L.M. Vleeshouwers

MODELLING WEED EMERGENCE PATTERNS

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MODELLING WEED EMERGENCE PATTERNS

Proefschrift
ter verkrijging van de graad van doctor
op gezag van de rector magnificus
van de Landbouwuniversiteit Wageningen,
dr. C.M. Karssen,
in het openbaar te verdedigen
op vrijdag 20 juni 1997
des namiddags te half twee in de Aula.

ISBN 90-5485-708-0

cover design: Ronald van Laar

Stellingen

1. Het maken van een onderscheid tussen de processen kiemrustbreking, kieming en vooropkomstgroei is essentieel voor het begrijpen van opkomstpatronen van akkeronkruiden.
Dit proefschrift

2. Het voorspellen van opkomstpatronen van akkeronkruiden wordt voornamelijk belemmerd door de onmogelijkheid om jaarlijkse cycli in kiemrust van onkruidzaden in de zaadbank met voldoende nauwkeurigheid te voorspellen.
Dit proefschrift

3. De grote en vaak onverklaarde verschillen in uitkomsten van kiemingsexperimenten met één soort duiden er op dat men in het zaadbiologisch onderzoek meer aandacht dient te besteden aan moederplanteffecten en kiemrustveranderingen, als oorzaken van kiemingsvariabiliteit.

4. Dat zaadfysiologen het begrip opgelegde kiemrust (*enforced dormancy*) gebruiken voor het onvermogen van zaden om te kiemen in het donker, is net zo onzinnig als wanneer medici het begrip opgelegde blindheid (*enforced blindness*) zouden hanteren voor het onvermogen van mensen te zien in het donker.
Bewley JD, Black M. 1982. Physiology and biochemistry of seeds. Berlin: Springer-Verlag.

5. Het rijgedrag van taxichauffeurs die passagiers vervoeren bewijst dat ze de verkeersregels kennen.

6. De sterke nadruk op de gevaren van klimaatverandering als gevolg van het gebruik van fossiele brandstoffen leidt er ten onrechte toe dat het belang van besparing op het gebruik ervan exclusief gekoppeld wordt aan het terugdringen van de CO_2-uitstoot.
n.a.v. De Volkskrant, 12 april 1997

7. Gezien het lage risico voor hart- en vaatziekten bij zowel landbouwers als academici zou het aanbevelenswaard zijn als de Landbouwuniversiteit het gezondheidsaspect een rol liet spelen bij de werving van studenten en personeel.
n.a.v. Trouw, 23 augustus 1995

8. Indien men duurzaamheid als maatstaf neemt, gaat de Nederlandse toerist te ver.
Gaan we te ver? Pleidooi voor een bezinning op de relatie toerisme-duurzaamheid-milieu. Rapport van de Raad voor het Natuurbeheer, 1994.

9. In Nederland zal invoering van een districtenstelsel niet leiden tot een grotere betrokkenheid van de kiezer bij de politiek.

Leo Vleeshouwers
Modelling weed emergence patterns
Wageningen, 20 juni 1997

ABSTRACT

Vleeshouwers LM. 1997. *Modelling weed emergence patterns*. PhD thesis, Wageningen Agricultural University, Wageningen, 165 pp.

Anticipating weed pressure may be important in selecting and timing weed control measures in order to optimize their effectiveness, and thus reduce herbicide use. Therefore, a predictive model of the time of emergence and the numbers of seedling emerging (the weed emergence pattern) after soil cultivation may be a useful tool in integrated weed management. In this study, a simulation model was developed in order to increase the quantitative understanding of weed emergence in the field in relation to weather, soil and cultivation measures. In the model, three phases were distinguished in the process of weed emergence in the field, and modelled in separate modules: annual changes in dormancy, germination, and pre-emergence growth. The model was parameterized and tested for three arable weed species: *Polygonum persicaria*, *Chenopodium album* and *Spergula arvensis*.

Simulation of annual cycles in dormancy and germination is based on a physiological model concerning the action of phytochrome in the seed. Dormancy is related to the amount of an hypothetical phytochrome receptor, that fluctuates in an annual pattern. The simulation model gave a reasonably accurate description of cyclic changes in germinability of seeds exhumed in a three years' burial experiment. The timing of germination was simulated by means of the thermal time concept.

A physiologically based model describes the effects of temperature, soil penetration resistance, burial depth and seed weight on pre-emergence growth of seedlings. The model provided a good description of seedling emergence observed in a laboratory experiment.

The separate modules simulating the consecutive processes of dormancy release, germination and pre-emergence growth were linked to form a model simulating seasonal weed emergence patterns in the field. Input variables of the model were the date and method of soil cultivation, soil temperature and soil penetration resistance. Output of the model was seedling density and the timing of seedling emergence. The model was evaluated with data from a field experiment. When using the germination results of the exhumed seed lots to estimate the degree of dormancy at the time of soil cultivation, the extent of the emergence flushes following soil cultivation could be described well. Although the dormancy model gave a good description of annual cycles in dormancy, the quantitative prediction of seasonal changes in dormancy and germination was not accurate enough for predicting field emergence, and appeared to be the weak point in predicting weed emergence patterns. When there was substantial emergence as a result of soil cultivation, the timing of emergence could be predicted accurately.

Keywords: *Polygonum persicaria*, redshank, *Chenopodium album*, fat hen, *Spergula arvensis*, corn spurrey, weeds, emergence pattern, dormancy, germination, pre-emergence growth, simulation model

DANKWOORD

Gedurende de jaren dat ik aan mijn promotie-onderzoek gewerkt heb, heb ik van velen belangrijke hulp en steun ontvangen. Van ganser harte wil ik op deze plaats ieder van hen bedanken.

Vanaf het prille begin tot aan de laatste loodjes is drs. B.J. Post betrokken geweest bij mijn werk aan dit proefschrift. Ben, van harte bedankt voor je voortdurende interesse en steun. Ik ben steeds bijzonder ingenomen geweest met onze prettige samenwerking. Mijn promotoren prof. dr. M.J. Kropff en prof. dr. C.M. Karssen wil ik hartelijk bedanken voor de begeleiding van het onderzoek. Martin Kropff heeft de ontwikkeling van het model en de neerslag daarvan in de verschillende manuscripten steeds van waardevol commentaar voorzien. Met grote voortvarendheid spoorde hij zwakke plekken op in mijn werk en daagde me uit die in sterke punten om te buigen. In vergelijking had ik met Cees Karssen weldadig rustige voortgangsbesprekingen, die waar nodig tot zeer gewaardeerde ondersteuning van zijn kant leidden.

Dr.ir. C.J.T. Spitters, die belangrijk pionierswerk verrichtte op het gebied van het modelleren van onkruidkieming, ben ik zeer erkentelijk voor het signaleren van de mogelijkheid die er lag om op dit terrein promotie-onderzoek te starten en voor zijn aansporingen om een projectvoorstel te formuleren. Kees Spitters overleed in het voorjaar van 1990. In gedachten heb ik nog regelmatig mijn resultaten aan zijn kritisch oordeel getoetst. Professor dr. P. Zonderwijk wil ik bedanken voor zijn stimulerende houding bij het opstellen van het projectvoorstel. Met Harro Bouwmeester heb ik vele, soms verhitte discussies gevoerd over kiemrustcycli van onkruidzaden. Bedankt, Harro. Onze gedachtenwisselingen en het gebruik van een aantal belangrijke gegevens uit je kiemrustonderzoek hebben grote betekenis gehad voor mijn proefschrift.

Voor het uitvoeren van de experimenten heb ik met veel genoegen een beroep gedaan op Herman van Oeveren, René Siep, Marita van den Bergh en Jaap Blijjenberg. Bij Jos Kroesbergen van de vakgroep Grondbewerking kon ik altijd terecht voor waardevolle hulp en advies. Rommie van der Weide heeft waardevolle aanwijzingen gegeven voor het uitvoeren van de experimenten over voor-opkomstgroei.

Jacques Withagen stond mij bij met raad en daad bij het uitvoeren van de statistische analyses. Willem Stol hielp me op weg met een aantal problemen die zich voordeden bij het simulatiewerk. Cees Daleboudt was aanspreekpunt bij wiskundige problemen.

Rudy Rabbinge en zijn groep van promovendi hebben een belangrijke rol gespeeld bij het vormen van mijn kritisch vermogen ten aanzien van eigen en andermans wetenschappelijk werk. Jacco Wallinga, Eddie Kremer, Bert Schnieders, Corné Kempenaar en Peter Schippers maakten het nog immer florerende lunch-overleg tot een succes. Het promovendi-overleg onder leiding van Martin Kropff was forum van discussie over talloze aspecten van het vakgebied (en wanneer het zich verplaatste naar de kroeg ook over verschillende aspecten van niet-vakgebieden). Indien nodig kon ik Henk Hilhorst en Ria Derkx altijd bereid vinden voor het bediscussiëren van mijn werk vanuit een plantenfysiologische invalshoek. I am very grateful to Bärbel Gerowitt (Göttingen), Professor Karl Hartmann (Erlangen-Nürnberg) and Louis Assemat (Dijon) for their hospitality during my visits to their institutes.

Gon van Laar gaf nuttig advies bij het lay-outwerk. Ben Post leverde de foto die de omslag siert. Ronald van Laar ontwierp de omslag en Bart Wemelsfelder zorgde voor de uitvoering ervan. Nico de Boer maakte een serie fraaie dia's die met grote regelmaat mijn voordrachten illustreerden.

Mijn kamergenoten Peter Kaspers en Bärbel Gerowitt (de hilarische discussies die we gedrieën voerden zijn nog steeds ongeëvenaard), Wietske van Dijk, Marita van den Bergh en Eddie Kremer bedank ik van harte voor hun kameraadschap. De menselijke belangstelling en adviezen van Aad van Ast heb ik enorm gewaardeerd. Evenzeer heb ik de aandacht en stimulans van Jan van Groenendael op prijs gesteld. Verder bedank ik alle collega's van de oud-vakgroepen VPO en TPE voor de prettige samenwerking.

Behalve een belangrijke stap in mijn loopbaan markeert dit proefschrift ook een belangrijke periode in mijn leven. Veel mensen hebben veel voor me betekend in deze periode. Bij voorkeur lieten we de onkruidproblemen links liggen. Bedankt voor jullie hulp bij het bijzetten van de zeilen toen het nodig was: Gait Groot Zevert, Ingrid van de Klundert en haar collega's. Bedankt voor alle liefde, belangstelling en steun: mijn moeder en vader, broers en zus, vrienden, familie, en Maria.

Leo

ACCOUNT

Parts of this thesis have been included, in part or in whole, in the following publications:

Chapter 1	**Vleeshouwers LM, Bouwmeester HJ, Karssen CM. 1995.** Redefining seed dormancy: an attempt to integrate physiology and ecology. *Journal of Ecology* **83**: 1031-1037.
Chapter 2	**Vleeshouwers LM, Bouwmeester HJ. 1997.** A simulation model for seasonal changes in dormancy and germination of weed seeds. *Plant, Cell and Environment* (submitted).
Chapter 3	**Vleeshouwers LM. 1997.** The effect of seed dormancy on percentage and rate of germination in *Polygonum persicaria* L., and its relevance for crop-weed interaction. *Annals of Applied Biology* (submitted).
Chapter 4	**Vleeshouwers LM. 1997.** Modelling the effect of temperature, soil penetration resistance, burial depth and seed weight on pre-emergence growth of weeds. *Annals of Botany* **79** (in press).
Chapter 5	**Vleeshouwers LM, Kropff MJ. 1997.** Field emergence patterns in three arable weed species. I. The effect of weather, soil and cultivation date. *New Phytologist* (submitted).
Chapter 6	**Vleeshouwers LM, Kropff MJ. 1997.** Field emergence patterns in three arable weed species. II. Modelling the effect of weather, soil and cultivation date. *New Phytologist* (submitted).

CONTENTS

1 GENERAL INTRODUCTION

1.1 Background of the problem

Without crop protection, almost half of the world's present agricultural production would be lost (Oerke *et al.*, 1994). To a high degree, crop protection relies on the use of pesticides. Environmental pollution and the development of resistance give rise to concern about the extent to which crop protection is dominated by chemical control. Recognizing the problems that attend the routine application of chemical control, the United Nations decided to promote the development of integrated pest management (IPM) as the best option for future crop protection (Johnson, 1993). IPM combines biological control, host plant resistance and appropriate farming practices, and minimizes the use of pesticides.

In terms of yield losses, the importance of weeds is approximately equal to that of animal pests and diseases: 31% of the losses that occur in spite of the present crop protection, are due to weeds (animal pests: 37%, diseases: 32%) (Oerke *et al.*, 1994). In terms of financial cost of chemical control, weeds are more important than insects and fungi: 44% of the world's expenditure on pesticides is spent on herbicides (insecticides: 29%, fungicides: 21%) (Oerke *et al.*, 1994). In contrast, the development of integrated weed management (IWM) lags behind integrated management of other pests. Detailed understanding of weed behaviour in relation to particular cropping practices is crucial for the development of integrated weed management systems (Fryer, 1977; Post and Wijnands, 1993). However, the biology of weeds is rather poorly studied compared to that of other pest organisms, particularly insects.

An important aspect of weed behaviour in relation to cropping practices in arable fields, is the development of a weed vegetation after soil cultivation. Many arable weeds are annual species that form a persistent seed bank (Thompson and Grime, 1979). Soil cultivation stimulates germination of weed seeds in the seed bank, and thus triggers the development of a weed vegetation. Anticipating weed pressure may be important in selecting and timing control measures in order to optimize their effectiveness. Therefore, prediction of the time of emergence, the numbers of seedlings emerging and the species composition of the weed vegetation (in short, the emergence pattern) after soil cultivation may be an important tool in integrated weed management (Forcella *et al.*, 1993*b*). However, the relationship between the composition of the seed bank and that of the weed vegetation, both in species and in numbers, is rather variable and poorly understood (Roberts and Ricketts, 1979; Ball and Miller, 1989; Forcella *et al.*, 1992; Cardina and Sparrow, 1996). Biological research is needed to understand and quantify the effect of cultural measures and environmental conditions on weed emergence patterns (Post, 1986; Post, 1988; Forcella *et al.*, 1992).

1.2 Dormancy, germination and pre-emergence growth

Arable weeds do not emerge at random over the year, but in clearly defined species-specific patterns. Seasonal emergence patterns of weeds in the field have been studied extensively. Table 1.1 gives an overview of the research in this field since 1900, comprising more than 250 weedy species in 17 countries. The major part of these studies (about 180 species) relate to arable weeds in temperate regions. Also the study that is reported in this thesis focuses on emergence patterns of arable weeds in temperate

Table 1.1 Summary of literature data on seasonal field emergence patterns of weeds. The table gives information about the seasonal distributions of emergence that are presented in either a table or a graph. It does not provide information about other aspects of the studies that are reported in these references. If different experiments are discussed in one paper, the experiments are numbered. Studies in which not all species occur as weeds are marked with an asterisk.

Reference	*Country*	*Number of species*	*Data allow comparison of emergence patterns between*	*Seeds buried or natural seed bank*	*Meteorological data presented*	*Simultaneous assessment of changes in dormancy*
Waldron (1904)	USA	7	species, burial depths	seeds buried (unknown quantity)	no	no
Chepil (1946*a*)	Canada	59	species, years after burial	1. seeds buried (unknown quantity); 2. seeds buried	no	no
Chepil (1946*b*)	Canada	5	species, burial depths, soil cultivation yes/no, soil packing yes/no, irrigation yes/no	seeds buried	no	no
Thurston (1961)	UK	2	species, years, burial depths, soil cultivation dates, soil cultivation frequencies	seeds buried	no	no
Allred & Tingey (1964)	USA	3	species, years, burial depths	seeds buried	soil temperature	no
Chancellor (1964*a*)	UK	16	species, years, soil cultivation yes/no, soil cultivation frequencies	natural seed bank	incidental rainfall data	no
Roberts (1964)	UK	11	species, years, years after burial	seeds buried	no	no
Dawson (1965)	USA	1	crop yes/no	seeds buried	incidental soil temperature, rainfall and irrigation data	no
Courtney (1968)	UK	1	soil cultivation yes/no, years, years after burial	seeds buried	no	yes
Budd (1970)	UK	1	sowing date	seeds buried	air temperature and rainfall	no
Popay & Roberts (1970)	UK	2	species, years, locations, buried seeds/natural seed bank	seeds buried, natural seed bank	soil temperature, rainfall, soil moisture	yes
Roberts & Feast (1970)	UK	20	species	seeds buried	no	no
Stoller & Wax (1973)	USA	8	species, years, burial depths	seeds buried	soil and air temperature, rainfall, soil moisture	no

Table 1.1 continued

Reference	*Country*	*Number of species*	*Data allow comparison of emergence patterns between*	*Seeds buried or natural seed bank*	*Meteorological data presented*	*Simultaneous assessment of changes in dormancy*
Lawson *et al.* (1974)	UK	18	1. species, locations 2. species, years, periods after soil cultivation	natural seed bank	monthly accumulated °Cdays over 5.6°C, rainfall	no
Twentyman (1974)	Australia	1	1. years 2. locations, vegetation cover yes/no	seeds buried	no	no
Roberts & Lockett (1978*a*)	UK	1	years, years after burial	seeds buried	no	no
Roberts & Lockett (1978*b*)	UK	1	years, years after burial, soil cultivation yes/no, depths of burial	seeds buried	incidental soil temperature data	yes
Roberts & Chancellor (1979)	UK	7	species, years years after burial, locations, depths of burial, soil cultivation frequencies	seeds buried	no	no
Roberts & Neilson (1980)	UK	10	species, years, years after burial	seeds buried	no	no
Roberts & Potter (1980)	UK	14	soil cultivation yes/no, soil cultivation dates	natural seed bank	rainfall, simulated soil moisture	no
Erviö (1981)	Finland	7	species, crops, years	natural seed bank	air temperature, rainfall	no
Håkansson (1983)	Sweden	12	species, soil cultivation yes/no	seeds buried	no	yes
Marks (1983)	Nigeria	14	species	natural seed bank	air temperature, rainfall	yes
Roberts & Boddrell (1983*a*)	UK	10	species, years, years after burial	seeds buried	no	no
Roberts & Boddrell (1983*b*)	UK	3	species, cultivation dates	seeds buried	no	no
Beuret (1984)	Switzerland	23	years	natural seed bank	no	no
Ogg & Dawson (1984)	USA	8	species, soil cultivation yes/no, years, years after burial	seeds buried	air temperature; soil continually irrigated	no
Roberts (1984)	UK	7	soil cultivation yes/no, soil cultivation dates	natural seed bank (seed numbers assessed by sampling)	rainfall, simulated soil moisture	no
Roberts & Boddrell (1984)	UK	4	species	seeds buried	no	no
Roberts & Boddrell (1985)	UK	11	species, years, years after burial	seeds buried	no	no

Table 1.1 continued

Reference	*Country*	*Number of species*	*Data allow comparison of emergence patterns between*	*Seeds buried or natural seed bank*	*Meteorological data presented*	*Simultaneous assessment of changes in dormancy*
Baskin *et al.* (1986)	USA	2	species, years	natural seed bank (seed numbers assessed by sampling)	air temperature, rainfall	no
Chancellor (1986)	UK	10	species, years, years after burial	natural seed bank	no	no
Dekker & Meggitt (1986)	USA	1	locations, years	natural seed bank	rainfall	no
Leguizamon (1986)	Argentina	1	years	seeds buried	soil temperature, rainfall	no
Roberts (1986)	UK	70*	species	seeds buried	no	no
Van den Brand (1986)	Netherlands	40	species, years	seeds buried (unknown quantity)	no	no
Longchamp *et al.* (1988)	France	4	species, years, soil cultivation dates	seeds buried	no	yes
Zimdahl *et al.* (1988)	Philippines	10	species, years	natural seed bank	rainfall and radiation	no
Cardina & Hook (1989)	USA	1	years, soil cultivation yes/no, soil cultivation dates, soil cultivation frequencies	natural seed bank	rainfall	no
Takayanagi & Kusanagi (1989)	Japan	1	soil cultivation dates	?	no	no
Benech-Arnold *et al.* (1990)	Argentina	1	shading of the soil yes/no, seed collecting dates	natural seed bank	soil temperature; soil continually irrigated	no
Bond & Baker (1990)	UK	?	soil cultivation dates, irrigation yes/no	natural seed bank	no	no
Boydston (1990)	USA	2	species, years, years after burial	seeds buried	soil temperature; soil continually irrigated	no
Egley & Williams (1991)	USA	6	species, years	seeds buried	water balance, incidental soil temperatures	no
Peters (1991)	UK	1	years, seeds from different positions on the panicle, seeds from different genetic lines	seeds buried rainfall	air temperature,	no
Reisman-Berman *et al.* (1991)	Israel	2	1. plots 2. species, soil cultivation dates	1. natural seed bank 2. seeds buried	soil temperature, rainfall and irrigation quantities	yes
Håkansson (1992)	Sweden	26	species, soil types	natural seed bank	no	yes

Table 1.1 continued

Reference	*Country*	*Number of species*	*Data allow comparison of emergence patterns between*	*Seeds buried or natural seed bank*	*Meteorological data presented*	*Simultaneous assessment of changes in dormancy*
Lutzeyer & Koch (1992)	Benin	4	species, soil cultivation yes/no	natural seed bank	rainfall	no
Sahile *et al.* (1992)	Ethiopia	10	species, locations	natural seed bank	rainfall	no
Alm *et al.* (1993)	USA	2	species, burial depths, watering regimes	seeds buried	soil temperature, soil water potential	no
Forcella (1993)	USA	1	years	seeds buried/ natural seed bank	soil temperature, rainfall, soil water potential	no
Harvey & Forcella (1993)	USA	1	years, locations	natural seed bank	soil temperature, rainfall, soil water potential	no
Van der Weide (1993)	Netherlands	1	1. soil cultivation dates 2. -	1. natural seed bank 2. seeds buried	no	yes
Anderson (1994)	USA	16	-	natural seed bank	rainfall	no
King & Oliver (1994)	USA	1	years, soil cultivation dates	natural seed bank	soil temperature, soil water potential	no
Popay *et al.* (1995)	New Zealand	10	species, years, countries	natural seed bank	air temperature, rainfall	no

climatic conditions. The most important environmental factors that are reported to affect the seasonal distribution of a species are temperature, rainfall and soil cultivation. To a large extent, the nature of the research summarized in Table 1.1 is descriptive. In six recent studies quantitative relationships between environmental conditions and weed seedling emergence were given. Takayanagi and Kusanagi (1989) presented a model that simulates emergence of *Digitaria adscendens* as a function of air temperature and soil moisture, Benech-Arnold *et al.* (1990) related emergence of *Sorghum halepense* to soil temperature, Alm *et al.* (1993) described a model simulating emergence of *Ipomoea hederacea* and *Abutilon theophrasti* in relation to soil temperature and soil water potential, Forcella (1993) simulated emergence of *Abutilon theophrasti* as a function of soil temperature and rainfall, Harvey and Forcella (1993) quantified emergence of *Chenopodium album* in relation to soil temperature, Van der Weide (1993) modelled emergence of *Galium aparine* as a function of soil temperature, depth of burial and penetration resistance of the soil, and King and Oliver (1994) presented a model that simulates emergence of *Digitaria sanguinalis* as influenced by soil temperature and soil water potential.

In order to obtain a quantitative explanation of emergence patterns, that may eventually lead to a model predicting the emergence of weeds in the field, it is necessary to identify the key factors in the environment that affect emergence patterns. In this respect it is crucial to distinguish between three processes that occur subsequently in the ploughing layer of an arable field, and lead to weed emergence (Cousens and Peters, 1993; Van der Weide, 1993). The first step is the release of dormancy of the buried seeds. Release of dormancy implies that the physiological state of the seeds changes in such a way that the seeds become increasingly sensitive to germination inducing factors like light and nitrate. Once dormancy has been released, the second step can take place. This is the germination process, that is triggered, for example, by irradiation. Inside the seed the rootlet starts to develop, and eventually protrudes from the seed. Finally, the cotyledons protrude from the seed coat, and the shoot grows to the surface. This third step is called pre-emergence growth. The rationale behind the distinction between these processes in the research is that they are physiologically different, that they work on different time scales, that they are affected by different environmental factors, and, in so far as they are affected by the same environmental factors, optimal values for those factors may be quite different. For example, changes in seed dormancy are reversible, while germination and pre-emergence growth are irreversible. In summer annual species breakage of dormancy occurs at low temperatures, and lasts for several months, while the germination process has its temperature optimum at higher temperatures, and lasts for only a few days. Soil compaction affects underground shoot elongation, but not dormancy and germination.

Protrusion of the radicle from the seed coat marks the transition from germination to pre-emergence growth. The separation between breakage of dormancy and induction of germination, however, is far more difficult to define. In the literature, no uniform concept of dormancy is used, and often viewpoints are only stated implicitly. Therefore, the concept used in this thesis will be discussed extensively in the next section (adapted from Vleeshouwers *et al.*, 1995). The concept was developed by the Seed Biology Group at the Department of Plant Physiology of Wageningen Agricultural University. Special attention will be given to the distinction between dormancy and germination. The definition of dormancy used in this thesis allows a clear separation between the processes of dormancy release and germination.

1.2.1 *Description of the processes*

Dormancy

Introduction. In the literature, there is no unanimity about the definition and significance of the phenomenon of seed dormancy. The statement made by Hobson (1981), that there may be as many definitions of dormancy as there are investigators concerned with the subject, can rightly be applied to the specific case of dormancy in seeds. This variety of ideas about dormancy is reflected in the number of classifications of dormancy employed by various authorities, as shown by Bewley and Black (1982).

Therefore, it is surprising that dormancy is not seen as a controversial subject. For example, in the book 'Seeds: the ecology of regeneration in plant communities' (Fenner, 1992) seed dormancy is dealt with in four separate chapters (Murdoch and Ellis, 1992; Pons, 1992; Probert, 1992; Karssen and Hilhorst, 1992), but none of the authors seeks to oppose his view against the others'. Nevertheless, they express different views on dormancy, between which there is friction, and sometimes plain contradiction. The fact that these contrasts are not stated explicitly in the literature may have an adverse effect on communication between researchers and on the understanding of each other's results and conclusions. This may lead to situations where scientists pose inaccurate research questions and set up defective experiments.

In this chapter I explain my position in the non-declared debate on dormancy, particularly in regard to the definition of dormancy, the classification of dormancy, the distinction between dormancy and germination, and the significance of seed dormancy in the life-cycle of plants. In addition, I will indicate the way in which the view that is discussed here is based on recently developed ideas in seed physiology. I believe that the use of a physiologically sound concept of dormancy may lead to a better definition of ecological research questions concerning dormancy and germination. The concept of seed dormancy that is discussed in this chapter is not the only one possible, but it is coherent, and it has enhanced the understanding of many observations on seed dormancy and germination.

I confine myself to those forms of dormancy named physiological dormancy by Baskin and Baskin (1989), since this is the most frequently occurring type of dormancy in seed banks in temperate regions, and do therefore not consider dormancy caused by a hard seed coat nor by underdevelopment of the embryo.

Definition and classification of dormancy. Harper (1959) distinguished two categories among plants living in a community: those which are growing and those which are dormant. This definition of dormancy implies that, according to Harper, seeds are dormant when they are not germinating. Harper recognized three types of seed dormancy: 'some seeds are born dormant (*innate*), some achieve dormancy (*induced*) and some have dormancy thrust upon them (*enforced*)'.

Many authors have adopted the essence of Harper's ideas. They have identified seed dormancy with the absence of a germination response, and have taken over his classification of dormancy (*e.g.* Murdoch and Ellis, 1992). In my opinion, however, the phenomenon that was classified by Harper should be called the seeds' inability to germinate, instead of the seeds' dormancy. There is a clear distinction between these two phenomena, as will be illustrated later on. Moreover, in his classification Harper did not make a distinct separation between the different causes for which a viable seed is unable to germinate. The causes he mentions are located both in the seed and in its environment, and are related to both dormancy and germination. I think that a sound concept of dormancy should clearly separate the internal and external factors that interact in seed germination. I prefer to reserve the term dormancy for a block or blocks within the seed that prevent germination, and distinguish it from the absence of factors required to evoke germination.

A classical notion of dormancy, which can be regarded as an elaboration of Harper's idea, is 'temporary failure of a viable seed to germinate, after a specified length of time, in a particular set of environmental conditions that later evoke germination when the restrictive state has been terminated by either natural or artificial means' (Simpson, 1990). Vegis (1964) considered that changes in the dormancy of seeds involve changes in their temperature requirements for germination. As dormancy is induced, the range of temperatures over which germination can proceed narrows, until germination is no longer possible at any temperature, and full dormancy is reached. As dormancy is broken, the temperature range widens, until it is maximal. This implies that the dormancy of a seed is not an all-or-nothing property (*cf.* Baskin and Baskin, 1985). However, a seed's 'failure to germinate in a particular set of environmental conditions' is an all-or-nothing property.

If one equates dormancy with failure of germination, Vegis' theory would imply that, except for seeds that are fully dormant, the dormancy of seeds kept at a temperature outside the range required for germination can be relieved by transferring them to a temperature inside this range. This view is shared by Bewley and Black (1982), who stated that dormancy may vary with external conditions, usually of temperature. On the other hand, dormancy is supposed to be an adaptive trait (*e.g.* Simpson, 1990). This implies that dormancy should *not* be a measure of the external conditions a seed is currently exposed to, but be a characteristic of the seed. I believe that these inconsistencies result from an inaccurate definition of dormancy. Firstly, dormancy should be able to have any value between all and nothing, and, secondly, it should be a seed trait (*cf.* Gordon, 1973).

Karssen (1982) emphasized that seasonal periodicity in the field-emergence of annuals is the combined result of seasonal periodicity in the field temperature and seasonal periodicity in the width of the range of temperatures suited for germination. Germination in the field is restricted to the period when the field temperature and the temperature range over which germination can proceed overlap (Fig. 1.1). Dormancy is only related

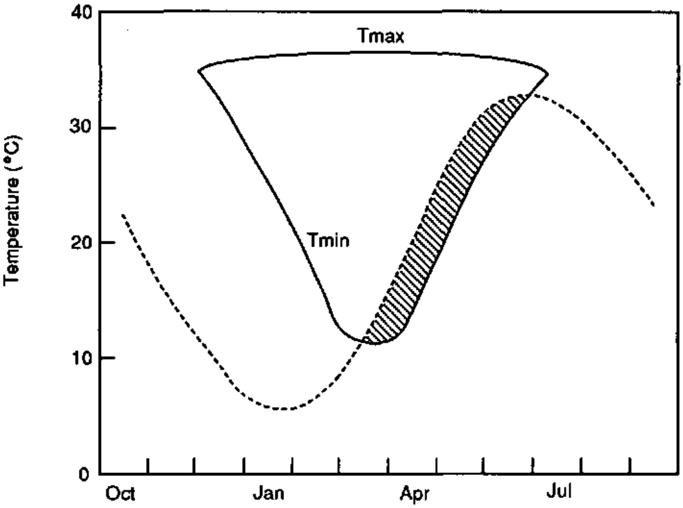

Fig. 1.1 Widening and narrowing of the temperature range of germination of a summer annual in relation to the temperature in the habitat during the seasons. The broken line indicates the mean daily temperature in the field. Solid lines indicate maximum (Tmax) and minimum (Tmin) temperature for germination. In the hatched area the actual and required temperatures overlap. (Adapted from Karssen, 1982).

to the width of the temperature range for germination, not to the question whether or not the current temperature is inside this range. Derkx and Karssen (1993*a*) showed that in *Sisymbrium officinale* changes in dormancy not only comprise changes in temperature requirements for germination, but also in its requirements for nitrate and light. Sensitivity to light and nitrate, both necessary stimuli for the germination of this species, increased when dormancy was broken and decreased when dormancy was induced.

Generalizing the concept of Karssen (1982), which is solely based on one factor, temperature, one may say that germination occurs when internal requirements and external factors meet. Dormancy is only related to the requirements for germination, not to the question whether or not these requirements are met in a particular environment. This is the reason why I oppose Harper's (1959) concept of dormancy. Standstill of plant growth, which he calls dormancy, only indicates that the requirements for growth are not met.

I propose a different definition of seed dormancy: *dormancy is a seed characteristic, the degree of which defines what conditions should be met to make the seed germinate.*

The wider the range of conditions at which a seed is able to germinate, the smaller its degree of dormancy (*cf.* Hilhorst, 1993). One could regard dormancy as the seed's fastidiousness about the germination conditions it requires, whereas germination is the seed's response to an overlap of the environmental conditions and the germination requirements, defined by the degree of dormancy (Fig. 1.2).

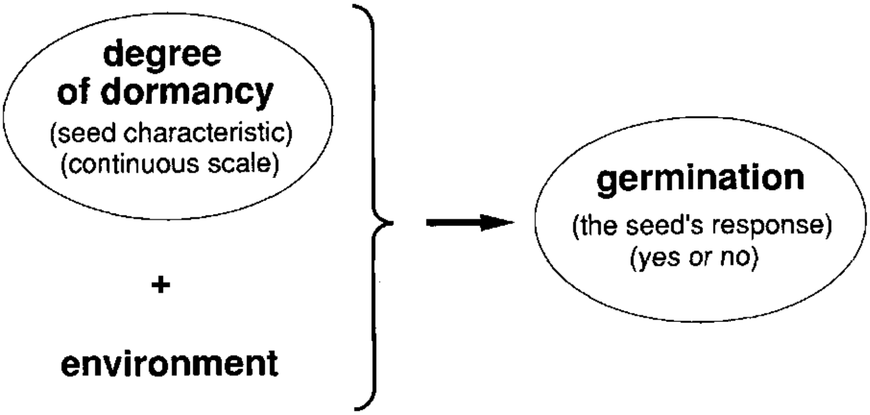

Fig. 1.2 Diagrammatic representation of the interaction of seed and environment in the process of germination. The degree of dormancy defines the germination requirements of the seed. If these requirements are met by the environment the seed will germinate, if they are not the seed will fail to germinate. It should be realized that the degree of dormancy of a seed at a certain moment is influenced by the environmental conditions it has experienced during its existence, back to the conditions in which it has ripened at the mother plant.

When doing experiments, one should realize that because of the different nature of germination and dormancy, the result of a germination test can only be an approximate representation of the dormancy state of seeds. This is especially true for a single seed. Whether or not the seed germinates in a germination test cannot be a measure of its dormancy. However, for a large seed population germination tests over a range of environmental conditions can give a satisfactory impression of the degree of dormancy.

No new classification of dormancy is attempted here. An adequate classification of dormancy is the existing one, introduced by Crocker (1916), that distinguishes primary and secondary dormancy. Primary dormancy is the dormancy state of the freshly shed seed. When primary dormancy has been relieved and suitable conditions are present, the seed germinates. If suitable conditions are not present, and germination does not occur, secondary dormancy may develop. Secondary dormancy of buried seeds can be relieved and re-induced during many successive seasons.

Factors affecting changes in dormancy and the actual germination process. The distinction between dormancy and germination that I advocate is not only based on theoretical considerations. It is shown experimentally that the processes of dormancy change and germination are regulated by different environmental factors. Besides, it is shown that both processes are regulated by temperature, but in a different way. An unfortunate circumstance is that it is, as yet, impossible to measure the dormancy state of a seed directly. One can only get an impression of the seed's dormancy by trying to make it germinate. This has led to the situation that many researchers do *not* make a clear distinction between changes in dormancy and the process of germination. Vincent and Roberts (1977), and Bewley and Black (1982), for example, call light and nitrate at one time factors that affect dormancy, at another time factors that promote germination. I do distinguish between dormancy release and stimulation of germination, and also between induction of dormancy and inhibition of germination.

Generally, changes in dormancy are investigated by storing seeds in imbibed conditions in an environment that allows seed survival but prevents germination (Baskin and Baskin, 1985). At regular intervals, samples of the stored seeds are taken and their germination is tested in a range of conditions. If the range of conditions allowing germination changes in the course of time, one can conclude that the storage conditions affected seed dormancy. Dormancy relieving factors will cause a widening of the range of conditions that allow germination, and dormancy inducing factors will cause a narrowing of this range. Factors that do not change the seeds' fastidiousness as to the germination conditions, but are at the same time indispensable to obtain a germination response, are germination inducing factors.

Bouwmeester and Karssen (1992) buried seeds of *Polygonum persicaria* in the field at a depth of 10 cm. At regular intervals over a period of three years, they exhumed samples of these seeds and tested them for germination over a range of temperatures. They showed that seasonal changes in the width of the temperature range over which exhumed seeds germinate (*i.e.* seasonal changes in dormancy) could be simulated by using only the soil temperature as an explanatory factor (Fig. 1.3). The changes in dormancy did not correlate with seasonal changes in soil moisture and soil nitrate content. The authors concluded that soil moisture and nitrate content do not influence changes in *dormancy*. Since the seeds were buried in continuous darkness, their conclusion can be extended to the factor light. However, nitrate, soil moisture and light are factors that strongly influence *germination* (*e.g.* Vincent and Roberts, 1977).

A complicating factor is that temperature has a dual role. It regulates the seasonal changes in dormancy, but also germination (*e.g.* Bouwmeester and Karssen, 1992, 1993*a*,*b*,*c*). The temperature requirements of both processes are, however, quite different. Dormancy of *Polygonum persicaria* can be broken at temperatures that will never allow germination of this species (Fig. 1.3, December 1986 until March 1987). Conversely, at the end of spring temperatures favour germination, but also induce dormancy (Fig. 1.3). If, at this time, the light-requiring seeds of *Polygonum persicaria* remain buried in the soil in darkness, germination is prevented by lack of light, and the prevailing temperatures will cause induction of dormancy. However, if the soil is disturbed, the seeds may be irradiated by daylight, and germination may take place at the prevailing temperatures. In this case, germination and induction of dormancy occur simultaneously. However, they do not really compete, because full induction of dormancy in buried seeds takes several months, while germination is completed in a few days.

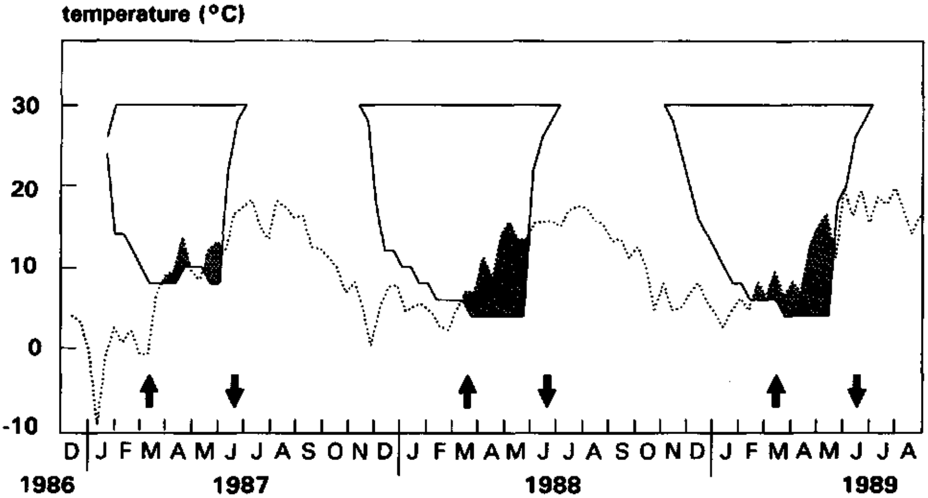

Fig. 1.3 Simulation of seasonal changes in the range of temperatures over which at least 50% of exhumed *Polygonum persicaria* seeds germinate. Solid lines represent maximum and minimum temperature required for 50% germination in water, calculated according to a descriptive model based on temperature derived parameters. The dotted line indicates air temperature at 1.50 m. Hatched areas indicate overlap of field temperature and germination temperature range. Arrows indicate the time when germination in Petri dishes outdoors actually increased above (↑) or decreased below (↓) 50%. (Adapted from Bouwmeester and Karssen, 1992).

Derkx and Karssen (1993*a*) showed that when *Sisymbrium officinale* seeds are buried in darkness germination is prevented. However, the temperature they are exposed to regulates the changes in the requirements for light, nitrate and temperature for subsequent germination (*i.e.* regulates dormancy). Changes in dormancy occur in spite of continuous darkness and are not correlated with changes in endogenous nitrate content (Derkx and Karssen, 1993*a*). From experiments in which *Sisymbrium officinale* seeds were incubated in darkness, Derkx *et al.* (1993*b*) concluded that changes in dormancy are not related to changes in respiratory activity. They reported that when the seeds are irradiated by red light, O_2 uptake starts to rise immediately as an early indication of the germination process having started. Consequently, Derkx and Karssen (1993*a*) called the effect of irradiation stimulation of germination instead of relief of dormancy. Generally, light requirement by seeds is considered to be a form of dormancy. This corresponds to my view. The effect of irradiation is usually called breakage of dormancy. I prefer to call this effect induction of germination. I think it consequent to describe as 'dormancy breaking' only those factors that mitigate the requirements for germination, like a low winter temperature, which, among other things, decreases the light intensity needed for germination of *Sisymbrium officinale* (Derkx and Karssen, 1993*a*).

Another factor, the effect of which should be reconsidered, is fluctuation of temperature. Alternating temperatures are widely thought to be dormancy relieving (*e.g.* Bewley and Black, 1982), but recent unpublished results of Bouwmeester indicate that in seeds of *Sisymbrium officinale* a pretreatment at alternating temperatures in darkness hampers subsequent germination at a constant temperature after irradiation. Alternating temperatures enhance germination of *Sisymbrium officinale* only when applied after irradiation of the seeds. Apparently, alternating temperatures cause *induction* of dormancy, but promote the germination process, once the seed has been irradiated.

Some considerations about the role of dormancy in the life-cycle of plants. Annual cycles in which dormancy is relieved and induced occur in buried seeds of many annual species throughout the lifetime of the seeds. The separation of dormancy from germination has shed new light on the role of seed dormancy within the life-cycle of plants. In my view, dormancy is not so much a device for surviving prolonged periods of unfavourable conditions, which is often claimed, as a device for surviving short periods of *favourable* conditions. In unfavourable conditions the lack of germination-stimulating factors will prevent germination, and the seed will survive ungerminated in the soil, independent of its dormancy state. Dormancy prevents germination in periods of conditions that are favourable for germination, at a time of the year when it can be expected that the plant that originates from the seed will not survive and produce offspring.

