** (2005). General approaches to modelling and practical issues of model choice: Series on model choice. Available at: http://www.toolkit.net.au/pdfs/MC-1.pdf. [Accessed 31/07/2007]

**Currence, H. D. and Lovely, W. G.** (1970). The analysis of soil surface roughness. *Transactions of the American Society of Agricultural Engineers*, **13** (6), 710-714.

**Curry, D.** (2002). Farming and Food: a Sustainable Future. Report of the Policy Commission on the Future of Farming and Food. London: Cabinet Office. 152 p. Available at: http://archive.cabinetoffice.gov.uk/farming/pdf/PC%20Report2.pdf.

**Dauer, J. T., Mortensen, D. A. and Vangessel, M. J.** (2007). Temporal and spatial dynamics of long-distance *Conyza canadensis* seed dispersal. *Journal of Applied Ecology*, **44** (1), 105-114.

**Davis, A. S., Dixon, P. M. and Liebman, M.** (2003). Cropping system effects on giant foxtail (*Setaria faberi*) demography: II. Retrospective perturbation analysis. *Weed Science*, **51** (6), 930-939.

**Davis, A. S., Dixon, P. M. and Liebman, M.** (2004a). Using matrix models to determine cropping system effects on annual weed demography. *Ecological Applications*, **14** (3), 655-668.

**Davis, H. G., Taylor, C. M., Lambrinos, J. G. and Strong, D. R.** (2004b). Pollen limitation causes an Allee effect in a wind-pollinated invasive grass (*Spartina alterniflora*). *Proceedings of the National Academy of Sciences of the United States of America*, **101** (38), 13804-13807.

**Davis, A. S. and Renner, K. A.** (2007). Influence of seed depth and pathogens on fatal germination of velvetleaf (*Abutilon theophrasti*) and giant foxtail (*Setaria faberi*). *Weed Science*, **55** (1), 30-35.

**Debaeke, P.** (1988a). Modélisation de l'évolution à long terme de la flore adventice. II: Application à trois dicotylédones annuelles en un site donné *Agronomie*, **8** (9), 767-777.

**Debaeke, P.** (1988b). Dynamique de quelques dicotylenes adventices en culture de cereale. II. Survie, floraison et fructification. *Weed Research*, **28** (4), 265-279.

**DEFRA** (2006). Basic Horticultural Statistics - Vegetable details 2006. Available at: http://statistics.defra.gov.uk/esg/publications/bhs/2006/vegetable%20details.pdf. [Accessed 18/02/2008]

**van Delden, A., Lotz, L. A. P., Bastiaans, L., Franke, A. C., Smid, H. G., Groeneveld, R. M. W. and Kropff, M. J.** (2002). The influence of nitrogen supply on the ability of wheat and potato to suppress *Stellaria media* growth and reproduction. *Weed Research*, **42** (6), 429-445.

**Department of the Environment** (1990). This Common Inheritance: Britain's Environmental Strategy. London: HMSO. Cm1200.

**Deregibus, V. A., Casal, J. J., Jacobo, E. J., Gibson, D., Kauffman, M. and Rodriguez, A. M.** (1994). Evidence that heavy grazing may promote the germination of *Lolium multiflorum* seeds via phytochrome-mediated perception of high red/far-red ratios. *Functional Ecology*, **8** (4), 536-542.

**Dessaint, F., Chadoeuf, R. and Barralis, G.** (1996). Influence of tillage on the vertical distribution of simulated plastic seeds. In: *Proceedings of the second international weed control congress, Copenhagen, Denmark, 25-28 June 1996: Volumes 1-4.* Edited by H. Brown, G. W. Cussans, M. D. Devine, S. O. Duke, C. Fernandez-Quintanilla, A. Helweg, R. E. Labrada, M. Landes, P. Kudsk and J. C. Streibig. Slagelse, Denmark: Department of Weed Control and Pesticide Ecology. pp. 95-100.

**Dicke, D., Gerhards, R., Buchse, A. and Hurle, K.** (2007). Modeling spatial and temporal dynamics of Chenopodium album L. under the influence of site-specific weed control. *Crop Protection*, **26** (3), 206-211.

**Donald, W. W.** (1993). Models and sampling for studying weed seed survival with wild mustard (*Sinapis arvensis*) as a case study. *Canadian Journal of Plant Science*, **73** (2), 637-645.

**Douglas, D. W., Thomas, A. G., Peschken, D. P., Bowes, G. G. and Derksen, D. A.** (1991). Effect of summer and winter annual scentless chamomile (*Matricaria perforata* Merat) interference on spring wheat yield. *Canadian Journal of Plant Science*, **71** (3), 841-850.

**Elsoms** (2007a). Roots. Available at: http://www.elsoms.com/PDFs/27-31.pdf. [Accessed 26/10/2007]

**Elsoms** (2007b). Alliums. Available at: http://www.elsoms.com/PDFs/23-26.pdf. [Accessed 29/08/2008]

**Elsoms** (2007c). Vegetable Production Guide. Available at: http://www.elsoms.com/PDFs/46-49.pdf. [Accessed 26/10/2007]

**Elsoms** (2009a). Sowing and harvest times for Nantes (Prepack) carrots. Available at: http://www.elsoms.com/Images/nantes-prod-new.aspx. [Accessed 27/11/2009/2009]

**Elsoms** (2009b). Carrots & Parsnips --> Carrots --> Nantes (Pre-pack). Available at: http://www.elsoms.com/vegetables/carrots---parsnips/carrots/nantes.aspx. [Accessed 6/10/2009]

**Farmers Guardian** (2007). Focus on the future of cereal weed control - one day Conference (12th July 2007) Peterborough, UK. Available at: http://www.farmersguardian.com/weedfocus. [Accessed 07/02/2008]

**Farmers Weekly Interactive** (2007). Double herbicide blow as trifluralin ban announced. Available at: http://www.fwi.co.uk/Articles/2007/03/21/102421/double-herbicide-blow-as-trifluralin-ban-announced.html. [Accessed 12/02/2008]

**Faculty of Agricultural Sciences (Aarhus University Denmark)** (2001). Pl@nteInfo - Crop protection online (Demo version). Available at: http://pvo.planteinfo.dk/cp/menu/menu.asp?subjectid=1&id=demo. [Accessed 01/04/2008]

**Feldman, S. R., Alzugaray, C., Torres, P. S. and Lewis, J. P.** (1998). Gap colonization by weeds in a wheat crop grown under different cultivation regimes. *Weed Research*, **38** (1), 35-45.

**Fenner, M., Cresswell, J. E., Hurley, R. A. and Baldwin, T.** (2002). Relationship between capitulum size and pre-dispersal seed predation by insect larvae in common Asteraceae. *Oecologia*, **130** (1), 72-77.

**Fernandez Quintanilla, C., Quadranti, M., Kudsk, P. and Barberi, P.** (2008). Which future for weed science? *Weed Research*, **48**, 297-301.

**Fernandez Quintanilla, C., Barroso, J., Recasens, J., Sans, X., Torner, C. and Sanchez del Arco, M. J.** (2000). Demography of *Lolium rigidum* in winter barley crops: analysis of recruitment, survival and reproduction. *Weed Research*, **40** (3), 281-291.

**Fernandez Quintanilla, C., Navarrete, L., Andujar, J. L. G., Fernandez, A. and Sanchez, M. J.** (1986). Seedling recruitment and age-specific survivorship and reproduction in populations of *Avena sterilis* L. ssp. *ludoviciana* (Durieu) Nyman. *Journal of Applied Ecology*, **23** (3), 945-955.

**Finch-Savage, W. E., Steckel, J. R. A. and Phelps, K.** (1998). Germination and post-germination growth to carrot seedling emergence: predictive threshold models and sources of variation between sowing occasions. *New Phytologist*, **139** (3), 505-516.

**Firbank, L. G. and Watkinson, A. R.** (1986). Modelling the population dynamics of an arable weed and its effects upon crop yield. *Journal of Applied Ecology*, **23** (1), 147-159.

**Firbank, L. G.** (1988). Biological Flora of the British Isles (series): *Agrostemma githago* L. . *Journal of Ecology*, **76** (4), 1232-1246.

**Fitter, A. H. and Peat, H. J.** (1994). The Ecological Flora Database (see http://www.ecoflora.co.uk). *Journal of Ecology*, **82**, 415-425.

**Fogelberg, F. and Gustavsson, A. M. D.** (1999). Mechanical damage to annual weeds and carrots by in-row brush weeding. *Weed Research*, **39** (6), 469-479.

**Fogelfors, H.** (1985). The importance of the field edge as a spreader of seed-propagated weeds. In: *Weeds and weed control*. Edited by G. Gummesson. Uppsala Sweden: 1. Reports. Sveriges Lantbruksuniversitet. pp. 178-189.

**Forcella, F., Arnold, R. L. B., Sanchez, R. and Ghersa, C. M.** (2000). Modeling seedling emergence. *Field Crops Research*, **67** (2), 123-139.

**Forcella, F.** (2003). Debiting the seed bank: priorities and predictions. *Aspects of Applied Biology*, **69**, 151-162.

**France, J. and Thornley, J. H. M.** (1984). Mathematical models in agriculture : a quantitative approach to problems in agriculture and related sciences. London [etc]: Butterworths. 335 p.

**Froud-Williams, R. J., Drennan, D. S. H. and Chancellor, R. J.** (1983). Influence of cultivation regime on weed floras of arable cropping systems. *Journal of Applied Ecology*, **20** (1), 187-197.

**Froud Williams, R. J., Drennan, D. S. H. and Chancellor, R. J.** (1984). The influence of burial and dry storage upon cyclic changes in dormancy, germination and response to light in seeds of various arable weeds. *New Phytologist*, **96** (3), 473-482.

**Froud-Williams, R. J., Chancellor, R. J. and Drennan, D. S. H.** (1984). The effects of seed burial and soil disturbance on emergence and survival of arable weeds in relation to minimal cultivation. *Journal of Applied Ecology*, **21** (2), 629-641.

**Gallandt, E. R., Liebman, M. and Huggins, D. R.** (1999). Improving soil quality: implications for weed management. *Journal of Crop Production*, **2** (1), 95-121.

**Gallandt, E. R.** (2006). How can we target the weed seedbank? *Weed Science*, **54** (3), 588-596.

**Garrett, K. A. and Dixon, P. M.** (1998). When does the spatial pattern of weeds matter? Predictions from neighborhood models. *Ecological Applications*, **8** (4), 1250-1259.

**Garthwaite, D. G., Thomas, M. R., Dawson, A., Stoddart, H. and Anderson, H.** (2004). Pesticide Usage Survey Report 195 - Outdoor vegetable crops in Great Britain 2003. Sand Hutton, York: Central Science Laboratory. 104 p. Available at: http://www.csl.gov.uk/newsAndResources/resourceLibrary/articles/puskm/outdoorveg2003.pdf.