In summer annuals, for example, changes in dormancy enable seeds to germinate in spring, but prevent germination in autumn, although the prevailing conditions in the field (light, nitrate, temperature, soil moisture) may be quite similar in both seasons. Germination in autumn, however, would not allow the completion of the life-cycle of the plant before winter, and has to be avoided. This was also acknowledged by Simpson (1990) who stated that dormancy is an adaptive trait that optimizes the distribution of germination over time within a population of seeds. The timing of germination in the field is the combined effect of changes in dormancy and changes in environmental conditions.

Another example is given by Ter Borg (1987) who showed that seeds of *Rhinanthus* species occurring in a lowland habitat need a longer period of chilling to relieve their dormancy than seeds of *Rhinanthus* species occurring in a mountain habitat, where winter is even longer. In the lowland habitat, however, low winter temperatures are generally interrupted by warmer spells, during which a high degree of dormancy is required to prevent germination. In the mountain habitat the soil is covered by snow during winter and this prevents the seeds from germinating too early, which makes an internal dormancy mechanism superfluous.

I do not agree with the claim that dormancy also optimizes the distribution of germination in space (*e.g.* Pons, 1989, 1992). Dormancy is not affected by the environmental factors by which seeds sense that their position in the soil is suitable for germination. The main factors that allow seeds to detect their depth of burial and the absence of competitors in their proximity are alternating temperatures, nitrate, light quantity and light quality, all of them stimulating germination.

A hypothetical physiological dormancy model. Hilhorst (1993) presented a hypothetical physiological model for the regulation of secondary dormancy and the stimulation of germination (Fig. 1.4) (see also Van Loon and Bruinsma, 1992). As yet there is only circumstantial evidence for the mechanism that is hypothesized in this model. The merit of the model is that it structures and integrates a large number of observations on dormancy and germination in a concise and comprehensible way. It corresponds to the concept of dormancy that is discussed in the former sections of this chapter, but now expressed in terms of a physiological mechanism.

In many species light is the primary inducer of germination. Irradiation by daylight converts the inactive form of the pigment phytochrome into the active form. In the model the response to light is supposed to be effected by an interaction between active phytochrome and its tentative receptor X. This receptor is assumed to be located in the plasma membrane. Hilhorst (1993) hypothesizes that modulation of the number of molecules of receptor X accounts for changes in dormancy.

I will explain the model for the case of a summer annual. Generally, in summer annuals low (winter) temperatures relieve dormancy, while high (summer) temperatures induce dormancy (Karssen, 1982). In the state of maximal dormancy the receptor is absent (Fig. 1.4a). At low temperatures, receptors are synthesized (Fig. 1.4b). This is the actual dormancy relieving process. At high temperatures, receptors are degraded. This is the actual dormancy inducing process.

The remaining part of the model concerns the stimulation of germination. Hilhorst (1993) assumes that a rise in temperature inducing an increase in fluidity of the membrane may be necessary to enable the receptor to move to the membrane surface and become exposed (Fig. 1.4c). The exposed receptor is activated by interaction with nitrate (Fig. 1.4d). The activated receptor can now bind its agonist phytochrome, which is activated by irradiation of the seed (Fig. 1.4e). The phytochrome-receptor complex generates a signal that leads to synthesis of gibberellins (GA) (Fig. 1.4f). In addition, either activated phytochrome or the phytochrome-receptor complex enhances the sensitivity of receptors to GA (Fig. 1.4g). Finally, a signal from the GA-receptor complex (Fig. 1.4h) leads to germination.

In this biochemical model, dormancy is directly related to the amount of phytochrome-receptor X. The amount of X determines the seed's responsiveness to light and nitrate, and also the width of the temperature range for germination (Vleeshouwers and Bouwmeester, 1993). The only factor effecting a change in the amount of X, and thus changing the seed's degree of dormancy, is temperature. All factors that are required to realize germination of a seed which has a sufficient amount of X are germination stimuli. The distinction between dormancy relieving and germination inducing factors that was made earlier in this chapter is therefore in agreement with this physiological model.

Primary and secondary dormancy

Although the classification into primary and secondary dormancy was originally based on the timing of the dormancy (Crocker, 1916; Karssen, 1982), it also seems to have a physiological background and ecological consequences. Derkx and Karssen (1993*a*) showed that during relief of primary dormancy of *Sisymbrium officinale* seeds, sensitivity to GA gradually increases. However, sensitivity to GA remains at a high level when secondary dormancy is induced and subsequently relieved. This implies that the relief of primary dormancy is physiologically different from the relief of secondary dormancy. On the other hand, in *Sisymbrium officinale* both types of dormancy are relieved by the same environmental factors (Karssen, 1982).

Bouwmeester and Karssen (1993*c*) reported that fresh *Sisymbrium officinale* seeds or seeds that were buried for a limited time (being in a state of primary dormancy) germinate better at high temperatures than at low temperatures, whereas seeds exhumed after more than five months' burial (being in a state of secondary dormancy) germinate better at low temperatures than at high temperatures. This implies that both types of dormancy may cause a different germination response. Possibly, this difference in germination response results from a change of the process controlling germination, which shifts from the binding of GA to its receptor in case of primary dormancy to the binding of phytochrome to its receptor in case of secondary dormancy.

In any case I conclude that one should be cautious when extrapolating germination results that were obtained with fresh seeds in order to predict germination of seeds that are buried in the seed bank.

> *'I watched the moths fluttering among the heath and hare-bells; listened to the soft wind breathing through the grass; and wondered how anyone could ever imagine unquiet slumbers, for the sleepers in that quiet earth.'*
> Emily Brontë, *Wuthering Heights*

Unquiet slumbers, for the sleepers in that quiet earth. Simpson (1990) mentioned that the English word 'dormancy' is derived from the Latin *dormire* (to sleep) and is defined in the *Concise Oxford Dictionary* as 'lying inactive in sleep'. In agreement with this definition, Ricklefs (1990) stated that by their dormancy mechanism plants ride out unfavourable conditions and await better ones before resuming an active and interactive state. However, from the foregoing, one may understand that seeds are far from passively asleep during their annual dormancy cycle. Throughout the seasons seeds continuously

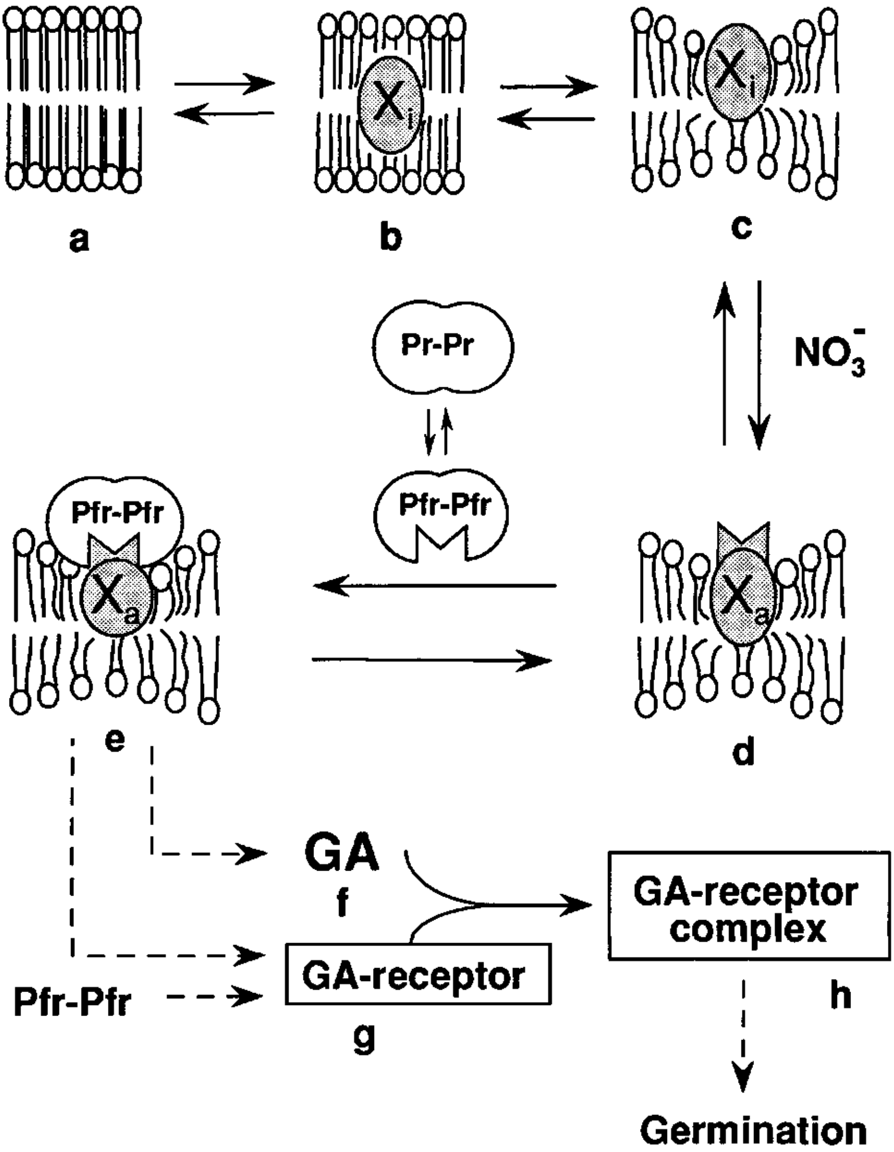

Fig. 1.4 Physiological model for relief and induction of dormancy, and stimulation of germination in light-requiring seeds. The phytochrome-receptor X is located in the plasma membrane. X_i denotes the inactive receptor, X_a the activated receptor. Pr-Pr: inactive phytochrome, Pfr-Pfr: activated phytochrome, GA: gibberellins. Letters in the figure refer to explanation in the text. (Adapted from Hilhorst, 1993).

sense their environment and adjust their level of dormancy to the changing environment. Thus, they increase the chance of completing their life-cycle successfully, once they have germinated. This sensing of the environment is independent of their degree of dormancy. Seeds are rather 'lying active in sleep' or 'watchfully asleep'.

Germination

In this study, germination is defined as the sequence of processes that is triggered by active phytochrome (Pfr), and culminates in radicle protrusion. Apart from the light that is needed to generate Pfr within a seed, germination is affected by many environmental factors. Here only a very short review of the most important factors in relation to weed seed germination is given. Extensive discussion of environmental effects on seed germination may be found in the textbooks by Bewley and Black (1982, 1994).

Light. Light affects seed germination through the photoreversible protein phytochrome. Phytochrome can be present in two forms. In darkness, the pigment is in an inactive form (Pr) with a light absorption maximum at 660 nm (red light). Upon irradiation with red light Pr is quickly converted into the active form (Pfr) with a light absorption maximum at 730 nm (far-red light). Irradiation by far-red light causes immediate reversion to Pr. Reversion of Pfr to Pr also occurs in darkness, but at a more reduced rate.

In several cases, dose-response curves relating the percentage germination to the quantity of light (*i.e.* fluence) during irradiation show a biphasic character. VanDerWoude (1985) used the dimeric model of the phytochrome molecule to explain the occurrence of biphasic fluence response curves. In this model, the phytochrome dimer exists in three forms, Pr-Pr, Pr-Pfr and Pfr-Pfr. The Pr-Pr form is inactive, the Pr-Pfr form is generated at very low fluences and is responsible for the first phase of the fluence response curve (the very low fluence response), the Pfr-Pfr form is generated at low fluences and is responsible for the second phase in the fluence response curve (the low fluence response). Derkx and Karssen (1993*a*) showed that seasonal changes in dormancy of buried seeds are reflected in seasonal changes in light sensitivity of seeds. During periods when the seeds have a relatively high degree of the dormancy, the very low fluence response may be absent. Photoinhibition may occur in continuous white light. Even seeds whose germination is triggered by short irradiations can be inhibited by prolonged exposure.

In weed seeds buried in the field, Pfr is generated by daylight irradiation during the cultivation of the soil, even when after soil cultivation seeds are covered with soil again. Daylight consists of a broad range of wavelengths, comprising both red light and far-red light. The relative amount of red to far-red light in daylight is such that it generates a sufficient amount of Pfr to trigger germination. When daylight is transmitted through green leaves, however, the chlorophyll absorbs red light, but allows far-red light to pass. Thus, the light under a leaf canopy is rich in far-red, which inhibits seed germination in most seeds. The very low fluence response enables seeds to react to very low amounts of daylight reaching them. In field experiments, Scopel *et al.* (1991) found that germination of buried seeds may be triggered by millisecond-exposures to sunlight. Photoinhibition may play a role in the prevention of germination of seeds at the soil surface.

Nitrate. Nitrate stimulates seed germination. Hilhorst and Karssen (1988) hypothesized that nitrate acts a an indispensable co-factor for Pfr action. Hilhorst (1993) proposed a model in which nitrate ions activate phytochrome receptors, thereby allowing the binding of Pfr to the receptors. Derkx and Karssen (1993*a*) showed that seasonal changes in seed dormancy are expressed as seasonal changes in the sensitivity for nitrate.

Levels of nitrate in the soil solution are often within the range that stimulate germination in laboratory tests. Germination of weed seeds in arable fields may be enhanced by fertilizer application (Espeby, 1989; Schimpf and Palmblad, 1980; Kleijn and Van der Voort, 1997), but data from several authors (Fawcett and Slife, 1978; Schimpf and Palmblad, 1980; Post, 1988; Espeby, 1989) show that the observed effect is small compared to that expected from laboratory tests.

Temperature. The germination percentage in a population of seeds and the rate at which it completes germination, are primarily determined by temperature. Generally the maximum percentage of germination is reached in a broad temperature range. On either side of this optimum temperature range, germination percentages decline until zero germination is reached at a certain minimum and maximum temperature for germination. The curve displaying the effect of temperature on the germination rate (*i.e.* the reciprocal of the time taken to complete germination) comprises two linear portions. The germination rate linearly increases with temperature until the temperature optimum is reached, above which the germination rate linearly decreases with temperature. Seasonal changes in dormancy are reflected in seasonal changes in the temperature range for germination (Karssen, 1982).

In many species, germination percentages increase with an increasing temperature amplitude around the mean (*e.g.* Totterdell and Roberts, 1980; Murdoch *et al.*, 1989). Germination rates, however, are not affected by the amplitude of the temperature fluctuation (Ellis and Barrett, 1994).

Temperature plays an important role in controlling germination in the field. Germination occurs when the field temperature overlaps the range required for germination. The timing and duration of the germination flush is dependent on the temperature. Differences in temperature requirements for germination between species may lead to peaks in field germination at different times of the season. The amplitude of the daily temperature fluctuations decreases with increasing depth in the soil. The effect of alternating temperatures on seed germination may therefore provide a mechanism to give positional information to seeds, which prevents them from germination at fatal depths.

Moisture. Increased water stress slows down the rate at which a population of seeds completes germination, or reduces total germination. Many seeds are desiccation tolerant, and survive seed water contents down to 5%. The early metabolic processes of germination that are initiated upon imbibition are arrested but not reversed by subsequent desiccation. Therefore, the time to complete germination in rehydrated seeds is shorter than in non-dried controls. In many species desiccation and subsequent remoistening also enhances the number of seeds that germinate, but in view of the definitions of dormancy and germination that are used in this thesis, this effect of desiccation should be considered breakage of dormancy and not stimulation of germination (Bouwmeester and Karssen, 1989).

In buried weed seeds, periods of moisture stress inhibit or delay germination. However, upon remoistening germination may be enhanced.

Integration of factors stimulating germination. A model that integrates the effects of temperature, light and nitrate on germination has been proposed by Hilhorst (1993) (Fig. 1.4). In this model, the transduction chain leading to germination begins with a membrane bound protein that becomes exposed as a result of a temperature-induced change in membrane fluidity. This facilitates binding of nitrate, resulting in an increased affinity of the protein for Pfr. Upon binding of Pfr the receptor protein complex is activated and the germination process is triggered (Hilhorst, 1990*a*,*b*; Karssen and Hilhorst, 1992). The rate at which the seed subsequently completes germination is primarily determined by temperature, but increased water stress delays the completion of germination.

The environmental factors that stimulate germination show numerous interactions, that are in their turn dependent on the degree of dormancy of the seeds. For example, alternating temperatures before irradiation may inhibit germination, while alternating temperatures after irradiation enhance germination; photoinhibition may only occur under water stress. Development of dormancy and germination models, either conceptual or quantitative, may be a indispensable tool to gain understanding in the complexity of these interactions.

Pre-emergence growth

Pre-emergence growth is the growth of the seedling shoot to the surface of the soil. In the phase prior to emergence, seedling growth is completely dependent on seed reserves. An important mortality factor in weed populations may be fatal germination (Fernandez-Quintanilla, 1988). Fatal germination is germination at such a depth in the soil that the seedlings that originate, exhaust their reserves before reaching the surface.

In contrast to the wealth of literature on seed dormancy and germination, hardly any literature on underground shoot growth can be found. Cousens and Peters (1993) reported that in *Bromus sterilis* the time taken to grow even short distances to the surface is much longer than the time taken to germinate. Van der Weide (1993) stressed the importance of the effects of environmental factors on pre-emergence growth in understanding patterns of field emergence in *Galium aparine*. The environmental factors she found to affect pre-emergence growth significantly were temperature, depth of burial, soil moisture and soil structure.

1.2.2 *Models*

Modelling weed emergence patterns may serve both a scientific and a practical goal (Schreiber, 1982; Harvey and Forcella, 1993; King and Oliver, 1994; Benech-Arnold and Sánchez, 1995). The development of quantitative models for complex ecological systems, like the seed-soil system, can be an important method to increase the understanding of the systems. Besides, quantitative knowledge of the processes that govern seedling emergence from seed banks may be used to improve weed control strategies. In this thesis the scientific objective of the model prevails. A recent review of the use of models regarding weed seed germination is given by Benech-Arnold and Sánchez (1995). Here only a short summary of relevant literature relating to weed seeds is given.

Dormancy

Several models simulating seasonal changes in dormancy of buried weed seeds (Spitters, 1989; Bouwmeester and Karssen, 1992, 1993*a*,*b*,*c*; Van der Weide, 1993) are based on the concept of dormancy introduced by Vegis (1964). He considered that changes in the dormancy of seeds involve changes in the temperature requirements for germination. As dormancy is induced, the range of temperatures over which germination can proceed narrows, until germination is no longer possible at any temperature, and full dormancy is reached. As dormancy is broken, the temperature range widens, until it is maximal. Spitters (1989) and Van der Weide (1993) used a fixed relationship between the calendar date and the temperature range over which seeds are able to germinate. Bouwmeester and Karssen (1992, 1993*a*,*b*,*c*) developed a model in which the temperature range for germination is regulated by the soil temperature in the field. In their model, dormancy patterns result from the simultaneous action of a dormancy breaking and a dormancy inducing factor, both of which are regulated by soil temperature. The dormancy breaking factor is the cold sum, calculated as the period spent below a critical border temperature; the dormancy inducing factor is the heat sum, calculated by accumulating the temperature during burial. The interaction of the cold sum and the heat sum defines the degree of dormancy.

Janssen (1974) modelled the process of after-ripening, and distinguishes between release of true dormancy and release of relative dormancy. Seeds in a state of true dormancy are unable to germinate. Seeds that have passed from the true into the relative dormancy state are able to germinate, and as relative dormancy is gradually released, the range of environmental conditions at which germination may take place increases. Both the release of true dormancy and the release of relative dormancy are modelled as a function of the temperature and the soil moisture content.

Benech-Arnold *et al.* (1990) developed a model in which two dormancy levels are distinguished in a seed population. Seeds from the inducible fraction are released from dormancy by fluctuating temperatures, seeds from the highly dormant fraction are not. The stimulatory activity of fluctuating temperatures on seeds belonging to the inducible fraction is exerted mainly through the thermal amplitude and the upper temperature of the daily temperature cycles.

Quantification of the concept developed by Vegis (1964) is a very convenient way to include dormancy in models simulating weed emergence patterns. Existing dormancy models of this type are descriptive. Recently hypotheses have been developed, however, on the mechanism of seed dormancy at a molecular level (Hilhorst, 1993; Derkx and Karssen, 1993*a*). The objective of the study reported in chapter 2 was to develop a model simulating annual changes in the temperature range for germination of weed seeds in the seed bank, that is based on the mechanism that was hypothesized by Hilhorst (1993).

Germination

In several models, germination of buried weed seeds is triggered either by soil cultivation (Spitters, 1989; Takayanagi and Kusanagi, 1989) or by irradiation of the seeds after exhumation (Bouwmeester and Karssen, 1992, 1993*a*,*b*,*c*). In the models by Van der Weide (1993) and Benech-Arnold *et al.* (1990) no triggering of germination takes place. In these models, all seeds whose dormancy has been released subsequently germinate.

The 'Vegis-type' models quantify the relationship between temperature and the germination percentage that is reached at this temperature, as a description of dormancy. Essentially, in these models, the percentage of germination in a seed population with a given degree of dormancy is determined by reading the percentage germination belonging to the temperature in the germination test or in the field from this relationship (Spitters, 1989; Bouwmeester and Karssen, 1992, 1993*a*,*b*,*c*; Van der Weide, 1993). In the model by Bouwmeester and Karssen (1992, 1993*a*,*b*,*c*), the function relating the germination percentage to the germination temperature, given a certain degree of dormancy, is modified by the presence or absence of nitrate, and the temperature during a period prior to exhumation.

In several models, the timing of germination of seeds whose dormancy has been released is described by the concept of thermal time (Spitters, 1989; Benech-Arnold *et al.*, 1990; Van der Weide, 1993). Daily differences between actual temperatures and a base temperature are accumulated until a set value is reached at which germination occurs. It is implicitly assumed by these authors that the rate of germination responds instantaneously to current temperature, and thus temperature fluctuation *per se* does not affect the thermal time required for seed germination.

In the models by Forcella (1993) and Harvey and Forcella (1993), the potential daily increase in the germination percentage is given as a function of the temperature. The actual increase in the germination percentage is calculated by multiplying the potential increase with a factor that decreases when the percentage germination approaches 100%.

Spitters (1989) modelled the effect of reduced soil moisture as a reduction factor on both the number of seeds germinating and their germination rate. In the model by Forcella (1993), the effect of water potential is quantified as a relative term that varies from 0 to 1 and is used to debit the germination rate when the water potential is lower than 0. Alm *et al.* (1993) modelled the germination rate as a function of temperature and soil water potential. It is calculated by multiplying the germination rate at standardized reference conditions with a factor dependent on both the mean temperature and the amplitude of the temperature fluctuation, and a factor dependent on the soil water potential.

Janssen (1974) modelled the process of germination by assuming several classes of seeds, which represent subsequent stages in the germination process. The transport of seeds from one class to the next is dependent on temperature and moisture conditions. The rate of germination increases with a decrease in the degree of relative dormancy of the seeds. In the early stages of germination, the process is assumed to be reversible during periods of drought or high temperatures, but in the later stages germinating seeds die upon desiccation.

A newly developed model to describe the rate of germination in relation to water stress is the concept of hydrotime (Bradford, 1995). Analogous to the effect of temperature, the effect of water potential on the timing of germination of seeds whose dormancy has been released, can be described by accumulating daily differences between actual water potentials and a base water potential until a set value is reached at which germination occurs. The hydrotime concept has not yet been used in weed germination models. A good description of experimental data with the hydrotime concept has been found in tomato (Dahal and Bradford, 1990). If the temperature and water potential responses of germination are combined into one single expression, hydrothermal time, a relatively poor agreement between predicted and actual germination curves in tomato was obtained (Dahal and Bradford, 1994). For application in field situations, however, the approximation may be sufficient (Bradford, 1995).

All weed germination models assume that the rate of germination is not dependent on the degree of dormancy of the seeds. However, as Gordon (1973) pointed out, a gradual induction of dormancy in a seed may first be noticed as an increased time to germination, prior to a complete block to germination. The objective of the study reported in chapter 3 was to quantify the delay in germination that is due to an increased degree of dormancy.

Pre-emergence growth

Van der Weide (1993) quantified the effects of environmental factors on pre-emergence seedling mortality by an empirical regression equation. Alm *et al.* (1993) modelled pre-emergence seedling elongation rate as a function of temperature and soil water potential. It is calculated by multiplying the elongation rate at standardized reference conditions with a factor dependent on the mean temperature and a factor dependent on the soil water potential. In the models by Forcella (1993) and Harvey and Forcella (1993), the delay of emergence owing to burial depth of the seed is accounted for by a time lag of one day per centimetre of burial depth. However, Harvey and Forcella (1993) concluded that for an accurate prediction of seedling emergence under more extreme conditions, a relationship between temperature and shoot elongation rate needs to be incorporated into the model.

In several models, the term germination or emergence is used for the combined process of seed germination and pre-emergence growth, and the effects of environmental factors on the combined process are quantified (*e.g.* Spitters, 1989; Takayanagi and Kusanagi, 1989; Benech-Arnold *et al.*, 1990). For example, the concept of thermal time is used to quantify the temperature dependence of the integrated process from seed germination to seedling emergence by Leblanc and Cloutier (1997). Takayanagi and Kusanagi (1989) simulated seasonal variation in seedling emergence as affected by air temperature and soil moisture, using a model that resembles the hydrothermal time concept applied to the combined process of seed germination and pre-emergence growth. Instead of a linear relationship between the emergence rate and the soil water potential, as is assumed in the hydrothermal time concept, they used a linear relationship between the emergence rate and the percentage soil moisture. King and Oliver (1994) fitted logistic equations to cumulative emergence curves at a range of constant temperatures and soil water potentials. They use the estimated parameters to simulate the time course of emergence under fluctuating field conditions. Forcella (1992) described an empirical equation that relates the percentage of seeds that emerge from the seed bank to accumulated temperature in April above a base temperature of 10°C. In this approach, dormancy, germination and pre-emergence growth are combined.

In this thesis, pre-emergence growth will be studied separately from dormancy and germination. Quantitative data on underground shoot growth are not available. Therefore, a model will be developed and parameterized, relating pre-emergence growth to seed weight, soil temperature and soil penetration resistance (chapter 4). Implicitly, this will also lead to a prediction of the percentage fatal germination.

Towards an explanatory model for weed emergence patterns

Most models for the processes involved in seedling emergence in the field are based on empirical relationships. For practical purposes, for example in weed management expert systems (Forcella *et al.*, 1993*a*), these models may serve well. In these models, combination of the processes of dormancy release, germination and pre-emergence growth may be fruitful (*e.g.* Forcella *et al.*, 1993*a*). In the study reported in this thesis, however, the objective was to build a model that was based on physiological principles, in order to increase the insight in the underlying processes and their interactions. Therefore, mechanistic models were developed for each of the three separate processes that lead to field emergence. Still, more descriptive approaches had to be used when explanatory approaches were hampered by a fragmentary knowledge of the physiological processes.

The relational diagram of the model that is described and evaluated in this thesis in presented in Fig. 1.5. The diagram contains only those environmental factors that are incorporated in the model. In order to keep the model as simple as possible, the effects of soil moisture and nitrate on germination and pre-emergence growth are not comprised in the model. The model for seed germination will be adopted from the literature. Field data on seedling emergence following different dates of soil cultivation will be collected (chapter 5), and used to validate the overall emergence model (chapter 6).

1.3 The species

The three species used in this study are all troublesome weeds in arable fields (Holm *et al.*, 1977). A short description of their agricultural importance and their seed biology will be given here, without attempting completeness.

1.3.1 ***Polygonum persicaria*** **L.**

P. persicaria is a principal weed in potatoes and wheat in the temperate regions (Holm *et al.*, 1977). In arable farming in the Netherlands, it is one of the four weed species that are frequently dominant and that largely determine the efforts needed in weed control (Anonymous, 1990).

Buried seeds display a seasonal dormancy pattern, that clearly shows the typical features of summer annuals. Dormancy is broken at low winter temperatures, the germination peak occurs in spring, and dormancy is re-induced at high summer temperatures (Bouwmeester and Karssen, 1992). Lauer (1953) reported that seeds may germinate in a range from 25°C to 35°C. However, Bouwmeester and Karssen (1992) found germination up to 100 per cent at 10°C. Light stimulates germination, especially in the presence of nitrate and at alternating temperatures (Vincent and Roberts, 1977). In the field, in peat soil, the optimal emergence depth was 0 to 1 cm, and the maximum

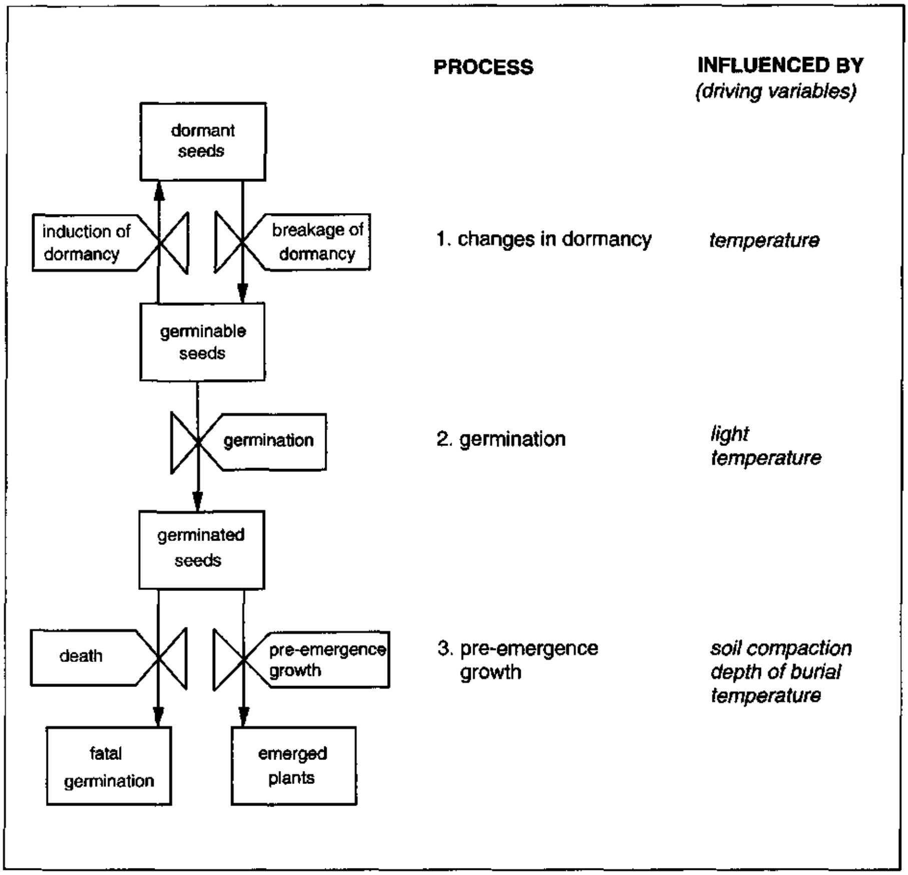

Fig. 1.5 Relational diagram of the model that is described and evaluated in this study.

emergence depth was 5 cm. In sandy loam, the optimal depth was 2 to 3 cm, and the maximum depth 7 cm. Emergence depths varied from year to year (Chancellor, 1964*b*). In a laboratory experiment, Macchia *et al.* (1990) found hardly any emergence from depths greater than 3 cm. Field emergence patterns observed by several authors (Fig. 1.6a) show that in general seedling emergence is restricted to spring, with a peak in April.

1.3.2 Chenopodium album L.

C. album L. is one of the most widely distributed weeds in the world. It is a troublesome weed in potato, wheat, maize, sugar beet and vegetables, wherever in the world they are grown (Holm *et al.*, 1977). In arable farming in the Netherlands, it is one of the four weed species that are frequently dominant and that largely determine the efforts needed in weed control (Anonymous, 1990).

Seasonal changes in dormancy of buried seeds are not very distinct (Bouwmeester and Karssen, 1992). The seasonal periodicity in emergence that occurs in the field is due to a seasonal periodicity in the field temperature, which only overlaps the temperature range required for germination from spring to late summer (Bouwmeester and Karssen, 1993*a*). Baskin and Baskin (1977), however, reported more distinct temporal differences in the germinability of buried seeds. Seeds may germinate in a temperature range from 2°C to 35°C, and maximum germination is reached at 20°C (Lauer, 1953). Both nitrate and light promote germination, while there is a strong positive interaction between the effects of these two factors (Vincent and Roberts, 1977). In the field, emergence from both clay loam and peat soil almost completely occurred from depths shallower than 4 cm (Chancellor, 1964*b*). Optimal emergence depth, however, varied from year to year. In both soil types, it was 1 to 2 cm in the first year, and 0 to 1 cm in the second year of the observations (Chancellor, 1964*b*). Macchia *et al.* (1990) reported that in a laboratory seedlings did not emerge from depths greater than 3 cm. Field emergence patterns observed by several authors (Fig. 1.6b) show that, in general, field emergence is concentrated in late spring and early summer, with a peak in May. However, emergence continues at a low level until October.

1.3.3 Spergula arvensis L.

S. arvensis is a troublesome cosmopolitan weed that is most widely distributed in the temperate zones. It has been reported to be a weed in cereals, potatoes, sugar beet and vegetables (Holm *et al.*, 1977).

Buried seeds exhibit annual cycles in dormancy (Bouwmeester and Karssen, 1993*b*). Bouwmeester and Karssen (1993*b*) reported that dormancy reacts to changes in temperature rather than to the absolute value of the temperature. The increase in temperature in spring causes release of dormancy, while the decrease in temperature in autumn causes induction of dormancy. Seeds may germinate in a temperature range from 2-35°C, with an optimum at 20-25°C (Lauer, 1953). Buried seeds have an absolute requirement for light in order to germinate (Wesson and Wareing, 1969; Bouwmeester and Karssen, 1993*b*). After desiccation, however, exhumed seeds germinate up to 90% in darkness (Bouwmeester and Karssen, 1993*b*). Hanf (1990) reported that in the field the majority of seedlings that emerge originate from seeds germinating at depths of 0.5-3 cm. Field emergence patterns observed by several authors (Fig. 1.6c) show that emergence occurs in a large part of the year, with a relatively smooth peak from May to July.

1.4 Objectives

The aim of this research project is to improve the quantitative understanding of weed seedling emergence patterns in the field. In order to achieve this goal, the knowledge of seed physiology and seed ecology of weeds has to be improved. Computer simulation will be used as a tool to get insight in the relevant processes. Special attention will be paid to the integration of existing knowledge related to the effect of environmental factors on

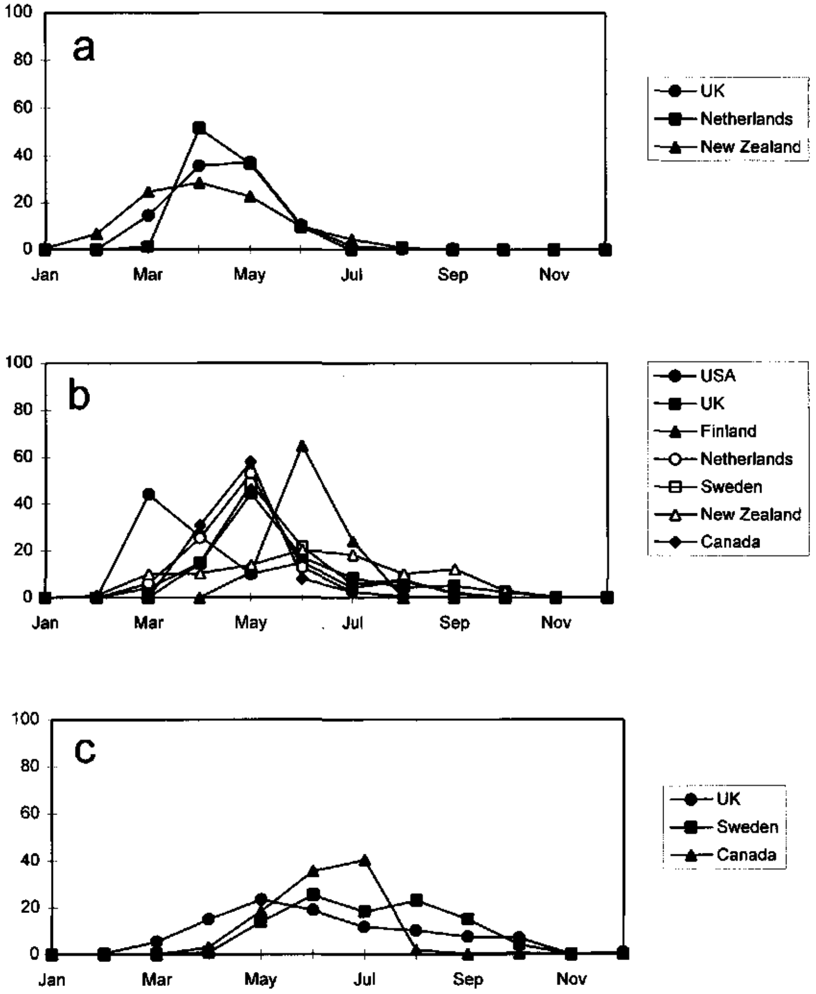

Fig. 1.6 Seedling emergence patterns in the field, as observed by several authors. Data are averaged per country.

A. *Polygonum persicaria*; UK: Chancellor (1964*a*), Roberts and Neilson (1980); Netherlands: Van den Brand (1986); New Zealand: Popay *et al.* (1995).

B. *Chenopodium album*; USA: Ogg and Dawson (1984); UK: Roberts (1964), Roberts and Feast (1970), Lawson *et al.* (1974); Finland: Erviö (1981); Netherlands: Van den Brand (1986); Sweden: Håkansson (1992); New Zealand: Popay *et al.* (1995); Canada: Chepil (1946*a*).

C. *Spergula arvensis*; UK: Roberts and Feast (1970), Lawson *et al.* (1974); Sweden: Håkansson (1992); Canada: Chepil (1946*a*).

Note that the time axis for the observations of Popay *et al.* (1995) from New Zealand was shifted by six months, to enable comparison with the patterns from the northern hemisphere.

dormancy changes, germination and emergence. Gaps in the existing knowledge will be identified and filled in.

The ultimate goal is a model that can predict weed emergence in the field. Such a prediction may help to reduce the use of herbicides in weed control.

1.5 Outline of the thesis

All experiments that are discussed in this thesis, and all simulation models that are made concern the three weed species *P. persicaria, C. album* and *S. arvensis*. The only exception is the study on the effect of dormancy on the rate of germination, which was only done with *P. persicaria*.

In chapter 2, a mechanistic model is discussed to simulate the annual dormancy cycles of buried weed seeds. The environmental factor that drives these changes is temperature.

Chapter 3 presents a study into the influence of dormancy on the extent and rate of germination of *Polygonum persicaria* in relation to the competition between *P. persicaria* and sugar beet.

In chapter 4, a mechanistic model for the growth of the seedling to the soil surface is described. This model relates the emergence percentage to seed weight, temperature, soil compaction and depth of burial. In the experiment to test this model pre-germinated seeds were used.

Chapter 5 deals with an experiment in which field emergence after soil disturbance was monitored in a detailed way. In this experiment known numbers of seeds were buried in plots with sterilized soil. The observed field emergence is discussed in relation to weather data that were collected during the experiments.

In chapter 6, the performance of the model that was made by integrating the models described in chapter 2 (dormancy) and chapter 4 (pre-emergence growth) and in the literature (germination), was tested with help of the field observations discussed in chapter 5. Gaps in the knowledge are evaluated.

Chapter 7 is devoted to a discussion of the experiments done and the models built in relation to the original aims of the research project and the needs for future research. The possible contribution of the integrated model discussed in chapter 6 to weed control practice is evaluated.

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2 A SIMULATION MODEL FOR SEASONAL CHANGES IN DORMANCY AND GERMINATION OF WEED SEEDS

Abstract A model has been developed to simulate the annual dormancy cycle of seeds in the seed bank, and the germination of exhumed seeds after irradiation. It applies to light-requiring species.

Simulation of dormancy and germination is based on a physiological model concerning the action of phytochrome in the seed. Dormancy is related to the amount of an hypothetical phytochrome receptor, that fluctuates in an annual pattern. Relief of dormancy is equivalent to an increase in the amount of receptor, and results in a widening of the range of temperatures over which germination can occur. Induction of dormancy is equivalent to a decrease in the amount of receptor, and results in a narrowing of this range. Annual changes in temperature are the driving force for annual changes in the amount of phytochrome receptor in seeds that are buried in the seed bank.

From the average amount of phytochrome receptor in the seeds of a population, the model calculates the germination percentage that is reached, when a seed sample from the population is exhumed, irradiated, and incubated at a given temperature in darkness. The model assumes that germination is triggered by light. The active phytochrome (Pfr) that is generated by a short irradiation of the seed, will bind to the receptor, from which it will subsequently gradually disappear by dark reversion. The seed will germinate when the residence time of Pfr to its receptor exceeds a certain period, called the escape time. The model derives the germination percentage from a comparison of the period Pfr is receptor-bound and the escape time. The outcome of the comparison depends on the temperature, which affects both dark reversion and escape time, and on the amount of phytochrome receptor present (and thus on the level of dormancy).

In the model, fourteen species-specific parameters define the annual changes in dormancy and germination. Using an optimization procedure, values for these parameters were estimated by fitting the model to data from a burial experiment. In this experiment, seeds of *Polygonum persicaria* L., *Chenopodium album* L. and *Spergula arvensis* L. were buried in the field. At regular time intervals during three years subsamples of these seeds were exhumed. The dormancy of these subsamples was assessed by irradiating them and testing their germination over a range of temperatures in the laboratory. The simulation model gave a reasonably accurate description of the observed cyclic changes in germinability of exhumed seeds.

2.1 Introduction

Viable seeds are dormant when their germination is inhibited by an internal block, so that they cannot germinate in an otherwise favourable environment (Bewley and Black, 1982). Dormancy may be partial. Seeds in persistent seed banks are often subject to annual cycles in the degree of dormancy (Karssen, 1982; Baskin and Baskin, 1985). Seed dormancy is regulated by temperature (Totterdell and Roberts, 1979; Bouwmeester and Karssen, 1992). In summer annuals, for example, low winter temperatures release seed dormancy and high summer temperatures induce seed dormancy.

Quantification of seasonal changes in dormancy of buried weed seeds may be an important step towards understanding and eventual prediction of seasonal emergence patterns of weeds. Existing simulation models (*e.g.* Spitters, 1989; Bouwmeester and Karssen, 1992, 1993*a*,*b*,*c*) use descriptive approaches to quantify seasonal changes in dormancy. These simulation models are based on an ecophysiological conceptual model of seed dormancy, in which the degree of dormancy is expressed as the width of the temperature range over which seeds are able to germinate. Seeds that are non-dormant germinate over a wide range of temperatures. When dormancy is induced the temperature range over which the seeds can germinate becomes narrower, until full dormancy is reached and germination cannot take place at any temperature (Vegis, 1964; Karssen, 1982). Seasonal patterns in dormancy of buried seeds are reflected in seasonal changes in the width of the temperature range suited for germination. Germination in the field is restricted to the period when the field temperature overlaps this range. Spitters (1989) used a fixed relationship between the calendar date and the temperature range over which seeds are able to germinate. With help of this relationship he simulated the seasonal patterns of field germination in *Ambrosia artemisiifolia* and *Lamium amplexicaule*. Bouwmeester and Karssen (1992, 1993*a*,*b*,*c*) developed a descriptive model of the seasonal changes in dormancy of four weedy species (*Polygonum persicaria*, *Chenopodium album*, *Spergula arvensis* and *Sisymbrium officinale*). In their model, dormancy patterns result from the simultaneous action of a dormancy breaking and a dormancy inducing factor, both of which are regulated by soil temperature. The dormancy breaking factor is the cold sum, calculated as the period spent below a critical border temperature; the dormancy inducing factor is the heat sum, calculated by accumulating the temperature during burial. A quadratic regression function related germination of exhumed seed samples to cold and heat sum, germination temperature, the presence or absence of nitrate, and the temperature during a period prior to exhumation.

Spitters (1989) stated that forecasting seedling flushes could improve by introducing more causality in his simulation model. He claimed that this may be achieved by storing the degree of dormancy as an integral, the value of which changes in time according to rates of induction and relief of dormancy. These rates depend on the factors controlling dormancy. Bouwmeester and Karssen (1992) stated that knowledge of the physiological processes responsible for the changes in dormancy should lead to a more mechanistic approach of the simulation of dormancy patterns.

Recently, Hilhorst (1993) and Derkx and Karssen (1993) developed a new concept for dormancy-related processes in seeds, which may be used in developing an explanatory model for dormancy patterns. Hilhorst (1993, see also Van Loon and Bruinsma, 1992) presented a biochemical conceptual model for secondary dormancy in light-requiring seeds, based on the action of phytochrome at a molecular level. I will describe his model here for a summer annual species (Fig. 2.1). In the model, regulation of dormancy is located in a membrane. The initial state of the membrane is that of a dormant, imbibed seed at low temperature (1). Breaking of dormancy at low temperatures implies synthesis of a phytochrome receptor protein X_a (2). Increase of the temperature increases membrane fluidity which makes lateral movement of the receptor possible (3). Nitrate activates the exposed receptor (X_a) (4). By irradiation with red light Pr is transformed to Pfr, that binds to the activated receptor (5). The presence of the X_a-Pfr complex triggers synthesis of gibberellins (GA) (6) and enhances the sensitivity of receptors to GA (7). Binding of GA to its receptors (8) induces germination. High summer temperatures cause degradation of the receptor protein and thus induce dormancy (1).

Both conceptual dormancy models that are described above have their specific merits. The ecophysiological concept, in which dormancy is related to the width of the temperature range for germination, can easily be quantified, and be used for predictions of germination in field conditions. The biochemical concept, in which dormancy is related

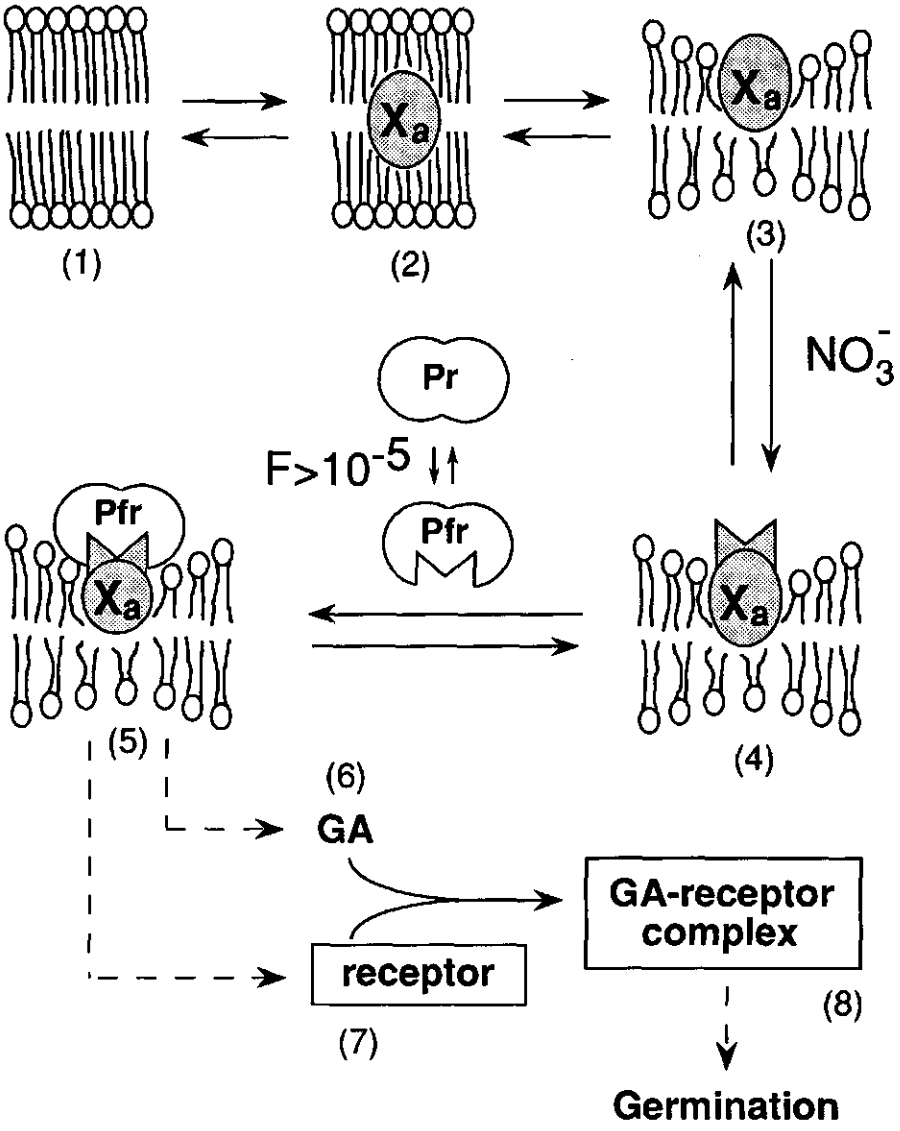

Fig. 2.1 Model for breakage and induction of dormancy, and stimulation of germination in light-requiring seeds. F = red light fluence (mol m^{-2}). For further explanation see text. After Hilhorst (1993).

to the amount of a phytochrome receptor, gives insight in the mechanism for changes in dormancy at a molecular level. In this chapter, a quantitative model is described, which is based on an integration of both conceptual models. A quantitative dynamic simulation approach was chosen, which allows the prediction of the dormancy cycle and germination on the basis of environmental factors.

The aim of this study was to quantify the relationships in the physiological model by Hilhorst (1993) and test whether this quantitative model can be used to understand seasonal changes in the temperature range over which germination occurs. The model was tested with data from a burial experiment with seeds of the arable weed species *Polygonum persicaria*, *Chenopodium album* and *Spergula arvensis*.

2.2 Materials and methods

2.2.1 Experiments

In December 1986 seed lots of *Polygonum persicaria*, *Chenopodium album* and *Spergula arvensis* were buried in the field at 10 cm in loamy sand. At regular intervals during three consecutive years subsamples of these seeds were exhumed. They were divided into smaller portions and incubated in Petri dishes in 50 mM KNO_3. Seeds were irradiated for 15 minutes with red light and germination was assessed in darkness at 10°C, 20°C and 30°C for *P. persicaria* and *C. album*, and at 2°C, 15°C and 30°C for *S. arvensis*. Subsamples were exhumed and tested for germination at 19 times during the experiment. The experiments are described in detail by Bouwmeester and Karssen (1992, 1993*a*,*b*).

2.2.2 Description of the simulation model

The simulation model uses the amount of the membrane-located phytochrome receptor protein X that was hypothesized by Hilhorst (1993) as a measure for the degree of dormancy. The dormancy model simulates seasonal changes in the amount of the receptor X in buried seeds, driven by seasonal changes in temperature. As yet, the hypothetical receptor X cannot be measured. In experiments it can only be made visible indirectly, by conducting germination tests over a range of conditions. Therefore, the dormancy model is coupled to a germination model. From the amount of X, the germination model calculates germination percentages of seed samples that are irradiated with red light and tested for germination at different temperatures.

The relational diagram of the simulation model is shown in Fig. 2.2. The dormancy part of the model is depicted in Fig. 2.2, *a1* and *a2*, and the germination part of the model in Fig. 2.2, *b* up to *f*. The variables used in the model are listed in Table 2.1, the parameters that were derived for the different species in Table 2.2. In the regulation of seasonal changes in dormancy and germination, temperature plays a dual role (Bouwmeester and Karssen, 1992). Field temperature determines the seasonal changes in dormancy of buried seeds, while the expression of the dormancy pattern is influenced by the temperature at which germination is tested. In the model, the dual role of temperature is reflected in the use of TB (burial temperature) in the simulation of dormancy, and TT (test temperature) in the simulation of germination (Fig. 2.2). In the present version of the model, TB represents the daily average temperature in the field, and TT the constant

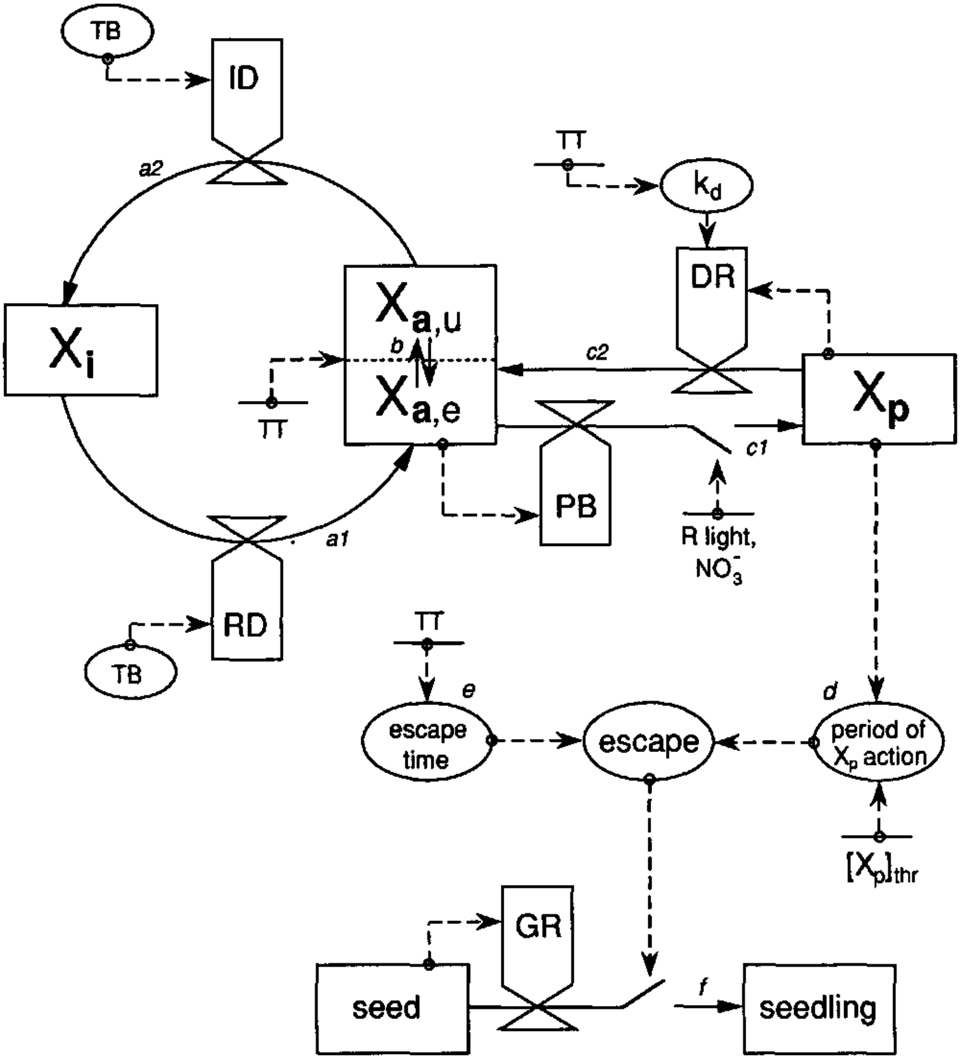

Fig. 2.2 Relational diagram corresponding to the biochemical dormancy model. $X_{a,u}$, $X_{a,e}$ and X_p correspond with (2), (3) and (5) in Fig. 2.1 respectively. Note that in Fig. 2.1 the reaction from $X_{a,e}$ to X_p occurs in two steps.

Table 2.1 List of variables used in this chapter. Dimensions in parentheses.

State variables	
X	: amount of receptor (-)
X_i	: unavailable (-)
X_a	: available (-)
$X_{a,u}$	: available, unexposed (-)
$X_{a,e}$	: available, exposed (-)
X_p	: occupied by Pfr (-)
Rate variables	
ID	: rate of dormancy induction (day^{-1})
RD	: rate of dormancy release (day^{-1})
PB	: rate of Pfr binding to receptor (s^{-1})
DR	: rate of dark reversion (h^{-1})
GR	: germination rate (h^{-1})
Driving variables	
R light	: red light
TB	: temperature during burial
TT	: temperature in the germination test
NO_3^-	: nitrate

temperature in the germination test. In the next section, the different parts of the simulation model will be described in detail, using Fig. 2.2 as a guide-line.

Dormancy cycle (Fig. 2.2, a1 and a2)

The assumption in the biochemical model that dormancy is related to the *amount* of receptor protein and that changes in dormancy result from synthesis and degradation of the receptor can be regarded as a convenient way to visualize the mechanism. The temperature requirements for dormancy release and induction vary strongly between species. It seems unlikely that the temperature relations for the turnover of the same receptor protein would differ that much between species. Furthermore, weed seeds can remain viable in the soil for decades. They have to maintain a low metabolism, and annual synthesis and degradation of a receptor protein may be too costly. A more plausible assumption is that the properties of the membrane in which the receptor is located determine the *availability* of receptor protein (*cf.* Derkx and Karssen, 1993). This would be in agreement with Baskin and Baskin (1985) who stated that annual dormancy cycles may be related to changes in membrane properties. The composition of the membrane in which the receptor is situated may vary between species and thus cause

Table 2.2 Estimated parameter values. The parameters in the model were estimated by calibration. In this calibration the model was run 2000 times. This table gives the best fitting parameter set for the three species. The figures in parentheses are the result of a sensitivity analysis. For each parameter, they indicate the range of values for which the fit of the model decreases with less then 10 percent compared to the best fitting set. In the sensitivity analysis the other parameters of the set were kept constant at their optimal level.

Parameter	Description (dimension in parentheses)	*Polygonum persicaria*		*Chenopodium album*		*Spergula arvensis*	
dormancy							
IX	initial amount of X_a (-)	**0.109**	(0.000, 0.178)	**0.175**	(0.135, 0.179)	**0.170**	(0.086, 0.198)
LX	lower limit of X_a (-)	**0.000**	(0.000, 0.048)	**0.159**	(0.012, 0.394)	**0.151**	(0.138, 0.190)
UX	upper limit of X_a (-)	**1**		**1**		**1**	
$\mathbf{T_{min,rd}}$	minimum temperature for the release of dormancy (°C)	**0.5**	(-0.6, 1.5)	**0.3**	(0.2, 1.0)	**4.1**	(3.2, 4.6)
$\mathbf{T_{opt,rd}}$	optimum temperature for the release of dormancy (°C)	**1.8**	(1.0, 4.1)	**9.0**	(6.4, 9.6)	**14.4**	(12.0, 16.1)
$\mathbf{T_{max,rd}}$	maximum temperature for the release of dormancy (°C)	**15.5**	(13.8, 16.5)	**16.6**	(12.8, 15.4) ∪ (16.1, 16.6)	**21.2**	(17.2, →)
$\mathbf{RD_{max}}$	maximal rate of release of dormancy (day^{-1})	**0.0239**	(0.0181, 0.0273)	**0.0117**	(0.0066, 0.0094) ∪ (0.0111, 0.0117)	**0.0184**	(0.0170, 0.0212)
$\mathbf{T_{min,id}}$	minimum temperature for the induction of dormancy (°C)	**8.1**	(7.5, 8.5)	**8.9**	(7.2, 9.4)	**2.4**	(-1.3, 3.4)
IDT	proportionality factor between the temperature and the rate of induction of dormancy ($day^{-1}°C^{-1}$)	**0.00109**	(0.00103, 0.00118)	**0.00084**	(0.00068, 0.00106)		
$\mathbf{T_{opt,id}}$	optimum temperature for the induction of dormancy (°C)					**10.6**	(9.4, 12.7)
$\mathbf{T_{max,id}}$	maximum temperature for the induction of dormancy (°C)					**20.9**	(20.3, 22.0)
$\mathbf{ID_{max}}$	maximal rate of induction of dormancy (day^{-1})					**0.00869**	(0.00841, 0.00938)
germination							
LTXE	lower temperature limit for X_a exposure (°C)	**1.7**	(-0.2, 3.2)	**3.1**	(0.9, 5.2)	**0.2**	(-0.3, 0.3)
UTXE	temperature above which the total amount of X_a is exposed (°C)	**37.1**	(34.5, 43.3)	**15.3**	(14.1, 17.7)	**6.2**	(5.2, 6.6)
$\mathbf{K_d20}$	rate constant of dark reversion at 20°C (h^{-1})	**0.0394**	(0.0321, 0.0537)	**0.0638**	(0.0601, 0.0729)	**0.0527**	(0.0417, 0.0599)
$\mathbf{Q_{10,dr}}$	Q_{10} of dark reversion (-)	**5.0**	(3.4, 6.8)	**9.2**	(8.7, 10.5)	**3.6**	(3.4, 4.2)
$\mathbf{[X_p]_{thr}}$	threshold for the activity of X_p (-)	**0.111**	(0.103, 0.130)	**0.209**	(0.191, 0.246)	**0.157**	(0.141, 0.168)
AET20	average escape time at 20°C (h)	**10**		**10**		**10**	
$\mathbf{Q_{10,et}}$	Q_{10} of escape (-)	**4**		**4**		**4**	

differences in the temperatures required to increase or decrease the availability of the receptor.

The present model assumes that changes in dormancy can be attributed to changes in the availability of the phytochrome receptor. The degree of dormancy is inversely related to the total amount of available receptor X_a, which can be unexposed ($X_{a,u}$) or exposed ($X_{a,e}$), where $X_a = X_{a,u} + X_{a,e}$. The absolute amount of available receptor cannot be quantified. In the model only relative changes in the amount of X_a are important, and it is therefore a dimensionless quantity.

The temperature relationships for the release and induction of dormancy are based on those suggested for *P. persicaria*, *C. album* and *S. arvensis* by Bouwmeester (1990). Dormancy release has a species-specific temperature optimum, ranging from 0°C to 15°C. The induction of dormancy increases linearly with increasing temperature.

Experiments of Totterdell and Roberts (1979) showed that even at constant temperatures a cyclic change in seed dormancy occurs. This implies that the dormancy cycle can reverse from release to induction and *vice versa* without a change in the temperature conditions. In the model, it is assumed that an internal switch causes the reversal from release to induction and from induction to release. This internal switch determines whether the prevailing temperature has a dormancy relieving or a dormancy inducing effect. Within a dormancy cycle there are separated periods of dormancy release and dormancy induction.

Primary dormancy is the dormancy state of the freshly shed seed. This is the initial situation of the seeds in the model. Secondary dormancy is the dormancy state of the seed in which dormancy has been reinduced after relief of primary dormancy (Karssen, 1982). I assumed that as far as the processes included in the model are concerned, release of

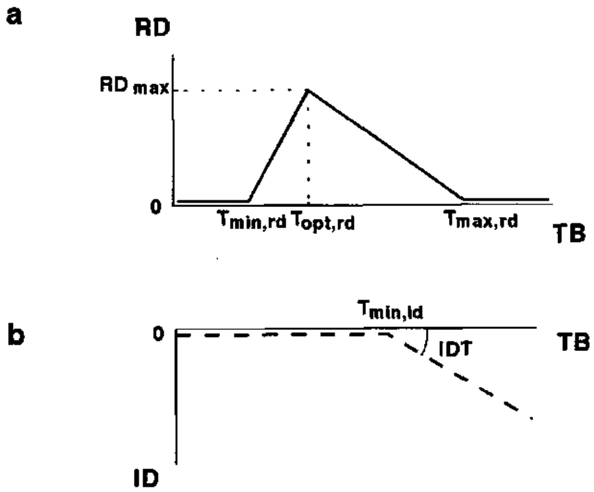

Fig. 2.3 The rate of dormancy release, RD (a), and the rate of dormancy induction, ID (b) as a function of the soil temperature in the field, TB.

primary and secondary dormancy are identical, and did not distinguish between them. Since the model starts when primary dormancy has already been induced, which occurs on the mother plant, in the model induction of dormancy concerns only induction of secondary dormancy.

Release of dormancy (Fig. 2.2a1). During periods of dormancy release, the rate at which the amount of available receptor increases, dX_a/dt, is called the rate of release of dormancy, RD (day^{-1}). Values of RD are always greater than or equal to zero. In the model the temperature dependence of RD is described as follows:

$$RD = 0 \qquad \text{if } TB < T_{min,rd} \qquad (2.1a)$$
$$RD = (TB-T_{min,rd})\cdot(RD_{max}/(T_{opt,rd}-T_{min,rd})) \qquad \text{if } T_{min,rd} < TB < T_{opt,rd} \qquad (2.1b)$$
$$RD = (T_{max,rd}-TB)\cdot(RD_{max}/(T_{max,rd}-T_{opt,rd})) \qquad \text{if } T_{opt,rd} < TB < T_{max,rd} \qquad (2.1c)$$
$$RD = 0 \qquad \text{if } TB > T_{max,rd}, \qquad (2.1d)$$

where TB is the field temperature (°C), $T_{min,rd}$, $T_{opt,rd}$ and $T_{max,rd}$ are the minimum, optimum and maximum temperature for the release of dormancy (°C), and RD_{max} is the maximum rate of dormancy release (day^{-1}) (Fig. 2.3a).

Induction of dormancy (Fig. 2.2a2). During periods of dormancy induction, the rate at which the amount of available receptor decreases, dX_a/dt, is called the rate of induction of dormancy, ID (day^{-1}). Values of ID are always less than or equal to zero. In the model the temperature dependence of ID is described as follows:

$$ID = 0 \qquad \text{if } TB < T_{min,id} \qquad (2.2a)$$
$$ID = -(TB-T_{min,id})\cdot IDT \qquad \text{if } TB > T_{min,id}, \qquad (2.2b)$$

where TB is the field temperature (°C), $T_{min,id}$ is the minimum temperature for the induction of dormancy (°C) and IDT is the slope of the curve ($day^{-1}{}^{\circ}C^{-1}$) (Fig. 2.3b).

In the model, alternating periods of dormancy induction and dormancy release result in cyclic changes in seed dormancy. The dormancy cycle of a seed shifts from induction to release when X_a equals its lower limit, LX, and from release to induction starts again when X_a equals its upper limit, UX. Output from the part of the model simulating the dormancy cycle is the amount of X_a in the average seed in the population. Among the seeds in the population there is a variation in the degree of dormancy. In the model this variation is simulated by a random generator drawing from a normal distribution of X_a around the simulated average.

Germination (Fig. 2.2, b-f)

The processes that determine the action of phytochrome in the seed constitute the germination part of the model (*cf.* chapter 1). The germination process of light-requiring seeds is triggered by red irradiation, converting the physiologically inactive form of phytochrome (Pr) to its active form (Pfr) (Bewley and Black, 1982). Pfr is thermodynamically unstable. Therefore, after a short irradiation, in darkness slow thermal reversion of Pfr to Pr occurs. The germination process has to be supported by the presence of Pfr for a certain period, the escape time. The germination process ceases if the life-time of Pfr is shorter than the escape time. Both the rate at which the processes that have to be supported by Pfr proceed (determining the escape time) and the rate at which Pfr is reverted to Pr in darkness are temperature dependent (Bewley and Black, 1982). A flash of light that produces some Pfr thus starts off a race between action and disappearance of Pfr within seeds. The outcome of this race (*i.e.* the final germination percentage) can be manipulated by choice of temperature (Borthwick, 1972). The exact relationship between temperature and germination percentage is defined by the temperature dependence of both Pfr action and Pfr disappearance. In the present model the idea that was put forward by Borthwick (1972) is extended by introducing seed dormancy as an additional factor determining the outcome of the race.

The processes denoted *b* up to *f* in Fig. 2.2 represent the germination process in a seed with a certain amount of X_a, when it is irradiated by red light.

Exposure of receptor (Fig. 2.2b). In order to be able to bind Pfr the receptor should be exposed to the outside of the membrane. Only available receptor molecules can be exposed. Therefore, unavailable receptor molecules cannot play a role in the germination process. Hilhorst (1993) hypothesized that the membrane fluidity increases with increasing temperature, which makes lateral movement of the receptor possible. The model assumes that the fraction of X_a that is exposed increases linearly with temperature:

$$X_{a,e}/X_a = 0. \qquad \text{if TT} < \text{LTXE} \qquad (2.3a)$$
$$X_{a,e}/X_a = (\text{TT}-\text{LTXE})/(\text{UTXE}-\text{LTXE}) \qquad \text{if LTXE} < \text{TT} < \text{UTXE} \qquad (2.3b)$$
$$X_{a,e}/X_a = 1. \qquad \text{if TT} > \text{UTXE}, \qquad (2.3c)$$

where TT is the temperature in the germination test (°C), LTXE is the lower temperature limit for X_a exposure (°C) and UTXE is the temperature above which the total amount of available receptor is exposed (°C) (Fig. 2.4).

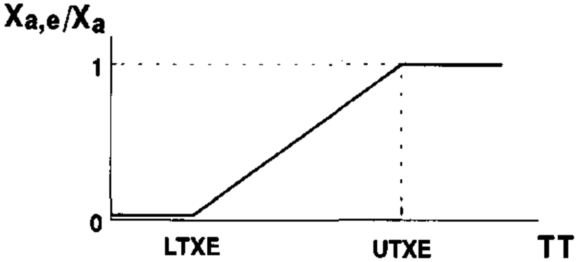

Fig. 2.4 The fraction of available receptor that is exposed, $X_{a,e}/X_a$ as a function of the temperature in the germination test, TT.

Binding of Pfr to the receptor (Fig. 2.2c1). Light with a wavelength of 660 nm (red light) converts 80 % of the phytochrome in the seed to Pfr (Hartmann, 1966). Photoconversion of Pr to Pfr by red light is independent of temperature (Nyman, 1961). In order to be able to bind Pfr, the exposed receptor must be activated by nitrate (Hilhorst, 1993). In the model it is assumed that the total amount of phytochrome in seeds in the seed bank is not limiting, and remains constant during burial. Provided that nitrate is present, a fraction f of $X_{a,e}$ is instantaneously occupied by Pfr when seeds are irradiated by red light, and thus turned into the receptor-phytochrome complex X_p. From data by Hilhorst (1990) it can be inferred that after red irradiation at the intensity that was used in the experiments all receptors were occupied, so f equals 1. Thus, in the time step Δt when the seeds are irradiated, the rate at which Pfr binds to the receptor PB (s^{-1}) equals

$$PB = dX_p/dt = X_{a,e}/\Delta t, \qquad (2.4a)$$

where Pfr_0 is the amount of Pfr immediately after irradiation,

$$\text{otherwise, } PB = 0. \qquad (2.4b)$$

Dark reversion (Fig. 2.2c2). Dark reversion is the process by which in darkness Pfr reverts to Pr. In plant tissue in general both dark reversion and Pfr destruction account for the decrease of Pfr. Bewley and Black (1982), however, stated that there is no clear evidence for Pfr destruction in seeds. This conclusion is supported by an *in vivo* study of phytochrome in seeds of *Pinus nigra* (Orlandini and Malcoste, 1972). Therefore, the simulation model attributes all Pfr decrease to dark reversion.

The kinetics of dark reversion were established by Schäfer and Schmidt (1974) in an *in vivo* experiment with *Cucurbita pepo* cotyledons:

$$Pfr_t = Pfr_0 \cdot \exp(-k_d t)$$

where Pfr_0 is the amount of Pfr immediately after irradiation, t is time, and k_d is the rate constant of dark reversion (note that Schäfer and Schmidt used the symbol k_b for this rate constant). A corresponding time course of Pfr during dark reversion in *Pinus nigra* seeds was found by Orlandini and Malcoste (1972).

In accordance with Quail and Schäfer (1974) and Hilhorst (1990), in the model an equilibrium between free and receptor-bound Pfr exists. It is assumed that the equilibrium is independent of temperature. The kinetics of the interaction between Pfr and its receptor are modelled by assuming that during the process of dark reversion the fraction of receptor molecules $X_{a,e}$ that are occupied by Pfr is proportional to the concentration of free Pfr present. Thus, the decrease in X_p after irradiation runs parallel with the decrease in Pfr:

$$[X_p]_t = [X_p]_0 \cdot \exp(-k_d t), \qquad (2.5)$$

where $[X_p]_t$ is the amount of occupied receptor at time t, $[X_p]_0$ is the amount of occupied receptor immediately after irradiation, and k_d is the rate constant of dark reversion (h^{-1}). From section *c1* it can be concluded that $[X_p]_0$ is equal to $X_{a,e}$.

Most likely, the kinetics of the interaction between Pfr and its receptor are more complex than assumed in the model (Hartmann and Cohnen Unser, 1972; Quail and Schäfer, 1974; Hilhorst, 1990), but too little concrete quantitative information is available to model the kinetics in more detail. In a future version of the model, the kinetics of the reaction may be incorporated. At present, I confine myself to the relation shown in eqn (2.5).

The rate of dark reversion strongly increases with increasing temperature (Taylorson and Hendricks, 1969). In the model this temperature dependence is quantified by the $Q_{10,dr}$, and all rates of dark reversion are related to the rate of dark reversion at 20°C. The k_d at the test temperature TT (°C) is calculated as:

$$k_d = k_d20 \; / \; (Q_{10,dr}{}^{((20-TT)/10)}), \qquad (2.6)$$

where k_d20 is the k_d at 20°C in h^{-1}.

Period of X_p action (Fig. 2.2d). Data from Karssen (1970) for *Chenopodium album* show that seeds need a threshold concentration of Pfr to stimulate germination. In the model this is interpreted as a threshold amount of X_p, $[X_p]_{thr}$, because only receptor-bound Pfr promotes germination. From eqn (2.5) it can be calculated that the period in which X_p promotes germination is equal to $(\ln([X_p]_0/[X_p]_{thr}))/k_d$.

Escape time (Fig. 2.2e). The germination process has to be supported by the presence of Pfr for a certain period, the escape time. Dark reversion causes conversion of Pfr to Pr, and thus terminates the germination process if the escape time has not yet passed.

In the model it is assumed that the germination process requires the presence of X_p until it reaches a stage from where it can proceed independently of the presence of X_p. Hilhorst (1993) suggested that the steps following the binding of Pfr to its receptor are synthesis of GA and activation of GA-receptors. For the calculation in the model, however, it is not essential what part of the germination process is dependent on X_p.

Escape times decrease with increasing temperature (Bewley and Black, 1982). In the model this temperature dependence of the escape time is quantified by the $Q_{10,et}$, and all escape times are related to the escape time at 20°C. The average escape time AET in h, at the test temperature TT (°C) is calculated as:

$$AET = AET20 \cdot (Q_{10,et}{}^{((20-TT)/10)}), \qquad (2.7)$$

where AET20 is the average escape time at 20°C in h.

Borthwick *et al.* (1954) showed the distribution of escape times in a seed population of *Lactuca sativa* at 20°C. In accordance to these data the model assumes a normal distribution of escape times within a population. A random generator drawing from this distribution simulates the variation in escape times in a seed population around the average that is calculated by the model.

Visible germination (Fig. 2.2f). The model simulates the germination percentage by counting the number of seeds for which the period of Pfr action exceeds the escape time. For this purpose, both the period of X_p action and the escape time are calculated as a function of the amount of X_a present and the test temperature. If in an individual seed of the seed lot that is tested for germination, the period of X_p action exceeds the escape time the germination rate GR (h^{-1}) equals

$$GR = 1/\Delta t \tag{2.8a}$$

in the time step Δt when the escape time is exceeded,

$$\text{otherwise } GR = 0. \tag{2.8b}$$

By counting the seeds for which GR reaches the value 1/Δt, the model determines the percentage of seeds that will germinate. Their time of emergence is not calculated. For this purpose the model could easily be extended with a calculation based on a temperature sum (Benech-Arnold and Sánchez, 1995).

Over all, the model input consists of the field temperature in the period when the seeds are buried (the driving variable for the dormancy model) and the temperatures used in the germination tests done at regular intervals after exhumation of the seeds (the driving variable for the germination model). If seeds are irradiated with red light and incubated in KNO_3, light and nitrate conditions are not limiting and germination only depends on the test temperature. Output of the model are the germination percentages in the tests.

2.2.3 Calibration of model parameters

Specific data to quantify the above-mentioned processes (Fig. 2.2, a-f) for *P. persicaria, C. album* and *S. arvensis* are lacking. Therefore parameters for the model relationships were estimated by calibrating the model with experimental germination data of *P. persicaria* (Bouwmeester and Karssen, 1992), *C. album* (Bouwmeester and Karssen, 1993*a*) and *S. arvensis* (Bouwmeester and Karssen, 1993*b*). In the calibration, parameter values were determined for which the simulated results fitted best to the observed data. For the burial temperature (TB) the daily average temperature at a depth of 10 cm in bare soil, measured at the meteorological station 'Haarweg' in Wageningen was used.

The FSEOPT-program developed by Stol *et al.* (1992) was used in the calibration procedure. This program uses a mathematical algorithm, the Price algorithm, for finding the best combination of model parameters for a given set of experimental data. The parameter set giving the best fit to the experimental data after 2000 reruns for each species was considered to be optimal. In the calibration, the goodness of fit of the model is quantified by a variable denoted as QT. First, for each of the three temperatures at which germination tests were done, an auxiliary variable QT′ was calculated as:

$$QT'(i) = \sqrt[IQT]{\sum_{k=1}^{19} (d_{ik}-m_{ik})^{IQT}} \qquad (i=1,2,3), \tag{2.9a}$$

where d_{ik} and m_{ik} represent the experimental data and the model output respectively for the k^{th} germination test in time at the i^{th} test temperature. The variable IQT can have the values 1 or 2, and determines how residuals are weighted. Subsequently, QT was calculated as:

$$QT = \max_{i=1,2,3}(QT'(i)), \tag{2.9b}$$

The optimal parameter set is considered to be the one with the lowest QT-value. Empirically it was found that for the data on *P. persicaria* and *C. album* the best criterion for the acceptability of a parameter set was the sum of absolute residuals between model output and experimental data, and for the data on *S. arvensis* the square root of the sum of squares of the residuals. This means that for *P. persicaria* and *C. album* the optional switch IQT was given the value 1, and for *S. arvensis* it was given the value 2. When IQT has the value 2, outliers have a greater influence on the value of QT (Stol *et al.*, 1992). In order to diminish the influence of the random generator on the value of QT for a given parameter set, the average QT of 10 reruns with the same parameter set was used in the calibration.

To enable comparison with other models, the percentage variance accounted for by the simulation model is calculated in analogy with the coefficient of multiple determination in regression models,

$$R^2 = 1 - \frac{\sum (d_{ik} - m_{ik})^2}{\sum (d_{ik} - \bar{d}_{ik})^2} \ . \tag{2.10}$$

In the calculation of R^2 all test temperatures were included.

The parameters and the initial value of X_a (IX), that were estimated in the calibration, are listed in Table 2.2. Three variables, however, were parameterized with a preset value that was the same for all three species, *viz.* UX, AET20 and $Q_{10,et}$. This was done for the following reasons. The amount of receptor is measured at a relative scale. The absolute quantities of receptor that are present in seeds are not known, and in the model only relative differences are important. I fixed the amount of X_a at which reversal from dormancy release to induction occurs (UX) at an arbitrary value of 1. This implies that in the model the amount of X is expressed as a fraction of the amount present at reversal.

The model calculates whether or not the seed will germinate by comparing the period of X_p action and the escape time. In this calculation it is only important which of these periods is longer. The period of X_p action is determined by the parameters k_d20 and $Q_{10,dr}$. The escape time is determined by the parameters AET20 and $Q_{10,et}$. Since only the ratio between these periods is important, the parameters estimated in the calibration are actually the ratios $(k_d20)^{-1}$/AET20 and $Q_{10,dr}/Q_{10,et}$. In order to be able to compare the estimated parameter values for k_d20 and $Q_{10,dr}$ to data from literature, the value of AET20 was fixed at 10 h, which value was reported by Borthwick *et al.* (1954) for *Lactuca sativa*, and the value of $Q_{10,et}$ was fixed at 4, which value was reported by Taylorson and Hendricks (1969) for *Amaranthus retroflexus*.

In all three species, the standard deviation of the distribution of X_a in the model was set at to 0.1. The standard deviation of the distribution of escape times was estimated at 0.2 times the average escape time, which was derived from data of Borthwick *et al.* (1954).

In the model, one has to indicate whether simulation starts in a period of dormancy release or in a period of dormancy induction. Since calibration was done with three summer annuals and the simulation started in December, the model was initialized in a state of dormancy release.

2.3 Results and discussion

Preliminary results of the simulation model showed that both *C. album* and *S. arvensis* deviated in one species-specific point from the basic model structure for the dormancy cycle. *C. album* differs from the two other species in the study in that the dormancy cycle does not only reverse from induction to release of dormancy when the amount of available receptor reaches its minimum, but also when the field temperature reaches $T_{min,id}$. The criteria for reversal used in the model are that either in autumn the average temperature over the last 10 days drops beneath $T_{min,id}$, or that the amount of X_a reaches LX. *S. arvensis* differs from the two other species in the study in that above a certain optimum temperature ID decreases with increasing temperature [*cf.* eqn (2.2)].

$$ID = 0. \qquad \text{if } TB < T_{min,id} \qquad (2.11a)$$
$$ID = -(TB - T_{min,id}) \cdot (ID_{max}/(T_{opt,id} - T_{min,id})) \qquad \text{if } T_{min,id} < TB < T_{opt,id} \qquad (2.11b)$$
$$ID = -(T_{max,id} - TB) \cdot (ID_{max}/(T_{max,id} - T_{opt,id})) \qquad \text{if } T_{opt,id} < TB < T_{max,id} \qquad (2.11c)$$
$$ID = 0. \qquad \text{if } TB > T_{max,id}, \qquad (2.11d)$$

where TB is the field temperature (°C), $T_{min,id}$, $T_{opt,id}$ and $T_{max,id}$ are the minimum, optimum and maximum temperature for the induction of dormancy (°C), and ID_{max} is the maximum rate of dormancy induction (day^{-1}).

2.3.1 Calibration of model parameters

In Table 2.2 the sets of optimum parameter values for the three species are shown. The results of the exhumation experiments with *P. persicaria*, *C. album* and *S. arvensis* are shown in Fig. 2.5, together with the simulated curves resulting from the optimum parameter set in the calibration. The experimental and simulated curves show that germination of exhumed seeds rose and fell in an annual pattern. In general the dormancy changes were fitted well. The fluctuations in the simulated germination percentages on a smaller time scale reflect the random variation in the population, and not short-term oscillations in dormancy.

The model was compared to the one by Bouwmeester and Karssen (1992, 1993*a*,*b*) that was fitted to the same data set, by examining R^2 values calculated according to eqn (2.10). For *P. persicaria*, *C. album* and *S. arvensis*, the model gave R^2 values of 0.74, 0.55 and 0.85, respectively. The model by Bouwmeester and Karssen (1992, 1993*a*,*b*) gave R^2 values of 0.69, 0.56 and 0.78, respectively. It should be noted that neither of the models has been calibrated with a maximal R^2 as a criterion. It appears that the most

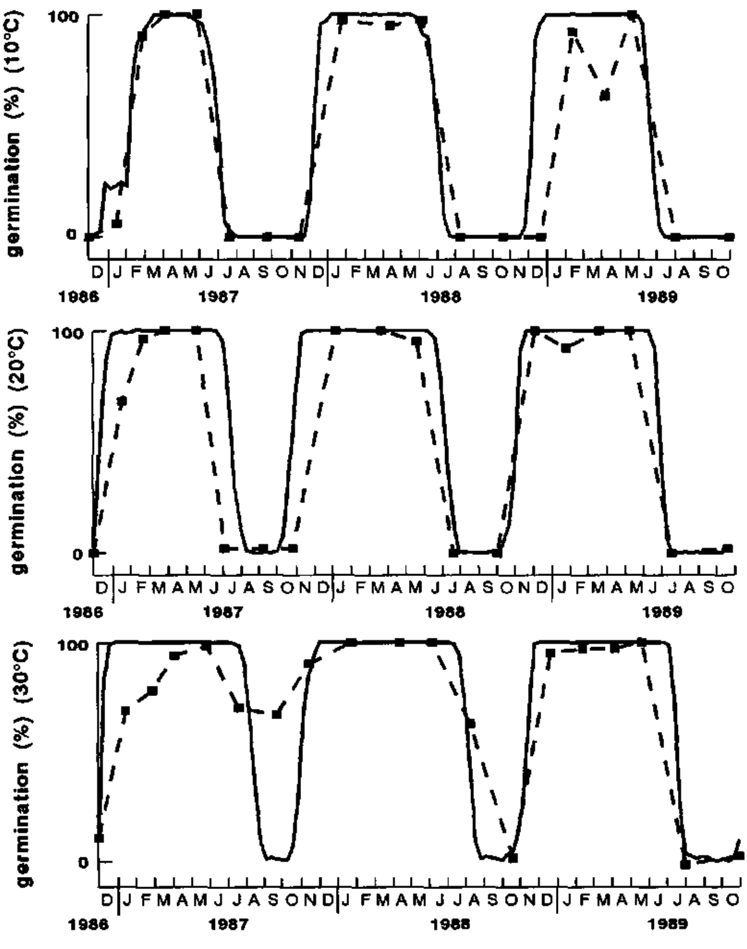

Fig. 2.5a Comparison between simulated results (————) and observed data (■) for *Polygonum persicaria*. Germination was tested at 10°C, 20°C and 30°C. Squares represent experimental data from Bouwmeester and Karssen (1992). The value of QT in the calibration was 212.5.