**Garthwaite, D. G., Thomas, M. R., Heywood, E. and Battersby, A.** (2006). Pesticide Usage Survey Report 213 - Arable crops in Great Britain 2006. Sand Hutton, York: Central Science Laboratory. 116 p. Available at: http://www.csl.gov.uk/newsAndResources/resourceLibrary/articles/puskm/arable2006.pdf.

**Gianessi, L. P. and Reigner, N. P.** (2007). The value of herbicides in U.S. crop production. *Weed Technology*, **21** (2), 559-566.

**Gillman, M., Bullock, J. M., Silvertown, J. and Hill, B. C.** (1993). A density-dependent model of *Cirsium vulgare* population-dynamics using field-estimated parameter values. *Oecologia*, **96** (2), 282-289.

**Gleadell** (2007). Cordiale - winter wheat. Available at: http://www.gleadell.co.uk/Cordiale.htm. [Accessed 11/06/2008]

**Goldberg, D. E., Turkington, R., Olsvig-Whittaker, L. and Dyer, A. R.** (2001). Density dependence in an annual plant community: variation among life history stages. *Ecological Monographs*, **71** (3), 423-446.

**Goldsworthy, P.** (2006). The Voluntary Initiative: successes and future challenges. *Proceedings of the HGCA Conference on Arable Crop Protection in the Balance: Profit and the Environment*, Grantham, UK, pp. 17.1-17.7. Available at: http://www.hgca.com/document.aspx?fn=load&media_id=2503&publicationId=1305.

**Gonzalez Andujar, J. L., Perry, J. N. and Moss, S. R.** (1999). Modeling effects of spatial patterns on the seed bank dynamics of *Alopecurus myosuroides*. *Weed Science*, **47** (6), 697-705.

**Gonzalez Andujar, J. L. and Fernandez Quintanilla, C.** (2004). Modelling the population dynamics of annual ryegrass (*Lolium rigidum*) under various weed management systems. *Crop Protection*, **23** (8), 723-729.

**Grant, W., Pedersen, E. K. and Marin, S. L.** (2000). Ecological Modelling: Systems Analysis and Simulation. In: *Handbook of Ecosystem Theories and Management*. Edited by S.E. Jørgensen and F. Müller. Boca Raton, FL: CRC Press - Lewis Publishers. pp. 103-110.

**Gregorczyk, A.** (1998). Richards Plant Growth Model. *Journal of Agronomy and Crop Science*, **181** (4), 243-247.

**Gressel, J. and Segel, L. A.** (1978). Paucity of plants evolving genetic resistance to herbicides - possible reasons and implications. *Journal of Theoretical Biology*, **75** (3), 349-371.

**Gressel, J.** (1995). Creeping resistances: the outcome of using marginally-effective or reduced rates of herbicides. *Proceedings of the Brighton crop protection conference: weeds*, Brighton, pp. 587-590.

**Grimme** (2003). Shaping, separating, planting: Innovative cultivation in 1 and 3 beds. Available at: http://www.grimme.de/Grimme_2003/PDF/Beetsystem_GB.pdf. [Accessed 31/08/2008]

**van Groenendael, J. M., de Kroon, H. and Caswell, H.** (1988). Projection matrices in population biology. *Trends in Ecology and Evolution.*, **3** (10), 264-269.

**Grundy, A. C., Mead, A. and Bond, W.** (1996). Modelling the effect of weed-seed distribution in the soil profile on seedling emergence. *Weed Research*, **36** (5), 375-384.

**Grundy, A. C.** (1997). The influence of temperature and water potential on the germination of seven different dry-stored seed lots of *Stellaria media*. *Weed Research*, **37** (4), 257-266.

**Grundy, A. C., Mead, A. and Burston, S.** (1999). Modelling the effect of cultivation on seed movement with application to the prediction of weed seedling emergence. *Journal of Applied Ecology*, **36** (5), 663-678.

**Grundy, A. C. and Mead, A.** (2000). Modeling weed emergence as a function of meteorological records. *Weed Science*, **48** (5), 594-603.

**Grundy, A. C., Mead, A. and Burston, S.** (2003a). Does weed seed sowing density significantly effect weed emergence response to burial depth? *Aspects of Applied Biology*, **69**, 39-46.

**Grundy, A. C., Mead, A. and Burston, S.** (2003b). Modelling the emergence response of weed seeds to burial depth: interactions with seed density, weight and shape. *Journal of Applied Ecology*, **40** (4), 757-770.

**Grundy, A. C.** (2003). Predicting weed emergence: a review of approaches and future challenges. *Weed Research*, **43** (1), 1-11.

**Grundy, A. C., Knott, C., Lutman, P. J., Marshall, E. J. P., Sunderland, K., Smith, B. and Fenlon, J.** (2003c). The impact of herbicides on weed abundance and biodiversity in horticulture. *Defra Project HH3403SX*, 287 pp.

**Grundy, A. C., Mead, A., Burston, S. and Overs, T.** (2004). Seed production of *Chenopodium album* in competition with field vegetables. *Weed Research*, **44** (4), 271-281.

**Gulden, R. H., Thomas, A. G. and Shirtliffe, S. J.** (2004). Secondary dormancy, temperature, and burial depth regulate seedbank dynamics in canola. *Weed Science*, **52** (3), 382-388.

**Gummerson, R. J.** (1986). The effect of constant temperatures and osmotic potential on the germination of sugar beet. *Journal of Experimental Botany*, **37**, 729-741.

**Guul-Simonsen, F., Jrgensen, M. H., Have, H. and Hakansson, I.** (2002). Studies of plough design and ploughing relevant to conditions in Northern Europe. *Acta Agriculturae Scandinavica*, **52** (2/3), 57-77.

**Haefner, J. W.** (2005). Modeling biological systems : Principles & applications. 2nd Edition. New York: Springer-Verlag. 480 p.

**Håkansson, S.** (2003). Weeds and weed management on arable land: an ecological approach. 1st Edition. Wallingford: CAB International. 274 p.

**Hamilton, J.** (2007). Vegetable News, December 2007. 4 p. Available at: http://www.ruralni.gov.uk/vegnews1207_chdb.pdf.

**Hansson, M. L., Bostrom, U. and Fogelfors, H.** (2001). Influence of harvest time and stubble height on weed seedling recruitment in a green cereal. *Acta Agriculturae Scandinavica*, **51** (1), 2-9.

**Hartmann, K., Krooß, C. and Mollwo, A.** (1997). Phytochrome-mediated photocontrol of the germination of the scentless mayweed, *Matricaria inodora* L.,and its sensitization by nitrate and temperature. *Journal Of Photochemistry And Photobiology B: Biology*, **40**, 240-252.

**Hartmann, K. M., Grundy, A. C. and Market, R.** (2005). Phytochrome-mediated long-term memory of seeds. *Protoplasma*, **227** (1), 47-52.

**Heath, O. V. S.** (1937). The growth in height and weight of the cotton plant under field conditions. *Annals of Botany*, **1** (3), 515-520.

**van Heemst, H. D. J.** (1985). The influence of weed competition on crop yield. *Agricultural Systems*, **18** (2), 81-93.

**Heggenstaller, A. H., Menalled, F. D., Liebman, M. and Westerman, P. R.** (2006). Seasonal patterns in post-dispersal seed predation of Abutilon theophrasti and Setaria faberi in three cropping systems. *Journal of Applied Ecology*, **43** (5), 999-1010.

**Hess, F. D.** (1994). Research needs in weed science. *Weed Technology*, **8** (2), 408-409.

**HGCA** (1997). Optimising broad-leaved weed control in cereals. Available at: http://www.hgca.com/publications/documents/cropresearch/TOPIC02.pdf. [Accessed 31/03/2008]

**HGCA** (2002). Harvest results 2002 - Winter wheat. Available at: http://www-dev.hgca.com/publications/documents/varieties/WW_T_yld.pdf. [Accessed 25/6/2008]

**HGCA** (2007). HGCA - Recommended list Winter wheat 2008/09. Available at: http://www.hgca.com/document.aspx?fn=load&media_id=4005&publicationId=240. [Accessed 11/06/2008]

**Hock, S. M., Knezevic, S. Z., Martin, A. R. and Lindquist, J. L.** (2006). Soybean row spacing and weed emergence time influence weed competitiveness and competitive indices. *Weed Science*, **54** (1), 38-46.

**Hodges, T. and Ritchie, J. T.** (1991). The Ceres-Wheat phenology model. In: *Predicting crop phenology*. Edited by. Boca Raton, USA: CRC Press pp. 133-141.

**Hof, L., Keizer, L. C., Elberse, I. A. and Dolstra, O.** (1999). A model describing the flowering of single plants, and the heritability of flowering traits of *Dimorphotheca pluvialis*. *Euphytica*, **110** (1), 35-44.

**Holmes, M. G. and Smith, H.** (1977). The function of phytochrome in the natural environment. 2. The influence of vegetation canopies on the spectral energy distribution of natural daylight. *Photochemistry and Photobiology*, **25** (6), 539-545.

**Holst, N., Rasmussen, I. A. and Bastiaans, L.** (2007). Field weed population dynamics: a review of model approaches and applications. *Weed Research*, **47** (1), 1-14.

**Honek, A., Saska, P. and Martinkova, Z.** (2006). Seasonal variation in seed predation by adult carabid beetles. *Entomologia Experimentalis et Applicata*, **118** (2), 157-162.

**Hulme, P. E.** (1994). Post-dispersal seed predation in grassland: its magnitude and sources of variation. *Journal of Ecology (Oxford)*, **82** (3), 645-652.

**Hulme, M., Jenkins, G. J., X., L., Turnpenny, J. R., Mitchell, T. D., Jones, R. G., Lowe, J., Murphy, J. M., Hassell, D., Boorman, P., McDonald, R. and Hill, S.** (2002). Climate change scenarios for the United Kingdom: The UKCip02 Scientific Report.: Tyndall Centre for Climate Change Research, University of East Anglia, Norwich, UK.

**Jackson, L. J., Trebitz, A. S. and Cottingham, K. L.** (2000). An introduction to the practice of ecological modeling. *Bioscience*, **50** (8), 694-706.

**Jones, M. G.** (1976). Carabid and staphylinid fauna of winter-wheat and fallow on a clay with flints soil. *Journal of Applied Ecology*, **13** (3), 775-791.

**Jones, N. E. and Naylor, R. E. L.** (1992). Significance of the seed rain from set-aside. In: *Set-aside: proceedings of a symposium organised by the British Crop Protection Council, held at Cambridge University, 15-18 September 1992.* Edited by J. Clarke. Farnham: British Crop Protection Council. p. 91.