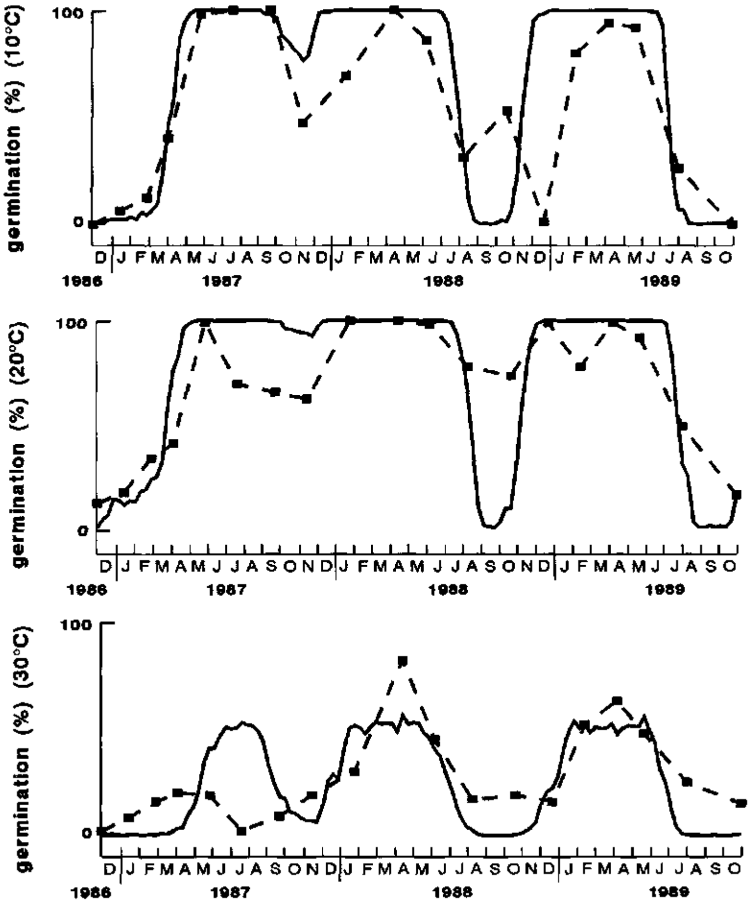

Fig. 2.5b Comparison between simulated results (————) and observed data (■) for *Chenopodium album*. Germination was tested at 10°C, 20°C and 30°C. Squares represent experimental data from Bouwmeester and Karssen (1993*a*). The value of QT in the calibration was 302.3.

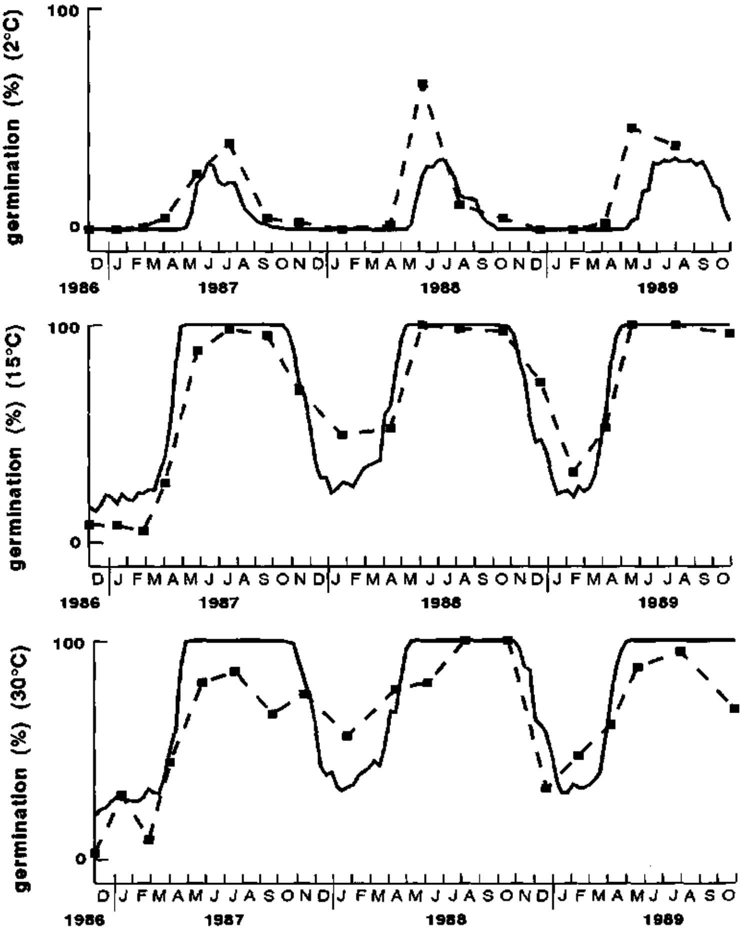

Fig. 2.5c Comparison between simulated results (————) and observed data (■) for *Spergula arvensis*. Germination was tested at 2°C, 15°C and 30°C. Squares represent experimental data from Bouwmeester and Karssen (1993*b*). The value of QT in the calibration was 72.4.

important improvement of the present model compared to the one by Bouwmeester and Karssen (1992, 1993*a*,*b*) is not the higher percentage variance accounted for, but its firmer basis in seed physiology.

2.3.2 Evaluation of parameter estimates

Description of dormancy patterns observed in the field is not a discriminative test of the model. Independent datasets are necessary to validate the model. The best way to test the model performance would be to compare simulated germination data with experimental results of germination tests over a range of test temperatures, using seeds that were pretreated at different temperature regimes ('burial temperatures') in the laboratory. However, these data are not available at present.

In this study all parameters in the model were estimated by calibration. If possible, it would be preferable to measure the parameters experimentally. Here I will try to get an impression of the validity of the parameter values estimated in the calibration, by comparing them with values reported in literature. Apart from the field experiments that were used in the calibration, Bouwmeester (1990) and Bouwmeester and Karssen (1992, 1993*a*,*b*) reported a number of data on dormancy release and induction of the three species in this study from experiments under controlled conditions. In an experiment with *P. persicaria* dormancy was relieved faster in a pretreatment at 2°C than at 6°C and 10°C, and was not relieved at all at 15°C (Bouwmeester, 1990). This agrees fully with the model (Table 2.2). In the calibration $T_{min,id}$ was estimated at 8.1°C. This estimate is too high; Bouwmeester and Karssen (1992) found that induction of dormancy in *P. persicaria* is also possible at 2°C. Experiments with *C. album* show that release of dormancy proceeds faster at 10°C than at 2°C, 6°C and 15°C (Bouwmeester and Karssen, 1993*a*, and unpublished results). This is in good agreement with the model, in which the maximum rate is reached at 9.0°C. Experimental results on *S. arvensis* showed that no release of dormancy occurs at 2°C. When the temperature increases, the rate of release increases to a maximum at 15°C, and then decreases to zero at 20°C (Bouwmeester and Karssen, 1993*b*). In these experiments dormancy induction was maximal at 10°C, lower at 6°C and 15°C, and about zero at 2°C and 20°C. These data agree fully with the model (Table 2.2). In contrast, Karssen *et al.* (1988) reported that primary dormancy of *S. arvensis* is released most effectively at 30°C. They found that the rate of dormancy release decreases with decreasing temperature, but dormancy is still being released at 2°C.

The parameter LTXE represents the theoretical minimum temperature at which germination can take place. The estimated values range from 0.2 to 3.1°C. These values are in accordance with the minimum germination temperature of so-called psychrophilic or cold-resistant weed species, ranging from 2 to 4°C (Fisyunov, 1976). Lauer (1953) reported germination of *C. album* and *S. arvensis* when tested at 2-5°C. As the minimum germination temperature for *P. persicaria* she mentioned 20-25°C. However, *P. persicaria* still germinated in a germination test at 3-4°C (Vleeshouwers, unpublished data). It should be noted that the parameter UTXE cannot be regarded as the theoretical maximum temperature for germination. No literature data are available that can be used as an estimate for UTXE.

Taylorson and Hendricks (1969) studied dark reversion and escape times in

Amaranthus retroflexus. They roughly estimated the half-time for dark reversion at 20°C to be 1.3 days, which implies a k_d20 of 0.0222 h^{-1}. The values estimated in the calibration range from 0.0394 h^{-1} to 0.0638 h^{-1}. The $Q_{10,dr}$ they estimated was 16. They considered this seemingly high value not unreasonable as the interaction of a protein and a chromophore is involved. The values estimated in the model were lower (from 3.6 to 9.2). The value estimated for $[X_p]_{thr}$ in *C. album* (0.209) lies within the range of Pfr to total phytochrome ratios found to promote germination of this species (Karssen, 1970), from about 0.05 to 0.4.

According to the model, the phytochrome receptor level required to induce maximal germination, defined as 99%, in *P. persicaria*, *C. album* and *S. arvensis*, amounts to 20%, 53% and 34%, respectively, of the level maximally present in the seeds. The percentages are of the same order of magnitude as the one for *Sisymbrium officinale* given by Hilhorst (1990), who calculated that the receptor level required to achieve full germination amounts to 40% of the maximal level.

In general, it is concluded that the parameters that produce a good fit between the model output and the experimental data have reasonable values compared to those that can be found in the literature.

2.3.3 Sensitivity analysis

Table 2.2 gives the results of a sensitivity analysis of the parameters in the model. For each parameter the range of values is given for which the QT-value increased with less than 10 percent compared to the best fitting set. In assessing the sensitivity of the model to one parameter the other parameters of the set were kept constant at their optimal level.

From the sensitivity analysis it can be concluded that there are no striking differences in the sensitivity of the model for the different parameters. No key parameters can be detected that have a disproportionately strong influence on the model output. The sensitivity analysis (Table 2.2) showed that, except for the initial value IX, no parameter could be assumed to have the same value for all three species.

2.3.4 Comparison of the species

The temperature dependence of the rate of dormancy release and induction for the three species is shown Fig. 2.6. *P. persicaria* and *C. album* only differ in the temperature optimum for dormancy release $T_{opt,rd}$, which is higher for *C. album* and in the maximal rate of dormancy release RD_{max}. *S. arvensis* has higher temperature requirements for dormancy release and lower temperature requirements for dormancy induction than both other species. For *S. arvensis* the induction of dormancy has an optimum temperature of 10.6°C. *P. persicaria* and *C. album* are likely to have a temperature optimum for the induction of dormancy too, but the optimum temperature is apparently so high that during the experiment it was not or seldom reached in the field at a depth of 10 cm, and therefore cannot be estimated from the available data. The slope of the curve showing the increase in dormancy induction rate with increasing temperature between $T_{min,id}$ and $T_{opt,id}$ for *S. arvensis* equals 0.00106 $day^{-1}{}^{\circ}C^{-1}$, and this is of the same order of magnitude as the IDT for *P. persicaria* and *C. album*. It can be concluded that the difference between the induction of dormancy of *S. arvensis* on the one hand and *P. persicaria* and *C. album* on the other hand is not a matter of model structure, but merely a matter of different parameter values.

The model offers a basis to characterize annuals on a continuous scale from pure winter annuals to pure summer annuals. A winter annual character coincides with a high $T_{opt,rd}$ and a low $T_{opt,id}$. A summer annual character coincides with a low $T_{opt,rd}$ and a high $T_{opt,id}$. For the three species in this study the summer annual character becomes more pronounced in the order *S. arvensis*, *C. album* and *P. persicaria*.

Fig. 2.7 shows the simulated changes in the minimum and maximum temperature required for 50% germination in 50 mM KNO_3 after irradiation with red light, in the period the burial experiment was done. Considering the test temperatures used, extrapolation of the temperature range was restricted to the range from 0°C to 35°C. Fig. 2.7 demonstrates that the simulation model, based on the hypothesis of Hilhorst (1993) that dormancy is related to the amount of a membrane-located phytochrome receptor, shows an annual widening and narrowing of the temperature range for germination and is thus compatible to the theory of Karssen (1982). It is able to build a bridge between the dormancy concepts of Hilhorst (1993) and Karssen (1982).

Fig. 2.7 clearly shows that for all three weed species the timing of germination in the field results from changes in both the minimum temperature required for germination and the prevailing temperature in the field. Already in December the temperature range for germination of *P. persicaria* is maximal. However, only in March-April the soil temperature has risen so far that germination in the field can occur. In *C. album* the timing of field germination depends more on the annual fluctuation in the soil temperature than on the annual fluctuation in the minimum temperature for germination. Since in *S. arvensis* broadening of the temperature range for germination coincides with the increase of soil temperature in spring and narrowing of the temperature range for germination coincides with the decrease of temperature in autumn, changes in dormancy and changes in the soil temperature reinforce each other in the timing of germination in the field.

2.3.5 Application of the model

During soil disturbance weed seeds are exposed to daylight. Afterwards most of the seeds are buried again at places where light cannot reach them. The experimental treatment of the seeds, consisting in exhumation, irradiation with red light and germination in the dark, corresponds with the effect of soil disturbance. The spectral composition of unfiltered daylight is such that it has the same effect on seed germination than red light. Therefore the model can also be used to predict weed germination in the field after disturbance of the soil. Only when the field temperature and the temperature range over which germination can proceed overlap, soil disturbance will cause a flush of weed seedlings (Fig. 2.7). The soil can be disturbed by soil cultivation but also by mechanical weed control measures. Predictions of weed germination in the field can be used to optimize weed management.

2.4 Conclusion

A simulation model for seed dormancy was developed that uses the amount of available membrane-located phytochrome receptor protein as a measure for the degree of

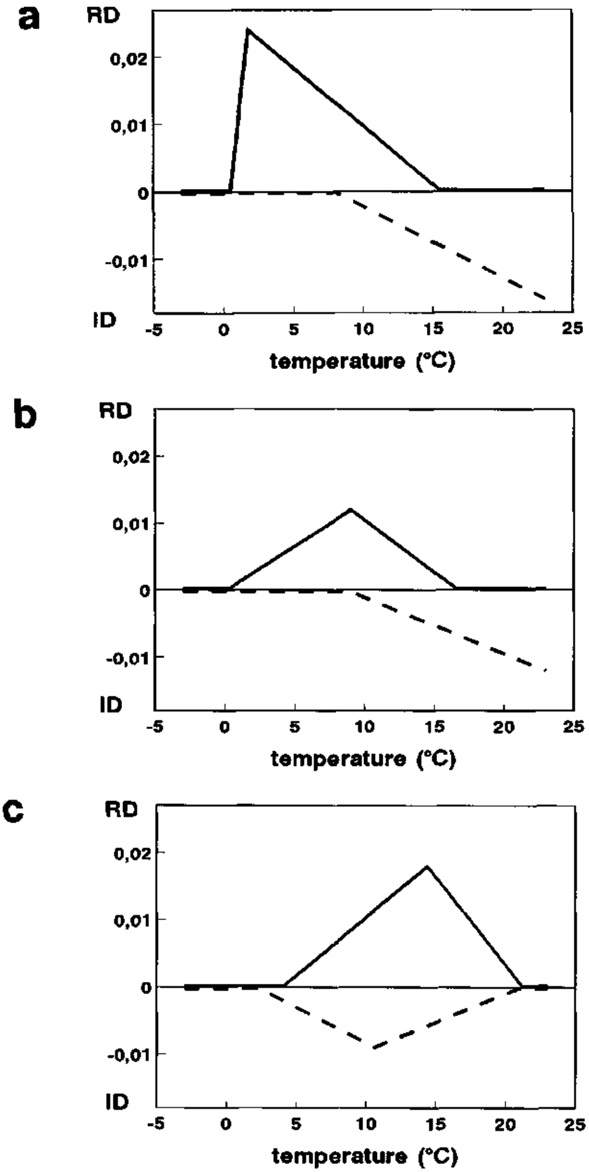

Fig. 2.6 Temperature dependence of the rate of dormancy release and induction in *Polygonum persicaria* (a), *Chenopodium album* (b) and *Spergula arvensis* (c). Note that release and induction of dormancy occur in separate periods, thus resulting in a cyclic increase and decrease in the availability of the phytochrome receptor.

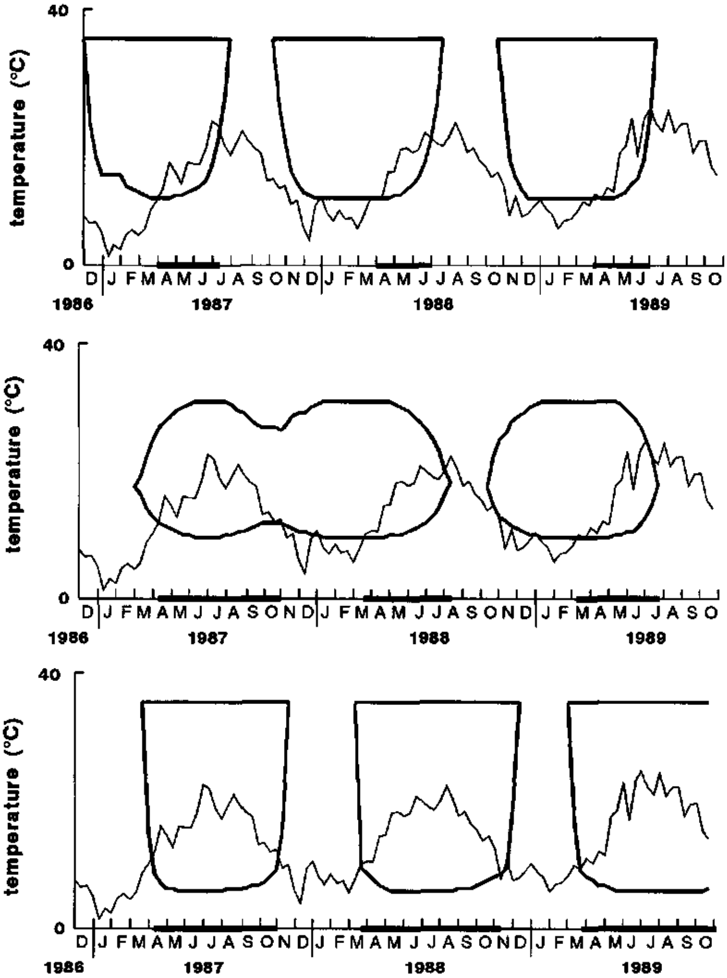

Fig. 2.7 Simulated seasonal changes in the range of temperatures over which exhumed seeds germinate. Thick lines represent the minimum and maximum temperature for 50% germination in 50 mM KNO_3 after red irradiation. The thin line indicates soil temperature at −10 cm. Line segments on the X-axis indicate periods when field temperature and germination temperature overlap.

dormancy. From this amount it calculates germination percentages of seed samples that are irradiated with red light and tested for germination at different temperatures. The model output can also be presented as the width of the temperature range in which germination occurs. Therefore, the model bridges the gap between the concept of dormancy hypothesized by Hilhorst (1993), in which dormancy is related to the amount of phytochrome receptor, and that presented by Karssen (1982), in which dormancy is related to the temperature range over which seeds germinate.

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3 THE EFFECT OF SEED DORMANCY ON PERCENTAGE AND RATE OF GERMINATION IN *POLYGONUM PERSICARIA* L., AND ITS RELEVANCE FOR CROP-WEED INTERACTION

Abstract Changes in germination percentage and germination rate of *Polygonum persicaria* resulting from loss of primary dormancy during chilling of imbibed seeds were quantified. Both percentage and rate of germination increased with increasing loss of dormancy. It was concluded that retardation of germination caused by dormancy was not due to dormancy release prior to germination, but to retardation of the germination process itself. When evaluated in relation to competition between sugar-beet and *P. persicaria*, the effect of dormancy on the germination percentage was more important than the effect on germination rate, but for an accurate prediction of yield loss, the latter effect cannot be neglected.

3.1 Introduction

Viable seeds are dormant when their germination is internally blocked, so that they cannot germinate in an otherwise favourable environment (Bewley and Black, 1982). Dormancy is not an all-or-nothing characteristic, but is measured on a continuous scale. Changes in dormancy involve gradual changes in the width of the temperature range in which seeds can germinate (Karssen, 1982). This concept is elaborated by Vleeshouwers and Bouwmeester (1993) who simulated the effect of dormancy on the relationship between temperature and the final germination percentage of the arable weed *Polygonum persicaria* (Fig. 3.1). Another aspect of the gradual nature of dormancy is the continuous decrease in the time to germination when dormancy is released (Gordon, 1973). Loss of primary dormancy during dry after-ripening causes an increase in both the percentage of seeds germinating and their rate of germination in barley and wheat (Gordon, 1973;

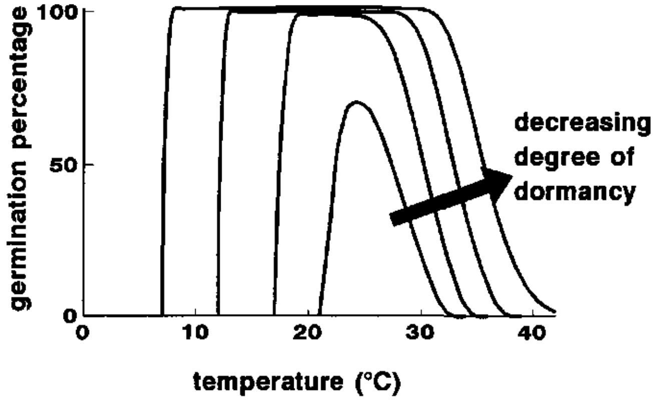

Fig. 3.1 The simulated relationship between temperature and the final germination percentage of *P. persicaria* at four degrees of dormancy. The lower the degree of dormancy, the wider the temperature range for germination.

Roberts and Smith, 1977; Favier, 1995) and the weed species *Avena fatua* (Naylor and Simpson, 1961). Loss of dormancy during chilling of imbibed seeds results in an increase in percentage and rate of germination in *Zinzania palustris* (Probert and Longley, 1989) and five wildflower species (Bratcher *et al.*, 1993).

Weed seeds in the soil seed bank are subjected to annual cycles in dormancy (Karssen, 1982). These changes in dormancy affect the germination of weed seeds triggered by soil cultivation. Weed control may be improved by a prediction of weed seed germination after soil cultivation. Both weed density and the time between crop and weed emergence are important parameters to quantify the competitive strength of a weed vegetation (Kropff *et al.*, 1992; Kropff and Van Laar, 1993). Therefore, prediction of germination should consist of the number of seeds germinating and the timing of their germination, both of which are affected by dormancy. In that respect, it is important to quantify the effects of dormancy on germination percentage and germination rate of weeds.

Models that predict weed emergence and contain the factor dormancy are those by Spitters (1989) and Benech Arnold *et al.* (1990). The model proposed by Spitters (1989) comprises the effect of dormancy on the density of *Ambrosia artemisiifolia* and *Lamium amplexicaule* after soil cultivation, but not on their rate of emergence. A study to the effect of dormancy on the germination of the weed species *Sorghum halepense* is reported by Benech Arnold *et al.* (1990), who presented a model to predict *S. halepense* seedling emergence. In the model three discrete dormancy states of the seeds are distinguished. Dormant seeds are released from dormancy by exposure to fluctuating temperatures. They then pass to the state from which they can germinate. The germination rate of the seeds that have their dormancy broken is only dependent on temperature. Therefore, the model implies that an increase in dormancy causes an increase in the time the seeds need to germinate. The retardation of germination is due to the time it takes to break their dormancy previously. Roberts and Smith (1977) gave an identical explanation for the increased germination period of freshly-harvested barley seeds over that of after-ripened seeds. They assume that the increase in the germination period corresponds to the duration of dormancy relief in freshly harvested seeds.

Temperature has a double effect on seed germination. Both the final germination percentage and the rate at which this percentage is reached are affected by temperature (Heydecker, 1977). Generally, the maximum final germination percentage is reached in a broad temperature range (Thompson, 1970), whereas the germination rate has a sharp optimum temperature (Garcia-Huidobro *et al.*, 1982). At temperatures below the optimum germination rate increases linearly with temperature (Hegarty, 1973; Garcia-Huidobro *et al.*, 1982).

The first objective of this study was to quantify the effect of dormancy on the percentage and rate of germination in *Polygonum persicaria* L. seeds, tested at different temperatures in the laboratory. The second objective was to quantify the relative importance of the changes in germination percentage and germination rate in relation to competition between *P. persicaria* and sugar-beet.

3.2 Materials and methods

The seeds of *P. persicaria* L. that were used in the experiment were harvested in July 1989 and stored dry at 3°C. Preliminary experiments in the spring of 1992 showed that the seeds were dormant and that the dormancy could be broken by imbibing the seeds in 10mM KNO_3 and pretreating them at 2°C for 5 days. This pretreatment caused germination percentages up to 98%. Periods of imbibition in 10mM KNO_3 at 2°C between 0 and 5 days caused intermediate degrees of dormancy.

The experiment was done in August and September 1992. Three different levels of dormancy were established by imbibing the dormant seeds in 10mM KNO_3 and pretreating them at 2°C in the dark for 1, 2 and 5 days. These levels of dormancy were called 3, 2 and 1, respectively. Thus, 3 indicates the highest level of dormancy, 1 the lowest level of dormancy. After the pretreatment the seeds were irradiated with red light for 15 minutes and germination was tested in incubators at temperatures of 5, 10, 15, 20, 25 and 30°C in the dark. Germination at every combination of dormancy level and temperature was tested in 4 portions of 100 seeds each. The light conditions experienced by the seeds at soil cultivation were mimicked by this experimental design. In general soil cultivation causes a short irradiation of the seeds during soil disturbance, after which most of the seeds will be buried again and germinate in the dark.

At regular intervals the number of germinated seeds was counted in green safe light. The observation intervals were adjusted to the rate at which germination proceeded. During the first days of germination this was a four hours' interval. Gradually the number of seeds germinating per time interval decreased and the counting frequency was reduced. After six weeks germination had come to an end in all of the experiments, and the observations were stopped.

The time course of germination was described by a Gompertz curve,

$$Y = a_1 \exp[-\exp(a_2+a_3t)], \tag{3.1}$$

where Y is the cumulative germination percentage, t is the time from red irradiation of the seeds, called the germination time, and a_1, a_2 and a_3 are empirically derived parameters. Several authors used the Gompertz curve to represent cumulative germination of spores (Lapp and Skoropad, 1976) and seeds (Tipton, 1984; Brown and Mayer, 1988).

In eqn (3.1) the final germination percentage is equal to a_1. The median of the distribution of germination times (t_{50}) is given by

$$t_{50} = [\ln(\ln 2)-a_2]/a_3. \tag{3.2}$$

In this chapter the germination rate is defined as the inverse median of the distribution of germination times ($1/t_{50}$) (*cf.* Garcia-Huidobro *et al.*, 1982), and equals

$$1/t_{50} = a_3/[\ln(\ln 2)-a_2]. \tag{3.3}$$

Equation (3.1) can be rewritten as

$$Y = a_1 \exp\{-\exp[a_2+(\ln(\ln 2)-a_2)a_4t]\}, \tag{3.4}$$

with $a_4 = a_3/[\ln(\ln 2)-a_2]$. For the analysis in this study, eqn (3.4) is a convenient way to describe the Gompertz curve because the germination rate is represented by parameter a_4.

For all different combinations of temperature and dormancy level, parameter a_1 was estimated as the cumulative germination percentage at the end of the six weeks' observational period, since the germination process had finished by then. Subsequently, parameters a_2 and a_4 were estimated by fitting the Gompertz curve, described as eqn (3.4), to the time course of germination by non-linear regression (SAS, procedure NLIN). Final germination percentage and germination rate were equalled to the estimated parameter values of a_1 and a_4, respectively. The 95% confidence interval of the final germination percentage was calculated by assuming a binomial distribution of the number of germinated seeds, from a total of 400 seeds that were tested. The 95% confidence interval of the germination rate was given by the SAS procedure NLIN as the confidence interval of the estimated parameter a_4. Finally, the dependence of germination percentage and germination rate on both temperature and dormancy was determined by comparing the results obtained under the different experimental conditions.

The results from the germination experiment were evaluated with respect to their significance for crop-weed competition, using data by Bos and Wallinga (1991). In their field experiment, yield reduction of sugar-beet was measured in relation to plant density and emergence date of *P. persicaria.* The experiment was conducted in 1990 in Wageningen on a sandy loam soil. Sugar-beet was sown on 6 April. The crop was grown at a density of 11.1 plants m^{-2}, at a spacing of 0.5 m between rows, and 0.18 m within rows. On 20 April, 25 April and 1 May, pre-germinated *P. persicaria* seeds were planted by hand in the crop rows, and, after emergence, thinned to densities of 2.8, 22.2 and 44.4 plants m^{-2}. Weed-free plots were used as a control. Sugar-beet was harvested on 2 October.

3.3 Results and discussion

3.3.1 Germination

The observed and the fitted time courses of germination at the different levels of dormancy and at the different temperatures is shown in Fig. 3.2. Hardly any germination occurred at 5°C, and no curves were fitted through the data at this temperature. The germination data are fitted well by the Gompertz curve, although a general feature of the regression is that the fitted curve rises to the final germination level too soon after the steep part of the curve. Estimates of the final germination percentages and germination rates, and their confidence intervals, in the temperature range from 10 to 30°C, are given in Table 3.1.

The estimated final percentage and rate of germination are depicted in Figs 3.3a and 3.3b. Fig. 3.3a shows that both dormancy and temperature influence the final germination percentage. A decrease in dormancy causes an increase of the final germination percentage. At all temperatures, final germination is higher at a lower dormancy level of the seeds. At all three levels of dormancy, final germination percentages are highest at the intermediate temperatures in the experiment. The data confirm the notion that release of dormancy widens the temperature range for germination. Fig. 3.3b shows that both dormancy and temperature affect the germination rate. A decrease in dormancy causes an increase of the germination rate. In the temperature range from 10°C to 25°C, germination rate is approximately linearly dependent on temperature at all levels of dormancy (R^2 values varying from 0.99 to 1.00). The effect of dormancy on the final

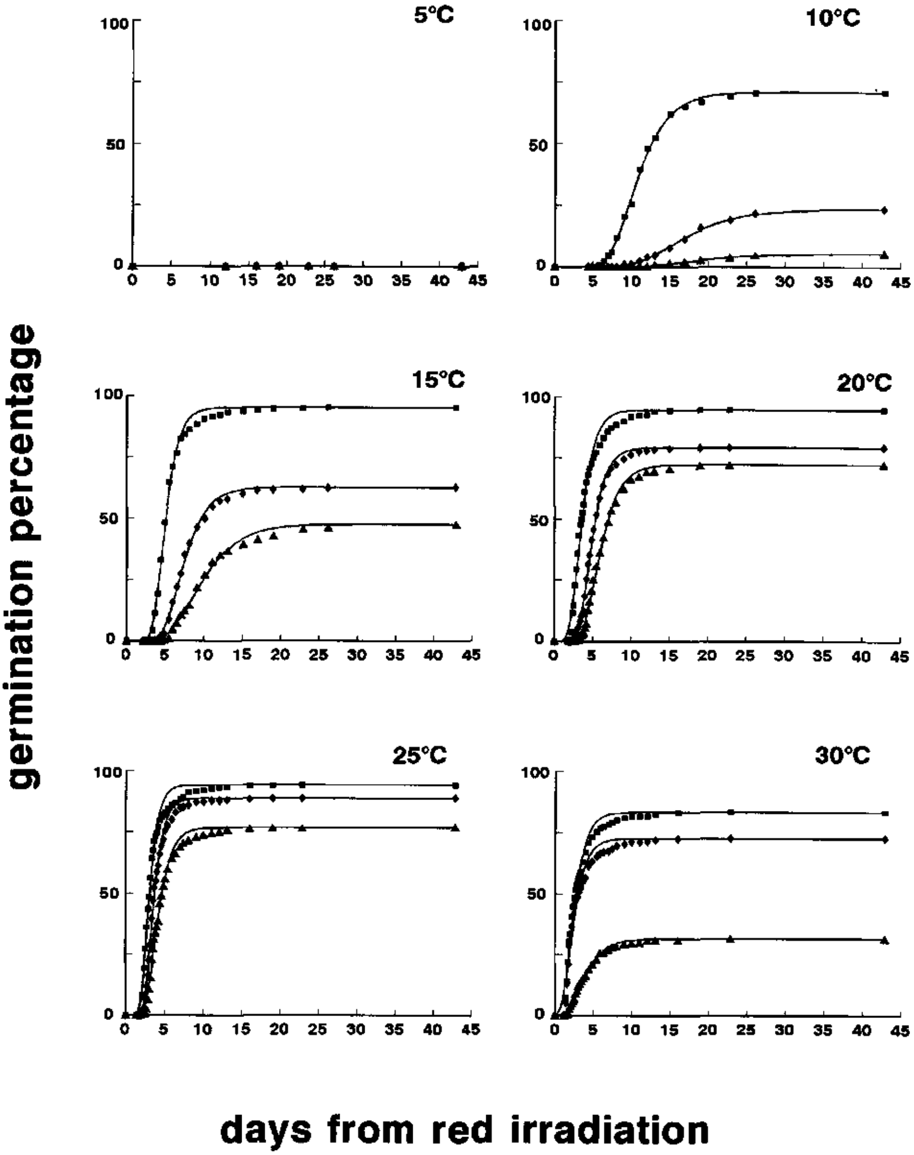

Fig. 3.2 The cumulative germination of *P. persicaria* at different levels of dormancy and different temperatures as observed (dormancy level 1: ■ , level 2: ◆ , level 3: ▲) and fitted by the Gompertz curve (————).

Table 3.1 Estimated final percentage and rate of germination at different temperatures (*T*) and levels of dormancy (95% confidence intervals in parentheses).

T (°C)	Final germination percentage (%)			Germination rate (day^{-1})		
	Dormancy level			*Dormancy level*		
	1	*2*	*3*	*1*	*2*	*3*
10	71.0 (66.3, 75.1)	23.5 (19.7, 27.9)	5.5 (3.7, 8.2)	0.093 (0.092, 0.094)	0.059 (0.058, 0.060)	0.053 (0.052, 0.054)
15	95.3 (92.7, 96.9)	62.8 (57.9, 67.2)	47.8 (43.1, 52.7)	0.202 (0.199, 0.205)	0.136 (0.134, 0.138)	0.103 (0.101, 0.106)
20	94.5 (91.8, 96.3)	79.3 (74.8, 82.8)	72.3 (67.6, 76.3)	0.282 (0.276, 0.288)	0.205 (0.203, 0.207)	0.167 (0.165, 0.169)
25	94.3 (91.5, 96.1)	88.8 (85.3, 91.4)	76.8 (72.3, 80.5)	0.330 (0.324, 0.337)	0.279 (0.275, 0.282)	0.242 (0.238, 0.245)
30	83.3 (79.3, 86.5)	72.5 (67.9, 76.5)	31.5 (27.3, 36.3)	0.415 (0.400, 0.430)	0.425 (0.406, 0.444)	0.259 (0.252, 0.267)

germination percentage is smallest at 25°C and increases with temperatures rising to 30°C or falling to 10°C (Fig. 3.3a). In contrast, the effect of dormancy on the rate of germination is smallest at 10°C and increases with increasing temperature (Fig. 3.3b).

The effect of the degree of dormancy on the rate of germination corresponds to that reported in the literature. Roberts and Smith (1977) and Benech-Arnold *et al.* (1990) interpreted the decrease of germination rate as an increase in the time needed to break dormancy previous to germination. They assumed that the process of radicle elongation (*i.e.* the germination process itself) is only dependent on temperature. In contrast, I argue that in *P. persicaria* germination itself is retarded by an increase in the degree of dormancy. The first reason is that dormancy of *P. persicaria* is only released at temperatures lower than 15°C (Bouwmeester and Karssen, 1992), so that release of dormancy could not have caused the delay of germination that occurred at 20, 25 and 30°C. Dormancy relief that does occur at 10°C and 15°C only involves small percentages of germination (Vleeshouwers, unpublished results). Thus, in the present experiment dormancy release during the germination test is negligible. The second reason is that after a pretreatment of 1 or 2 days at 2°C in 10 mM KNO_3, germination of *P. persicaria* seeds was completely dependent on light (Vleeshouwers, unpublished results). In the experiment, the germination process was started by a single red irradiation, after which germination was completed in the dark. This means that seeds in which dormancy was

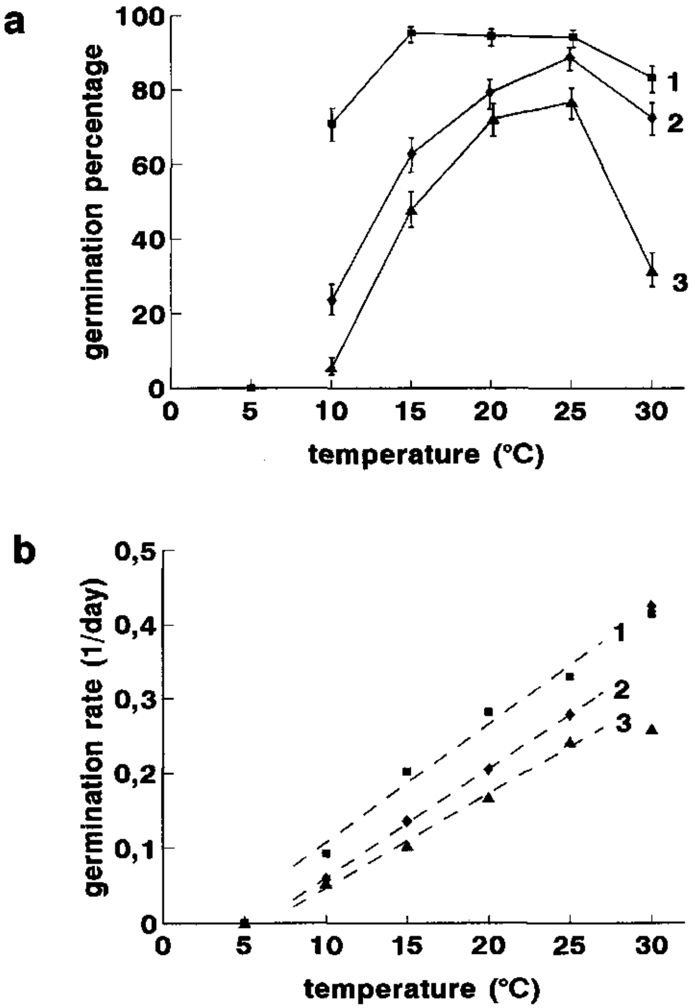

Fig. 3.3 The final germination percentage (a) and rate of germination (b) in *P. persicaria* at three levels of dormancy (level 1 ■ , level 2: ◆ , level 3: ▲) in relation to temperature. Vertical bars indicate 95% confidence intervals. Most 95% confidence intervals of the germination rates were smaller than the symbols and are not indicated. Standard errors never exceeded 2%. Linear regression curves of the germination rate on temperature in the range from 10°C to 25°C are shown.

broken after having been irradiated, missed the necessary trigger to start the germination process. In only a small fraction of seeds breakage of dormancy prior to germination may have played a role in the delay in germination. These are the seeds in which temperatures of 10°C and 15°C released dormancy, and in which the active form of phytochrome formed by irradiation was present for such a long time, that they were still able to germinate in darkness after release of dormancy. The majority of seeds that germinated in the test, however, were already able to germinate before they were irradiated, and did not lose dormancy during their stay in the incubators. The increased time to germination at a higher degree of dormancy must have been due to retardation of the germination process itself.

3.3.2 Competition

Release of dormancy of *P. persicaria* implies that more seeds germinate in a wider temperature range, and that germination of those seeds that germinate proceeds at a faster rate. Both weed seedling density and the timing of weed seedling emergence relative to crop emergence determine crop yield loss resulting from crop-weed interactions (Kropff *et al.*, 1992; Kropff and Van Laar, 1993). In this section, an estimation of the relative importance of the effects of dormancy on germination percentage and germination rate in relation to weed interference with crop growth will be made with help of field data by Bos and Wallinga (1991).

In the field experiment by Bos and Wallinga (1991), sugar-beet was sown on 6 April, and emerged on 24 April. Pre-germinated *P. persicaria* seeds were planted within the crop, and emerged 1, 8, and 13 days after crop emergence. Weed densities were 2.8, 22.2 and 44.4 plants m^{-2}. Sugar-beet yield was measured after harvesting at 2 October, and yield loss was expressed as

$$RYL = 1 - (Y_P/Y_0), \qquad (3.5)$$

where RYL is relative yield loss (-), Y_P (kg m^{-2}) is sugar-beet yield in competition with *P. persicaria*, and Y_0 (kg m^{-2}) is sugar-beet yield in a weed-free situation. Results are depicted in Fig. 3.4.

In order to evaluate the potential effect of the degree of dormancy in *P. persicaria* on yield loss in sugar-beet, and to estimate the effects of the changes in germination percentage and germination rate separately, yield loss in a hypothetical sugar-beet field infested by *P. persicaria* was calculated. The field conditions, and the species characteristics determining crop-weed interaction were assumed to be equal to those in the experiment by Bos and Wallinga (1991). The germination characteristics of *P. persicaria* were assumed to be equal to those in the laboratory experiment (Table 3.1). I compared yield losses caused by *P. persicaria* at the three levels of dormancy present in the germination experiment. The seed lot with the lowest degree of dormancy was used as a reference. In the calculation it was assumed that the germination process of *P. persicaria* was triggered by soil disturbance related to sowing of sugar-beet, on 6 April. Seed bank density of *P. persicaria* in the upper soil layer was assumed to be 50 seeds m^{-2}. Average air temperature in the Netherlands in April is roughly 10°C. At a temperature of 10°C, times to 50% germination for seeds at the dormancy levels 1, 2 and 3 were estimated at

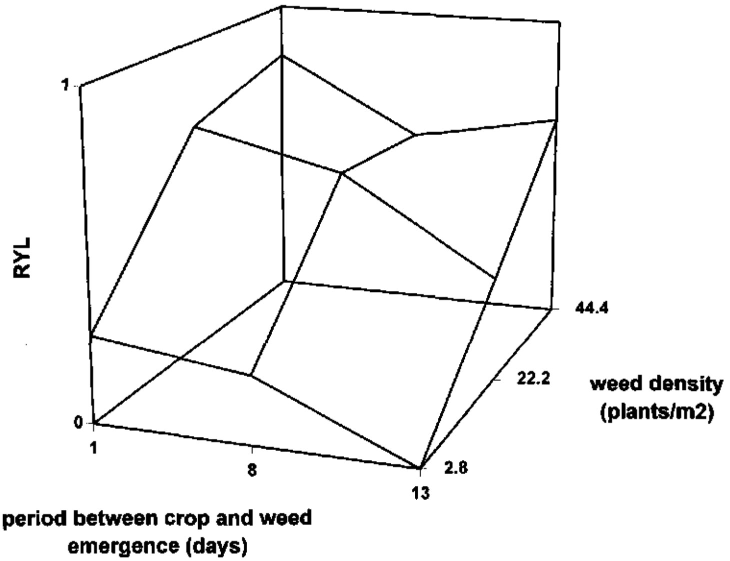

Fig. 3.4 Relative yield loss (*RYL*) in sugar-beet caused by competition with *Polygonum persicaria* in different densities, and emerging at different dates relative to crop emergence. Data from Bos and Wallinga (1991).