**Jones, R. E. and Medd, R. W.** (2000). Economic thresholds and the case for longer term approaches to population management of weeds. *Weed Technology*, **14** (2), 337-350.

**Jurado Exposito, M., Lopez Granados, F., Gonzalez Andujar, J. L. and Garcia Torres, L.** (2004). Spatial and temporal analysis of *Convolvulus arvensis* L. populations over four growing seasons. *European Journal of Agronomy*, **21** (3), 287-296.

**Jurik, T. W. and Zhang, S.** (1999). Tractor wheel traffic effects on weed emergence in central Iowa. *Weed Technology*, **13** (4), 741-746.

**Juroszek, P., Gerhards, R. and Kühbauch, W.** (2002). Photobiologische Unkrautregulierung annueller Ackerunkräuter. *Journal of Agronomy and Crop Science*, **188** (6), 389-397.

**Juroszek, P. and Gerhards, R.** (2004). Photocontrol of weeds. *Journal of Agronomy and Crop Science*, **190** (6), 402-415.

**Juzwik, J., Kromroy, K. and Allmaras, R.** (2002). Comparison of tillage equipment for improving soil conditions and root health in bareroot nurseries. Proceedings - Rocky Mountain Research Station USDA Forest Service. Rocky Mountain Research Station Fort Collins USA: 2002. RMRS-P-24 103-111. 7 ref.

**Karlsson, P. S. and Méndez, M.** (2005). The resource economy of plant reproduction. In: *Reproductive allocation in plants*. Edited by E.G. Reekie and F. A. Bazzaz. Burlington, MA.: Academic Press. pp. 1-49.

**Kay, Q. O. N.** (1994). *Tripleurospermum inodorum* (L.) Schultz Bip. (*Matricaria inodora* L., *Matricaria maritima* auct. p.p. non L., *Matricaria perforata* Merat, *Tripleurospermum perforatum* (Merat) Wagenitz, *Tripleurospermum maritimum* (L.) Schultz Bip. p.p. non L.). *Journal of Ecology*, **82** (3), 681-697.

**Kegode, G. O. and Pearce, R. B.** (1998). Influence of environment during maternal plant growth on dormancy of shattercane (*Sorghum bicolor*) and giant foxtail (*Setaria faberi*) seed. *Weed Science*, **46** (3), 322-329.

**Kelpsas, B. R. and Campbell, S. J.** (1994). Influence of mechanical incorporation method on dazomet distribution in conifer nursery soil. *Tree Planters' Notes*, **45** (2), 53-57.

**Kessler, D.** (1989). Scentless chamomile - seed production and germination. Regina, SK: Agriculture Canada. 2 p.

**King, D. and Roughgarden, J.** (1983). Energy allocation patterns of the California grassland annuals *Plantago erecta* and *Clarkia rubicunda*. *Ecology*, **64** (1), 16-24.

**Klinkhamer, P. G. L., Meelis, E., de Jong, T. J. and Weiner, J.** (1992). On the analysis of size-dependent reproductive output in plants. *Functional Ecology*, **6** (3), 308-316.

**Klostermyer, J.** (1989). Competition by *Stellaria media* (L.) Vill. and *Matricaria inodora* L. in oilseed winter rape (*Brassica napus* L. var. *napus*) and development of an empirical decision-model for postemergence weed control. 88 pp. p.

**Knezevic, S. Z., Horak, M. J. and Vanderlip, R. L.** (1997). Relative time of redroot pigweed (*Amaranthus retroflexus* L.) emergence is critical in pigweed-sorghum [*Sorghum bicolor* (L.) Moench] competition. *Weed Science*, **45** (4), 502-508.

**Knezevic, S. Z., Vanderlip, R. L. and Horak, M. J.** (2001). Relative time of redroot pigweed emergence affects dry matter partitioning. *Weed Science*, **49** (5), 617-621.

**Knott, C. M.** (2002). Weed control in other arable and field vegetable crops. In: *Weed Management Handbook*. Edited by R.E.L. Naylor. Oxford: Blackwell Science. p. 432.

**Knott, C. M.** (2004a). Filling the gaps in vegetable herbicides. *HDC News*, **108** (December 2004), 18-21.

**Knott, C. M.** (2004b). Fresh challenges for carrot growers. *HDC News*, **99** (January 2004), 9-11.

**Knott, C. M.** (2006). Vegetable herbicide countdown. *HDC News*, **128** (November 2006), 22-25.

**Kosmas, C., Gerontidis, S., Marathianou, M., Detsis, B., Zafiriou, T., Muysen, W. N., Govers, G., Quine, T. and van Oost, K.** (2001). The effects of tillage displaced soil on soil properties and wheat biomass. *Soil & Tillage Research*, **58** (1/2), 31-44.

**Kropff, M. J. and van Laar, H. H.** (1993). Modelling crop - weed interactions. Wallingford [etc.]: CAB International [etc.]. 274 p.

**Kropff, M. J., Bastiaans, L. and Cousens, R. D.** (1999). Approaches used in the prediction of weed population dynamics. *Proceedings of the 1999 Brighton crop protection conference: weeds*, Farnham, pp. 399-408.

**Kropff, M. J. and Walter, H.** (2000). EWRS and the challenges for weed research at the start of a new millennium. *Weed Research*, **40** (1), 7-10.

**Kropff, M. J., Bastiaans, L., Kempenaar, C. and Van der Weide, R. Y.** (2008). The changing role of agriculture and tomorrow's weed research agenda. *Journal of Plant Diseases and Protection* (Special Issue XXI), 3-8.

**Kruk, B., Insausti, P., Razul, A. and Benech-Arnold, R.** (2006). Light and thermal environments as modified by a wheat crop: effects on weed seed germination. *Journal of Applied Ecology*, **43** (2), 227-236.

**Kucewicz, M. and Hodynski, C.** (2003). Germination of *Matricaria maritima* subsp. *inodora* (L.) dostal (scentless mayweed) achenes depending on their maturity and position on the mother plant. *Journal of Plant Protection Research*, **43** (2), 143-153.

**Kudsk, P.** (2002). Optimising herbicide performance. In: *Weed management handbook*. Edited by R. E. L. Naylor. Oxford: Blackwell Science. pp. 323-344.

**Kudsk, P. and Streibig, J. C.** (2003). Herbicides - a two-edged sword. *Weed Research*, **43** (2), 90-102.

**Lande, R., Engen, S. and Saether, B. E.** (2003). Stochastic Population Dynamics in Ecology and Conservation. *Oxford Series in Ecology and Evolution*. Oxford: Oxford University Press. 224 p.

**Lapham, J. and Drennan, D. S.** (1990). The fate of yellow nutsedge (*Cyperus esculentus*) seed and seedlings in soil. *Weed Science*, **38** (2), 125-128.

**Lawson, H. M., Wright, G. M., Wilson, B. J. and Wright, K. J.** (1993). Seedbank persistence of five arable weed species in autumn-sown crops. *Proceedings of the Brighton crop protection conference, weeds*, Farnham, pp. 305-310.

**Leblanc, M. L., Cloutier, D. C., Legere, A., Lemieux, C., Assemat, L., Benoit, D. L. and Hamel, C.** (2002). Effect of the presence or absence of corn on common lambsquarters (*Chenopodium album* L.) and barnyardgrass [*Echinochloa crus-galli* (L.) Beauv.] emergence. *Weed Technology*, **16** (3), 638-644.

**Lecoeur, J. and Sinclair, T. R.** (2001). Harvest index increase during seed growth of field pea. *European Journal of Agronomy*, **14** (3), 173-180.

**Légère, A., Beckie, H. J., Stevenson, F. C. and Thomas, A. G.** (2000). Survey of management practices affecting the occurrence of wild oat (*Avena fatua*) resistance to acetyl-CoA carboxylase inhibitors. *Weed Technology*, **14** (2), 366-376.

**Leguizamon, E. S. and Roberts, H. A.** (1982). Seed production by an arable weed community. *Weed Research*, **22** (1), 35-39.

**Lewis, J.** (1973). Longevity of crop and weed seeds: survival after 20 years in soil. *Weed Research*, **13** (2), 179-191.

**Liebman, M. and Dyck, E.** (1993). Crop-rotation and intercropping strategies for weed management. *Ecological Applications*, **3** (1), 92-122.

**Liebman, M., Mohler, C. L. and Staver, C. P.** (2001). Ecological management of agricultural weeds. Cambridge: Cambridge University Press. 532 p.

**Lintell Smith, G., Freckleton, R. P., Firbank, L. G. and Watkinson, A. R.** (1999). The population dynamics of *Anisantha sterilis* in winter wheat: comparative demography and the role of management. *Journal of Applied Ecology*, **36** (4), 455-471.

**Lonchamp, J. P., Chadoeuf, R. and Barralis, G.** (1984). Evolution de la capacite de germination des semences de mauvaises herbes enfouies dans le sol. *Agronomie*, **4** (7), 671-682.

**Lutman, P. J. W., Cussans, G. W., Wright, K. J., Wilson, B. J., Wright, G. M. and Lawson, H. M.** (2002). The persistence of seeds of 16 weed species over six years in two arable fields. *Weed Research*, **42** (3), 231-241.

**Lutman, P. J. W.** (2002). Estimation of seed production by *Stellaria media, Sinapis arvensis* and *Tripleurospermum inodorum* in arable crops. *Weed Research*, **42** (5), 359-369.

**Lutman, P. J. W., Peters, N. C. B., Berry, K., Hull, R. I., Perry, N. H. and Wright, K. J.** (2003). The persistence of seeds of two populations of six arable weeds. *Aspects of Applied Biology*, **69**, 195-202.

**Lutman, P. J. W.** (2006). SID 5 - Research project final report - Parameterising the biology and population dynamics of weeds in arable crops to support more targeted weed management - AR0409. 37 p. Available at: http://randd.defra.gov.uk/Document.aspx?Document=AR0409_6358_FRP.doc.

**Malo, J. E.** (2002). Modelling unimodal flowering phenology with exponential sine equations. *Functional Ecology*, **16** (3), 413-418.

**'t Mannetje, A., McLean, D., Cheng, S., Boffetta, P., Colin, D. and Pearce, N.** (2005). Mortality in New Zealand workers exposed to phenoxy herbicides and dioxins. *Occup Environ Med*, **62** (1), 34-40.

**Marshall, E. J. P.** (1989). Distribution patterns of plants associated with arable field edges. *Journal of Applied Ecology*, **26** (1), 247-257.

**Marshall, E. J. P. and Brain, P.** (1999). The horizontal movement of seeds in arable soil by different soil cultivation methods. *Journal of Applied Ecology*, **36** (3), 443-454.

**Marshall, E. J. P., Brown, V. K., Boatman, N. D., Lutman, P. J. W., Squire, G. R. and Ward, L. K.** (2003). The role of weeds in supporting biological diversity within crop fields. *Weed Research*, **43** (2), 77-89.

**Martin, R. J., Cullis, B. R. and McNamara, D. W.** (1987). Prediction of wheat yield loss due to competition by wild oats (*Avena* spp.). *Australian Journal of Agricultural Research*, **38** (3), 487-499.

**Martin, D.** (2005). Weed control overview and update of HDC project. *Proceedings of the UK Onion and Carrot Conference and Exhibition 2005*, Peterborough, UK, p. 4.

**MathWorks** (2007). MatLab 7.5 Product Description. Available at: http://www.mathworks.com/products/matlab/description1.html. [Accessed 2/09/2007]

**Mauchline, A. L., Watson, S. J., Brown, V. K. and Froud-Williams, R. J.** (2005). Post-dispersal seed predation of non-target weeds in arable crops. *Weed Research*, **45** (2), 157-164.

**Maxwell, B. D. and Mortimer, M. M.** (1994). Selection for herbicide resistance. In: *Herbicide resistance in Plants: Biology and Biochemistry*. Edited by S.B. Powles and J.A.M. Holtum. Boca Raton, Florida: CRC Press. pp. 1-25.

**Mayer, D. G. and Butler, D. G.** (1993). Statistical validation. *Ecological Modelling*, **68** (1-2), 21-32.

**McCanny, S. J. and Cavers, P. B.** (1988). Spread of proso millet (*Panicum miliaceum* L.) in Ontario, Canada. II. Dispersal by combines. *Weed Research*, **28** (2), 67-72.

**Mead, A., Grundy, A. C. and Burston, S.** (1998). Predicting the movement of seeds following cultivation. *Aspects of Applied Biology*, **51**, 91-98.

**Meagher, T. R. and Delph, L. F.** (2001). Individual flower demography, floral phenology and floral display size in *Silene latifolia*. *Evolutionary Ecology Research*, **3** (7), 845-860.

**Medd, R. W.** (1996). Ecology of wild oats. *Plant Protection Quarterly*, **11** (Suppl. 1), 185-187.

**van Melick, P. W. H.** (1996). Transport van onkruidzaden in de bouwvoor door risterploegen. Wageningen: Soil Technology group, Wageningen University. 65 p.

**Mennan, H. and Zandstra, B. H.** (2006). The effects of depth and duration of seed burial on viability, dormancy, germination, and emergence of ivyleaf speedwell (*Veronica hederifolia*). *Weed Technology*, **20** (2), 438-444.

**Mertens, S. K. and Jansen, J.** (2002). Weed seed production, crop planting pattern, and mechanical weeding in wheat. *Weed Science*, **50** (6), 748-756.

**Mertens, S. K., van den Bosch, F. and Heesterbeek, J. A. P.** (2002). Weed populations and crop rotations: exploring dynamics of a structured periodic system. *Ecological Applications*, **12** (4), 1125-1141.

**Milberg, P., Andersson, L. and Noronha, A.** (1996). Seed germination after short-duration light exposure: implications for the photo-control of weeds. *Journal of Applied Ecology*, **33** (6), 1469-1478.

**Milberg, P. and Andersson, L.** (1997). Seasonal variation in dormancy and light sensitivity in buried seeds of eight annual weed species. *Canadian Journal of Botany*, **75** (11), 1998-2004.

**Milberg, P. and Andersson, L.** (1998). Does cold stratification level out differences in seed germinability between populations? *Plant Ecology*, **134** (2), 225-234.

**Ministry of Agriculture Fisheries and Food** (2000). Towards Sustainable Agriculture - A Pilot set of Indicators. London: MAFF. PB 4583. Available at: http://www1.oecd.org/agr/biodiversity/pilotind.pdf.

**Mohler, C. L.** (1993). A model of the effects of tillage on emergence of weed seedlings. *Ecological Applications*, **3** (1), 53-73.

**Mohler, C. L., Frisch, J. C. and McCulloch, C. E.** (2006). Vertical movement of weed seed surrogates by tillage implements and natural processes. *Soil & Tillage Research*, **86** (1), 110-122.

**Montgomery, J. A., McCool, D. K., Busacca, A. J. and Frazier, B. E.** (1999). Quantifying tillage translocation and deposition rates due to moldboard plowing in the Palouse region of the Pacific Northwest, USA. *Soil & Tillage Research*, **51** (3/4), 175-187.

**Moonen, A. C. and Barberi, P.** (2004). Size and composition of the weed seedbank after 7 years of different cover-crop-maize management systems. *Weed Research*, **44** (3), 163-177.

**Mortensen, D. A., Bastiaans, L. and Sattin, M.** (2000). The role of ecology in the development of weed management systems: an outlook. *Weed Research*, **40** (1), 49-62.

**Moss, S. R.** (1988). Influence of cultivations on the vertical distribution of weed seeds in the soil. *Proceedings of the VIIIe Colloque International sur la Biologie, l'Ecologie et la Systematique des Mauvaises Herbes.*, Paris, France, pp. 71-80.

**Moss, S. R.** (2003). Herbicide resistance in weeds: current status in Europe and guidelines for management. *Pesticide Outlook*, **14** (4), 164-167.

**Moss, S. R.** (2006). Herbicide resistance: new threats, new solutions? *Proceedings of the HGCA Conference on Arable Crop Protection in the Balance: Profit and the Environment*, Grantham, UK, pp. 12.1-12.9. Available at: http://www.hgca.com/document.aspx?fn=load&media_id=2498&publicationId=1305.

**Moss, S. R.** (2007). Weed Management: is it a case of trying to predict the unpredictable? *Proceedings of the 14th EWRS Symposium*, Hamar (Norway), p. 10.

**Moss, S. R. and Perryman, S. A.** (2007). The incidence of herbicide-resistant *Alopecurus myosuroides* (black-grass) in England and its development in relation to past herbicide use. *Aspects of Applied Biology*, **83**, 109-113.

**Motulsky, H. and Christopoulos, A.** (2004). Comparing models using the extra sum-of-squares F test. In: *Fitting models to biological data using linear and nonlinear regression: A practical guide to curve fitting*. Edited by H. Motulsky and A. Christopoulos. USA: Oxford University Press. pp. 138-142.

**van Mourik, T. A., Stomph, T. J. and Murdoch, A. J.** (2005). Why high seed densities within buried mesh bags may overestimate depletion rates of soil seed banks. *Journal of Applied Ecology*, **42** (2), 299-305.

**Murphy, S. D., Yakubu, Y., Weise, S. F. and Swanton, C. J.** (1996). Effect of planting patterns and inter-row cultivation on competition between corn (*Zea mays*) and late emerging weeds. *Weed Science*, **44** (4), 865-870.

**Navas, M. L.** (1991). Using plant population biology in weed research: a strategy to improve weed management. *Weed Research*, **31** (4), 171-179.

**Naylor, R. E. L.** (2002). Weed management handbook. Oxford [etc.]: Blackwell. VII, 423 p; pp.

**Neve, P. and Powles, S.** (2005). Recurrent selection with reduced herbicide rates results in the rapid evolution of herbicide resistance in *Lolium rigidum*. *Theoretical and Applied Genetics*, **110** (6), 1154-1166.

**Neve, P.** (2007). Challenges for herbicide resistance evolution and management: 50 years after Harper. *Weed Research*, **47** (5), 365-369.

**Ngugi, H. K., Scherm, H. and NeSmith, D. S.** (2002). Distribution of pseudosclerotia of *Monilinia vaccinii-corymbosi* and risk of apothecial emergence following mechanical cultivation. *Phytopathology*, **Paul, USA** (2002. 92: 8), 877-883.

**Noronha, A., Andersson, L. and Milberg, P.** (1997). Rate of change in dormancy level and light requirement in weed seeds during stratification. *Annals of Botany*, **80** (6), 795-801.

**Norris, R. F. and Légère, A.** (2004). Introduction to the Symposium on 'Weed ecology in long term experiments: status and future needs' *Weed Science*, **52** (5), 863-903.

**Norsworthy, J. K.** (2004). Soybean canopy formation effects on pitted morningglory (*Ipomoea lacunosa*), common cocklebur (*Xanthium strumarium*), and sicklepod (*Senna obtusifolia*) emergence. *Weed Science*, **52** (6), 954-960.

**O'Donovan, J. T. and McClay, A. S.** (2002). Relationship between relative time of emergence of Tartary buckwheat (*Fagopyrum tataricum*) and yield loss of barley. *Canadian Journal of Plant Science*, **82** (4), 861-863.

**O'Donovan, J. T., Blackshaw, R. E., Harker, K. N., Clayton, G. W., Moyer, J. R., Dosdall, L. M., Maurice, D. C. and Turkington, T. K.** (2007). Integrated approaches to managing weeds in spring-sown crops in western Canada. *Crop Protection*, **26** (3), 390-398.

**Obeid, M., Machin, D. and Harper, J. L.** (1967). Influence of density on plant to plant variation in fiber flax, Linum usitatissimum L. *Crop Science*, **7**, 471-473.

**Oerke, E. C.** (2006). Crop losses to pests. *Journal of Agricultural Science*, **144** (1), 31-43.

**Orrock, J. L. and Damschen, E. I.** (2007). The effect of burial depth on removal of seeds of *Phytolacca americana*. *Southeastern Naturalist*, **6** (1), 151-158.

**Orson, J. H.** (1999). The cost to the farmer of herbicide resistance. *Weed Technology*, **13** (3), 607-611.

**Otsu, N.** (1979). A threshold selection method from gray-level histograms. *IEEE Transactions on Systems, Man and Cybernetics*, **9** (1), 62-66.

**Park, S. E., Benjamin, L. R., Aikman, D. P. and Watkinson, A. R.** (2001). Predicting the growth interactions between plants in mixed species stands using a simple mechanistic model. *Annals of Botany*, **87** (4), 523-536.

**Parker, I. M.** (2000). Invasion dynamics of *Cytisus scoparius*: a matrix model approach. *Ecological Applications*, **10** (3), 726-743.

**Peachey, R. E. and Mallory-Smith, C.** (2007). Influence of winter seed position and recovery date on hairy nightshade (*Solanum sarrachoides*) recruitment and seed germination, dormancy, and mortality. *Weed Science*, **55** (1), 49-59.

**Penning de Vries, F. W., Jansen, D. M., Berge, H. F. and Bakema, A.** (1989). Simulation of ecophysiological processes of growth in several annual crops. *Simulation Monographs 29*. Wageningen, The Netherlands: Centre for Agricultural Publishing and Documentation (PUDOC), Wageningen. 271 p.