11, 17 and 19 days after the start of the germination process (Table 3.1). A pre-emergence growth phase of 6 days (Bos and Wallinga, 1991) implies that the times to 50% emergence for *P. persicaria* seedlings originating from seeds at the dormancy levels 1, 2 and 3 were estimated at 17, 23 and 25 days after the start of the germination process. Thus, calculated *P. persicaria* seedling emergence was 1 day before, and 5 and 7 days after sugar-beet emergence on 24 April. Germination percentages were 71.0, 23.5 and 5.5% (Table 3.1), leading to weed densities of 36, 12 and 2.8 plants m^{-2}, respectively.

By linear interpolation and extrapolation of the relationship shown in Fig. 3.4, curves relating *RYL* in sugar-beet to weed density of *P. persicaria* emerging 1 day before, and 5 and 7 days after sugar-beet were estimated (Fig. 3.5). Reading the *RYL* at weed densities of 36, 12 and 2.8 plants m^{-2}, at the three curves respectively, *RYL* in sugar-beet caused by *P. persicaria* at the three levels of dormancy was estimated at 0.85, 0.44 and 0.22 (Fig. 3.5: 1, 2, 3). If only differences in germination percentage resulting from an increase in dormancy in *P. persicaria* were taken into account, *RYL* was estimated at 0.85, 0.51 and 0.29 (Fig. 3.5: 1, 2', 3'). If only differences in germination rate resulting from an increase in dormancy in *P. persicaria* were taken into account, *RYL* was estimated at 0.85, 0.68 and 0.62 (Fig. 3.5: 1, 2'', 3''). This shows that in the field situation that was evaluated, the effect of dormancy through a change in weed seedling density was stronger than its effect through a change in weed germination rate. However, by neglecting the effect of dormancy on the rate of germination, relative yield loss in sugar-beet caused by *P. persicaria* at the two higher degrees of dormancy was overestimated by a fraction 0.07.

The above calculation applied to a specific case, in which the temperature was 10°C and the seed density in the upper soil layer was 50 seeds m^{-2}. From Figs 3.3 and 3.5 it can be inferred that the effect of weed seed dormancy on relative yield loss of the crop through reductions of germination percentage and germination rate depends on soil temperature and weed seed density. For example, at both higher temperatures and higher weed seed densities, the effect of dormancy through a reduced germination rate becomes relatively more important. The tentative conclusion that can be made at present, therefore, is that when models predicting weed germination and emergence in the field are to be used to make an early estimation of crop yield loss in a range of circumstances, the effect of weed seed dormancy on germination rate should be taken into account.

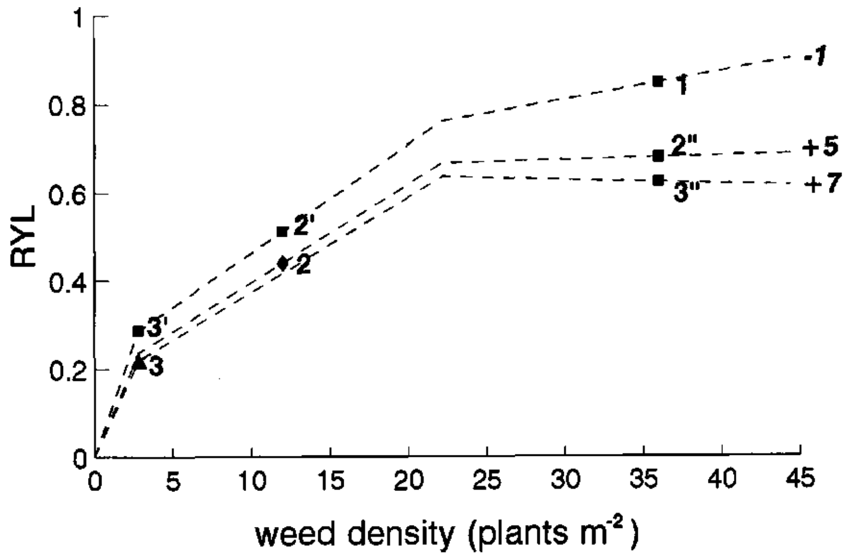

Fig. 3.5 Estimated relationships between weed density of *P. persicaria* and relative yield loss (*RYL*) of sugar-beet, for different periods between crop and weed emergence. Based on data by Bos and Wallinga (1991). For further explanation see text.

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4 MODELLING THE EFFECT OF TEMPERATURE, SOIL PENETRATION RESISTANCE, BURIAL DEPTH AND SEED WEIGHT ON PRE-EMERGENCE GROWTH OF WEEDS

Abstract Emergence of the weed species *Polygonum persicaria* L., *Chenopodium album* L. and *Spergula arvensis* L. was studied experimentally, after burial of pre-germinated seeds at different depths in soil with different penetration resistances at a range of constant temperatures in the laboratory.

Final percentages of emergence tended to be unaffected by temperature in the range 10-25°C, while they were lower at 5°C. Emergence percentages decreased with increasing soil penetration resistance and increasing burial depth. Rates of emergence increased with increasing temperature, and decreased with increasing soil penetration resistance and increasing burial depth.

A physiologically based model was developed to describe the effects of temperature, soil penetration resistance, burial depth and seed weight on pre-emergence growth of seedlings. The model was used to analyse the experimental data in order to obtain insight into the effects of these factors on seedling emergence. The model provided a good description of the trends observed in the experiment.

4.1 Introduction

Knowledge of weed emergence patterns in relation to weather and soil conditions is important for weed management, since the number of seedlings that emerge and the distribution of emergence times affect the degree of interference with subsequent crop growth (Kropff, 1988; Kropff and Van Laar, 1993). Emergence of weeds in the field is the combined result of seed germination in the soil and pre-emergence seedling growth. Many researchers (*e.g.* Doneen and Macgillivray, 1943; Dawson and Bruns, 1962; Wiese and Davis, 1967; Roberts and Potter, 1980; Benech Arnold *et al.*, 1990) have studied the effect of environmental factors on the combined process of seed germination and seedling growth to the soil surface. Several other authors, however, working on the emergence of crops (Parker and Taylor, 1965; Taylor, Parker and Robertson, 1966; Finch-Savage, 1986; Carberry and Campbell, 1989) or weeds (Boydston, 1989; Van der Weide, 1993) have acknowledged that there are physiological differences between germination and underground seedling growth, and that studying these processes separately may lead to a better understanding of the effect of environmental factors on field emergence.

Germination and underground seedling growth are affected by different environmental factors, or in a different way by the same environmental factors. For example, emergence of calabrese, carrot, onion and sugar beet decreases with increasing soil impedance, owing to the failure of seedlings to penetrate the soil, rather than to the failure of seeds to germinate (Hegarty and Royle, 1978). Seed germination in onion has greater sensitivity to moisture stress than subsequent radicle growth (Ross and Hegarty, 1979). Interfacial mechanical stress of 1.7 MPa limits coleoptile elongation of wheat, whereas germination can still proceed up to an interfacial mechanical stress of 3.0 MPa (Collis-George and Yoganathan, 1985). Increased burial depth does not significantly affect germination of *Avena sterilis*, but strongly reduces emergence (Fernandez-Quintanilla, 1988).

There are, on the other hand, environmental factors that affect germination and shoot elongation in the same way. For example, both processes have a similar base temperature in onion (Wheeler and Ellis, 1992) and pearl millet (Carberry and Campbell, 1989), which enables these authors to describe germination and pre-emergence seedling growth as one process, using the thermal time approach.

Besides being an important factor with respect to crop-weed competition, pre-emergence seedling growth may have a large impact on the population dynamics of weeds. Fernandez-Quintanilla (1988) states that in the life-cycle of *Avena sterilis* unsuccessful emergence is a major mortality factor. Pre-emergence mortality results from a cessation of seedling growth before the soil surface has been reached. Thus, for predictions of the demography of weed populations it may be crucial to quantify pre-emergence growth of seedlings.

A mathematical model relating pre-emergence seedling growth to weather data and soil characteristics may be a helpful tool to predict field emergence and pre-emergence mortality. The percentage of seedlings emerging, their mean time of emergence and the spread around this mean time of emergence are the three most important parameters describing the time course of seedling emergence. Empirical relationships between these parameters and environmental factors have been given by several authors. For example, for a description of the emergence of onion seedlings from a fixed burial depth of 1 cm, Wheeler and Ellis (1992) related the level of emergence to temperature and soil water content, and the rate of emergence to temperature. Blacklow (1973) presented a dynamic model simulating the influence of temperature on shoot elongation of maize. Hegarty and Royle (1978) described the percentage emergence of four crop species as a function of soil moisture and soil compaction. For *Galium aparine*, Van der Weide (1993) reported that temperature and burial depth are the most important factors determining emergence rate, and soil penetration resistance and burial depth are the most important factors determining the percentage of emergence. She used a regression model to relate the emergence percentage of *Galium aparine* to soil penetration resistance and burial depth. Weaver *et al.* (1988) used a cumulative distribution curve to describe the time of emergence of tomato and four weed species, and attempted to relate the parameters in the curve to temperature and soil moisture. However, the relationships between temperature, soil moisture and the parameters in the model, which they found in their experiments, were too complex to express the model parameters as a function of temperature and soil moisture.

None of the authors mentioned in the preceding paragraph give a full mathematical description of the time course of seedling emergence. Furthermore, most of the relationships they present between environmental conditions and emergence patterns are purely descriptive, and concern the combined process of germination and pre-emergence growth. In this study, a physiologically based model was developed for the effects of temperature, burial depth, soil penetration resistance and seed weight on pre-emergence growth of weeds. The model comprises both the number of seedlings emerging and the distribution in time of their emergence. It was tested with experimental data on the weed species *Polygonum persicaria* L., *Chenopodium album* L. and *Spergula arvensis* L.

4.2 Materials and methods

4.2.1 Experiments

Pre-germinated seeds of the weed species *P. persicaria*, *C. album* and *S. arvensis* were buried at five different depths in PVC tubes that were filled with soil at three different compactions. The tubes were placed in incubators at five different temperatures, and the emergence of weed seedlings was scored every day.

The seeds used in the experiment were harvested in arable fields in the vicinity of Wageningen in July 1989 (*P. persicaria*), October 1991 (*C. album*) and July 1988 (*S. arvensis*). They were kept in open trays at room temperature for about two months in order to dry, and subsequently stored at 2°C. The experiments were conducted in autumn 1993 (*P. persicaria* and *C. album*) and spring 1995 (*S. arvensis*).

The distribution of seed weights was determined by weighing individual seeds in samples taken from the seed lots used in the experiments. The samples consisted of 150 seeds for *P. persicaria*, and of 100 seeds for *C. album* and *S. arvensis*. Seed polymorphism was present in all three species. The seed lot of *P. persicaria* consisted of two morphs. Biconvex seeds made up 44% of the seed lot, and trigonous seeds 56%. In both categories seed weights were normally distributed, which resulted in a bimodal distribution of seed weights in the *P. persicaria* seed lot as a whole. In *C. album*, all seed coats were smooth and shiny, but their colour varied from light-brown to black. In *S. arvensis*, both papillate and non-papillate seed coat morphs were present. In spite of the seed polymorphism, distributions of seed weight in *C. album* and *S. arvensis* could be characterized by unimodal probability functions. Seed weight in *S. arvensis* was normally distributed, and in *C. album* the logarithm of seed weight was normally distributed. Data are summarized in Table 4.1.

Table 4.1 Mean μ and standard deviation σ of the seed weight (mg) of the seed lots used in the experiments.

Species		μ	σ
Polygonum persicaria	biconvex	2.78	0.65
	trigonous	3.30	0.85
Chenopodium album		0.843	0.181
Spergula arvensis		0.395	0.076

The soil used in the experiment was a loamy sand taken from an arable field, sterilized by 1.8 MRad X-ray radiation. In preliminary experiments this treatment had proven to be 100% effective in killing weed seeds present in the soil (unpublished results).

Seeds of the three weed species were pre-germinated according to procedures developed in preliminary experiments (unpublished results). In this study, pre-germination is defined as protrusion of the rootlet, whereas the cotyledons are still fully covered by the seed coat. *P. persicaria* seeds were imbibed in petri dishes in 10 mM KNO_3, and pretreated for 7 days at 2°C in darkness in order to break dormancy. They were then pre-germinated at a temperature of 20°C in darkness, after a red irradiation of 15 minutes. Seeds of *C. album* were pre-germinated in petri dishes in 10 mM KNO_3 at an alternating temperature of 20/30°C in 12 h light and 12 h darkness, after a red irradiation of 15 minutes. Seeds of *S. arvensis* were pre-germinated at 15°C in 12 h light and 12 h darkness. Under these conditions they were first imbibed in 10 mM KNO_3 for 7 days, subsequently desiccated by opening the petri dishes and, after 7 days, remoistened with water. No red irradiation was given to the *S. arvensis* seeds.

Pre-germinated seeds with a rootlet shorter than 5 mm were selected from the petri dishes and temporarily stored at 2°C. Since *C. album* rootlets of that size kept growing at 2°C, the criterion for use in the experiment was extended to a root length less than 2 cm. Growth of *P. persicaria* and *S. arvensis* at 2°C was negligible, and only seeds with a rootlet shorter than 5 mm were used in the experiment.

The soil in which the pre-germinated seeds were buried had a soil moisture content of 14.1%, corresponding to pF 2. This soil moisture content was considered optimal for both water and oxygen supply of growing roots. Penetration resistance was measured at this moisture content over a range of bulk densities, using a penetrometer with a conical probe of 2 mm diameter. From these measurements the relationship between bulk density and penetration resistance for the soil used was determined. PVC tubes with a diameter of 5.8 cm and a height of 10 cm were filled with moist soil at three different bulk densities (1.285 g cm^{-3}, 1.392 g cm^{-3} and 1.461 g cm^{-3}), resulting in penetration resistances of 0.4 MPa, 0.7 MPa and 1.0 MPa. This range of soil penetration resistances was representative of the arable field from which the soil was taken. The amount of soil that was needed to achieve the desired penetration resistance was put into the tubes in three layers and compressed. Before adding the next layer of soil, the previous layer was superficially raked with a fork, and at the desired depth 20 pre-germinated seeds were placed on this layer. Table 4.2 gives the depths of burial used for the three species. The tubes were filled to 1 cm below the upper edge.

Table 4.2 Burial depths of the pre-germinated seeds.

Species	Burial depths (cm)
Polygonum persicaria	0.5, 1, 2, 4, 8
Chenopodium album	0.5, 1, 2, 3, 4
Spergula arvensis	0.5, 1, 1.5, 2, 3

After being filled, the tubes were placed in incubators at 5 different temperatures (5, 10, 15, 20 and 25°C). All combinations of soil penetration resistance, burial depth and temperature were used with three replicates of each. The three replicates were placed on different shelves in the incubators, with tubes on each shelf being randomly distributed, to give a complete randomized block design.

The emergence of weed seedlings was scored every day. Seedlings were considered to have emerged when both cotyledons were unfolded above the ground. Evaporation was minimized by covering the tubes with perforated plastic caps. The tubes were weighed at regular intervals during the experiment and evaporated water was replenished.

Analysis of variance was used to check whether the three experimental factors had a significant effect on the number of seedlings emerged, and on their mean emergence time. Analysis of seedling numbers was based on a binomial distribution of the number of seedlings emerged. In order to check whether there was a significant block effect, the factor incubator shelf and the interaction between shelf and temperature were included in the analysis.

4.2.2 *The emergence model*

The emergence model is essentially a mathematical description of the emergence pattern of seedlings, the parameters of which are related to temperature, burial depth, soil penetration resistance and seed weight. The emergence pattern is expressed as the time course of cumulative emergence, described with a Gompertz curve,

$$Y = a_1 \exp[-\exp(a_2 - a_3 t)], \tag{4.1}$$

where Y is cumulative emergence (-), t is the time from germination in the soil (day), and a_1 (-), a_2 (-) and a_3 (day^{-1}) are parameters. Germination is defined as the protrusion of the rootlet from the seed. For the seeds in the experiment, t is the time from burial of the pre-germinated seeds. Cussans *et al.* (1996) also use a Gompertz curve to describe the cumulative distribution of the time to emergence. In plant biology, the Gompertz curve has been used to describe the growth of shoots (Lapp and Skoropad, 1976), and the germination of seeds (Tipton, 1984; Brown and Mayer, 1988). The distribution function used by Weaver *et al.* (1988) was not adopted, since it has one parameter more than the Gompertz curve without giving a better description of the emergence data in this study, and a biological interpretation of the parameters was more difficult than with a Gompertz curve.

In this chapter, the cumulative emergence Y will be expressed as the fraction of germinated seeds producing emerged seedlings. In order to be able to attribute biological significance to the parameters in the Gompertz equation, eqn (4.1) is rewritten as

$$Y = Y_{max} \exp\{-\exp[\mathrm{e}/D + \ln(\ln 2) - (\mathrm{e}/D)rt]\}, \tag{4.2}$$

where e=exp(1). The modified Gompertz curve [eqn (4.2)] contains three parameters (Y_{max}, r and D), which are functions of the parameters a_1, a_2 and a_3 in the original Gompertz curve [eqn (4.1)] (see Appendix). The final fraction of emergence is equal to Y_{max} (-). Thus, the fraction of pre-emergence seedling mortality equals $1 - Y_{max}$. In analogy with the definition of germination rate introduced by Hegarty (1973), the emergence rate is defined as the inverse median of the distribution of emergence times, and is rendered by r (day^{-1}). Parameter D (-) is the relative dispersion of emergence times, and indicates the spread of emergence in time, relative to the median of the distribution of emergence times. It is similar to the coefficient of variation of the distribution of emergence times.

The model relates the final fraction of emergence, the emergence rate and the relative dispersion of emergence times to temperature, soil penetration resistance, depth of burial and seed weight. Pre-emergence growth of the seedling shoot to the soil surface is the central process in the model. Some relationships in the model are adapted from literature on the effect of environmental factors on root growth, since relevant quantitative data on underground shoot growth are unavailable.

The final fraction of emergence (Y_{max})

The model considers the growth of the seedling through the soil layer covering the seed. This growth phase is subjected to the limiting condition that the seedling does not receive light to enable photosynthesis. Growth and respiration of the seedling are completely dependent on the carbon reserves stored in the seed. The depth from which the seedling is able to emerge is therefore limited by the amount of seed reserves.

In the model, the shape of the seedling is approximated by a cylinder. It is assumed that the shoot grows straight to the surface. The maximal depth, d_{max} (cm) from which a seedling can emerge is calculated as

$$d_{max} = S\, f_{sh}\, w_{sl}, \tag{4.3}$$

where S is the specific shoot length (cm $\mathrm{g}^{-1}_{\mathrm{dw\ sh}}$)*, f_{sh} is the fraction of the shoot in the total seedling biomass ($\mathrm{g}_{\mathrm{dw\ sh}}\ \mathrm{g}^{-1}_{\mathrm{dw\ sl}}$), and w_{sl} is the dry weight of the seedling ($\mathrm{g}_{\mathrm{dw\ sl}}$) at the time when the seed reserves are completely exhausted. In the model it is assumed that the shoot/root ratio is not affected by burial depth, soil penetration resistance and temperature, and thus f_{sh} is constant.

Seedling weight, w_{sl} depends on seed weight by

$$w_{sl} = c_g\, p\, w_{sd}, \tag{4.4}$$

where w_{sd} is the fresh weight of the intact seed ($\mathrm{g}_{\mathrm{fw\ sd}}$), and c_g ($\mathrm{g}_{\mathrm{dw\ sl}}\ \mathrm{g}^{-1}_{\mathrm{dw\ sr}}$) and p ($\mathrm{g}_{\mathrm{dw\ sr}}\ \mathrm{g}^{-1}_{\mathrm{fw\ sd}}$) are proportionality factors. Growth respiration is modelled as a conversion factor c_g from seed reserves into structural plant material. Factor p represents the fraction of the fresh seed weight consisting in dry matter seed reserves. It is dependent on the water content of the seed and the fraction of the seed weight made up by the seed coat, and is assumed to be constant.

Maintenance respiration of the seedling during pre-emergence growth was calculated by assuming a maintenance coefficient of 0.015 g g^{-1} day^{-1} at 25°C, a Q_{10} of 2, and a

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**Abbreviations*: dw: dry weight; fw: fresh weight; sd: seed; sh: shoot; sl: seedling; sr: seed reserves conversion factor for growth respiration of 0.7 g g^{-1} (Penning de Vries and Van Laar, 1982). Using these values, the average total maintenance respiration during the emergence process was estimated at 1.4% of the initial seed reserves. During pre-emergence growth a maximum of 5.5% of the initial seed reserves were consumed by maintenance respiration. These percentages were so low that, as yet, maintenance respiration is neglected in the model.

Osborne (1977) reported that when pea shoots meet an impedance, ethylene production in the bud is increased, and, as a result, cell elongation is inhibited and radial growth is promoted. Eavis (1969) studied the penetration of pea seedling roots in soil at different mechanical impedances, measured with help of a penetrometer and found that the fresh weight per unit length of the root is approximately proportional to mechanical impedance. In the model it is assumed that this relationship also holds for the dry weight of the shoot. Thus, the inverse specific shoot length ($g_{\mathrm{dw\ sh}}$ cm^{-1}) is proportional to penetration resistance

$$1/S = k_1 + k_2\,Q, \tag{4.5}$$

where Q is penetration resistance (MPa), and k_1 ($g_{\mathrm{dw\ sh}}$ cm^{-1}) and k_2 ($g_{\mathrm{dw\ sh}}$ cm^{-1} MPa^{-1}) are empirically derived parameters.

If eqns (4.3), (4.4) and (4.5) are combined, and parameters k_1 and k_2 are divided by the constant fraction $f_{sh}\ c_g\ p$ ($g_{\mathrm{dw\ sh}}$ $g^{-1}_{\mathrm{fw\ sd}}$) and renamed b_1 ($g_{\mathrm{fw\ sd}}$ cm^{-1}) and b_2 ($g_{\mathrm{fw\ sd}}$ cm^{-1} MPa^{-1}), d_{max} can be expressed as

$$d_{max} = \frac{1}{b_1 + b_2 Q}\, w_{sd}, \tag{4.6}$$

Equation (4.6) is in accordance with data on *Melilotus officinalis* by Haskins and Gorz (1975), who reported that the depth from which seedlings emerge increases with increasing seed mass. Parameters b_1 and b_2 describe the conversion of seed fresh weight into shoot length, in relation to soil penetration resistance. The factor ($b_1 + b_2 Q$) is the amount of seed fresh matter that is invested per cm shoot, when the seed develops into a seedling. The investment includes all seed fresh matter that is not converted into shoot material, like seed coat, growth respiration losses and root material.

Equation (4.6) can also be interpreted such that a minimum seed weight $w_{sd,min}$ ($g_{\mathrm{fw\ sd}}$) is needed to obtain emergence from a fixed burial depth d (cm),

$$w_{sd,min} = (b_1 + b_2\,Q)\,d. \tag{4.7}$$

If $\phi(w)$ represents the probability distribution of seed weight w in the population, the fraction of seeds emerging from depth d, at a soil penetration resistance Q can be expressed as

$$Y_{max} = \int_{(b_1+b_2Q)d}^{\infty} \phi(w)\,\mathrm{d}w. \tag{4.8a}$$

Preliminary analysis revealed that in all three species, emergence fractions were not affected by a temperature range of 10-25°C, whereas emergence at 5°C was significantly lower. In the model it is assumed that at 5°C conversion of seed fresh weight to shoot length is less efficient than that at temperatures from 10 to 25°C. Consequently, at 5°C,

$$Y_{max} = \int_{(b_1+b_2Q)d/C}^{\infty} \phi(w)\,\mathrm{d}w, \tag{4.8b}$$

where the conversion efficiency of seed fresh weight into shoot length at 5°C relative to that in the range 10-25°C is denoted C (-).

The rate of emergence (*r*)

In the model, the rate of emergence (day^{-1}) is defined as the inverse of the time needed by the median seedling to reach the surface and unfold its cotyledons, after germination of the seed at a certain depth in the soil. The shoot elongation rate is defined as the rate at which the shoot tip approaches the soil surface (cm day^{-1}).

Blacklow (1972) showed that in a temperature range from 10 to 30°C, radicle and shoot elongation of maize increase, approximately linearly, with temperature. Garcia-Huidobro *et al.* (1982) reported that a linear relationship also holds for other developmental processes, such as germination, the appearance of a series of leaves, and flowering. Greacen and Oh (1972) and Dexter (1987) found that the rate of root elongation decreases linearly with increasing soil mechanical resistance.

In the model it is assumed that the shoot elongation rate is independent of burial depth, and linearly dependent on temperature and penetration resistance. If d is the depth of burial (cm), the time needed for the growth of the shoot to the surface t_1 (day) equals

$$t_1 = d \,/\, (c_1 + c_2\,T - c_3\,Q), \tag{4.9}$$

where T is the temperature (°C), Q is the penetration resistance of the soil (MPa), and c_1 (cm day^{-1}), c_2 (cm day^{-1} °C^{-1}) and c_3 (cm day^{-1} MPa^{-1}) are parameters. Implicitly, it is assumed in eqn (4.9) that there is no interaction between temperature and penetration resistance in their effect on the elongation rate of the shoot.

When a seed germinates, the rootlet protrudes earlier from the seed than the shoot. This means that some time proceeds between germination and the start of shoot elongation. When the shoot has reached the soil surface, it also takes some time before the cotyledons are unfolded, and the seedling is considered to have emerged. The rate of initialization of shoot elongation after germination, and the rate of unfolding of the cotyledons are supposed to be linearly related to temperature, both in the same way, and to be independent of depth of burial and soil penetration resistance. The total time needed to initialize shoot elongation and to unfold the cotyledons t_2 (day) equals

$$t_2 = 1/(c_4 + c_5 T), \tag{4.10}$$

where c_4 (day^{-1}) and c_5 (day^{-1} °C^{-1}) are parameters.

Summarizing, the emergence rate r equals

$$r = \frac{1}{t_1 + t_2} = \frac{1}{\dfrac{d}{c_1 + c_2 T - c_3 Q} + \dfrac{1}{c_4 + c_5 T}}, \tag{4.11}$$

where c_1, c_2, c_3, c_4 and c_5 relate to the seed having the median shoot elongation rate in the population.

The relative dispersion of emergence times (D)

Since no explicit data on the variation in pre-emergence growth between individual seedlings are available, in the model the *relative* dispersion of emergence times is assumed to be constant. This means that the dispersion of emergence times increases when emergence rate decreases. A constant relative dispersion implies that parameter D is assumed to be independent of temperature, soil penetration resistance, burial depth and seed weight.

Summarizing, in the model, Y_{max} is a function of T, Q, d and $\phi(w)$ [eqns (4.8a) and (4.8b)], r is a function of T, Q and d [eqn (4.11)] and D is independent of T, Q, d and $\phi(w)$.

4.2.3 Parameterization of the model

For each of the three species, eqns (4.8a), (4.8b) and (4.11) were fitted to the observed emergence fractions and the calculated median emergence times respectively (SAS, procedure NLIN), and parameters b_1, b_2, C, c_1, c_2, c_3, c_4 and c_5 estimated. Parameter D in eqn (4.2) was calculated by averaging relative dispersions of emergence times over all separate curves.

4.3 Results

4.3.1 Experiments

Emergence of *P. persicaria* from depths of 4 cm and 8 cm, of *C. album* from depths of 3 cm and 4 cm, and of *S. arvensis* from a depth of 3 cm was negligible (2, 0, 0, 4 and 1 seedlings respectively, out of the 900 buried at each of these depths), and was therefore not included in the analysis.

In all three species the percentage emergence was significantly affected by temperature, soil penetration resistance and burial depth ($P<0.01$). Soil penetration resistance and burial depth showed a significant interaction ($P<0.01$). Besides, temperature and burial

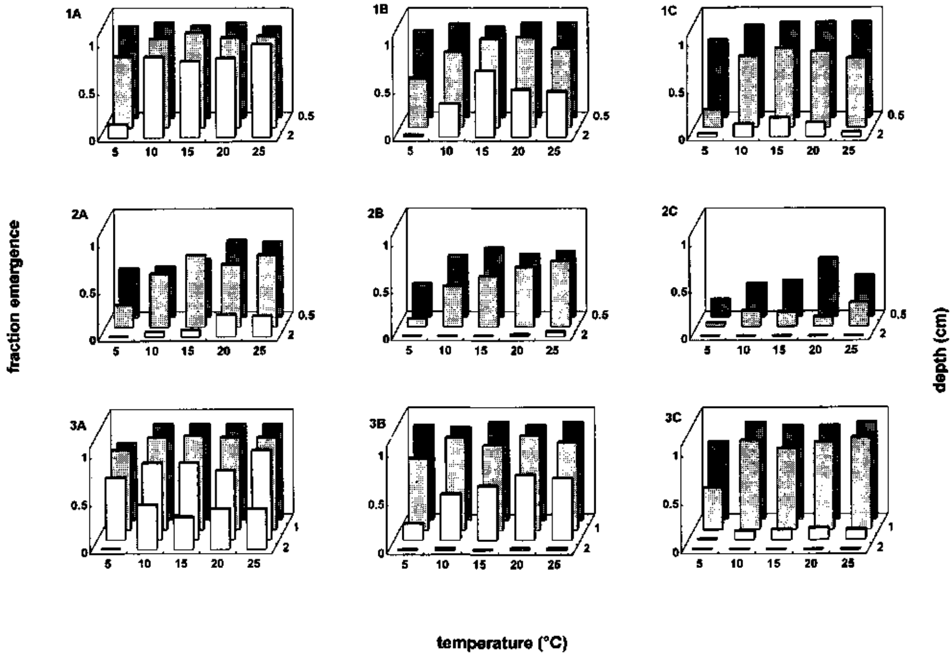

Fig. 4.1 Observed emergence fractions at different temperatures following planting of pregerminated seeds at different depths. Species: 1, *P. persicaria*; 2, *C. album*; 3, *S. arvensis*. Soil penetration resistances: A, 0.4 MPa; B, 0.7 MPa; C, 1.0 MPa.

depth showed a significant interaction in their effect on the percentage emergence of *S. arvensis* (P=0.036).

In all three species, temperature, soil penetration resistance and burial depth had a significant effect on the mean time of emergence (P<0.01). The species differed in the significance of interaction factors. None of the interaction factors significantly affected the mean emergence time in *C. album*. In *P. persicaria* there was a significant interaction between soil penetration resistance and depth of burial and a significant three way interaction between temperature, soil penetration resistance and depth of burial (P<0.01). In *S. arvensis* all interactions were significant (P<0.05). In none of the three species were there significant differences in the final percentage of emergence and the mean time of emergence between the three shelves of the incubator (P>0.10).

Replicates were pooled, and Gompertz curves [eqn (4.2)] were fitted through the cumulative emergence curves. In Figs 4.1, 4.2 and 4.3 the observed fraction emergence, emergence rate and relative dispersion of emergence times are depicted for the three species at all temperatures, burial depths and soil penetration resistances used in the

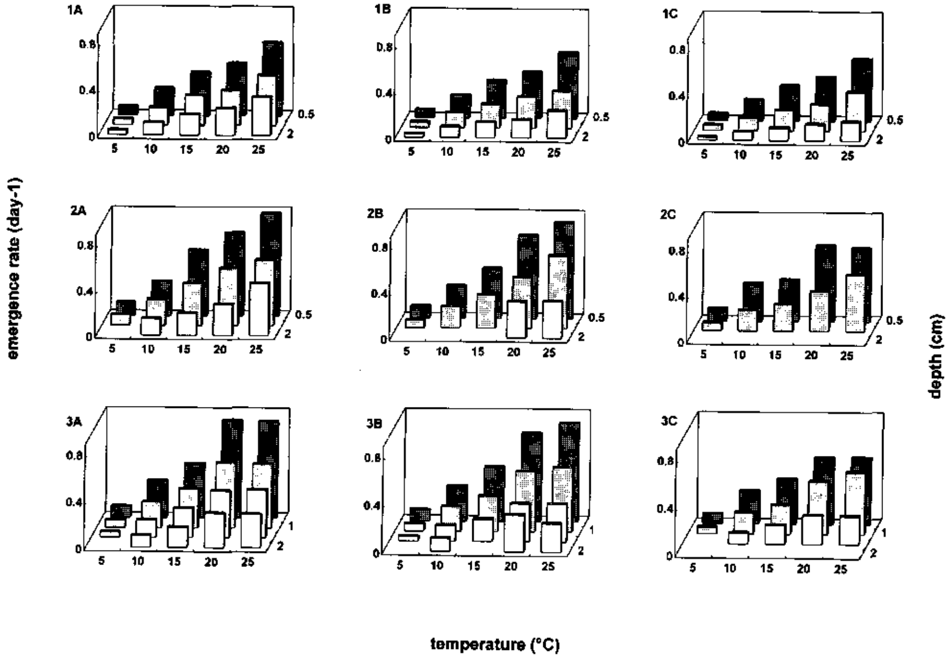

Fig. 4.2 Emergence rates, calculated from the observations, at different temperatures following planting of pre-germinated seeds at different depths. Species: 1, *P. persicaria*; 2, *C. album*; 3, *S. arvensis*. Soil penetration resistances: A, 0.4 MPa; B, 0.7 MPa; C, 1.0 MPa.

experiment. The overall trend in the fraction emergence in relation to temperature was a reduction at 5°C compared to a constant level from 10-25°C (Fig. 4.1). Fraction emergence tended to decrease with increasing burial depth and increasing soil penetration resistance (Fig. 4.1). The rate of emergence tended to increase with increasing temperature, decreasing burial depth and decreasing soil penetration resistance (Fig. 4.2). The relative dispersion of emergence times displayed quite some variation, but there were no consistent trends (Fig. 4.3).

4.3.2 Parameterization of the model

The final fraction of emergence

Using the distribution of seed weights summarized in Table 4.1, eqns (4.8a) and (4.8b) were fitted to the fraction of emergence of the three species. Accounting for the fact that even under optimal conditions, emergence of *C. album* did not exceed 75%, it was

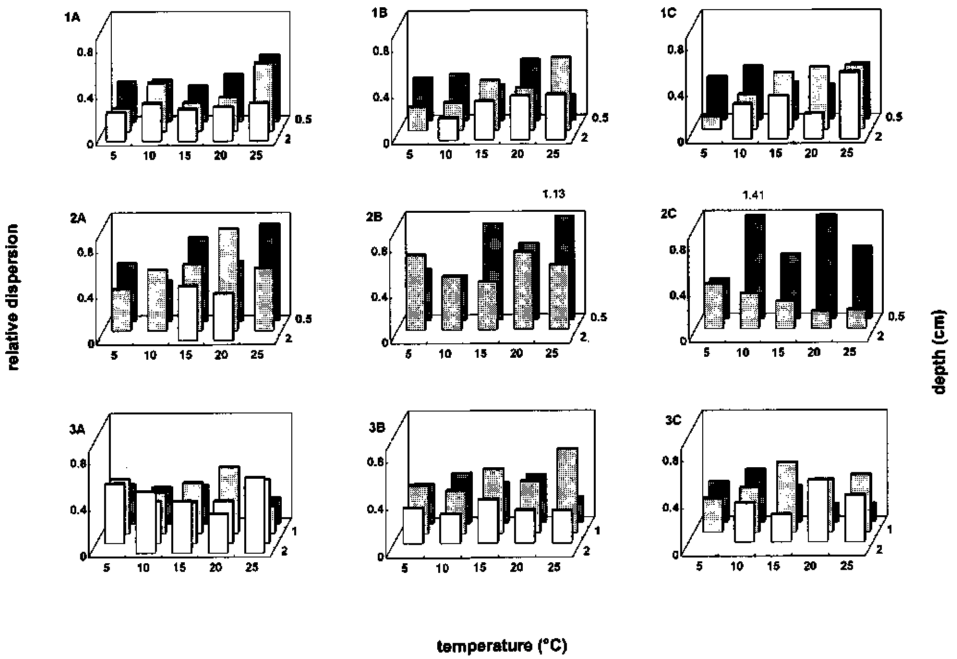

Fig. 4.3 Relative dispersions of emergence times, calculated from the observations, at different temperatures following planting of pre-germinated seeds at different depths. Species: 1, *P. persicaria*; 2, *C. album*; 3, *S. arvensis*. Soil penetration resistances: A, 0.4 MPa; B, 0.7 MPa; C, 1.0 MPa.

assumed that there was a background mortality of *C. album* seedlings of 25%, independent of temperature, soil moisture and burial depth. In Fig. 4.4 the fitted emergence fractions of the three species are plotted against those observed in the temperature range from 5-25°C. The model shows a good fit (*P. persicaria*: $R^2=0.94$; *C. album*: $R^2=0.79$; *S. arvensis*: $R^2=0.97$). The three strongest outliers, in the top centre of the graph, represent emergence of *C. album* when buried at a depth of 0.5 cm at a penetration resistance of 1.0 MPa, which is overestimated by the model. Estimates of parameters b_1, b_2 and C are given in Table 4.3.

Parameter b_1 is the extrapolated value of the amount of seed fresh weight that is invested per cm shoot length at a soil penetration resistance of 0 MPa. Parameter b_2 is the proportionality factor between soil penetration resistance and the amount of seed fresh weight invested per cm shoot length. Both b_1 and b_2 increase in the order *S. arvensis* < *C. album* < *P. persicaria*, and thus with increasing seed weight.

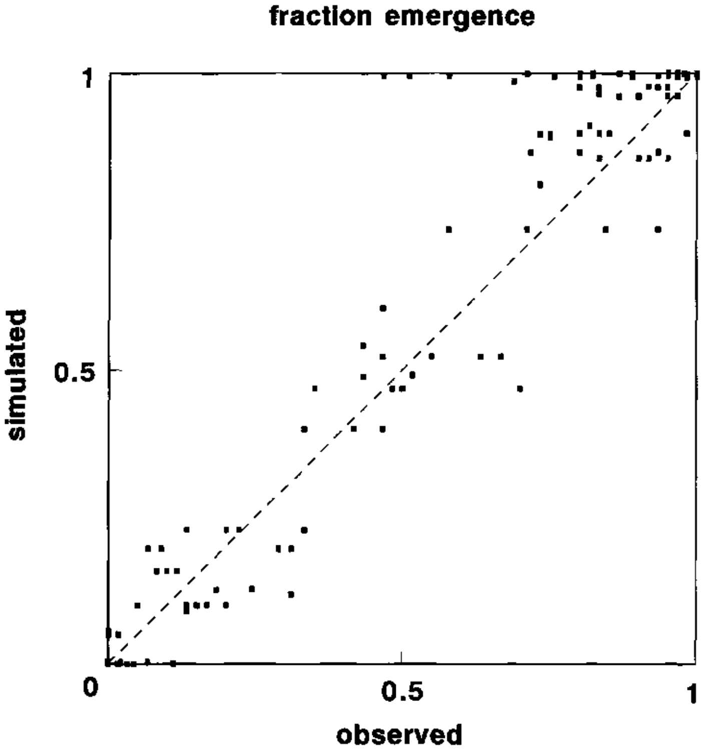

Fig. 4.4 The simulated versus the observed fraction of emergence for all experimental conditions and species combined. *C. album* data are corrected for background seedling mortality.

The rate of emergence

Equation (4.11) was fitted to the emergence rates for all three species. A temperature of 25°C appeared to be supra-optimal for the rate of emergence of *S. arvensis*, so that emergence rates at 25°C were overestimated by the model. Therefore, in the analysis of the data for *S. arvensis* the emergence rate at 25°C was assumed to be equal to the emergence rate at 20°C. With this adjustment for *S. arvensis*, the model gave a good fit for the data on the rate of emergence of the three species (*P. persicaria*: $R^2=0.99$; *C. album*: $R^2=0.96$; *S. arvensis*: $R^2=0.96$). In Fig. 4.5, the fitted emergence rates of the three species are plotted against the ones calculated from the observations. Estimates of parameters c_1 to c_5 are given in Table 4.3.

The relationship between seed weight and the effect of soil penetration resistance,

Table 4.3 Estimates of the parameters in the emergence model, with 95% confidence intervals in parentheses.