**Perry, J. N. and Gonzalez Andujar, J. L.** (1993). Dispersal in a metapopulation neighbourhood model of an annual plant with a seedbank. *Journal of Ecology*, **81** (3), 453-463.

**Pesticides Safety Directorate** (2004). Project addressing EU minor use gaps: Weed Management in Carrots (*Daucus carota*) and Parsnips (*Pastinaca sativa*). Available at: http://www.pesticides.gov.uk/uploadedfiles/Web_Assets/PSD/MUN_TG_carrots_parsnips1.pdf. [Accessed 31/08/2007]

**Pesticides Safety Directorate, Scottish Executive, DARDNI, Welsh Assembly Government and DEFRA** (2006). Pesticides and the Environment - A Strategy for the Sustainable Use of Plant Protection Products and Strategy Action Plans. London: DEFRA. PB 11721. Available at: http://www.pesticides.gov.uk/uploadedfiles/Web_Assets/PSD/PB11721_Pesticidesenvironment_Lo.pdf.

**Pesticides Safety Directorate** (2008). Specific Off Label Approvals for use in the UK. Available at: https://secure.pesticides.gov.uk/offlabels/search.asp. [Accessed 14/02/2008]

**Pino, J., Sans, F. X. and Masalles, R. M.** (1998). Population dynamics of *Rumex obtusifolius* under contrasting lucerne cropping systems. *Weed Research*, **38** (1), 25-33.

**Povey, F. D., Smith, H. and Watt, T. A.** (1993). Predation of annual grass weed seeds in arable field margins. *Annals of Applied Biology*, **122** (2), 323-328.

**Powles, S. B., Monjardino, M., Llewellyn, R. S. and Pannell, D.** (2001). Proactive versus reactive herbicide resistance management: understanding the economic sense of herbicide conservation versus exploitation. *Proceedings of the Third International Weed Science Congress*, Foz do Iguacu, Brazil., pp. 148-149.

**Puricelli, E., Faccini, D., Orioli, G. and Sabbatini, M. R.** (2005). Seed survival and predation of *Anoda cristata* in soyabean crops. *Weed Research*, **45** (6), 477-482.

**Puricelli, E., Vitta, J. I., Sabbatini, M. R. and Orioli, G.** (2007). Modeling population dynamics of *Anoda cristata* in a glyphosate-resistant soybean crop under different management systems. *Agriscientia*, **XXIV** (1), 1-9.

**Rabbinge, R. and de Wit, C. T.** (1989). Systems, models and simulation. In: *Simulation and system management in crop protection*. Edited by R. Rabbinge, S.A. Ward and H. H. van Laar. Wageningen: Pudoc. pp. 3-15.

**Radics, L., Glemnitz, M., Hoffmann, J. and Czimber, G.** (2004). Composition of weed floras in different agricultural management systems within the European climatic gradient. *Proceedings of the 6th EWRS Workshop on Physical and Cultural Weed Control*, Lillehammer, pp. 58-68.

**Rahman, A., James, T. K., Mellsop, J. and Grbavac, N.** (2000). Effect of cultivation methods on weed seed distribution and seedling emergence. In: *New Zealand Plant Protection*. Edited by S. M. Zydenbos. Rotorua New Zealand: New Zealand Plant Protection Society. pp. 28-33.

**Ramula, S. and Lehtila, K.** (2005). Importance of correlations among matrix entries in stochastic models in relation to number of transition matrices. *Oikos*, **111** (1), 9-18.

**Rao, V. S.** (2000). Principles of weed science. Enfield: Science Publishers Inc. . Ed. 2, viii + 555 pp.

**Rasmussen, I. A. and Holst, N.** (2003). Computer model for simulating the long-term dynamics of annual weeds: from seedlings to seeds. *Aspects of Applied Biology*, **69**, 277-284.

**Reader, R. J.** (1985). Temporal variation in recruitment and mortality for the pasture weed *Hieracium floribundum*: implications for a model of population dynamics. *Journal of Applied Ecology*, **22** (1), 175-183.

**Reader, R. J.** (1991). Control of seedling emergence by ground cover - a potential mechanism involving seed predation. *Canadian Journal of Botany*, **69** (9), 2084-2087.

**Rees, M. and Crawley, M. J.** (1989). Growth, reproduction and population dynamics. *Functional Ecology*, **3** (6), 645-653.

**Rees, M. and Brown, V. K.** (1991). The effects of established plants on recruitment in the annual forb *Sinapis arvensis*. *Oecologia*, **87** (1), 58-62.

**van der Reest, P. J. and Rogaar, H.** (1988). The effect of earthworm activity on the vertical distribution of plant seeds in newly reclaimed polder soils in the Netherlands. *Pedobiologia*, **31** (3-4), 211-218.

**Reuss, S. A., Buhler, D. D. and Gunsolus, J. L.** (2001). Effects of soil depth and aggregate size on weed seed distribution and viability in a silt loam soil. *Applied Soil Ecology*, **16** (3), 209-217.

**Rew, L. J., Froud-Williams, R. J. and Boatman, N. D.** (1996). Dispersal of *Bromus sterilis* and *Anthriscus sylvestris* seed within arable field margins. *Agriculture, Ecosystems & Environment*, **59** (1/2), 107-114.

**Richards, F. J.** (1959). A flexible growth function for empirical use. *Journal of Experimental Botany*, **10**, 290-300.

**Richter, O., Zwerger, P. and Bottcher, U.** (2002). Modelling spatio-temporal dynamics of herbicide resistance. *Weed Research*, **42** (1), 52-64.

**Roach, D. A. and Gampe, J.** (2004). Age-specific demography in Plantago: Uncovering age-dependent mortality in a natural population. *American Naturalist*, **164** (1), 60-69.

**Roberts, H. A.** (1962). Studies on the weeds of vegetable crops II. Effect of six years of cropping on the weed seeds in the soil. *Journal of Ecology*, 803-813.

**Roberts, H. A.** (1964). Emergence and longevity in cultivated soil of seeds of some annual weeds. *Weed Research*, **4** (4), 296-307.

**Roberts, H. A. and Dawkins, P. A.** (1967). Effect of cultivation on the numbers of viable weed seeds in soil. *Weed Research*, 290-301.

**Roberts, H. A. and Feast, P. M.** (1972). Fate of seeds of some annual weeds in different depths of cultivated and undisturbed soil. *Weed Research*, **12** (4), 316-324.

**Roberts, H. A. and Feast, P. M.** (1973). Emergence and longevity of seeds of annual weeds in cultivated and undisturbed soil. *Journal of Applied Ecology*, **10** (1), 133-143.

**Roberts, H. A. and Feast, P. M.** (1974). Observations on the time of flowering of mayweeds. *Journal of Applied Ecology*, **11** (1), 223-229.

**Roberts, H. A. and Lockett, P. M.** (1975). Germination of buried and dry-stored seeds of *Stellaria media*. *Weed Research*, **15** (3), 199-204.

**Roberts, H. A. and Potter, M. E.** (1980). Emergence patterns of weed seedlings in relation to cultivation and rainfall. *Weed Research*, **20** (6), 377-386.

**Roberts, H. A. and Boddrell, J. E.** (1983). Seed survival and periodicity of seedling emergence in ten species of annual weeds. *Annals of Applied Biology*, **102** (3), 523-532.

**Robinson, R. A. and Sutherland, W. J.** (2002). Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology*, **39** (1), 157-176.

**Robinson, S.** (2006). Issues in conceptual modelling for simulation: setting a research agenda. *Proceedings of the Operational Research Society Simulation Workshop 2006*, Birmingham, UK, pp. 165-174.

**Roger-Estrade, J., Colbach, N., Leterme, P., Richard, G. and Caneill, J.** (2001). Modelling vertical and lateral weed seed movements during mouldboard ploughing with a skim-coulter. *Soil & Tillage Research*, **63** (1/2), 35-49.

**Rohrig, M. and Stutzel, H.** (2001). Dry matter production and partitioning of *Chenopodium album* in contrasting competitive environments. *Weed Research*, **41** (2), 129-142.

**Roller, A. and Albrecht, H.** (2006). Effects of tillage systems on the seed bank persistence and seedling emergence of ten arable weeds. *Journal of Plant Diseases and Protection*, 257-265.

**Rottele, M. and Koch, W.** (1981). Distribution of weed seed in the soil and consequences for seed density estimations. *Zeitschrift fur Pflanzenkrankheiten und Pflanzenschutz*, **Sonderheft 9**, 383-391.

**Rowse, H. R., McKee, J. M. T. and Higgs, E. C.** (1999). A model of the effects of water stress on seed advancement and germination. *New Phytologist*, **143**, 273-279.

**Rowse, H. R. and Finch-Savage, W. E.** (2003). Hydrothermal threshold models can describe the germination response of carrot (*Daucus carota*) and onion (*Allium cepa*) seed populations across both sub- and supra-optimal temperatures. *New Phytologist*, **158** (1), 101-108.

**Russell, G.** (1996). Spatial aspects of modelling in applied biology. In: *Modelling in applied biology: spatial aspects (AAB 46)*. Edited by E.M. White, G. Russel, L. Benjamin, M. Mugglestone, P. Brain, P. Hamer and K. Topp. Great Britain: The Association of Applied Biologists. pp. 1-4.

**Sagar, G. R. and Mortimer, A. M.** (1976). An approach to the study of the population dynamics of plants with special reference to weeds. *Applied Biology*, **1**, 47.

**Samson, D. A. and Werk, K. S.** (1986). Size-dependent effects in the analysis of reproductive effort in plants. *American Naturalist*, **127** (5), 667-680.

**San Roman, E. and Fernandez, O. A.** (1991). Influence of soil compaction on the emergence of *Polygonum convolvulus* L. seedlings. *Proceedings of the Proceedings of the 12th Argentine meeting on weeds and their control, Mar del Plata, Argentina, 9-11 October 1991.. 1991. Vol. 1, 119-122. 16 ref.*

**Sanchez del Arco, M. J., Torner, C. and Quintanilla, C. F.** (1995). Seed dynamics in populations of Avena sterilis ssp. ludoviciana. *Weed Research*, **35** (6), 477-487.

**Sattin, M., Zanin, G. and Berti, A.** (1992). Case-history for weed competition / population ecology – Velvetleaf (*Abutilon theophrasti*) in corn (*Zea mays*). *Weed Technology*, **6** (1), 213-219.

**Scaife, A., Cox, E. F. and Morris, G. E. L.** (1987). The relationship between shoot weight, plant density and time during the propagation of four vegetable species. *Annals of Botany*, **59** (3), 325-334.

**Schnieders, B. J.** (1999). A quantitative analysis of inter-specific competition in crops with a row structure. AB-DLO. Wageningen, Wageningen University. **Doctoral:** 165.

**Schuster, C. L., Shoup, D. E. and Al-Khatib, K.** (2007). Response of common lambsquarters (*Chenopodium album*) to glyphosate as affected by growth stage. *Weed Science*, **55** (2), 147-151.

**Scopel, A. L., Ballare, C. L. and Ghersa, C. M.** (1988). Role of seed reproduction in the population ecology of *Sorghum halepense* in maize crops. *Journal of Applied Ecology*, **25** (3), 951-962.

**Scursoni, J., Benech-Arnold, R. and Hirchoren, H.** (1999). Demography of wild oat in barley crops: effect of crop, sowing rate, and herbicide treatment. *Agronomy Journal*, **91** (3), 478-485.

**Seed Science Group** (2008). Simulation of seed germination and seedling emergence. Available at: http://www2.warwick.ac.uk/fac/sci/whri/research/seedscience/simulation/. [Accessed 23/09/2008]

**Seguer Millàs, J.** (2002). Influence of weather conditions and seed features on the burial rate of weed seeds on the soil surface. Wageningen, Wageningen University. **M.Sc:** 79.

**Selman, M.** (1970). The population dynamics of *Avena fatua* (wild oats) in continuous spring barley; desirable frequency of spraying with tri-allate. *Proceedings of the 10th British Weed Control Conference*, pp. 1176-1188.

**Sester, M., Delanoy, M., Colbach, N. and Darmency, H.** (2004). Crop and density effects on weed beet growth and reproduction. *Weed Research*, **44** (1), 50-59.

**Sester, M., Durr, C., Darmency, H. and Colbach, N.** (2006). Evolution of weed beet (Beta vulgaris L.) seed bank: Quantification of seed survival, dormancy, germination and pre-emergence growth. *European Journal Of Agronomy*, **24** (1), 19-25.

**Shitaka, Y. and Hirose, T.** (1998). Effects of shift in flowering time on the reproductive output of *Xanthium canadense* in a seasonal environment. *Oecologia*, **114** (3), 361-367.

**Shoji, K.** (2007). Development of a spot plow providing complete inversion for effective weed control. *Weed Biology and Management*, **7** (1), 14-22.

**Silvertown, J. and Charlesworth, D.** (2001). Introduction to Plant Population Biology. 4th Edition. Oxford: Blackwell Publishing. 347 p.

**Singh, S.** (2002). The serendipity of Science. Available at: http://www.bbc.co.uk/radio4/science/serendipity.shtml. [Accessed 30/08/2008]

**Sly, J. M.** (1978). The usage of pesticides on vegetables grown as part of an arable farm rotation. *Pesticide Science*, **9** (3), 245-258.

**Smith, R. G., Gross, K. L. and Januchowski, S.** (2005). Earthworms and weed seed distribution in annual crops. *Agriculture, Ecosystems & Environment*, **108** (4), 363-367.

**Sobey, D. G.** (1981). Biological flora of the British Isles. No. 150. *Stellaria media* (L.) Vill. *Journal of Ecology*, **69** (1), 311-335.

**Soil Association** (1999a). Organic Carrot Production - Soil Association technical guides for organic crop and livestock production.

**Soil Association** (1999b). Organic Onion Production - Soil Association Technical Guides for Organic Crop and Livestock production.

**Soltani, A., Galeshi, S., Attarbashi, M. R. and Taheri, A. H.** (2004). Comparison of two methods for estimating parameters of harvest index increase during seed growth. *Field Crops Research*, **89** (2/3), 369-378.

**Sosnoskie, L. M., Herms, C. P. and Cardina, J.** (2006). Weed seedbank community composition in a 35-yr-old tillage and rotation experiment. *Weed Science*, **54** (2), 263-273.

**Spink, J. H., Semere, T., Sparkes, D. L., Whaley, J. M., Foulkes, M. J., Clare, R. W. and Scott, R. K.** (2000). Effect of sowing date on the optimum plant density of winter wheat. *Annals of Applied Biology*, **137** (2), 179-188.

**Spitters, C. J. T.** (1983). An alternative approach to the analysis of mixed cropping experiments. 1. Estimation of competition effects. *Netherlands Journal of Agricultural Science*, **31**, 1-11.

**Squire, G. R., Brooks, D. R., Bohan, D. A., Champion, G. T., Daniels, R. E., Haughton, A. J., Hawes, C., Heard, M. S., Hill, M. O., May, M. J., Osborne, J. L., Perry, J. N., Roy, D. B., Woiwod, I. P. and Firbank, L. G.** (2003). On the rationale and interpretation of the Farm Scale Evaluations of genetically modified herbicide-tolerant crops. (Special issue: The farm-scale evaluations of spring-sown genetically modified crops). *Philosophical Transactions of the Royal Society of London*, **358** (1439), 1779-1799.

**Stace, C. A.** (1997). New Flora of the British Isles. 2nd Edition. Cambridge: Cambridge University Press. 1226 p.

**Staricka, J. A., Burford, P. M., Allmaras, R. R. and Nelson, W. W.** (1990). Tracing the vertical distribution of simulated shattered seeds as related to tillage. *Agronomy Journal*, **82** (6), 1131-1134.

**Steinmaus, S. J. and Norris, R. F.** (2002). Growth analysis and canopy architecture of velvetleaf grown under light conditions representative of irrigated Mediterranean-type agroecosystems. *Weed Science*, **50** (1), 42-53.

**Storkey, J.** (2004). Modelling seedling growth rates of 18 temperate arable weed species as a function of the environment and plant traits. *Annals of Botany*, **93** (6), 681-689.

**SUFFOLKRB** (2008). JD 6200 Destoning. Available at: http://www.youtube.com/watch?v=1bQk9urnYJg. [Accessed 31/08/2008]

**Sugiyama, H. and Hirose, T.** (1991). Growth schedule of *Xanthium canadense*: Does it optimize the timing of reproduction? *Oecologia*, **88** (1), 55-60.

**Swanton, C. J., Huang, J., Deen, W., Tollenaar, M., Anil, S. and Rahimian, H.** (1999). Effects of temperature and photoperiod on *Setaria viridis*. *Weed Science*, **47** (4), 446-453.

**Swanton, C. J., Shrestha, A., Knezevic, S. Z., Roy, R. C. and Ball-Coelho, B. R.** (2000). Influence of tillage type on vertical weed seedbank distribution in a sandy soil. *Canadian Journal of Plant Science*, **80** (2), 455-457.

**Tamis, W. L. M., Van't Zelfde, M., Van der Meijden, R. and De Haes, H. A. U.** (2005). Changes in vascular plant biodiversity in the Netherlands in the 20th century explained by their climatic and other environmental characteristics. *Climatic Change*, **72** (1-2), 37-56.

**Taylor, I. N., Walker, S. R. and Adkins, S. W.** (2005). Burial depth and cultivation influence emergence and persistence of *Phalaris paradoxa* seed in an Australian sub-tropical environment. *Weed Research*, **45** (1), 33-40.

**Tei, F., Scaife, A. and Aikman, D. P.** (1996). Growth of lettuce, onion, and red beet. 1. Growth analysis, light interception, and radiation use efficiency. *Annals of Botany*, **78** (5), 633-643.

**Theaker, A. J., Boatman, N. D. and Froud Williams, R. J.** (1995). Variation in *Bromus sterilis* on farmland - evidence for the origin of field infestations. *Journal of Applied Ecology*, **32** (1), 47-55.

**Thomas, A. G., Lefkovitch, L. P., Woo, S. L., Bowes, G. G. and Peschken, D. P.** (1994). Effect of temperature on germination within and between diploid and tetraploid populations of *Matricaria perforata* Merat. *Weed Research*, **34** (3), 187-198.

**Thomas, A. G., Derksen, D. A., Blackshaw, R. E., van Acker, R. C., Légère, A., Watson, P. R. and Turnbull, G. C.** (2004). A multistudy approach to understanding weed population shifts in medium- to long-term tillage systems. *Weed Science*, **52** (5), 874-880.

**Thompson, B. K., Weiner, J. and Warwick, S. I.** (1991). Size-dependent reproductive output in agricultural weeds. *Canadian Journal of Botany*, **69** (3), 442-446.

**Thompson, K., Band, S. R. and Hodgson, J. G.** (1993). Seed size and shape predict persistence in soil. *Functional Ecology*, **7** (2), 236-241.

**Thompson, K., Bakker, J. P. and Bekker, R. M.** (1997). Soil seed banks of North West Europe : methodology, density and longevity. Cambridge: Cambridge University Press. 276 p.

**Thomson, J. D.** (1980). Skewed flowering distributions and pollinator attraction. *Ecology*, **61** (3), 572-579.

**Thorup-Kristensen, K. and van den Boogaard, R.** (1999). Vertical and horizontal development of the root system of carrots following green manure. *Plant and Soil*, **212** (2), 143-151.

**van Tienderen, P. H.** (1995). Life cycle trade-offs in matrix population models. *Ecology*, **76** (8), 2482-2489.

**Timmons, F. L.** (2005). A history of weed control in the United States and Canada. *Weed Science*, **53** (6), 748-761.

**Tooley, J. A., Froud-Williams, R. J., Boatman, N. D. and Holland, J. M.** (1999). Weed seed predation in arable field margins by carabid beetles (Carabidae: Coleoptera). *Aspects of Applied Biology*, **54**, 211-216.

**Univercoman** (2008a). Onion windrower. Available at: http://www.youtube.com/watch?v=U5KYQyLQIs4. [Accessed 11/9/2008]

**Univercoman** (2008b). Carrot harvester. Available at: http://www.youtube.com/watch?v=4B5KVdpZ7U8. [Accessed 11/9/2008]

**Vanhala, P. and Pitkanen, J.** (1998). Long-term effects of primary tillage on above-ground weed flora and on the weed seedbank. *Aspects of Applied Biology*, **51**, 99-104.

**Vasileiadis, V. P., Froud-Williams, R. J. and Eleftherohorinos, I. G.** (2007). Vertical distribution, size and composition of the weed seedbank under various tillage and herbicide treatments in a sequence of industrial crops. *Weed Research*, **47** (3), 222-230.

**van der Vegte, F. W.** (1978). Population differentiation and germination ecology in *Stellaria media*. *Oecologia*, **37** (2), 231-246.

**Verhulst, P. F.** (1838). Notice sur la loi que la population suit dans son accroissement. *Correspondance Math´ematique et Physique*, **10**, 113-117.

**Vidotto, F., Ferrero, A. and Ducco, G.** (2001). A mathematical model to predict the population dynamics of *Oryza sativa* var. *sylvatica*. *Weed Research*, **41** (5), 407-420.