Parameter (dimension)		*Polygonum persicaria*		*Chenopodium album*		*Spergula arvensis*	
D	(-)	0.36	(0.19, 0.59)	0.56	(0.15, 1.41)	0.37	(0.15, 0.64)
b_1	($g_{fw\ sd}$ cm^{-1})	0.00041	(0.00019, 0.00064)	0.00017	(0.00005, 0.00029)	0.00013	(0.00012, 0.00014)
b_2	($g_{fw\ sd}$ cm^{-1} MPa^{-1})	0.00162	(0.00130, 0.00194)	0.00080	(0.00060, 0.00099)	0.00018	(0.00017, 0.00020)
C	(-)	0.51	(0.46, 0.56)	0.46	(0.40, 0.56)	0.80	(0.76, 0.83)
c_1	(cm day^{-1})	0.262	(0.148, 0.377)	0.397	(0.132, 0.663)	0.193	(0.028, 0.359)
c_2	(cm day^{-1} $°C^{-1}$)	0.020	(0.016, 0.024)	0.030	(0.021, 0.040)	0.034	(0.027, 0.041)
c_3	(cm day^{-1} MPa^{-1})	0.307	(0.208, 0.405)	0.459	(0.243, 0.675)	0.345	(0.200, 0.489)
c_4	(day^{-1})	−0.181	(−0.247, −0.115)	−0.247	(−0.389, −0.105)	−0.431	(−0.610, −0.252)
c_5	(day^{-1} $°C^{-1}$)	0.053	(0.044, 0.061)	0.075	(0.057, 0.092)	0.104	(0.077, 0.132)

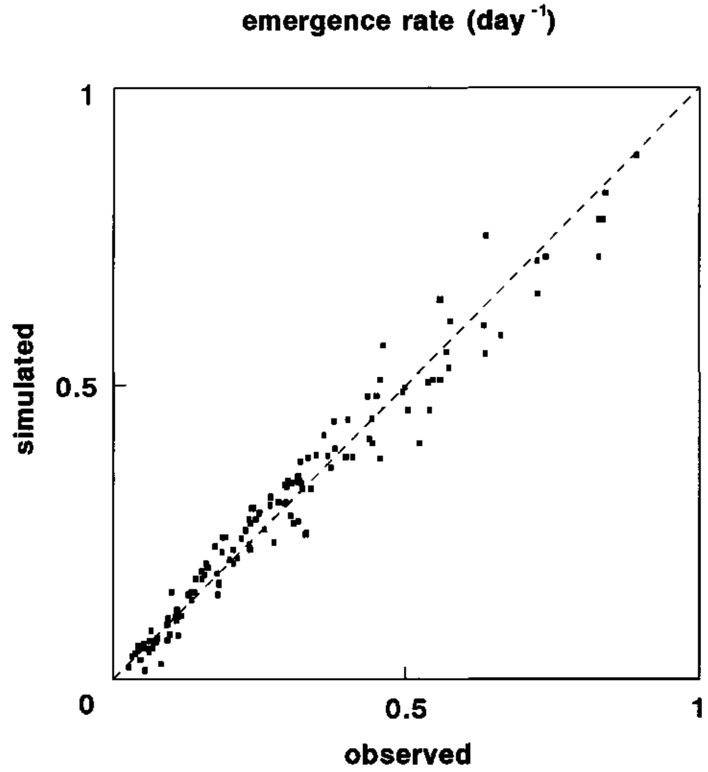

Fig. 4.5 The simulated versus the observed rate of emergence for all experimental conditions and species combined.

which was observed for the fraction of emergence, did not occur with respect to the rate of emergence (parameter c_3). An increase in soil penetration resistance delayed emergence of *C. album* more than emergence of *S. arvensis* and *P. persicaria*. The effect of temperature on the rate of emergence (defined by parameter c_2, affecting t_1, and parameter c_5, affecting t_2) increases in the order *P. persicaria* < *C. album* < *S. arvensis*, and thus with decreasing seed weight.

The relative dispersion of emergence times

The assumption that relative dispersion of emergence times is constant for a species was affirmed in that no consistent trends with temperature, burial depth or soil penetration resistance were present. However, values were rather variable and ranged from 0.11 to

0.62 in *P. persicaria*, from 0.15 to 1.41 in *C. album*, and from 0.10 to 0.71 in *S. arvensis*. Estimates of parameter *D* are given in Table 4.3. The relative dispersion of emergence times was approximately equal in *P. persicaria* and *S. arvensis*, but had a higher value in *C. album*.

4.4 Discussion

For weed control purposes, the most important characteristics describing emergence patterns of weeds are the number of seedlings emerging and their time of emergence. Pre-emergence seedling growth plays an important role in determining emergence patterns. For *P. persicaria*, *C. album* and *S. arvensis*, pre-emergence growth could be related to temperature, soil penetration resistance, depth of burial and seed weight by a mathematical model. The stable nature of the relationships over species suggests that in these dicotyledonous species pre-emergence growth is ruled by the same physiological principles, and species only differ in the parameter values describing these relationships. In this chapter a simple description of the model is presented for pre-emergence growth from a fixed depth at constant temperatures in the range 5-25°C through homogeneous soil. For predictions of field emergence this model must be adapted, in order to simulate emergence of weed seeds with a known vertical distribution in the soil, at temperatures changing in time, and in soils with heterogeneous compaction.

4.4.1 Further improvement of the model

The model presented in this chapter should be regarded as a first step towards an understanding of underground seedling growth. Its final aim is to predict how the environment affects pre-emergence growth. It is based on physiological principles to a larger extent than other emergence models in the literature (Hegarty and Royle, 1978; Wheeler and Ellis, 1992; Van der Weide, 1993). The model comprises, however, a number of empirical relationships, the parameters of which can only be estimated by fitting the model to experimental observations. The description of experimental data was good. Therefore, it may be used as a tool to direct future experimental work aimed at an understanding of processes.

As yet, the model has been parameterized with the use of experimental observations on seedling emergence at the population level. The result of pre-emergence growth, *i.e.* emergence, rather than the process of pre-emergence growth has been observed in these experiments. The scope for further improvement of the model lies in an evaluation of the process of pre-emergence growth at an individual plant level. This can be done by assessing how characteristics of individual seedlings, such as shoot elongation rate, specific shoot length, growth respiration and shoot/root ratio respond to temperature, burial depth, soil penetration resistance and seed weight. In this respect, time series of underground seedling development, obtained by washing out seedlings prior to emergence will be indispensable. For example, the empirical relationship given by eqn (4.6) shows that the amount of seed fresh weight invested per cm emergence depth increases with increasing soil penetration resistance. In the model the effect of increasing soil penetration resistance on emergence depth is explained by a decrease in specific shoot length [eqn (4.5)]. Alternatively, the effect may be explained by a decreased shoot/root ratio or a more tortuous growth of the seedling shoot in response to an increased soil penetration resistance. The hypotheses can be tested by studying processes in the soil.

The model parameter on which least physiological or empirical knowledge exists, is the spread of emergence in time. Dispersion of emergence times results from variation in underground shoot elongation rates between individual seedlings. No literature data were available on the relationship between the environment and variation in underground shoot elongation rates. In the model, it was assumed that the variation in emergence times was proportional to the median of the distribution of emergence times. Parameter D, the relative dispersion of emergence times, was assumed to be constant. Observed values of D, however, were rather variable. Research into processes in soil at the level of individual seedlings is needed to identify the environmental factors and seedling characteristics that affect variation in shoot elongation rates. For practical application of the model, however, the assumption of a constant relative dispersion of emergence times is reasonable, since the time course of cumulative emergence is rather insensitive to differences in parameter D within the range observed.

An important factor which has yet to be incorporated in the model is soil moisture. A decrease in soil moisture content results in an increase of both penetration resistance and matric potential, and both factors can decrease the rate of root elongation (Bengough and Mullins, 1990). Authors differ in their opinions on whether increased penetration resistance should be considered a moisture effect. For example, Finch-Savage and Phelps (1993), who report an overriding effect of water stress on the timing of onion seedling emergence in the field, and a less significant effect of soil impedance, included increased penetration resistance in the effect of water stress. This is also done by Hegarty and Royle (1978), who derived a relationship to quantify the effect of penetration resistance and decreased soil moisture content on the fraction seedling emergence. In contrast, Van der Weide (1993) distinguished between the two effects of increasing moisture stress, and reported that an increased matric potential reduced the fraction and rate of emergence of *Galium aparine* stronger at increased soil resistances. Dexter (1987) presented a relationship to describe the effect of mechanical stress and external water potential on root elongation rate separately. For a better understanding of the process of emergence in relation to a decreased soil moisture content, it may be preferable to separate the increased penetration resistance from the actual moisture stress.

4.4.2 Characterization of the species by the model

The model enables a calculation of the maximum depth of emergence for each species [eqn (4.6)] in relation to soil penetration resistance. In all three species, the maximum depth from which a seedling can emerge is hardly affected by temperature, but strongly dependent on soil penetration resistance. At a penetration resistance of 0.4 MPa, and at temperatures from 10-25°C, the burial depths at which the fraction of emergence is reduced to 0.01, are 4.9 cm for *P. persicaria*, 2.7 cm for *C. album* and *S. arvensis*. At a soil penetration resistance of 1.0 MPa these depths are 2.4 cm, 1.4 cm and 1.8 cm, respectively. From this example it can be seen that maximum emergence depth in *S. arvensis* is less sensitive to an increase in soil penetration resistance than in the other two species.

The time of emergence of the earliest seedlings in a seedling flush is important with respect to the competitive strength of the weed. Weeds that emerge simultaneously with the crop or shortly after the crop cause severe yield losses even at very low densities (Kropff and Van Laar, 1993). The time of emergence of the first weed seedlings depends on both the median emergence time (t_{50}) and the relative dispersion of emergence times. Of the three species in this study *C. album* has the lowest t_{50} (the highest emergence rate) and also the highest relative dispersion of emergence times, which implies that when seeds germinate simultaneously, the earliest seedlings of *C. album* appear before those of *P. persicaria* and *S. arvensis*. With help of the model it can be calculated that, for example, at a temperature of 10°C, a soil penetration resistance of 0.4 MPa and a burial depth of 1 cm, the time of emergence for the earliest 5% of the seedlings ($t_{0.05}$) is 4.8 day for *P. persicaria*, 2.8 day for *C. album* and 3.3 day for *S. arvensis*. This illustrates that in terms of species characteristics concerning pre-emergence growth, *C. album* is more competitive than *S. arvensis* and *P. persicaria*.

The model makes it possible to quantify unsuccessful emergence after soil cultivation in the field. The following calculations are done for a soil at field capacity, at temperatures in the range of 10-25°C. In the three species used in the study, the percentage germination after soil cultivation decreased with increasing burial depth (Vleeshouwers, data not published). If it is assumed that the percentage of seeds germinating after soil cultivation linearly decreases with burial depth to 0% at 15 cm, and soil penetration resistance after soil cultivation is 0.2 MPa, which is a fair estimate for loamy sand (Van der Weide, pers. comm.), the estimated fraction of unsuccessful emergence amounts to 0.50 for *P. persicaria*, 0.70 for *C. album*, and 0.72 for *S. arvensis*. From data on *Avena sterilis* by Fernandez-Quintanilla (1988) a fraction of 0.55 can be calculated. Again, these figures stress the importance of the emergence phase in the life-cycle of arable weeds.

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Appendix

Cumulative emergence Y is described with the Gompertz equation,

$$Y = a_1 \exp(-\exp(a_2 - a_3 t)), \tag{4A.1}$$

where t is the time from germination of the seeds in the soil (day), and a_1 (-), a_2 (-) and a_3 (day^{-1}) are (positive) parameters.

The maximum level of emergence, Y_{max} is the level reached when t approaches infinity. From eqn (4A.1) it can be calculated that

$$Y_{max} = \lim_{t \to \infty} Y = a_1. \tag{4A.2}$$

The median of the distribution of emergence times t_{50} (day) is the time when the emergence reaches 50% of its maximum level,

$$Y = a_1 \exp[-\exp(a_2 - a_3 t_{50})] = 0.5\, a_1. \tag{4A.3}$$

From this equation it can derived that

$$t_{50} = [a_2 - \ln(\ln 2)]/a_3. \tag{4A.4}$$

The emergence rate r (day^{-1}) is defined as $1/t_{50}$ and equals

$$r = a_3/[a_2 - \ln(\ln 2)]. \qquad (4A.5)$$

The rate of increase in the number of emerged plants equals

$$\mathrm{d}Y/\mathrm{d}t = a_1 a_3 \exp(a_2 - a_3 t) \exp[-\exp(a_2 - a_3 t)]. \qquad (4A.6)$$

The second derivative of the cumulative emergence curve equals

$$\mathrm{d}^2Y/\mathrm{d}t^2 = \{1 - \exp(a_2 - a_3 t)\} \{-a_1 a_3^2 \exp[-\exp(a_2 - a_3 t)] \exp(a_2 - a_3 t)\}. \qquad (4A.7)$$

The mode of the distribution of emergence times is the time when $\mathrm{d}Y/\mathrm{d}t$ reaches its maximum $(\mathrm{d}Y/\mathrm{d}t)_{max}$. This is the inflection point in the curve, at which $\mathrm{d}^2Y/\mathrm{d}t^2=0$. From eqn (4A.7) it can be derived that $\mathrm{d}^2Y/\mathrm{d}t^2=0$ when $t=a_2/a_3$. By filling in $t=a_2/a_3$ in eqn (4A.6) it can be calculated that

$$(\mathrm{d}Y/\mathrm{d}t)_{max} = a_1 a_3 \exp(-1) = a_1 a_3/\mathrm{e}. \qquad (4A.8)$$

The steeper the curve at the inflection point, the smaller the dispersion of emergence times. The steepness of the curve, relative to the maximum level of emergence reached, is given by $(\mathrm{d}Y/\mathrm{d}t)_{max}/a_1$. In this chapter the dispersion of emergence times is defined as $a_1/(\mathrm{d}Y/\mathrm{d}t)_{max}$ (day). The *relative* dispersion of emergence times D (-) is calculated as

$$D = \frac{a_1/(\mathrm{d}Y/\mathrm{d}t)_{max}}{t_{50}} = \frac{a_1/(a_1 a_3/\mathrm{e})}{(a_2 - \ln(\ln 2))/a_3} = \frac{\mathrm{e}}{a_2 - \ln(\ln 2)}, \qquad (4A.9)$$

where $\mathrm{e}=\exp(1)$. The relative dispersion of emergence times bears resemblance to the coefficient of variation of the distribution of emergence times.

Combining eqn (4A.1) with eqns (4A.2), (4A.5) and (4A.9) leads to the representation of the Gompertz curve used in the emergence model [eqn(4.2)],

$$Y = Y_{max} \exp\{-\exp[\mathrm{e}/D + \ln(\ln 2) - (\mathrm{e}/D)rt]\}. \qquad (4A.10)$$

5 FIELD EMERGENCE PATTERNS IN THREE ARABLE WEED SPECIES
I. THE EFFECT OF WEATHER, SOIL AND CULTIVATION DATE

Abstract Emergence of *Polygonum persicaria*, *Chenopodium album* and *Spergula arvensis* was monitored in the field. Field plots were sterilized and seeds of the three species were mixed through the soil in winter. Separate field plots were cultivated once only during spring, and seedling emergence was monitored regularly. Seedling emergence was also monitored in undisturbed plots. Simultaneously, seasonal changes in seed dormancy of the buried weed seeds were assessed by exhuming seed lots buried in envelopes, and testing their germination in the laboratory. Seed survival at the end of the period of field observations was assessed by sampling the soil in the plots.

The date of soil cultivation had a strong effect on seedling numbers in the spring emergence flushes, and on the timing of these flushes. A high correlation existed between mean seed-bed temperature in the week after soil cultivation and the number of seedlings in the spring emergence flush. The onset of the spring flushes could be described well by a temperature sum. Summer emergence flushes in *C. album* and *S. arvensis* resulted from remoistening of the seed-bed by rainfall after periods of drought. Like seedling emergence, seed survival was affected by the date of soil cultivation. The correlation between emergence and depletion of the seed bank, however, is slight.

5.1 Introduction

The seasonal distribution of weed seedling emergence under field conditions in temperate regions has been studied intensively (*e.g.* Waldron, 1904; Chepil 1946*a*,*b*; Chancellor, 1964; Roberts, 1964; Roberts and Feast, 1970; Stoller and Wax, 1973*a*; Lawson *et al.*, 1974; Roberts and Potter, 1980; Roberts, 1984; Ogg and Dawson, 1984; Van den Brand, 1986; Longchamp *et al.*, 1988; Håkansson, 1992; Van der Weide, 1993; Popay *et al.*, 1995). Cultivation measures and weather conditions affect emergence patterns of weeds, which differ in seedling density and in the distribution of emergence over time. Insight in the effects of soil cultivation and weather conditions on weed emergence patterns is important for weed management, since weed density and the timing of weed emergence strongly affect the degree of interference with crop growth (Roberts and Potter, 1980; Kropff and Van Laar, 1993).

All authors mentioned in the preceding paragraph stress the importance of species characteristics in the seasonal distribution of field emergence. This can primarily be attributed to differences between species in the annual cycling of dormancy (Karssen, 1982). Superimposed on this species-specific seasonal variation in germinability, there is an effect of temperature, mainly influencing the onset of field germination (Roberts, 1964; Stoller and Wax, 1973*a*; Roberts and Potter, 1980; Ogg and Dawson, 1984), and an effect of rainfall, mainly influencing the timing of subsequent germination flushes (Roberts, 1964; Stoller and Wax, 1973*a*; Roberts and Potter, 1980; Roberts, 1984). There is a close correspondence between the peaks of emergence on disturbed and undisturbed plots. However, a single soil cultivation enhances seedling density (Lawson *et al.*, 1974; Roberts and Potter, 1980; Roberts, 1984; Van den Brand, 1986), while repeated soil cultivations either increase or decrease the number of seedlings emerging, dependent on the species present (Chepil, 1946*a*,*b*; Chancellor, 1964; Ogg and Dawson, 1984). The effect of soil cultivation is mainly due to the stimulation of germination by exposure to daylight (Wesson and Wareing, 1967, Scopel *et al.*, 1994). Distribution of emergence over the year is not influenced by the number of years the seeds have been buried in the soil (Chepil, 1946*a*; Roberts, 1964; Roberts and Feast, 1970). However, in some species emergence from seeds buried in the soil for only one winter was earlier than that from seeds buried for more than one year (Ogg and Dawson, 1984), and in some species ageing in the soil reduced the markedness of the periodicity of emergence (Popay *et al.*, 1995). In natural conditions, weed emergence patterns depend on cropping history and past weed control measures, as these factors determine the species composition of the seed bank and the numbers of seeds in the soil (Lawson *et al.*, 1974). Soil penetration resistance affects the emergence of weeds because of its effect on pre-emergence growth of seedlings (Van der Weide, 1993).

The decrease in seed numbers in the seed bank in relation to emergence was documented by Waldron (1904), Chepil (1946*a,b*), Roberts (1964), Roberts and Feast (1972), Stoller and Wax (1973*a*), Longchamp *et al.* (1988) and Wilson and Lawson (1992). They did not provide data, however, on the influence of the timing of a single soil cultivation on the decline in the number of viable seeds in the seed bank.

The experiments conducted in the studies mentioned differed in the weed species studied, the use of the natural seed bank or the burial of pre-collected seeds, the timing and frequency of soil tillage, the duration of the observations and the recording of meteorological data. The majority of the studies were qualitative in nature. They identified the factors that affect field emergence of weeds, and established some general relationships between these factors and weed emergence patterns. A further step towards understanding weed emergence patterns, and towards application of the knowledge on weed emergence in weed management may be quantification of the relationships between species characteristics, weather conditions and cultivation measures on the one hand and weed seedling emergence patterns on the other hand. The first objective of this study was to quantitatively analyse of field emergence patterns of three summer annual weeds, following a single soil cultivation at different times in spring. For this purpose, emergence patterns were related to the main factors affecting emergence, which were either controlled (initial seed bank) or measured (seed dormancy, soil temperature, soil compaction, rainfall). The second objective of this study was to assess the loss of seeds from the soil seed bank in relation to the timing of a single soil cultivation and to concomitant seedling emergence. For this purpose, seed bank depletion was assessed at the end of the experiment.

5.2 Materials and methods

The weed seeds used in this experiment were collected in July 1993 (*Polygonum persicaria* and *Spergula arvensis*) and September 1993 (*Chenopodium album*) in arable fields in the vicinity of Wageningen. The seeds were dried in open trays at room temperature for one month. Subsequently they were cleaned and stored at 2°C. Average seed weights were 2.13 mg for *P. persicaria*, 0.78 mg for *C. album* and 0.39 mg for *S. arvensis*.

In November 1993, 18 circular field plots were created in an experimental arable field by sinking 18 open-ended PVC cylinders, which were 20 cm deep and had a diameter of 30 cm, into the soil, so that approximately 0.5 cm projected above the surface. The experiment was laid out in three blocks, each consisting of a row of 6 plots. The distance between the plots in a row was about 40 cm, the distance between the rows was about 3 m. The soil was a sandy loam. The soil inside the cylinders was removed, bulked, thoroughly mixed and divided into 18 equal portions. The soil portions were irradiated with X-ray radiation to an amount of 1 MRad, to ensure that seeds present in the soil were killed.

In December 1993, 18 equal seed samples of each of the three weed species were weighed out. In a concrete mixer these were mixed through the 18 portions of sterilized soil, after which the soil was put back into the cylinders in the field. The starting situation for the experiment created in this way thus consisted in 18 plots divided in 3 blocks with qualitatively and quantitatively exactly the same seed bank. The approximate seed density in the soil profile of 20 cm depth was 141,500 seeds m^{-2} for *P. persicaria*, 212,200 seeds m^{-2} for *C. album* and 99,000 seeds m^{-2} for *S. arvensis*.

Emergence of seedlings in the plots was observed from December 1993 until September 1994. The observation intervals ranged from 1 to 20 days, dependent on the rate of emergence. After being counted, seedlings were cut off to prohibit double counting. No crop was grown in the experimental field where the plots were situated. The field was regularly sprayed with glyphosate in order to prevent growth of weeds and contamination of the plots with seeds from outside. During herbicide application the plots were covered with plastic lids.

In all blocks, five plots were cultivated, each at a different date in spring, and one plot remained uncultivated. The dates of soil cultivation were 8 March, 21 March, 12 April, 21 April and 3 May 1994. These dates span the period when the soil is cultivated for the planting of summer-grown crops in the Netherlands. In each block cultivation dates were attributed randomly to the plots to obtain a randomized block design, in which the treatment was date of soil cultivation. Soil cultivation consisted in a thorough mixing of the soil. At the date of soil cultivation the soil in the cylinders concerned was dug out with a trowel to a depth of 15 cm, and put into a shallow plastic tray. In order to expose the seeds buried in the soil to daylight and to redistribute them randomly, the soil in this tray was stirred and subsequently transferred to another tray in small portions. The stirring and transferring was repeated twice before the soil was put back in the cylinder. The layer from 15 to 20 cm functioned as a buffer zone to avoid mixing with the soil from the arable field containing the natural seed bank.

From 8 March onwards, soil temperature in the experimental field was measured at one hour intervals at a depth of 1 cm in two separate, undisturbed plots that were also surrounded by PVC cylinders dug into the soil. Daily rainfall was measured at the meteorological station 'Haarweg' in Wageningen, at a distance of 1.7 km from the experimental field.

Parallel to the field observations on the emergence of the three weed species, seasonal changes in dormancy of seeds buried in the field were assessed. For this purpose, in December 1993 envelopes made of fine mesh nylon gauze were filled with sterilized soil containing 100 seeds. For each species 30 envelopes were filled. The envelopes were buried in the field, close to the experimental plots, at a depth of approximately 8 cm below the soil surface. At dates as close as possible to the dates of soil cultivation, 6 envelopes of each species were exhumed according to a random scheme in order to test germination. The exhumation dates were 9 March, 22 March, 12 April, 21 April and 1

May. The soil containing the seeds was put into 50 mm petri dishes with one layer of filter paper, moistened with 10 mM KNO_3. Nitrate concentration was in accordance with the average value of 9.1 mM in soil water, reported by Fitter and Hay (1981). The soil layer in the petri dish had a depth of approximately 3 mm. It was irradiated with red light from both above and below for 20 minutes. Subsequently the petri dishes were placed in incubators at temperatures of 5°C, 7.5°C, 10°C, 15°C, 20°C and 25°C in darkness. Observations in green safe light were continued until no additional germination occurred.

To assess the remaining seed bank at the end of the experiment, soil samples were taken immediately after finishing the observations in September 1994. In all plots of block 1, four soil cores with a diameter of 5.9 cm were taken and separated in layers of 0-1, 1-2, 2-3, 3-4, 4-6, 6-8, 8-10 and 10-15 cm deep. The four samples from the same depth were bulked, thoroughly mixed, and a sub-sample was taken, corresponding to 27.3 ml of soil *in situ*. The sub-samples were sieved through a sieve with a mesh width of 0.5 mm, and from the remaining coarse fraction the seeds that were resistant to gentle pressure were collected. To assess the number of viable seeds, germination tests were done. *P. persicaria* seeds were pretreated at 2°C for 8 weeks and germination was tested at 20°C in 10 mM KNO_3. Germination of *C. album* seeds was tested at 20°C in 25 mM KNO_3, without pretreatment. Seeds of *S. arvensis* were tested at 20°C in a medium with 10 mM KNO_3 and 50 ppm GA_{4+7}, without pretreatment. The pretreatment of exhumed *P. persicaria* seeds did not result in substantial germination. Therefore, after the germination test, viability of remaining *P. persicaria* seeds was assessed by a tetrazolium test (Moore, 1973).

Core samples taken from the plots in block 3 at a depth of 1 to 6 cm were used to determine penetration resistance at the end of the experiment. The soil in the core samples was brought at pF 2, and penetration resistance was measured by penetrating the soil with a cone with a top angle of 30° and a diameter of 2 mm. Resistance measurements were averaged over the soil profile. Measurements closer than 0.5 cm to both surfaces of the core samples were excluded.

Analysis of variance was used to test differences in seedling numbers on the plots cultivated at different dates. Multiple regression was used to correlate differences in seedling numbers with differences in temperature, temperature amplitude, rainfall and soil penetration resistance following soil cultivation, and seed dormancy at the moment of soil cultivation. Since seed survival data were collected in only one block, differences between plots were tested with help of Friedman's non-parametric test. In this test, soil cultivation was regarded as the treatment, and soil layers, which were sampled separately, as blocks.

5.3 Results and discussion

5.3.1 Seedling emergence

Fig. 5.1 shows the emergence patterns of the three weed species as affected by soil cultivation at different dates, and their emergence pattern in undisturbed soil. Seedling numbers were clearly affected by soil cultivation. In all three species, soil cultivation at the last two dates in the experiment resulted in much higher emergence levels than soil cultivation at the first three dates. In *P. persicaria*, cultivation at any date enhanced seedling emergence relative to the undisturbed plots. In *C. album*, however, emergence

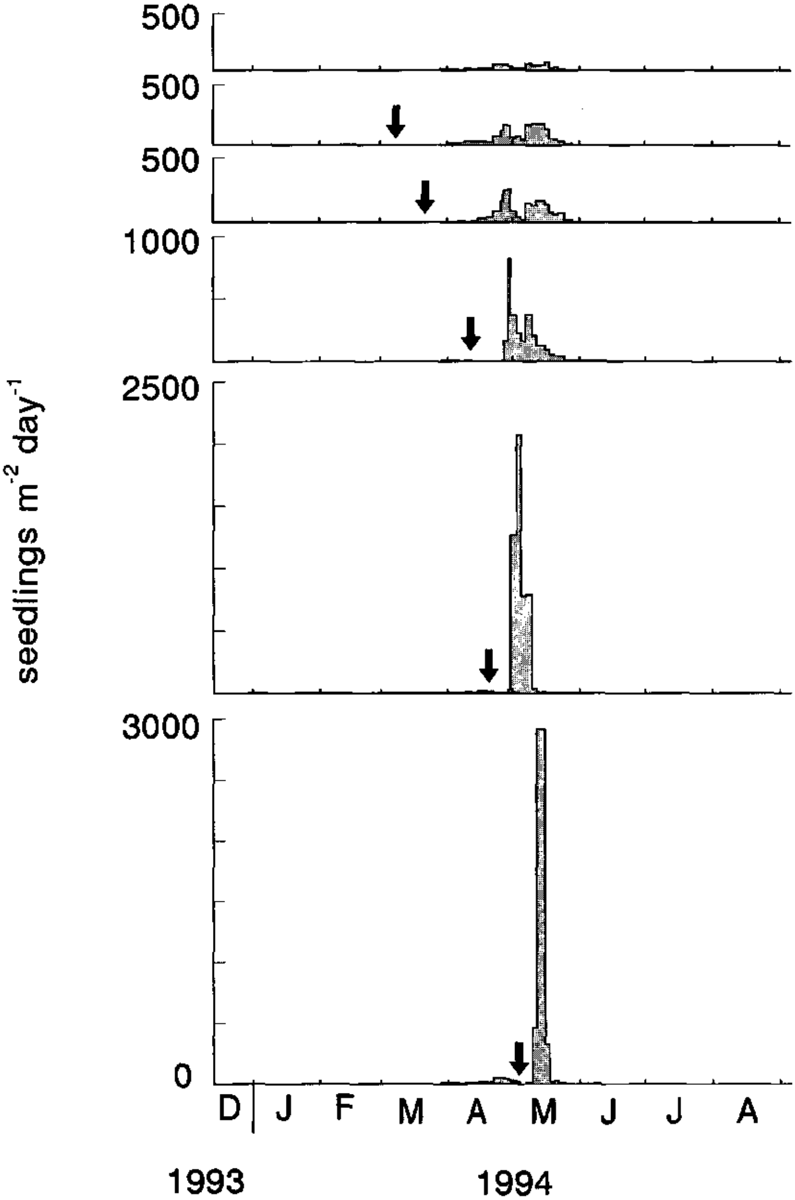

Fig. 5.1a Weed seedling emergence (seedlings m^{-2} day^{-1}) of *Polygonum persicaria* in undisturbed soil, and following soil cultivation at different dates. Arrows indicate the dates of soil cultivation.

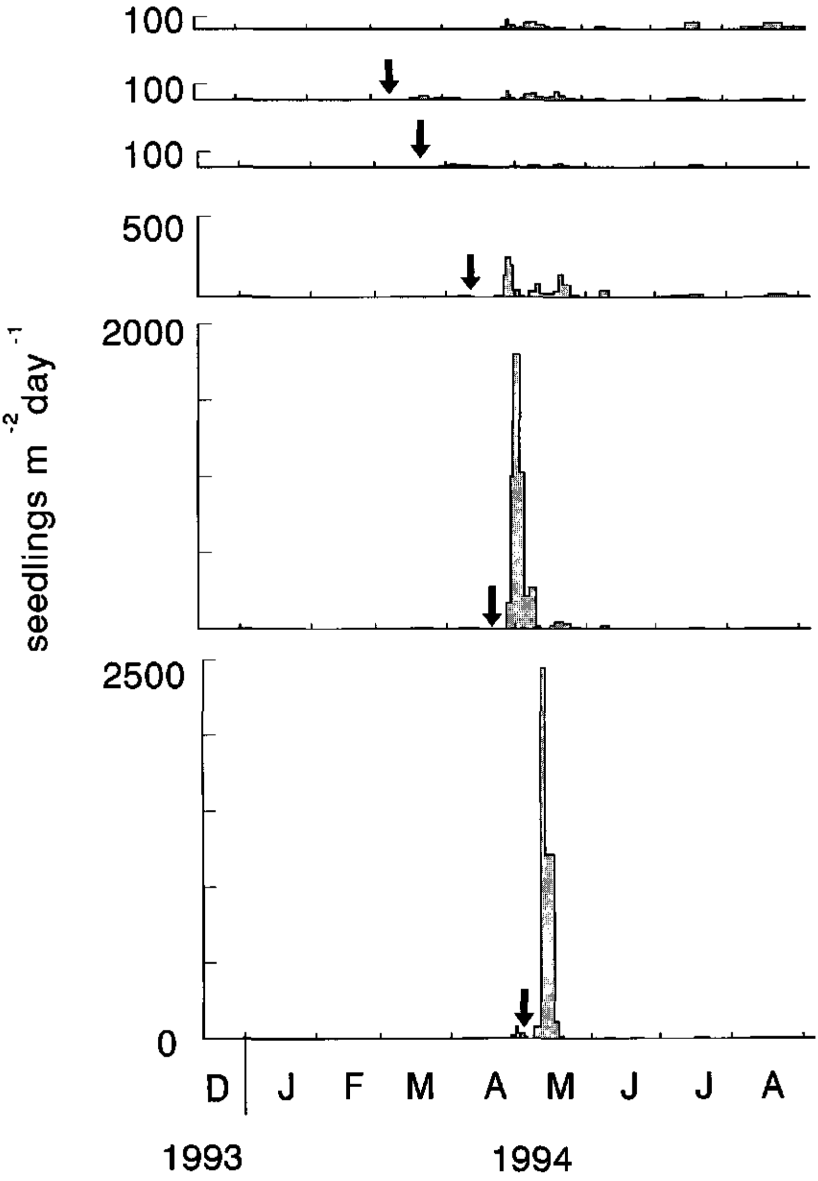

Fig. 5.1b Weed seedling emergence (seedlings m^{-2} day^{-1}) of *Chenopodium album* in undisturbed soil, and following soil cultivation at different dates. Arrows indicate the dates of soil cultivation.

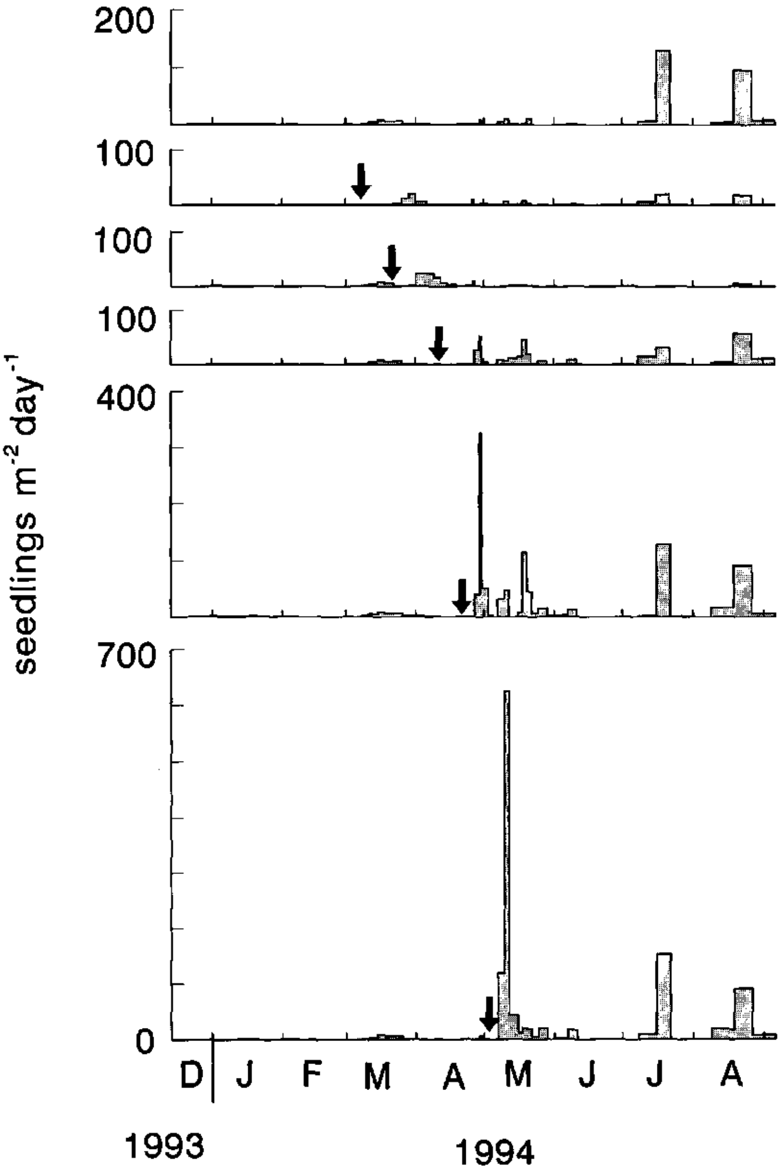

Fig. 5.1c Weed seedling emergence (seedlings m^{-2} day^{-1}) of *Spergula arvensis* in undisturbed soil, and following soil cultivation at different dates. Arrows indicate the dates of soil cultivation.

following the soil cultivations in March was lower than emergence in the uncultivated plots. In *S. arvensis*, soil cultivation on 8 March, 21 March and 12 April reduced seedling emergence relative to uncultivated soil.

The period of field emergence in the three species was not dependent on soil cultivation date. Emergence of *P. persicaria* started in the beginning of April and lasted until the end of May (Fig. 5.1a). Small numbers of *C. album* and *S. arvensis* seedlings emerged soon after burial in winter, and emergence still occurred when the experiment was finished in summer (Figs 5.1b and 5.1c). The distribution of peaks in seedling emergence within this period was dependent on soil cultivation. In general, soil cultivation was followed by a period when emergence ceased, after which a seedling flush occurred. In July and August, however, seedling flushes of *C. album* and particularly *S. arvensis* appeared, whose timing and duration were independent of the date of soil cultivation. The absence of an obvious effect of cultivation on the period of weed emergence was also reported by Lawson *et al.* (1974). The effect of soil cultivation on the distribution of peaks in the seedling flushes contrasted with observations by Roberts and Potter (1980), who reported a close correspondence between peaks of emergence on uncultivated plots and plots that were cultivated at different dates from April to October. However, by using an observation interval of one week and by combining observations on all species that emerged, Roberts and Potter (1980) emphasized the overall tendency in emergence rather than the differences at the finer scale that was used in this study.

In Fig. 5.2, the weekly average soil temperature at a depth of 1 cm in undisturbed soil, and weekly rainfall in the period from 8 March until 1 September are shown. From

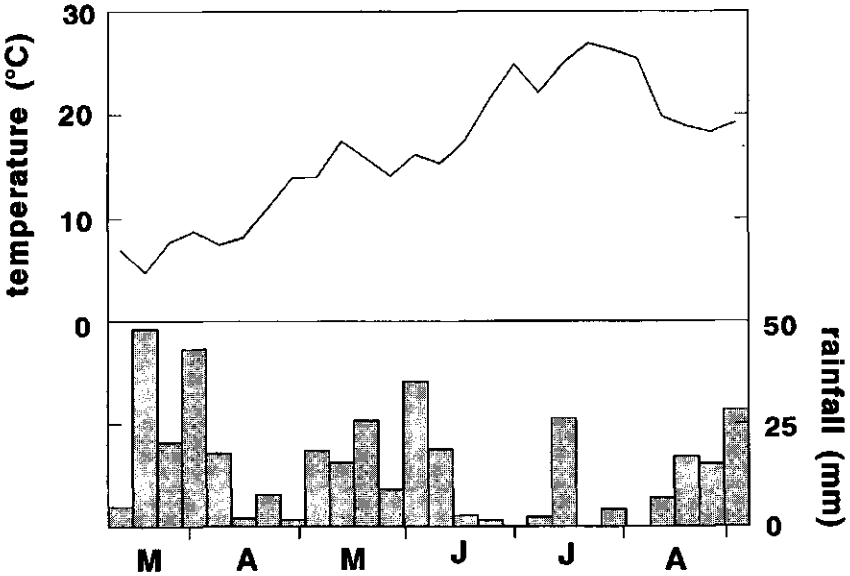

Fig. 5.2 Weekly average soil temperature (°C) at a depth of 1 cm in undisturbed soil and weekly rainfall (mm) in the period from 8 March until 1 September 1994.

March to July the average soil temperature increased gradually, and rainfall was relatively high. In July and August high soil temperatures coincided with an alternation of dry and wet periods.

Fig. 5.3 shows germination fractions in the seed portions that were exhumed shortly before or shortly after soil cultivation, and tested in a range of temperatures. In all three species, dormancy decreased (germinability increased) in the period from 9 March to 1 May. In *P. persicaria* dormancy reached its minimum in the beginning of April. From that moment the fraction germinated seeds remained constant, and was practically independent of temperature in a range from 7.5°C to 25°C. In *C. album* germinability gradually increased during March and April. The fraction germinated seeds increased with increasing temperature from 5°C to 20°C, while germination at 25°C was comparable to that at 20°C. *S. arvensis* had a considerably higher degree of dormancy than the other two species during the test period. Dormancy in *S. arvensis* stayed at approximately the same level during March and April, while some relief in dormancy occurred between 21 April and 1 May.

In Table 5.1a penetration resistance measurements are given as an average for each plot in block 3. At the end of the field experiment, penetration resistances were highest in the plots where the soil had been cultivated at the two dates in March. From 21 March on, the penetration resistance was lower when plots were cultivated later in the season.

5.3.2 Emergence flushes in spring

In this study, the spring emergence flush is defined as the emergence flush that is the direct result of soil cultivation in spring. The extent and timing of weed emergence in the field following soil cultivation is determined by the degree of dormancy of the seeds in the soil at the moment of cultivation, the subsequent germination of seeds and pre-emergence growth of seedlings. Germination of all three species in this study is stimulated by light (Bouwmeester, 1990), which penetrates into the soil during soil cultivation. By cultivating the soil at different dates, seeds were stimulated to germinate at different stages of their dormancy cycle, but also at different weather conditions, which causes differences in the germination process. At different dates of soil cultivation, the soil conditions may be affected differently, which influences the pre-emergence growth of seedlings.

It was assumed that field emergence after 30 June did not result from the soil cultivations in spring. Thus, the emergence flush in spring is defined as the emergence between the day of soil cultivation and 30 June. In all three species, analysis of variance showed a significant effect of the date of soil cultivation on the number of seedlings in the spring emergence flush ($P<0.0001$). No significant block effects were detected.

Multiple linear regression was used in order to analyse the possible contribution of different variables to the explanation of variance in seedling numbers in the spring emergence flush. The five variables that were used in the regression were average field temperature, temperature fluctuation, soil moisture and soil penetration resistance in the period following soil cultivation, and the degree of dormancy at the moment of soil cultivation (Table 5.1a). The four environmental factors in the analysis are all reported to affect seed germination and emergence (Bewley and Black, 1982; Stoller and Wax, 1973*b*; Bradford, 1995; Van der Weide, 1993). It was assumed that the stimulating effect

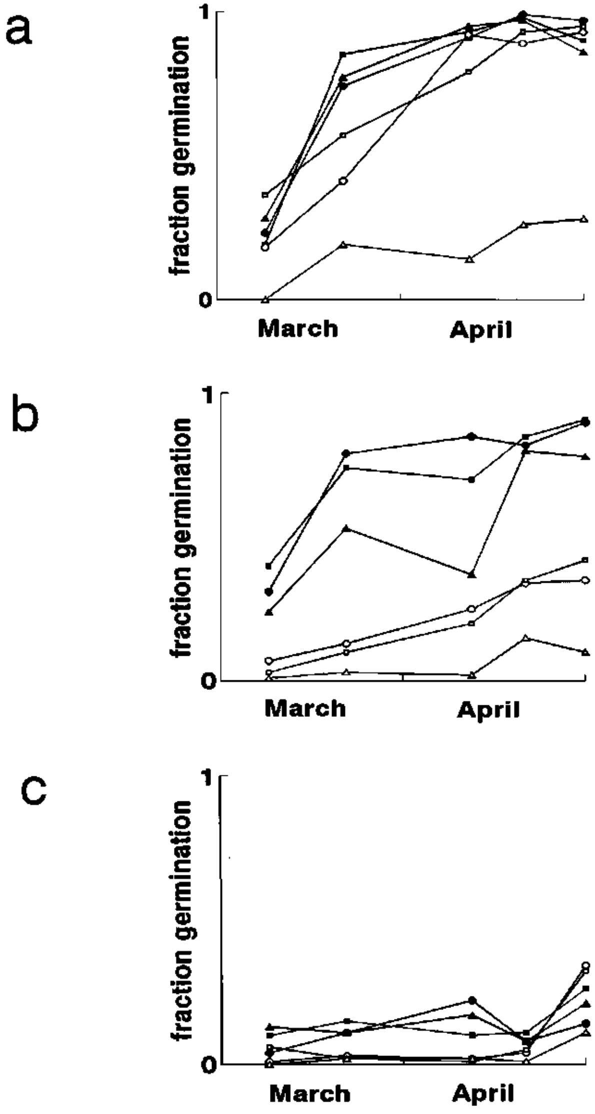

Fig. 5.3 Germination of exhumed seeds of *Polygonum persicaria* (a), *Chenopodium album* (b) and *Spergula arvensis* (c) as a function of exhumation date. After red irradiation, germination was tested in a range of temperatures (△ 5°C; □ 7.5°C; ○ 10°C; ▲ 15°C; ■ 20°C; ● 25°C).

Table 5.1a Seedling density caused by soil cultivation at different dates, and seedling density on uncultivated soil (N), in relation to four environmental factors (T, A_T, R, Q), and the degree of dormancy (D). N is given in thousands of seedlings m^{-2} (± standard error). For the cultivated plots seedling emergence between the date of soil cultivation and 30 June is given, for the uncultivated ones emergence between 8 March and 30 June. T is the average temperature at a depth of 1 cm in the week after soil cultivation. A_T is the average amplitude of the day-night temperature fluctuation at a depth of 1 cm in the week after soil cultivation. R is the rainfall in the period from one week before until one week after cultivation. Q is the soil penetration resistance measured at the end of the season. D is the average fraction of germination of seed portions exhumed simultaneously to soil cultivation in the field, and tested in a range of temperatures.

					P. persicaria		*C. album*		*S. arvensis*	
Cultivation date	T (°C)	A_T (°C)	R (mm)	Q (MPa)	D (-)	N (m^{-2})	D (-)	N (m^{-2})	D (-)	N (m^{-2})
uncultivated	-	-	-	0.51	-	1.6 ±0.2	-	1.1 ±0.4	-	0.2 ±0.04
8 March	6.9	6.6	18.6	1.64	0.21	4.0 ±0.2	0.18	1.1 ±0.1	0.06	0.2 ±0.03
21 March	6.9	7.2	68.5	1.69	0.59	4.2 ±0.1	0.39	0.5 ±0.1	0.07	0.3 ±0.07
12 April	8.2	10.2	15.8	0.73	0.77	5.7 ±0.4	0.40	2.2 ±0.4	0.09	0.4 ±0.06
21 April	12.3	10.6	10.6	0.54	0.84	12.1 ±0.7	0.55	10.5 ±0.6	0.06	1.2 ±0.02
3 May	14.0	9.3	19.8	0.44	0.82	13.5 ±0.9	0.58	10.3 ±0.9	0.23	2.1 ±0.14

Table 5.1b R^2 values for linear regression of seedling density caused by soil cultivation at different dates, on soil temperature (T), temperature amplitude (A_T), rainfall (R), soil penetration resistance (Q) and degree of dormancy (D). For more details see Table 5.1a.

Factor	R^2		
	P. persicaria	*C. album*	*S. arvensis*
T	0.99	0.95	0.95
A_T	0.45	0.46	0.27
R	0.23	0.28	0.14
Q	0.74	0.71	0.62
D	0.51	0.70	0.68

of the daylight reaching the seeds as a result of soil cultivation did not differ between treatments. In a linear regression on each of the five factors separately, the field temperature following soil cultivation, taken as the average field temperature at a depth of 1 cm in the week after soil cultivation, gave the highest correlation with the number of seedlings emerging in spring (*P. persicaria*: R^2 = 0.99, *C. album*: R^2 = 0.95, *S. arvensis*: R^2 = 0.95) (Table 5.1b). In a multiple regression, none of the other variables average daily temperature amplitude in the week following soil cultivation, rainfall in the period from one week before cultivation until one week after cultivation, penetration resistance after soil cultivation and fraction of germination of the seed lots that were exhumed simultaneously, averaged over the germination tests at the different temperatures, could add significantly to the explanation of residual variance in seedling numbers after linear regression on the average soil temperature in the field.

Forcella (1992) related annual totals of seedling emergence of four weed species in maize to temperature and rainfall data. Seedlings emerging after crop sowing in spring were the primary contributors to total annual emergence. He found the best correlation with the number of degree-days above 10°C in April, *i.e.* in the month preceding soil cultivation and sowing the maize crop. However, the correlation for *Chenopodium album* was low (R^2 = 0.35) compared to that for the other three species in his study, and also compared to the correlation of *C. album* emergence with soil temperature after cultivation in this study.

The temporary cessation of seedling emergence caused by soil cultivation may be due to the killing of seedlings that had not yet reached the soil surface by soil disturbance. The temperature-sum approach (Garcia-Huidobro *et al.*, 1982*a*,*b*) was used to describe the timing of emergence following soil cultivation. The temperature sum is calculated by accumulating daily average temperature above a base temperature T_b, starting at the day of soil cultivation. When the temperature sum reaches a thermal time θ_x, a fraction x of the final number of seedlings is attained. Values for T_b and θ_x were estimated by trial and error. In this way, the onset of emergence after soil cultivation could be described reasonably well (Table 5.2). Onset of emergence was defined as the date when 5% of the seedlings in the seedling flush have emerged. Estimates for T_b and $\theta_{0.05}$ were 5.2°C and 78.1°Cday for *P. persicaria*, 0.0°C and 101.5°Cday for *C. album*, and 2.0°C and 87.3°Cday for *S. arvensis*. Description of later stages in the emergence process, like the median of the distribution of emergence times, was poor. This may be due to periods of reduced soil moisture, which temporarily cease the emergence process (Roberts, 1984; Finch-Savage and Phelps, 1993).

Table 5.2 The observed and expected onset of emergence after different dates of soil cultivation. Onset of emergence is defined as the date when 5% of the seedlings in the seedling flush have emerged. Expected onset of emergence is calculated by accumulating daily average temperature above a base temperature T_b, starting at the day of soil cultivation, until a thermal time $\theta_{0.05}$ is reached. *P. persicaria*: T_b=5.2°C, $\theta_{0.05}$=78.1°Cday; *C. album*: T_b=0.0°C, $\theta_{0.05}$=101.5; *S. arvensis*: T_b=2.0°C, $\theta_{0.05}$=87.3°C.

Cultivation date	*P. persicaria*		*C. album*		*S. arvensis*	
	obs.	exp.	obs.	exp.	obs.	exp.
8 March	11 April	+3	21 March	+3	25 March	+3
21 March	21 April	−2	31 March	+2	5 April	−1
12 April	28 April	0	26 April	−3	28 April	−4
21 April	2 May	−1	29 April	0	28 April	+1
3 May	11 May	+1	11 May	−1	9 May	+1

5.3.3 Emergence flushes in summer

In this study, emergence flushes in summer are defined as emergence flushes after 30 June, which were assumed not to be the direct result of soil cultivation in spring. Karssen (1982) hypothesized that the smaller flushes of seedling emergence in summer following the major flush in spring may be due to the alternation of desiccation and imbibition of the seeds buried in the soil. Desiccation relieves dormancy, which becomes apparent when the seeds are remoistened. Bouwmeester (1990) reports that desiccation became stimulatory to germination only after seeds have been buried in the soil for approximately 1.5 months (*S. arvensis*), 6 months (*C. album*) and 12 months (*P. persicaria*). Desiccation has a stronger effect on germination of *S. arvensis* than on germination of the two other species (Bouwmeester, 1990). The reaction of *S. arvensis* on the alternation of desiccation and rehydration has also been documented by Post (1984), Karssen *et al.*

(1988) and Bouwmeester and Karssen (1993). In *S. arvensis*, and to a lesser extent also in *C. album*, two emergence flushes were observed, one in July and one in August (Figs 5.1b and 5.1c), each time when a period of drought was followed by rainfall (Fig. 5.2). In this experiment, burial of *P. persicaria* was shorter than 12 months and no reaction to dry-wet-alternation took place.

In *C. album* and *S. arvensis*, seedling numbers in the emergence flushes in summer depended on the date of soil cultivation in spring. In *S. arvensis* the extent of summer emergence was negatively correlated with soil penetration resistance (R^2 = 0.91). In *C. album* correlation with soil penetration resistance was absent. This may have been caused by a major depletion of the seed bank in the upper soil layer after cultivations on 21 April and 3 May, so that little additional emergence could take place in these treatments.

5.3.4 Seed survival in the soil

Initial viability of the seeds was not tested, but from the germination percentages of the exhumed samples and the viability tests of the seeds recovered at the end of the season it can be concluded that viability at the moment of burial was close to 100%. In *P. persicaria* and *C. album*, firmness of the seed was a good criterion for viability. The fraction of firm seeds recovered at the end of the experiment that appeared to be viable was 0.88 for *P. persicaria*, and 0.95 for *C. album*. In *S. arvensis*, however, this fraction was only 0.58. In *S. arvensis* the number of firm seeds recovered was systematically higher than the number of seeds buried at the start. A substantial percentage of these firm seeds did not germinate when tested, or showed aberrant germination. Only seeds that germinated in the test were considered to be viable. In general, the test conditions applied to *S. arvensis* are known to stimulate germination to approximately 100% (Vleeshouwers, unpublished results). In the arable soil that was used in the experiment many *S. arvensis* seeds occur. It was concluded that X-ray radiation used to sterilize the soil did not kill these seeds, but ceased their ability to germinate, possibly by disrupting the meristematic tissue. This assumption was supported by the observation that the number of seeds germinating in the test, and thus the number of seeds considered viable, maximally amounted to the number of seeds added to the soil.

Fig. 5.4 shows the fate of the seeds that were buried in the upper 15 cm of the soil, divided in the categories seeds producing emerged seedlings, seeds dying before or after germination and seeds remaining viable. When expressed as the percentage of seeds buried in the upper 15 cm, emergence ranged from 1.4 to 13.5 in *P. persicaria*, from 0.5 to 6.9 in *C. album*, and from 0.6 to 5.8 in *S. arvensis*. When expressed as a fraction of seeds that were lost from the soil seed bank in the upper 15 cm, emergence ranged from 3.7 to 29.5 in *P. persicaria*, from 3.1 to 14.0 in *C. album*, and from 1.5 to 11.5 in *S. arvensis*.

The effect of soil cultivation on seed survival was tested with help of Friedman's test, in which soil cultivation was regarded as treatment and the soil layers as blocks. In all three species, the fraction of seeds surviving in the soil was significantly affected by soil cultivation (*P. persicaria* and *C. album*: $P<0.001$; *S. arvensis*: $P=0.003$). In *P. persicaria* and *C. album*, the differences in seed survival are mainly caused by a relatively high seed loss in the plots cultivated on 21 April and 3 May, and a relatively low seed loss in the plots cultivated on 21 March. In *S. arvensis* relatively low seed loss

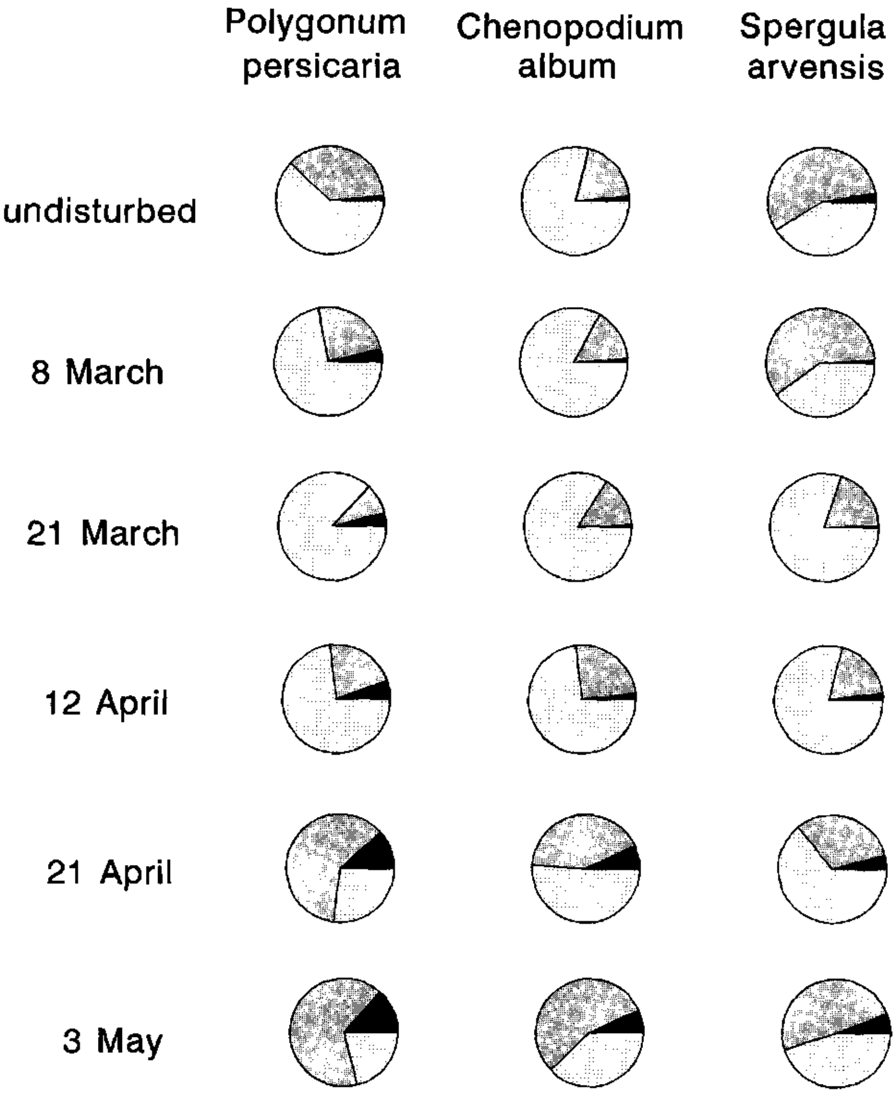

Fig. 5.4 Fate of the seeds in the upper 15 cm soil layer in the period from December 1993 till September 1994, classified in fraction emergence (black area), seed and seedling mortality (grey area) and survival (dotted area), in relation to soil cultivation.

in the plots cultivated on 21 March and 12 April was the main reason for the effect of soil cultivation on seed survival.

Roberts (1972) stated that the most important factor in the depletion of weed seed populations in the soil is germination, which either leads to emergence or to the death of the seedling. Therefore, a close correlation between loss of viable seeds from the soil and seedling emergence on the plots was expected. Indeed, in *C. album* an increase in seed loss from the soil coincides with an increase in seedling emergence (Fig. 5.4). However, in the two other species the correlation appeared to be absent. In *P. persicaria* soil cultivation at 8 March, 21 March and 12 April enhanced seedling emergence compared to the uncultivated plot, but reduced seed loss. In *S. arvensis* the same holds for soil cultivation at 21 April and 3 May, whereas cultivation at 8 March reduced emergence compared to uncultivated soil by a factor three, but slightly increased seed loss. Possibly seed mortality (before germination) and seedling mortality (before emergence) differ between cultivation dates, thereby interfering with the correlation between seed loss and seedling emergence.

Germination in the uncultivated plots may be caused by light penetration in the soil (Woolley and Stoller, 1978), by dry-wet alternations (*S. arvensis*, Bouwmeester and Karssen, 1993) and by the activity of the soil fauna, generating a natural soil cultivation (Willems and Huijsmans, 1994). Comparing undisturbed plots and plots cultivated twice or four times a year, Roberts and Dawkins (1967) concluded that for a combination of more than twenty British weed species the rate of depletion of seeds increases with increasing frequency of soil disturbance. In all three species in this study, however, a single soil cultivation at some dates decreased seed loss compared to the undisturbed plots (Fig. 5.4). In *P. persicaria* loss of viable seeds was reduced by soil cultivation at 8 March, 21 March and 12 April, in *C. album* by soil cultivation at 8 March and 21 March, in *S. arvensis* by soil cultivation at 21 March, 12 April, 21 April and 3 May. Only cultivation at 21 April and 3 May increased the rate of depletion of the seed bank of the three species combined, relative to that in uncultivated soil.

The distribution of viable seeds over the soil profile at the end of the experiment averaged over all cultivated plots is shown in Fig. 5.5. In *P. persicaria* and *C. album* the numbers of viable seeds show an increasing trend with increasing burial depth over the upper 15 cm. In *S. arvensis* the average percentage of seeds remaining in the soil was about 30% in the top 2 cm, and about 60% in deeper layers. The increase in seed survival with increasing burial depth in the cultivated plots may be explained by a decrease in germination after soil cultivation with increasing burial depth. All seeds in the soil were treated in the same way by soil cultivation, and the redistribution of seeds nullified any possible existing relationship between burial depth and the condition of the seeds. Therefore, the influence of burial depth must have been initiated after soil cultivation. The decrease in germination with increasing depth is often attributed to a reduction in temperature fluctuation (Bewley and Black, 1982; Karssen, 1982). After irradiation, germination of *P. persicaria* and *C. album* is stimulated by alternating temperatures (Vincent and Roberts, 1977), and germination of *C. album* increases with increasing temperature amplitude (Murdoch *et al.*, 1989). In the exhumed seed samples of these two species, however, high germination percentages are reached at constant temperatures in the laboratory (Fig. 5.3). In the regression analysis, no effect of the fluctuation in soil temperature on the level of emergence could be shown. In

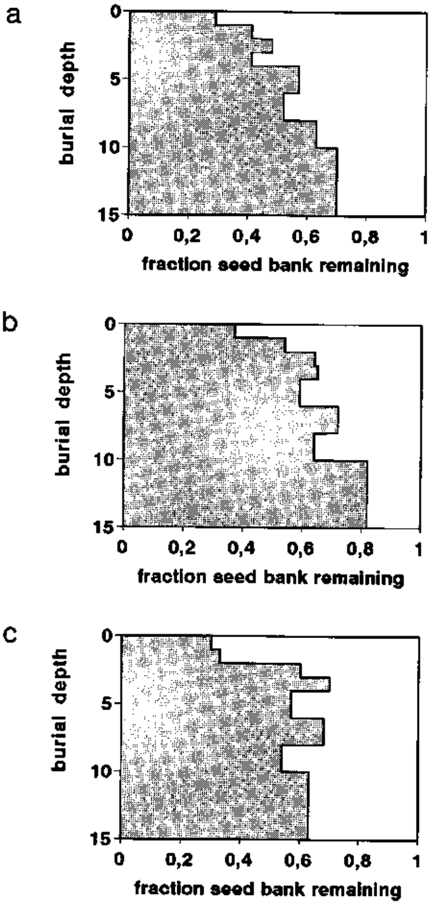

Fig. 5.5 Vertical distribution of the fraction of seeds surviving in the upper 15 cm of the soil profile, in *Polygonum persicaria* (a), *Chenopodium album* (b) and *Spergula arvensis* (c).

S. arvensis, temperature fluctuation even tends to inhibit germination (Vincent and Roberts, 1977). Therefore, in the present experiment, the decreased amplitude of the diurnal temperature fluctuation does not seem to be the factor that inhibits seed germination at greater depths. More likely, the gaseous environment in the soil may inhibit seed germination. Benvenuti and Macchia (1995) postulated that an increased difficulty in eliminating toxic fermentation products with an increased burial depth in soil accounts for the germination inhibiting effect of burial depth. They show that in *Datura stramonium* pre-incubation under anaerobic conditions leads to a strong increase in the degree of dormancy within a few days from incubation. Wesson and Wareing (1969) showed that inhibition of germination of *S. arvensis* seeds by burial was caused by a gaseous inhibitor produced by the seeds themselves. In *S. arvensis*, the effect of desiccation during periods of drought may have been an additional factor causing a difference in seed survival between the superficial and the deeper layers. Germination of remoistened *S. arvensis* seeds increases linearly with an increasing level of preceding desiccation (Bouwmeester, 1990). Only in the upper 2 cm the soil moisture content may have been so low periodically that subsequent germination was stimulated.

5.4 Conclusions

The date of soil cultivation in spring had a strong effect on weed seedling emergence. The later in spring the soil was cultivated, the more seedlings emerged, and the sooner after soil cultivation emergence started. Both the extent of the spring seedling flush and the timing of its onset showed a good correlation with the soil temperature in the period after soil cultivation, which increased during spring. Later in the season, the alternation of desiccation and remoistening of the soil determined the timing of emergence flushes. Seedling numbers in these flushes were probably dependent on soil penetration resistance.

Seed survival in the soil was also dependent on soil cultivation date. Knowledge on the relative importance of the various factors that lead to depletion of the seed bank is too limited to give a quantitative explanation of the relationship between cultivation date and seed survival, and of the relationship between seed loss from the soil and seedling emergence.

Whether or not soil cultivation increases the number of seedlings emerging and the number of viable seeds lost from the soil, depends on the date of soil cultivation and the weed species. Regarding the effect on seedling emergence and seed bank depletion, preparation of a stale seed-bed only seems useful at the end of April or the beginning of May, and thus preceding the growing of maize, provided that the emerged weed seedlings can be controlled effectively.

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6 FIELD EMERGENCE PATTERNS IN THREE ARABLE WEED SPECIES II. MODELLING THE EFFECT OF WEATHER, SOIL AND CULTIVATION DATE

Abstract A model was developed to simulate weed emergence patterns after soil cultivation. In the model, the consecutive processes of dormancy release, germination and pre-emergence growth were modelled in separate modules. Input variables of the model are the date and method of soil cultivation, soil temperature and soil penetration resistance. Output of the model is seedling density and the timing of seedling emergence. The model was parameterized for *Polygonum persicaria*, *Chenopodium album* and *Spergula arvensis* with help of previous field and laboratory experiments.

The model was evaluated with data from a field experiment, in which separate plots were cultivated once only, at five different times in spring. When using germination data of exhumed seed lots to estimate the degree of dormancy at the time of soil cultivation, the extent of the emergence flushes following soil cultivation could be described well. When there was substantial emergence as a result of soil cultivation, the timing of emergence could be predicted accurately. Improvement of the model should focus on increasing the precision of the simulation of dormancy release, and on the simulation of emergence flushes that are not related to soil cultivation. Analysis with the simulation model revealed that the high correlations between seed-bed temperature and both the extent and rate of seedling emergence were only partly based on causal relationships.

6.1 Introduction

Seasonal patterns of field emergence have been documented for more than 180 annual weed species (chapter 1). Generally, weed seedlings emerge in species-specific patterns that are modulated by the environment. There may be large differences in the seasonal distribution of emergence between species (Roberts and Feast, 1970; Ogg and Dawson, 1984), and in the seasonal distribution of a certain species between years (Roberts and Potter, 1980; Ogg and Dawson, 1984). In several field studies, seasonal emergence patterns were related to soil cultivation, temperature and rainfall, which led to some qualitative understanding of the effects of these factors on seedling emergence. Extensive laboratory research has been done to study the effect of environmental factors on the germination of seeds of many weed species. However, few attempts have been made to use the physiological knowledge generated in these laboratory experiments to explain field emergence patterns of arable weeds quantitatively.

Quantitative models predicting weed emergence patterns are expected to have two important agronomic applications (Forcella, 1993). First, when coupled with models predicting crop emergence, they will allow an early estimation of crop yield reduction from weed interference. Second, they will permit a better determination of the optimal timing of both mechanical and chemical weed control. The development of quantitative models may also have the scientific objective of increasing the understanding of complex ecological systems. To my knowledge, quantitative models that describe seasonal emergence patterns were developed for seven weed species only (Takayanagi and Kusanagi, 1989; Benech-Arnold *et al.*, 1990; Alm *et al.*, 1993; Forcella, 1993; Harvey and Forcella, 1993; Van der Weide, 1993; King and Oliver, 1994). Some characteristics of these models are presented in Table 6.1. Three models were used to simulate field emergence patterns in conditions where emergence was not water-limited, and therefore do not comprise the effect of water stress (Benech-Arnold *et al.*, 1990; Harvey and Forcella, 1993; Van der Weide, 1993). In five models, emergence was normalized according to the final seedling number that was observed in the field (Takayanagi and Kusanagi, 1989; Alm *et al.*, 1993; Forcella, 1993; Harvey and Forcella, 1993; King and Oliver, 1994). These models predict the relative distribution of seedling emergence over time, but not the absolute number of seedlings emerging. The models by Benech-Arnold *et al.* (1990) and Van der Weide (1993) predict both seedling numbers and the timing of their emergence, provided that seed numbers in the seed bank are known.

Table 6.1 Some characteristics of published models simulating weed emergence patterns.

Reference	*Species*	*Weather parameters used in simulation*	*Output of the simulation*
Takayanagi & Kusanagi (1989)	*Digitaria adscendens*	air temperature, soil moisture content	timing of emergence
Benech-Arnold *et al.* (1990)	*Sorghum halepense*	soil temperature	seedling numbers, timing of emergence
Alm, Stoller & Wax (1993)	*Ipomoea hederacea* *Abutilon theophrasti*	soil temperature soil water potential	timing of emergence
Forcella (1993)	*Abutilon theophrasti*	soil temperature, rainfall	timing of emergence
Harvey & Forcella (1993)	*Chenopodium album*	soil temperature	timing of emergence
Van der Weide (1993)	*Galium aparine*	soil temperature	seedling numbers, timing of emergence
King & Oliver (1994)	*Digitaria sanguinalis*	soil temperature, soil water potential	timing of emergence

The model described in this chapter is grafted onto the framework presented by Cousens and Peters (1993) for the development of a mechanistic model for the quantitative prediction of emergence in the field. Cousens and Peters (1993) distinguished three consecutive processes in the events leading to field emergence. These processes can be denoted as dormancy release, germination, and pre-emergence growth: 'It is important to separate the stimuli required to cause a qualitative change in seed status, from the environmental factors determining the rate of germination and growth when dormancy has been removed. When the time of emergence is observed in the field, it is the result of the confounded effects of:

1. the time taken to come out of dormancy,
2. the time taken to respond (germinate) when conditions become favourable,
3. the time taken to grow to the surface.'

In addition to their time of emergence, also the *number* of seedlings emerging is the result of the successive processes of dormancy release, germination and pre-emergence growth.

The separation of the three consecutive processes that lead to emergence may be an important step in the quantitative understanding of weed emergence in the field. The rationale behind the distinction between these processes is that they are physiologically different, that they work on different time scales, that they are affected by different environmental factors, and, in so far as they are affected by the same environmental factors, optimal values for those factors may be quite different. For example, dormancy release is reversible, and seeds may go through several annual cycles of dormancy release and induction, while germination and pre-emergence growth are irreversible. In summer annual species breakage of dormancy occurs at low temperatures, and lasts for several months, while the germination process has its temperature optimum at higher temperatures, and lasts for only a few days. Soil compaction affects underground shoot elongation, but not dormancy and germination.

Takayanagi and Kusanagi (1989) and King and Oliver (1994) did not simulate changes in dormancy, and combined simulation of germination and pre-emergence growth. Forcella (1993) and Harvey and Forcella (1993) did not simulate changes in dormancy; they simulated germination, and included subsequent pre-emergence growth as a fixed delay per cm seed burial depth. Alm *et al.* (1993) did not simulate changes in dormancy; they simulated germination and subsequent seedling elongation separately. Benech-Arnold *et al.* (1990) simulated dormancy release and germination separately; they included pre-emergence growth as a fixed delay after germination. Van der Weide (1993) is the only author who explicitly simulated both changes in dormancy, germination and pre-emergence growth.

For the greater part, existing models for field emergence patterns (Table 6.1) consist of descriptive, empirical relationships to quantify emergence in relation to the environment. Physiologically based models have been developed for annual changes in seed dormancy (chapter 2), germination (*e.g.* Garcia-Huidobro *et al.*, 1982*a*,*b*; Finch-Savage and Phelps, 1993; chapter 2) and pre-emergence growth (chapter 4). In this study, three physiologically based models simulating the processes of dormancy breakage, germination and pre-emergence growth were combined into a model simulating field emergence patterns of weeds. The first objective was to test the overall model with the results of a field experiment concerning emergence patterns of the weed species *Polygonum persicaria* L., *Chenopodium album* L. and *Spergula arvensis* L. (chapter 5). The second objective was to interpret the effect of weather, soil and cultivation date on the emergence patterns, and to quantify the contributions of the three processes to these patterns with help of the overall model.

6.2 Materials and methods

6.2.1 Model description

General structure of the model

The model simulates the pattern of weed emergence in the field after soil cultivation. The model consists of three submodels, each using the output of its predecessor as an input. In Fig. 6.1 input and output variables of the three submodels, and the parameters needed to characterize the weed species and the soil are presented. In Table 6.2 definitions and dimensions of the species parameters are given. The number of environmental variables used in the model was reduced to a minimum: only the date and method of soil cultivation, soil temperature and soil penetration resistance were included.

Submodel I simulates the seasonal changes in dormancy of the seeds buried in the seed bank. Output is the degree of dormancy, characterized by the availability of a membrane protein in the seeds, which acts as a phytochrome receptor. Inputs are the degree of dormancy of the seeds at the time of burial, and the daily average temperature at a depth of 5 cm in the soil.

Submodel II simulates the germination process of the seeds buried in the soil. The germination process is triggered by irradiation. In the field, irradiation occurs *in situ* as a result of soil cultivation. The method of soil cultivation determines the depth to which the soil is disturbed, and the fraction of seeds buried in the cultivated soil layer that are exposed to daylight. Output variables of the germination submodel are the number of seeds germinating after soil cultivation, and the distribution of germination times. Input variables are the availability of phytochrome receptor (*i.e.* the degree of dormancy), the seed density in the soil seed bank, the date and method of soil cultivation, and the hourly temperature at a depth of 1 cm in the soil.

Submodel III simulates the pre-emergence growth of seedlings starting from the moment of underground germination. Output variables are the number of seedlings emerging and the distribution of emergence times. Input variables are the time course of germination, the distribution of seed weights, the depth of burial of the seeds that germinate, and the hourly soil temperature at a depth of 1 cm.

Dormancy

In the dormancy submodel, dormancy is defined as the availability of a hypothetical phytochrome receptor X, located in the membrane of the seeds (Hilhorst, 1993). The availability of the receptor increases by the process of dormancy release and decreases by the process of dormancy induction. No distinction is made between primary and secondary dormancy. Induction and release of dormancy alternate over the course of the year as a function of the temperature in the field (Fig. 6.2). The dormancy status of the seed population is characterized by the mean availability of the phytochrome receptor in the population. An extensive description of the dormancy model is given in chapter 2.

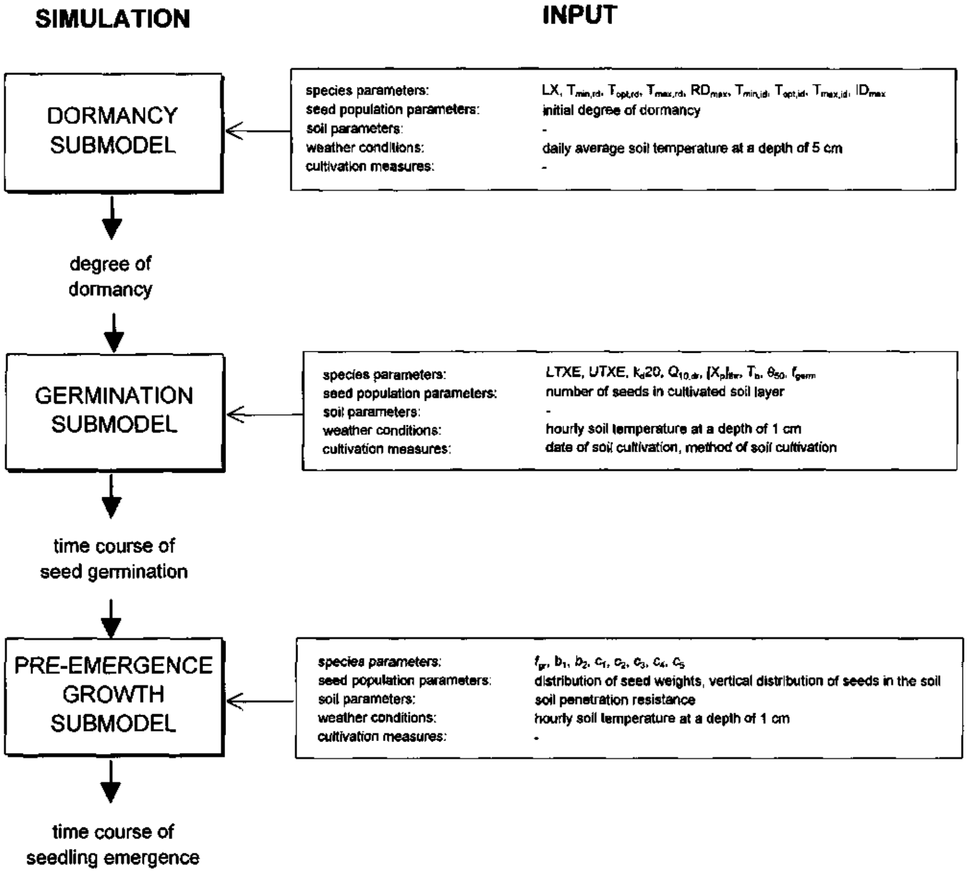

Fig. 6.1 Input and output variables of the three submodels used in the simulation, and the parameters needed to characterize the species and the soil. The input variables are classified in seed population parameters, which characterize the seed population at the start of the experiment, and weather conditions. The degree of dormancy is output of the dormancy submodel and input for the germination submodel. The time course of germination is output of the germination model and input for the pre-emergence growth submodel. The time course of emergence is the output of the overall model.

Germination

In the germination submodel, the germination percentage and the timing of germination are simulated in two separate subroutines, which are denoted submodel IIA and submodel IIB respectively. The germination percentage is determined by the temperature in the

Table 6.2 Definitions and dimensions of the species parameters used in the model.

Parameter	Definition and dimension (in parentheses)
dormancy (submodel I)	
LX	lower limit of X_a (-)
$T_{min,rd}$	minimum temperature for the release of dormancy (°C)
$T_{opt,rd}$	optimum temperature for the release of dormancy (°C)
$T_{max,rd}$	maximum temperature for the release of dormancy (°C)
RD_{max}	maximal rate of release of dormancy (day^{-1})
$T_{min,id}$	minimum temperature for the induction of dormancy (°C)
$T_{opt,id}$	optimum temperature for the induction of dormancy (°C)
$T_{max,id}$	maximum temperature for the induction of dormancy (°C)
ID_{max}	maximal rate of induction of dormancy (day^{-1})
germination (submodel II)	
LTXE	lower temperature limit for X_a exposure (°C)
UTXE	temperature above which the total amount of X_a is exposed (°C)
k_d20	rate constant of dark reversion at 20°C (h^{-1})
$Q_{10,dr}$	Q_{10} of dark reversion (-)
$[X_p]_{thr}$	threshold for the activity of X_p (-)
T_b	base temperature permitting germination (°C)
θ_{50}	thermal time to 50% germination (°C day)
f_{germ}	coefficient of variation of the distribution of germination rates (-)
pre-emergence growth (submodel III)	
f_{gr}	coefficient of variation of the distribution of shoot elongation rates (-)
b_1, b_2	regression parameters describing the effect of soil penetration resistance on the conversion efficiency of seed fresh weight into shoot length (g cm^{-1}, g cm^{-1} MPa^{-1})
c_1, c_2, c_3, c_4, c_5	regression parameters describing the effect of temperature and soil penetration resistance on cotyledon protrusion and shoot elongation rate during pre-emergence growth (cm day^{-1}, cm day^{-1} $°C^{-1}$, cm day^{-1} MPa^{-1}, day^{-1}, day^{-1} $°C^{-1}$)

period following irradiation of the seeds (chapter 2). The model described in chapter 2 was developed for calculating germination percentages of exhumed seed lots after red irradiation, in a laboratory test at constant temperatures. In the field, germination is triggered by daylight irradiation during soil cultivation. Since field temperatures fluctuate, the analytical solution used in chapter 2 to calculate the germination percentage was not adequate any more, and was replaced by a dynamic model subroutine using the hourly

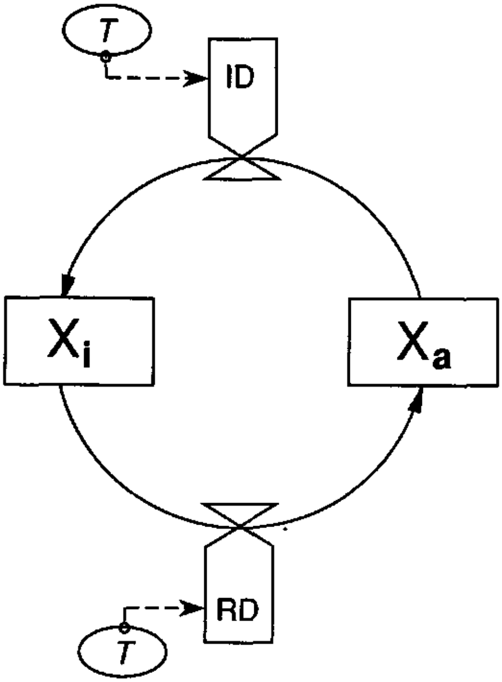

Fig. 6.2 Structure of the submodel simulating the annual dormancy cycle of buried seeds. The phytochrome receptor can be present in two forms (X_i and X_a). X_i denotes the receptor in its unavailable form, X_a denotes the receptor in its available form. The degree of dormancy of the seed is related to the amount of X_a. The proportions of X_i and X_a change by release of dormancy (RD) and induction of dormancy (ID), which are both dependent on the soil temperature T.

temperature (T) (submodel IIA; Fig. 6.3) It is assumed that in the field nitrate and the quantity of light reaching the seeds as a result of soil cultivation, are not limiting for germination.

For the simulation of the timing of seed germination (submodel IIB), the thermal time concept (Garcia-Huidobro *et al.*, 1982*a*) was used. For constant temperatures below the temperature optimum, the thermal time concept can be presented as

$$1/t_{50} = (T - T_b)/\theta_{50} \qquad \text{if } T > T_b, \tag{6.1a}$$

$$1/t_{50} = 0 \qquad \text{if } T < T_b, \tag{6.1b}$$

where t_{50} is the time to 50% germination (day), T is the temperature (°C), T_b is the base temperature (°C), and θ_{50} is the thermal time to 50% germination (°C day).

The development rate during the germination process is called the germination rate *GR*

(day^{-1}). Germination of a seed is completed at time t_g, which is reached when the accumulated germination rate reaches the value 1,

$$\int_{t=0}^{t_g} GR\,dt = 1, \tag{6.2}$$

where t=0 at the moment of irradiation. At constant temperatures, the mean germination rate GR_{mean} in the seed population equals $1/t_{50}$ (day^{-1}). According to Ellis and Barrett

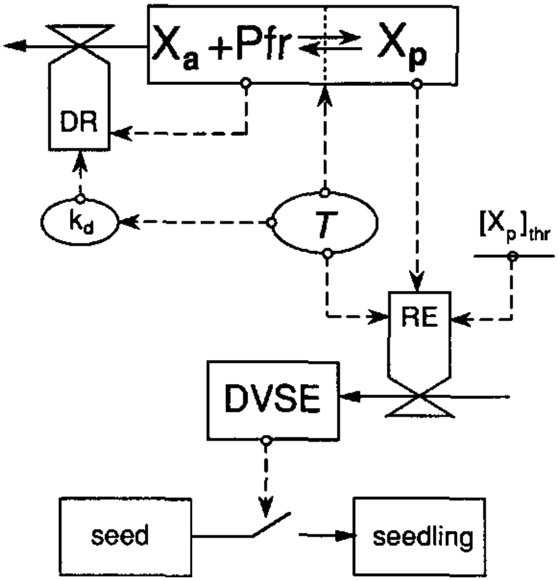

Fig. 6.3 Structure of the subroutine simulating the germination percentage at a fluctuating temperature *T*. By irradiation phytochrome is converted to its active form (Pfr), which binds to the available phytochrome receptor X_a, to form a phytochrome-receptor-complex X_p. An equilibrium exists between X_a, Pfr and X_p. If the temperature *T* increases, the exposure of the phytochrome receptor X_a increases. This allows Pfr to occupy a larger part of the receptor molecules present, and the equilibrium will shift in the direction of X_p. Pfr is reverted to its inactive form in a process called dark reversion. The rate of dark reversion is temperature dependent. Since an equilibrium between free and receptor-bound phytochrome exists, dark reversion withdraws X_p from the system. As long as X_p is present above a threshold level $[X_p]_{thr}$, it promotes the first stage of the germination process, the escape process, proceeding at a temperature dependent rate RE. As soon as the developmental stage DVSE is reached, the germination process in the seed is beyond the point up to which stimulation by X_p is needed, and eventually the seed will germinate. If presence of X_p is too short, the escape process will not reach the developmental stage DVSE, and irradiation of the seed will not result in germination.

(1994), the germination rate reacts instantaneously to temperature, which implies that in a fluctuating temperature regime, at any time the mean germination rate can be given by

$$GR_{mean} = (T - T_b)/\theta_{50} \qquad \text{if } T > T_b, \qquad (6.3a)$$

$$GR_{mean} = 0 \qquad \text{if } T < T_b. \qquad (6.3b)$$

In the model, it is assumed that the germination rates in the seed population are normally distributed around GR_{mean}, with a constant coefficient of variation f_{germ}. This assumption leads to cumulative distributions of germination times t_g that are skew in the way it is often observed with germination data. It was assumed that germination rates of the seeds in which germination is triggered by soil cultivation are not affected by their degree of dormancy. Since the model will be applied to field data in the Netherlands in spring, when temperatures are relatively low, the reaction of germination to supra-optimal temperatures is not included.

Pre-emergence growth

In chapter 4, a model is presented using a Gompertz curve to describe the time course of emergence, after planting pre-germinated seeds in homogeneous soil. The variables affecting emergence that were incorporated in the model were the temperature, which was kept constant, the depth at which the seeds were planted, the penetration resistance of the soil and the distribution of seed weights. In the present study, the Gompertz curve has been remodelled to a dynamic model, in order to simulate pre-emergence growth at fluctuating temperature, after non-simultaneous underground germination of seeds that are homogeneously distributed in the soil. Pre-emergence growth is modelled as two consecutive processes, cotyledon protrusion and shoot elongation. Cotyledon protrusion is assumed to be dependent on temperature only, and modelled with help of a temperature sum. Once the cotyledons have protruded, shoot elongation starts. A relational diagram of the simulation of shoot elongation is shown in Fig. 6.4.