**Vleeshouwers, L. M., Bouwmeester, H. J. and Karssen, C. M.** (1995). Redefining seed dormancy: an attempt to integrate physiology and ecology. *Journal of Ecology*, **83** (6), 1031-1037.

**Vleeshouwers, L. M. and Kropff, M. J.** (2000). Modelling field emergence patterns in arable weeds. *New Phytologist*, **148** (3), 445-457.

**Vleeshouwers, L. M. and Bouwmeester, H. J.** (2001). A simulation model for seasonal changes in dormancy and germination of weed seeds. *Seed Science Research*, **11** (1), 77-92.

**Walker, A., Farrant, D. M., Bryant, J. H. and Brown, P. A.** (1976). The efficiency of herbicide incorporation into soil with different implements. *Weed Research*, **16** (6), 391-397.

**Walsh, M. J. and Minkey, D. M.** (2006). Wild radish (*Raphanus raphanistrum* L.) development and seed production in response to time of emergence, crop-topping and sowing rate of wheat. *Plant Protection Quarterly*, **and F.J. Richardson, Meredith, Australia** (2006. 21: 1), 25-29.

**Wang, J., Kropff, M. J., Lammert, B., Christensen, S. and Hansen, P. K.** (2003). Using CA model to obtain insight into mechanism of plant population spread in a controllable system: annual weeds as an example. *Ecological Modelling*, **166** (3), 277-286.

**Watkinson, A. R., Lonsdale, W. M. and Andrew, M. H.** (1989). Modeling the population dynamics of an annual plant *Sorghum intrans* in the wet-dry tropics. *Journal of Ecology*, **77** (1), 162-181.

**Watson, S. J., Mauchline, A. L., Brown, V. K. and Froud-Williams, R. J.** (2003). Post-dispersal losses of *Stellaria media* and *Polygonum aviculare* seeds in spring barley (*Hordeum vulgare*). *Aspects of Applied Biology*, **69**, 203-208.

**Weaver, S., Cluney, K., Downs, M. and Page, E.** (2006). Prickly lettuce (Lactuca serriola) interference and seed production in soybeans and winter wheat. *Weed Science*, **54** (3), 496-503.

**WeedFocus** (2008). Best practice overview. Available at: http://www.weedfocus.com/output_weedfocus.aspx?sec=1278&con=1284. [Accessed 17/02/2008]

**Weiner, J. and Solbrig, O. T.** (1984). The meaning and measurement of size hierarchies in plant populations. *Oecologia*, **61**, 334-336.

**Weiner, J.** (1988). The influence of competition on plant reproduction. In: *Plant reproductive ecology: patterns and strategies*. Edited by J. Lovett Doust and L. Lovett Doust. New York: Oxford University Press Inc., pp. 228-245.

**Weiner, J., Griepentrog, H. W. and Kristensen, L.** (2001). Suppression of weeds by spring wheat *Triticum aestivum* increases with crop density and spatial uniformity. *Journal of Applied Ecology*, **38** (4), 784-790.

**Welsh, J. P., Bulson, H. A. J., Stopes, C. E., Froud-Williams, R. J. and Murdoch, A. J.** (1999). The critical weed-free period in organically-grown winter wheat. *Annals of Applied Biology*, **134** (3), 315-320.

**Wesson, G. and Wareing, P. F.** (1969). The induction of light sensitivity in weed seeds by burial. *Journal of Experimental Botany*, **20** (63), 414-425.

**Westerman, P. R., van der Werf, W. and Brussaard, L.** (2003a). Measuring causes of seed bank mortality: a method. *Aspects of Applied Biology*, **69**, 217-222.

**Westerman, P. R., Wes, J. S., Kropff, M. J. and van der Werf, W.** (2003b). Annual losses of weed seeds due to predation in organic cereal fields. *Journal of Applied Ecology*, **40** (5), 824-836.

**Westerman, P. R., Hofman, A., Vet, L. E. M. and van der Werf, W.** (2003c). Relative importance of vertebrates and invertebrates in epigeaic weed seed predation in organic cereal fields. *Agriculture, Ecosystems & Environment*, **95** (1/3), 417-425.

**Westerman, P. R., Liebman, M., Heggenstaller, A. H. and Forcella, F.** (2006). Integrating measurements of seed availability and removal to estimate weed seed losses due to predation. *Weed Science*, **54** (3), 566-574.

**Westerman, P. R., van Ast, A., Stomph, T. J. and van der Werf, W.** (2007). Long-term management of the parasitic weed *Striga hermonthica*: Strategy evaluation with a population model. *Crop Protection*, **26**, 219-227.

**Whalley, W. R., Finch-Savage, W. E., Cope, R. E., Rowse, H. R. and Bird, N. R. A.** (1999). The response of carrot (Daucus carota L.) and onion (Allium cepa L.) seedlings to mechanical impedance and water stress at sub-optimal temperatures. *Plant, Cell and Environment*, **22**, 229-242.

**Willenborg, C. J., May, W. E., Gulden, R. H., Lafond, G. P. and Shirtliffe, S. J.** (2005). Influence of wild oat (*Avena fatua*) relative time of emergence and density on cultivated oat yield, wild oat seed production, and wild oat contamination. *Weed Science*, **53** (3), 342-352.

**Williams, M. M., II and Boydston, R. A.** (2006). Volunteer potato interference in carrot. *Weed Science*, **54** (1), 94-99.

**Wilson, B. J., Peters, N. C. B., Wright, K. J. and Atkins, H. A.** (1988). The influence of crop competition on the seed production of *Lamium purpureum*, *Viola arvensis* and *Papaver rhoeas* in winter wheat. *Aspects of Applied Biology*, **18**, 71-80.

**Wilson, B. J. and Lawson, H. M.** (1992). Seedbank persistence and seedling emergence of 7 weed species in autumn-sown crops following a single years seeding. *Annals of Applied Biology*, **120** (1), 105-116.

**Wilson, B. J., Wright, K. J., Brain, P., Clements, M. and Stephens, E.** (1995). Predicting the competitive effects of weed and crop density on weed biomass, weed seed production and crop yield in wheat. *Weed Research*, **35** (4), 265-278.

**Wilson, P. and King, M.** (2008). Arable plants: a field guide - Introduction. Available at: http://www.arableplants.fieldguide.co.uk/?P=introduction#survival. [Accessed 02/03/2008]

**Woebbecke, D. M., Meyer, G. E., Bargen, K. v. and Mortensen, D. A.** (1995). Color indices for weed identification under various soil, residue, and lighting conditions. *Transactions of the ASAE*, **38** (1), 259-269.

**Woo, S. L., Thomas, A. G., Peschken, D. P., Bowes, G. G., Douglas, D. W., Harms, V. L. and McClay, A. S.** (1991). The biology of Canadian weeds. 99. *Matricaria perforata* Merat (Asteraceae). *Canadian Journal of Plant Science*, **71** (4), 1101-1119.

**Woods, S., Haydock, P. P. J., Evans, K., Robinson, R. C. and Dawkins, T. C. K.** (1999). Use of fluorescent tracer techniques and photography to assess the efficiency of tillage incorporated granular nematicides into potato seed-beds. *Soil & Tillage Research*, **51** (1/2), 17-23.

**WRAG** (2003). Managing and preventing herbicide resistance in weeds - WRAG guidelines. Available at: http://www.pesticides.gov.uk/uploadedfiles/Web_Assets/RAGs/WRAG_Guidelines_2003.pdf.

**WRAG** (2007). Response from Weed Resistance Action Group in relation to trifluralin and Annex 1. Available at: http://www.pesticides.gov.uk/uploadedfiles/WRAG%20Trifluralin%20response%20updated%20May%202007.pdf. [Accessed 15/02/2008]

**Wright, K. J.** (1993). Weed seed production as affected by crop density and nitrogen application. *Proceedings of the Brighton crop protection conference, weeds*, Farnham, pp. 275-280.

**Yenish, J. P., Doll, J. D. and Buhler, D. D.** (1992). Effects of tillage on vertical distribution and viability of weed seed in soil. *Weed Science*, **40** (3), 429-433.

**Yin, X., Goudriaan, J. A. N., Lantinga, E. A., Vos, J. A. N. and Spiertz, H. J.** (2003). A flexible sigmoid function of determinate growth. *Annals of Botany*, **91** (3), 361-371.

**Yoda, K., Kira, T., Ogawa, H. and Hozumi, K.** (1963). Self-thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of Biology, Osaka City University*, **14**, 107-129.

**Zhang, J., Hamill, A. S., Gardiner, I. O. and Weaver, S. E.** (1998). Dependence of weed flora on the active soil seedbank. *Weed Research*, **38** (2), 143-152.

**Zhixiong, L., Nan, C., Perdok, U. D. and Hoogmoed, W. B.** (2005). Characterisation of soil profile roughness. *Biosystems Engineering*, **91** (3), 369-377.

**Ziska, L. H.** (2004). Rising carbon dioxide and weed ecology. In: *Weed biology and management*. Edited by Inderjit. the Netherlands: Kluwer Academic Publishers. pp. 159-176.

# Appendix 1 – Questionnaire to carrot/onion growers

Date: Name + Address (optional):

1. **Cultivation**
    a) Do you plough the area where the carrots are grown? Yes ☐ No ☐
    b) If yes, how deep do you plough the soil?
    c) What secondary cultivation do you use?
    d) Do you use a de-stoner? Yes ☐ No ☐
    e) Do you use a sub-soiler? Yes ☐ No ☐

2. **Soil characteristics**
    a) How would you characterise the soil where you grow onions (e.g. sandy loam etc.)?
    b) If you happen to have more specific soil type information (e.g. from ADAS) what are the soil characteristics?
    c) What type of growing system do you use? Bed system ☐ Ridges ☐ Other ☐
    d) If you ticked the 'Other' box in the previous question could you please explain this.

3. **Weed control**
    a) Which weeds do you consider the most problematic within your carrot growth system?
    b) Which weed control strategy do you apply to prevent / control weeds within the carrot crop?

4. **Land use**
    a) How do you grow your onions / carrots? Cropping rotation ☐ Continuous ☐
    b) If you use a crop rotation, could you please specify the current (or last used) rotation?
    c) Do you have a specific crop to precede a carrot crop? If so, could you specify please

**Agricultural calendar:**

d) With regard to the soil where carrots are grown, could you indicate in chronological order which activities (cultivation, weeding, fertilising and harvesting) happen and when (by shading the appropriate times in the table), from the moment of harvesting the crop preceding a carrot crop, to the moment the carrots are harvested. See below for an example:

| **Activities:** | **Timing depends on:** | Jan | | Feb. | | Mar | | Apr | | May | | June | | July | | Aug | | Sept. | | Oct. | | Nov. | | Dec. | |
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For example:

| **Activities:** | **Timing depends on:** | Jan | | Feb. | | Mar | | Apr | | May | | June | | July | | Aug | | Sept. | | Oct. | | Nov. | | Dec. | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Power harrowing | Weather, type of carrot grown | | | | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | | | | | | | | | | | | | |

Extra remarks:

# Appendix 2 – Determination of leaf and flower area through image analysis in MatLab

```
mlvalid = 0;
        while imlvalid==0
                      dirname = uigetdir('M:\Projects\AG\AG0190\Objective 4 - PhD - Bastiaan Brak\Ph.D files\growth parameter estimation', 'Pick the
                      directory where the target images are stored')
            if dirname==0
                disp('*** You must give the directory where the target images are stored - try again ***')
            else
                imlvalid=1;
            end
        end

        cd(dirname)

        txtfile = dir('imagelist.txt');

        if isempty(txtfile)
            jpgfiles = dir('*.jpg');

            fid=fopen('imagelist.txt','wt+');

            fprintf (fid, '%s', dirname);
            fprintf (fid, '%c\n', 92);

            for n=1:length(jpgfiles)
                if n==length(jpgfiles)
                    fprintf (fid, '%s\n\n\n', jpgfiles(n).name);
                else
                    fprintf (fid, '%s\n', jpgfiles(n).name);
                end
            end
            fclose(fid);
        end

        cd ..

        flbwvalid = 0;
        while flbwvalid==0
            [flbwfiles,flbwpath]=uiputfile('xxxxxx.tif',...
                'Give the path where BW flower tif images will be saved');
            if flbwpath==0
                disp('*** You must give the path where the BW flower images are to be stored - try again! ***')
            else
                flbwvalid=1;
            end
        end
        disp(['BW flower images are put in: ',flbwpath])
```

```
maxgrcbwvalid = 0;
while maxgrcbwvalid==0
    [maxgrcbwfiles,maxgrcbwpath]=uiputfile('xxxxxx.tif',...
        'Give the path where b&w tif images for max groundcover will be saved');
    if maxgrcbwpath==0
        disp('*** You must give the path where the BW - max grc - images are to be stored - try again! ***')
    else
        maxgrcbwvalid=1;
    end
end
disp(['BW max groundcover images are put in: ',maxgrcbwpath])

plmanvalid = 0;
while plmanvalid==0
    [plmanfiles,plmanpath]=uiputfile('xxxxxx.tif',...
        'Give the path where manipulated images will be saved');
    if plmanpath==0
        disp('*** You must give the path where the manipulated images are to be stored - try again! ***')
    else
        plmanvalid=1;
    end
end
disp(['Manipulated (2G-R-B) images are put in: ',plmanpath])

grcbwvalid = 0;
while grcbwvalid==0
    [grcbwfiles,grcbwpath]=uiputfile('xxxxxx.tif',...
        'Give the path where b&w tif images for ground cover will be saved');
    if grcbwpath==0
        disp('*** You must give the path where the BW - ground cover - images are to be stored - try again! ***')
    else
        grcbwvalid=1;
    end
end
disp(['BW groundcover images are put in: ',grcbwpath])

labwvalid = 0;
while labwvalid==0
    [labw1files,labwpath]=uiputfile('xxxxxx.tif',...
        'Give the path where BW tif images for pure leaf area will be saved');
    if labwpath==0
        disp('*** You must give the path where the BW - pure leafarea - images are to be stored - try again! ***')
    else
        labwvalid=1;
    end
end
disp(['BW pure leafarea images are put in: ',labwpath])

excvalid = 0;
```

```
while excvalid==0
    [excelfile,excelpath]=uiputfile('Result_logfile.xls',...
        'Give the path to the spreadsheet with the results.');
    if excelpath==0
        disp('*** You must give the path where the Excel file with the results is to be stored - try again! ***')
    else
        excvalid=1;
    end
end

load fllevel.dat;

PLOT=[];
PLANT=[];
PLLEVEL=[];
MODPLLEVEL=[];
TOTAREACM2=[];
FLOWERLEVEL255=[];
FLOWERAREACM2=[];
INCOMPLETE_GROUNDCOVERAREACM2=[];
MAXGROUNDCOVERAREACM2=[];
GROUNDCOVERAREACM2=[];
PURELEAFAREACM2=[];

cd(dirname)
fid1=fopen('imagelist.txt');

imagepath = fgetl(fid1);

fprintf('\nCurrently processing:\n\n')
b=0;
while 1
    imagefile = fgetl(fid1);
    if isempty(imagefile)
        fprintf('\n\n')
        disp(['number of analysed files: ',int2str(b)])
        fprintf('\n')
        break
    end

    renamedIMG=strrep(lower(imagefile),'.jpg','.tif');
    flbw=[flbwpath,renamedIMG];
    plman=[plmanpath,renamedIMG];
    grcbw=[grcbwpath,renamedIMG];
    maxgrcbw=[maxgrcbwpath,renamedIMG];
    labw=[labwpath,renamedIMG];


    if exist(flbw)==2
        disp(['The file "',flbw,'" already exists and the code can not proceed!'])
```

```
else
    if exist(plman)==2
        disp(['The file"',plman,'" already exists and the code can not proceed!'])
    else
        if exist (grcbw)==2
            disp(['The file"',grcbw,'" already exists and the code can not proceed!'])
        else
            if exist (maxgrcbw)==2
                disp(['The file"',maxgrcbw,'" already exists and the code can not proceed!'])
            else
                if exist (labw)==2
                    disp(['The file"',labw,'" already exists and the code can not proceed!'])
                else
                    imfilp=[imagepath,imagefile];

                    fprintf('%s\n',imagefile);

                    origIMG=imread(imfilp);

                    redIMG =   origIMG(:,:,1);
                    greenIMG = origIMG(:,:,2);
                    blueIMG =  origIMG(:,:,3);

                    flowerlevel255=fllevel(b+1);
                    flowerlevel=(fllevel(b+1))/255;

                    flbwIMG=im2bw(redIMG,flowerlevel);

                    flbwfiltIMG=bwareaopen(flbwIMG,75);

                    imwrite(flbwfiltIMG,flbw,'tif');

                    flpixels=bwarea(flbwfiltIMG);

                    origdblIMG = double(origIMG)/255;

                    reddblIMG =   origdblIMG(:,:,1);
                    greendblIMG = origdblIMG(:,:,2);
                    bluedblIMG =  origdblIMG(:,:,3);

                    mandblIMG=(2*greendblIMG-reddblIMG-bluedblIMG);

                    manuint8IMG=uint8(round(mandblIMG*255));

                    totpixels=prod(size(manuint8IMG));

                    imwrite(manuint8IMG,plman,'tif');

                    pllevel=graythresh(manuint8IMG);
```

```
    maxgrcbwIMG=im2bw(manuint8IMG,0.003922);
    maxgrcbwfiltIMG=bwareaopen(maxgrcbwIMG,150);
    maxgrcpixels=bwarea(maxgrcbwfiltIMG);

    imwrite(maxgrcbwfiltIMG,maxgrcbw,'tif');
    modpllevel=0.52*pllevel;

    incomplgrcbwIMG=im2bw(manuint8IMG,modpllevel);

    incomplgrcbwsoftIMG=medfilt2(incomplgrcbwIMG,[3 3]);

    incomplgrcpixels=bwarea(incomplgrcbwsoftIMG);

    grcbwIMG=flbwfiltIMG | incomplgrcbwsoftIMG;

    grcpixels=bwarea(grcbwIMG);

    imwrite(grcbwIMG,grcbw,'tif');

    labwIMG=grcbwIMG-flbwfiltIMG;

    labwpixels=bwarea(labwIMG);

    imwrite(labwIMG,labw,'tif');

    s=double(imagefile);

    plot=str2double(char([s(1,2),s(1,3)]));
    plant=str2double(char([s(1,6)]));
    totareacm2=str2double(char([s(1,8),s(1,9),s(1,10),s(1,11),s(1,12)]));

    flowerareacm2=totareacm2*(flpixels/totpixels);
    incomplete_groundcoverareacm2=totareacm2*(incomplgrcpixels/totpixels);
    pureleafareacm2=totareacm2*(labwpixels/totpixels);
    groundcoverareacm2=totareacm2*(grcpixels/totpixels);
    maxgroundcoverareacm2=totareacm2*(maxgrcpixels/totpixels);

    PLOT=[PLOT;plot];
    PLANT=[PLANT;plant];
    FLOWERLEVEL255=[FLOWERLEVEL255;flowerlevel255];
    FLOWERAREACM2=[FLOWERAREACM2;flowerareacm2];
    PLLEVEL=[PLLEVEL;pllevel];
    MODPLLEVEL=[MODPLLEVEL;modpllevel];
    TOTAREACM2=[TOTAREACM2;totareacm2];

   INCOMPLETE_GROUNDCOVERAREACM2=[INCOMPLETE_GROUNDCOVERAREACM2;incomplete_groundcoverareacm2];
    MAXGROUNDCOVERAREACM2=[MAXGROUNDCOVERAREACM2;maxgroundcoverareacm2];
    GROUNDCOVERAREACM2=[GROUNDCOVERAREACM2;groundcoverareacm2];
    PURELEAFAREACM2=[PURELEAFAREACM2;pureleafareacm2];
end
```

```
                    end
                end
            end
        end
        b=b+1;
    end

    exc=[excelpath,excelfile];

    excel=actxserver('excel.application');

    set(excel,'visible',1);

    workbooks=excel.workbooks;
    workbook=invoke(workbooks,'add');

    sheets=excel.activeworkbook.sheets;
    sheet=get(sheets,'item',1);

    headerrange=get(sheet,'range','A1','A1');
    colheaderrange=get(sheet,'range','A3','K3');
    datarange=get(sheet,'range','A4',['K' num2str(b+3)]);

    set(headerrange,'Value','Results of Image Analysis')
    set(colheaderrange,'Value',{'Plot','Plant','Pllevel','Modpllevel',...
        'Totareacm2','Flowerlevel','Flowerareacm2','Incgrcareacm2',...
        'Maxgroundcoverareacm2','Groundcoverareacm2','Pureleaf1areacm2'})
           set(datarange,'Value',[PLOT,PLANT,PLLEVEL,MODPLLEVEL,TOTAREACM2,...
        FLOWERLEVEL255,FLOWERAREACM2,INCOMPLETE_GROUNDCOVERAREACM2,...
        MAXGROUNDCOVERAREACM2,GROUNDCOVERAREACM2,PURELEAFAREACM2])

    invoke(workbook, 'SaveAs', exc);

    fclose('all');
    fprintf('\n')
    toc
end

disp('All relevant information is saved in the Excel file and the program now closes')
```