Variation in the ability of seedlings to emerge from a certain depth arises from variation in the amount of seed reserves. Variation in emergence times is generated by assuming a normal distribution of pre-emergence growth rates in the population, with a constant coefficient of variation f_{gr}. This is in accordance with the findings of Finch-Savage and Phelps (1993), who reported that the normal distribution applied to rates provided the best fit to the emergence data of onion seedlings. In a constant environment, a normal distribution of pre-emergence growth rates generates a skew distribution of emergence times that exactly resembles a Gompertz curve when plotted cumulatively.

Heterogeneity in the seed population

Following soil cultivation, only a fraction of the seeds in the cultivated soil layer emerges as seedlings, and their emergence is spread in time. Whether or not a seed will develop into a seedling that will emerge after soil cultivation, is affected by its degree of dormancy, seed weight, and burial depth, all of which vary within the population. Spread in emergence times results from a vertical distribution of seed burial depths, and from a variation within the population in germination and pre-emergence shoot elongation rates.

Parameterization and initialization

The dormancy submodel and the subroutine in the germination model simulating the germination percentage (submodels I and IIA) were parameterized and initialized according to chapter 2. Parameters T_b, θ_{50} and f_{germ} in the subroutine simulating the germination rate (submodel IIB) were estimated from the germination curves observed in the exhumation experiments. For this purpose, data from the exhumation dates were pooled. Estimation of T_b and θ_{50} is shown in Fig. 6.5. Pre-emergence growth

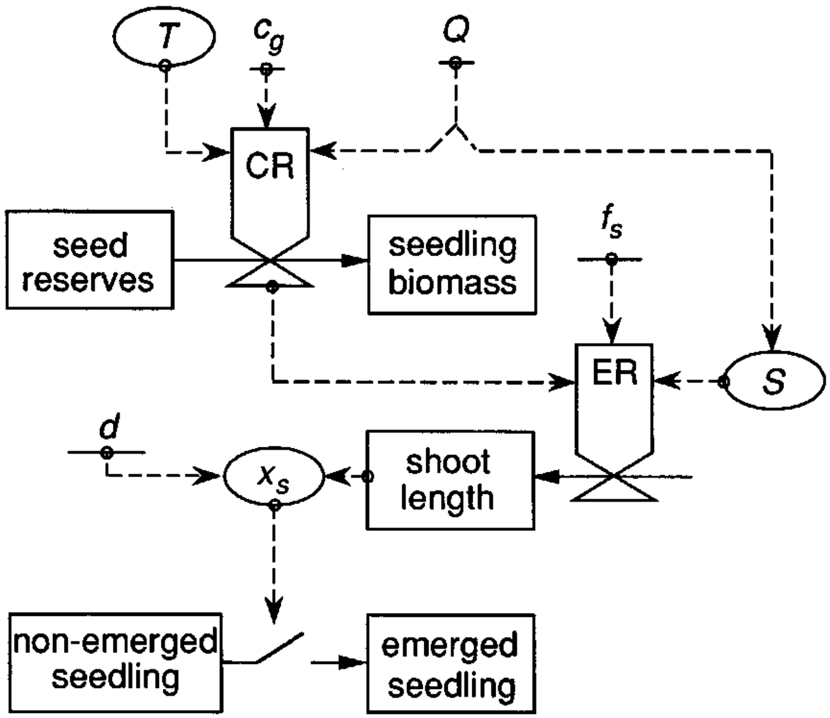

Fig. 6.4 Structure of the submodel simulating shoot elongation. Seed reserves are converted to seedling biomass at a rate (CR) that is dependent on both temperature (*T*) and soil penetration resistance (*Q*). A conversion factor (c_g) accounts for growth respiration losses. A fixed fraction f_s of the carbohydrates that are mobilized from the seed reserves are allocated to the shoot. Shoot elongation rate (ER) is calculated by multiplying the increase in shoot biomass (f_s·CR) with the specific shoot length (*S*), which is also dependent on soil penetration resistance (*Q*). It is assumed that the shoot grows to the soil surface in a straight line. Thus, the distance of the shoot tip to the soil surface (x_s) can be calculated by subtracting the shoot length from the depth of burial of the seed (*d*). As soon as x_s has decreased to zero, the seedling will emerge. If the seed reserves are depleted, CR will drop to zero. If by then the shoot tip has not yet reached the soil surface, the seedling will die.

(submodel III) was parameterized according to chapter 4. The coefficient of variation of the normal distribution of pre-emergence growth rates f_{gr} that replaces the relative dispersion of emergence times D used in chapter 4 was estimated by fitting the dynamic model to the emergence curves observed in chapter 4. No reduction of the conversion efficiency from seed reserves into shoot elongation at low temperatures was assumed. Newly estimated parameters in this study are given in Table 6.3.

In the model, the seed population is characterized by the number of seeds buried in the cultivated soil layer and their vertical distribution over the soil profile (see chapter 5), their degree of dormancy at the time of burial (see chapter 2), and the distribution of seed weights (see the description of the field experiment). The method of soil cultivation is characterized by the depth of soil cultivation, and the fraction of seeds within the cultivated layer that are exposed to daylight (see the description of the field experiment).

Assessment of goodness-of-fit

In analogy with the coefficient of multiple determination in regression models, the fraction variance accounted for by the simulation model R^2 is calculated as

$$R^2 = 1 - \frac{\sum (y_{obs} - y_{sim})^2}{\sum (y_{obs} - \bar{y}_{obs})^2} , \qquad (6.4)$$

where y_{obs} is the observed value and y_{sim} the simulated value.

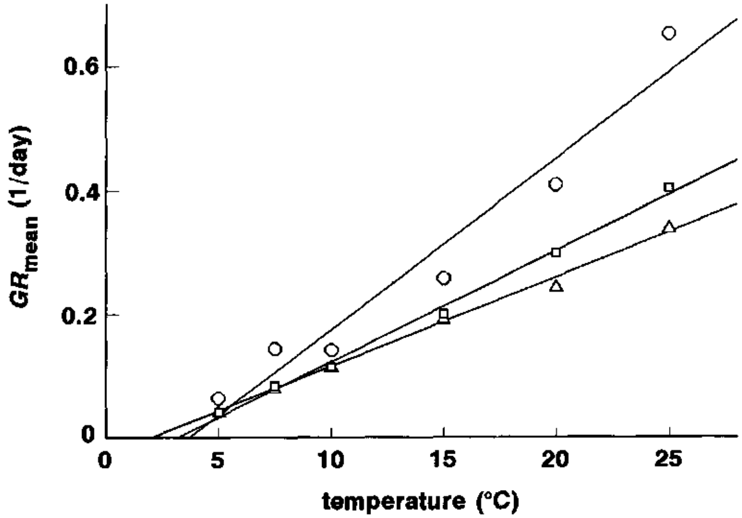

Fig. 6.5 Relationships between the mean germination rate GR_{mean} (= $1/t_{50}$) and temperature for *Polygonum persicaria* (□), *Chenopodium album* (△) and *Spergula arvensis* (○); r^2 values for the linear regressions were 0.998, 0.998 and 0.975, respectively.

Table 6.3 Newly estimated species parameters in the study.

	Polygonum persicaria	*Chenopodium album*	*Spergula arvensis*
T_b	3.2	2.0	3.7
θ_{50}	55.3	68.9	36.1
f_{germ}	0.3	0.3	0.3
f_{gr}	0.15	0.25	0.15

6.2.2 Field experiment

In December 1993, seeds of *Polygonum persicaria*, *Chenopodium album* and *Spergula arvensis* were mixed through the upper 20 cm soil layer of 18 field plots. Seed densities were 141,500 seeds m^{-2}, 212,200 seeds m^{-2} and 99,000 seeds m^{-2}, respectively. Average seed weights were 2.45 mg for the triangular *P. persicaria* seeds (37% of the population), 2.01 mg for the oval *P. persicaria* seeds (63% of the population), 0.78 mg for *C. album* and 0.39 mg for *S. arvensis*. In accordance with chapter 4, seed fresh weights in both the triangular and the oval subpopulation of *P. persicaria*, and in the population of *S. arvensis* were assumed to be normally distributed; in *C. album* a log-normal distribution of seed fresh weights was assumed. Coefficients of variation of the seed weights were equalled to the ones measured in chapter 4. The soil in the plots was a sandy loam, that was previously sterilized by X-ray radiation. In spring 1994, 15 plots were cultivated once only at five different dates, down to a depth of 15 cm, and 3 plots remained uncultivated. Cultivation consisted in a thorough mixing of the soil, and it was assumed that all seeds that were buried in the cultivated soil layer were irradiated at the time of soil cultivation. The method of soil cultivation was not varied in the experiment. In all plots, emergence of the three weed species was monitored. Observation intervals ranged from 1 to 5 days in the period from March to May, dependent on the rate of seedling emergence. Soil temperature under bare ground was measured during the experiment. Immediately after finishing the observations in September 1994, pF-curves and soil penetration resistances at pF 2.0 in the plots were measured. Further weather data were collected from a weather station 1.7 km from the experimental field.

In order to facilitate the interpretation of field emergence patterns, additional measurements on seasonal changes in dormancy and germination of the buried seeds were done. Changes in dormancy and germination were assessed by exhuming seed lots wrapped in nylon gauze envelopes that were buried close to the field plots. The exhumed seeds were irradiated with red light and their germination was tested at a range of temperatures in the laboratory. Exhumation dates corresponded with dates of soil cultivation. Further details of the experiment are given in chapter 5.

6.3 Results and discussion

6.3.1 Simulation of dormancy release

Prior to testing the overall simulation model with the emergence patterns observed in the field, the submodel simulating release of dormancy (submodel I), and the subroutine simulating the percentage of seeds germinating (submodel IIA) were tested with data from the exhumation experiment. Output from submodel I is the availability of a receptor protein that cannot be measured directly as yet. Submodel IIA translates the amount of available receptor into germination percentages in the seed population. Therefore, only the combination of submodels I and IIA (*i.e.* simulated germination percentages) can be tested. In Fig. 6.6 simulated germination percentages are compared to those in the exhumed seed portions. It shows that in general germination percentages in the laboratory tests are largely overestimated by the model. The results suggest that dormancy release simulated by submodel I occurred too early in the season. Apparently, the model that gives a good description of annual cycles in dormancy and germination when applied over several years (chapter 2), falls short when predictions are required within a growing season, with an accuracy on a time scale of weeks. As an alternative, I tested the model by Bouwmeester and Karssen (1992, 1993*a*,*b*) that also simulates germination percentages of exhumed seeds tested at constant temperatures in the laboratory. However, also data simulated by this model deviate largely from the ones observed in the exhumation experiment.

Options to improve the simulation of seasonal changes in dormancy and germination may be found in both the parameterization and the structure of the model. Parameterization of the submodels simulating seasonal changes in dormancy and germination may be improved by storing seeds in different temperature regimes in artificial conditions, by testing samples of the stored seeds for germination at regular time intervals in a range of temperatures, and thus estimate the exact temperature relations of dormancy release, dormancy induction, and germination. However, the most important progress on these submodels (I and IIA) is to be expected from research at a molecular physiological level. Submodels I and IIA quantify a highly hypothetical system (chapters 1 and 2). Improved knowledge on the physiological mechanism that causes changes in the width of the temperature range for germination may lead to a refinement of the model structure and to a more precise estimation of parameters.

In order to bypass the defective simulation of dormancy release, submodels I and IIA were skipped from the model. Field germination percentages were estimated from the exhumation data, rather than simulated by the model. By interpolating the relationship between the test temperature and the germination percentage of the exhumed seed lot in the laboratory, the germination percentage at the current field temperature was estimated. For this purpose, the average field temperature in the week after soil cultivation was used. Subsequent simulation runs with the model were done with these estimates as input.

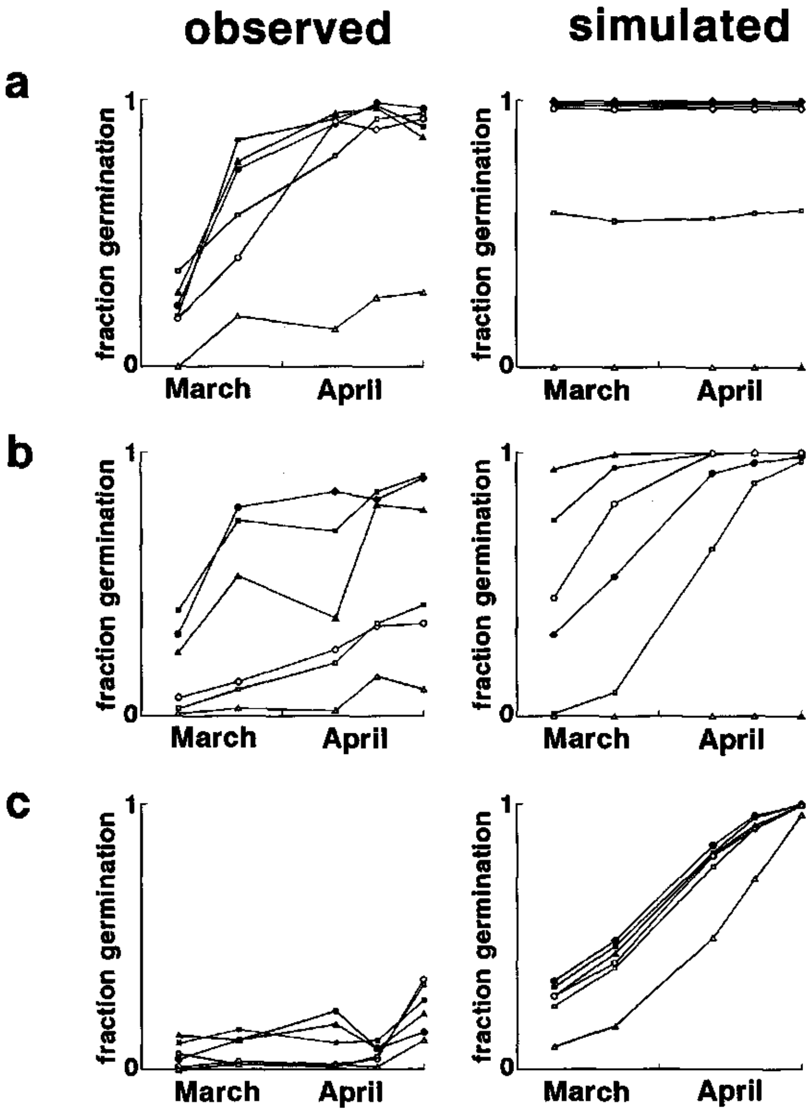

Fig. 6.6 Observed and simulated germination of exhumed seeds of *Polygonum persicaria* (a), *Chenopodium album* (b) and *Spergula arvensis* (c) as a function of exhumation date in 1994. After red irradiation, germination was tested in a range of temperatures (△ 5°C; □ 7.5°C; ○ 10°C; ▲ 15°C; ■ 20°C; ● 25°C).

6.3.2 The overall emergence pattern

In Fig. 6.7 simulated emergence patterns are compared to those observed in the field. Simulations were done using the model described in the Materials and Methods section, apart from the use of exhumation data to estimate the germination percentage in the field (Fig. 6.6). To allow a detailed comparison of observed and simulated emergence patterns, only the period from March to May has been depicted. Simulated emergence was restricted to this period, whereas there was only minor emergence observed outside this period. Observed emergence in the complete period from December 1993 until September 1994 was given in chapter 5. In *P. persicaria*, emergence after soil cultivation on 21 April and 3 May was simulated well. Observed emergence flushes after soil cultivations at 8 March, 21 March and 12 April, and also in the undisturbed plots exhibited two peaks. In all four treatments, there was a second emergence peak in May. Only the first peak was simulated by the model. Simulated emergence after soil cultivation on 12 April started too early. In *C. album*, emergence after soil cultivation on 21 April and 3 May was simulated well. Timing of simulated emergence after the soil cultivations in March did not coincide with the one observed in the field. Seedling numbers in these treatments, however, were negligible compared to those after the later soil cultivations, and hardly exceeded those in the undisturbed plots. After soil cultivation at 12 April, the model only simulated the first peak after soil cultivation, which started too early. In *S. arvensis*, in all treatments of the experiment, the first emergence peak after soil cultivation was followed by several others. The timing of the later flushes was often correlated with those in the other treatments, including those in the undisturbed plots. There was a broad parallel between *S. arvensis* and *C. album*. The first peak of emergence after soil cultivations at 21 April and 3 May was simulated well. Simulated emergence after soil cultivation at 12 April occurred in one peak, which started too early. The time of emergence after the soil cultivations on 8 March and 21 March did not coincide with the observed data. Emergence following soil cultivation at 8 March, 21 March and 12 April hardly exceeded that in undisturbed soil.

In *S. arvensis* and to a lesser extent in *P. persicaria* and *C. album*, emergence occurred in several flushes. The most obvious difference between the experimental treatments was the extent and timing of the first flush of seedling emergence following soil cultivation. Seedling flushes later in the season coincided in the different treatments, including the undisturbed treatment, and were thus independent of soil cultivation. I concluded that only the first seedling flush following soil cultivation was triggered by soil cultivation, and later flushes were triggered by other factors. The model simulates weed emergence that is directly related to soil cultivation, and will therefore not generate these later seedling flushes. Therefore, in all experimental treatments, the model simulated only one seedling flush. Consequently, I will relate the performance of the model to the first flush after soil cultivation.

In Table 6.4 simulated seedling numbers are compared to numbers observed in the first emergence peak. In general, there was good correspondence between simulated and observed numbers (*P. persicaria*: R^2 = 0.80, *C. album*: R^2 = 0.92, *S. arvensis*: R^2 = 0.95). Exceptions were the seedling numbers of *P. persicaria* and *C. album* that emerged after soil cultivation at 12 April, which were overestimated by the model. In *P. persicaria*, it can be concluded that this resulted from an overestimation of field

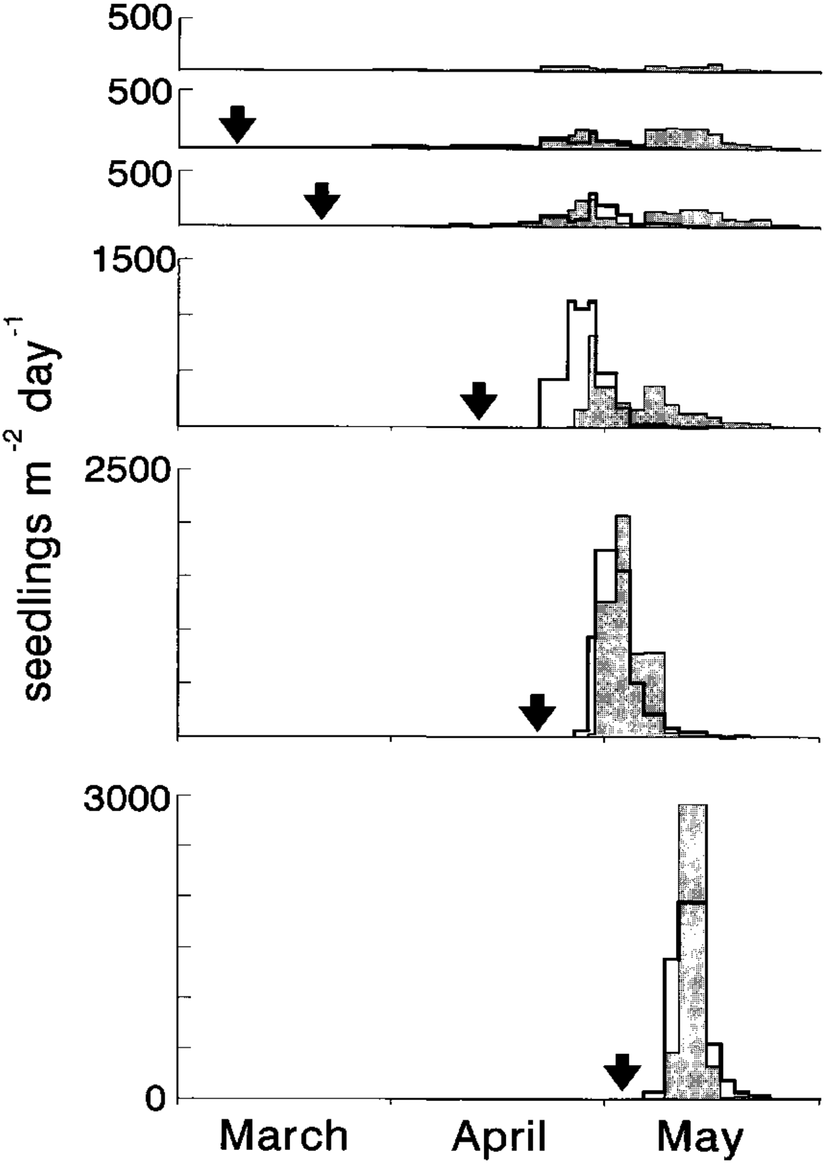

Fig. 6.7a Observed (▨) and simulated (□) weed seedling emergence (seedlings m^{-2}day^{-1}) of *Polygonum persicaria* in the undisturbed and the cultivated treatments in 1994. In the undisturbed treatment, only observed weed emergence is shown. In the cultivated treatments, only weed emergence following soil cultivation is depicted. Arrows indicate the dates of soil cultivation.

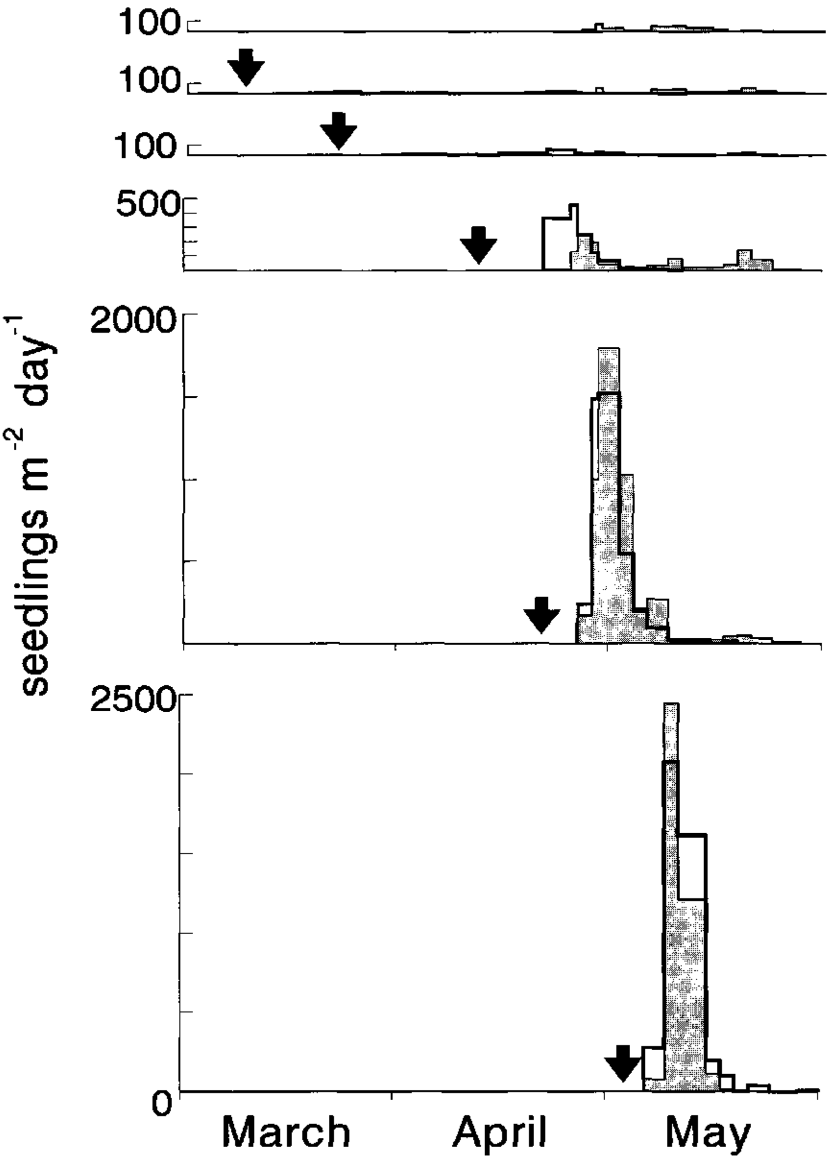

Fig. 6.7b Observed (□) and simulated (▣) weed seedling emergence (seedlings m^{-2}day^{-1}) of *Chenopodium album* in the undisturbed and the cultivated treatments in 1994. In the undisturbed treatment, only observed weed emergence is shown. In the cultivated treatments, only weed emergence following soil cultivation is depicted. Arrows indicate the dates of soil cultivation.

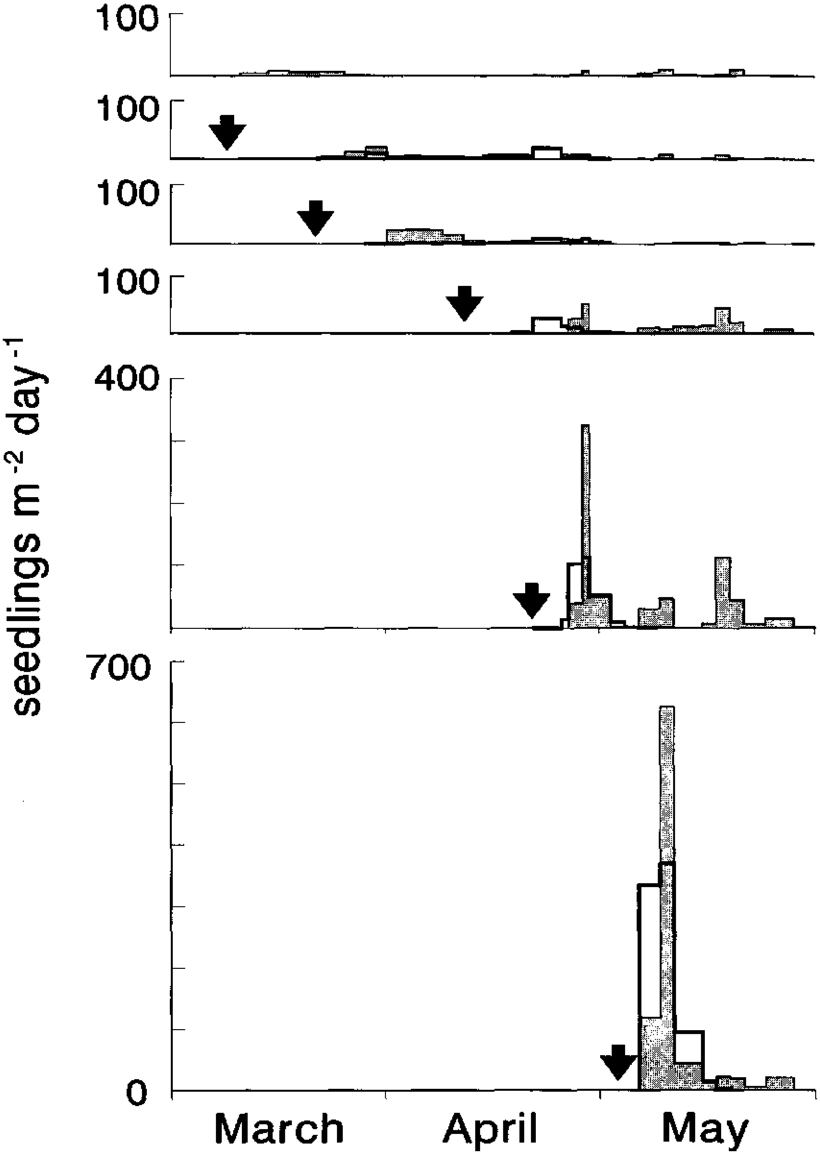

Fig. 6.7c Observed (▨) and simulated (☐) weed seedling emergence (seedlings m^{-2}day^{-1}) of *Spergula arvensis* in the undisturbed and the cultivated treatments in 1994. In the undisturbed treatment, only observed weed emergence is shown. In the cultivated treatments, only weed emergence following soil cultivation is depicted. Arrows indicate the dates of soil cultivation.

Table 6.4 Observed and simulated seedling numbers (in thousands of seedlings m^{-2}) in the first emergence flush after soil cultivation.

Date of soil cultivation (1994)	*Polygonum persicaria*		*Chenopodium album*		*Spergula arvensis*	
	obs.	sim.	obs.	sim.	obs.	sim.
8 March	1.8	1.3	0.3	0.2	0.2	0.2
21 March	1.9	2.3	0.3	0.5	0.3	0.1
12 April	3.0	8.1	1.0	2.8	0.1	0.2
21 April	12.1	11.5	10.0	8.5	0.6	0.5
3 May	13.5	12.6	10.2	12.1	1.8	2.2

germination. Based on the exhumation experiment, a fraction germination of 0.82 was expected, but this cannot be reconciled to the observation that in the field only a fraction 0.51 of the seeds was lost from the upper 2 cm soil layer.

For the emergence curves in cultivated soil, it was calculated how many days passed between soil cultivation and the attainment of an emergence percentage of 5% and 50 %. Timing of the first emergence flushes was predicted well in *P. persicaria*. There was good correspondence between simulated and observed number of days to 5% emergence (R^2 = 0.89) and to 50% emergence (R^2 = 0.97). As a result of an incorrect simulation of a part of the data in *C. album* and *S. arvensis*, *viz.* emergence after soil cultivations in March, R^2 values for these species were < 0. In these two species, simulated emergence after the soil cultivations in March was later than observed emergence. A possible reason may be that in order to simulate emergence from these plots, the relationship between soil penetration resistance and underground shoot elongation rate given in chapter 4 had to be extrapolated quite far. The relationship was estimated from measurements in a range of soil penetration resistances from 0.4 MPa to 1.0 MPa, while soil penetration resistances in the plots cultivated at 8 and 21 March were 1.64 MPa and 1.69 MPa, respectively. Probably, in *C. album* and *S. arvensis*, shoot elongation rates at soil penetration resistances above 1.0 MPa were underestimated in the model, which caused simulated emergence to be later than observed emergence. Besides, in several species, detailed analysis revealed that a linear relationship between temperature and germination rate tends to underestimate germination rates at temperatures slightly above T_b (Thompson and Fox, 1976). Fig. 6.5 suggests that this may also have been the case in *S. arvensis*, and, therefore, in this species this may be another reason for the overestimation of the time to emergence at the low field temperatures in March.

For all three species together, there was a strong correlation between the quantitative importance of the emergence flush and its predictability by the model. All quantitatively important emergence flushes could be predicted well. Comparison with emergence patterns in undisturbed plots shows that, since seedling numbers in *C. album* and *S. arvensis* after the soil cultivations in March were low, these flushes could hardly be distinguished from the background noise. This implies that assessment of the model predictions for these treatments was less reliable than for the other ones.

6.3.3 *Effect of soil moisture content*

The omission of soil moisture effects was based on the consideration that the model would be applied to spring-emerging weed species, and in spring soil moisture conditions in the Netherlands are seldom an important impediment to germination and emergence (Van der Weide, 1993). Spitters (1989) showed that field emergence is unrestricted at soil moisture tensions between pF 2.0 and 2.7, and that both seedling number and emergence rate are progressively reduced between pF 2.7 and 4.2. Soil moisture tension in the upper 2 cm of the soil, in relation to rainfall, was simulated by the simulation model presented by Spitters (1989), extended with a Penman evaporation subroutine for bare soil according to Kropff and Van Laar (1993) (Fig. 6.8). The simulation showed that in the period from March until May the soil moisture tension hardly ever exceeded pF 2.7. Thus, over the period when the emergence model simulated weed emergence patterns, the effect of water stress could be neglected.

The reaction of seeds to remoistening after a period of desiccation (chapter 5) can be inferred from Fig. 6.8. Especially in July and August, emergence flushes of *C. album* and particularly *S. arvensis* occurred that coincided with periods of high soil moisture following periods of low soil moisture. However, also in May and June emergence peaks in these two species may be correlated with dry-wet-alternations. As yet, the extent and the exact timing of these flushes are not quantitatively understood.

6.3.4 *Effect of soil cultivation date*

Soil cultivation triggers germination, and consequently, the timing of soil cultivation determines the environmental conditions in which germination and pre-emergence growth take place. Since the dormancy state of buried weed seeds changes continuously over the

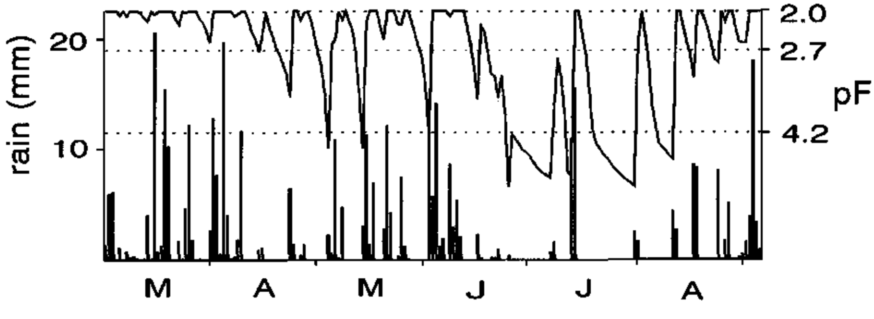

Fig. 6.8 Observed daily rainfall (mm) (bars) and simulated soil moisture tension (pF-values) in the upper 2 cm of the soil (line) in the period from March until August 1994.

seasons, the timing of soil cultivation also determines the degree of dormancy when the seeds are triggered to germinate. In the simulations, differences in seedling numbers in the simulated emergence flushes after the different dates of soil cultivation were caused by differences in three factors: the degree of dormancy of the buried seeds at the time of soil cultivation, the soil temperature after soil cultivation (the seed-bed temperature), and the soil penetration resistance after soil cultivation. As a measure for the degree of dormancy at the time of soil cultivation, germination percentages of seed portions exhumed simultaneously to soil cultivation were used. Differences in the timing of the emergence flushes after the different dates of soil cultivation were effected by two factors: seed-bed temperature and soil penetration resistance. Measurements of the environmental factors are given in chapter 5. Measurements of seed dormancy are presented in Fig. 6.6. An analysis was carried out to assess the relative contribution of differences in dormancy, seed-bed temperature and soil penetration resistance to differences in the simulated seedling numbers, and the relative contribution of differences in seed-bed temperature and soil penetration resistance to differences in the simulated timing of emergence.

In the simulation, the effect of a factor was removed by using the average value of the factor over all soil cultivation dates, instead of using the actual, different values that were measured at each cultivation date. The simulation results of the reduced model were compared to those of the complete model. The effect of the withdrawal of variation in one or two factors on the result of the simulation was quantified by $R^{2\prime}$, defined as

$$R^{2\prime} = 1 - \frac{\sum (y'_{sim} - y_{sim})^2}{\sum (y_{sim} - \bar{y}_{sim})^2} , \tag{6.5}$$

where y_{sim} is the simulated value with the complete model, and y'_{sim} is the value simulated with the reduced model. The more $R^{2\prime}$ approaches 1, the less differences in the factor or factors that were withdrawn contributed to the simulation of differences in emergence. Results from the analyses are shown in Tables 6.5 and 6.6.

Table 6.5 shows that simulated differences in the extent of the spring emergence flushes of *S. arvensis* were almost completely due to differences in dormancy at the different cultivation dates. In *P. persicaria*, simulated variation in seedling numbers emerging was caused by differences in both dormancy and soil penetration resistance. In *C. album* simulated differences in both dormancy and seed-bed temperature and soil penetration resistance were responsible for differences in seedling numbers in the emergence flushes.

The simulation model accounted for 80 to 95% of the variance in the numbers of seedlings emerging after soil cultivation at different times in spring. Linear regression of the number of seedlings emerging in spring (*i.e.* before 30 June) on seed-bed temperature accounted for 95 to 99% of the variance (chapter 5). Linear regression of the number of seedlings emerging in the first emergence flush after soil cultivation on seed-bed temperature accounted for 86 to 99% of the variance. The present analysis, however, revealed that differences in seed-bed temperature had little or no effect on the simulation of seedling numbers emerging in the first flush after soil cultivation. The high correlation between seed-bed temperature and the number of seedlings emerging, either before 30 June (chapter 5) or in the first flush, was due to a high correlation between seed-bed temperature and the other factors affecting emergence, *viz.* dormancy and soil penetration resistance. It is clear that the correlation did not result from a direct causal relationship: the model evaluation shows that within the range temperatures that occurred in the experiment, the temperature of the seed-bed hardly influenced the number of seedlings emerging.

Table 6.5 Fraction variance in simulated seedling numbers ($R^{2\prime}$) accounted for by models incorporating variation in dormancy (dorm), soil penetration resistance (Q), or seed-bed temperature (T).

Model comprises variation in	*Polygonum persicaria*	*Chenopodium album*	*Spergula arvensis*
dorm, Q, T	1.00	1.00	1.00
dorm, Q	0.99	0.40	0.70
dorm, T	0.40	0.57	0.81
Q, T	0.86	0.20	0.49
dorm	0.42	0.03	0.96
Q	0.76	0.17	0.25
T	0.00	0.19	0.24

Table 6.6 shows that in all three species, variation in the simulated timing of seedling emergence after soil cultivation was the result of variation in the combination of soil penetration resistance and seed-bed temperature. In the simulations, the time to germination amounted to 27 to 81% of the total time between soil cultivation and emergence, dependent on species and soil cultivation date (results not shown). In *C. album* and *S. arvensis*, analysis of the performance of the model under a range of hypothetical conditions, with respect to the timing of emergence, should only be regarded as an exploration of model behaviour. In *P. persicaria*, it has also practical value, since the model gives a good prediction of the timing of emergence over the complete range of conditions present in the field experiment.

Only in *P. persicaria*, the simulation model could explain the variance in the time to first emergence after soil cultivation at different times in spring (R^2 = 0.89). In chapter 5, the concept of thermal time was used to predict the onset of emergence after soil cultivation. The onset of emergence was defined as the moment when 5% of the seedlings

Table 6.6 Fraction variance in median of simulated emergence times, $R^{2\prime}$, (in days after soil cultivation) accounted for by models incorporating variation in soil penetration resistance (Q) or seed-bed temperature (T).

Model comprises variation in	*Polygonum persicaria*	*Chenopodium album*	*Spergula arvensis*
Q, T	1.00	1.00	1.00
Q	0.39	0.20	0.10
T	0.33	0.37	0.35

emerging in spring (*i.e.* before 30 June) had emerged. Using daily average soil temperatures at a depth of 1 cm, they described the combined process of germination and emergence in *P. persicaria*, *C. album* and *S. arvensis* with base temperatures of 5.2°C, 0.0°C and 2.0°C respectively. Regarding the number of days passing between soil cultivation and the attainment of an emergence percentage of 5%, R^2 values calculated according to eqn (6.4) were 0.97, 0.26 and 0.75, respectively. The present analysis, however, shows that a model that is fitted on daily average soil temperature at a depth of 1 cm may give a good correlative description of the onset of emergence, but it is not based on a causal relationship, and has little predictive value. The averaged base temperatures that were determined in laboratory experiments and used in the present model are 3.0°C, 2.5°C and 4.1°C, respectively. Table 6.6 shows that differences in the timing of emergence between the soil cultivation treatments were only partly dependent on differences in soil temperature alone. Furthermore, simulation revealed that when the daily average temperature approximately equalled the base temperature for germination and pre-emergence growth in a species, and when there were large daily temperature fluctuations around the daily average, simulation results based on hourly temperatures deviated largely from those based on daily average values (results not shown) (*cf.* Yin *et al.*, 1996). When using the daily average temperature in these cases, progress in germination and pre-emergence growth during the daytime is neglected. In this study, this was especially important for the simulation of emergence patterns after the soil cultivations in March. For the later treatments, the use of hourly or daily average temperatures did not make an important difference.

In chapter 5, it was suggested that the exact time course of field emergence after its onset was not to be described by the thermal time concept because of periods of reduced soil moisture that temporarily ceased the emergence process. Simulation showed that periods of reduced soil moisture that inhibited emergence were short (Fig. 6.8). The defective description of later stages of the emergence process in chapter 5 was rather an effect of dry-wet-alternations that triggered subsequent emergence flushes than of periods of reduced soil moisture that interrupted the emergence process.

6.3.5 Comparison with existing models

Harvey and Forcella (1993) developed a model for the prediction of *C. album* emergence in spring. In Fig. 6.9 emergence patterns simulated with help of the model by Harvey and Forcella (1993) are compared to the ones observed in this study. In order to simulate the emergence patterns, total emergence was equalled to the one observed in the period from 1 March until 31 May. In the model by Harvey and Forcella (1993) emergence flushes are spread over longer time periods than in the present model (Fig. 6.7b). The simulated onset of emergence after soil cultivation in March was later than the observed one, which corresponded with the present model. After soil cultivation on 12 April, the model by Harvey and Forcella (1993) simulated a seedling flush extending from the end of April to the end of May, which corresponded with the period over which three subsequent flushes occurred in the field. The present model only simulated the first of these three flushes. However, after soil cultivations on 21 April and 3 May, the seedling flush simulated by the model of Harvey and Forcella (1993) lasted until mid June and end June respectively, while in the field no substantial emergence occurred after mid May. Here, both the timing of peak emergence and the duration of the flushes were simulated more accurately by the present model.

The *timing* of the significant emergence flushes that were triggered by soil cultivation could be predicted well by the present model. Also existing models for weed emergence patterns (Table 6.1) show that the distribution of seedling emergence in time is generally well understood. Benech-Arnold and Sánchez (1995) stressed the fact that usually dormancy is present in weed seed populations. As a consequence, estimation of the proportion of non-dormant seeds is needed in order to predict the *number* of seedlings emerging. Five of the seven models summarized in Table 6.1 only comprise the timing of seedling emergence (Takayanagi and Kusanagi, 1989; Alm *et al.*, 1993; Forcella, 1993; Harvey and Forcella, 1993; King and Oliver, 1994). They fix the final extent of emergence at 100%, and simulate how 100% field emergence is reached in the course of time. However, they do not predict whether 100% emergence concerns *e.g.* 20 or 2000 weed seedlings per square meter. The present study shows that a mechanistic model simulating changes in seed dormancy that is accurate enough to be used in predictive models, is still beyond reach. As yet, descriptive models for seed dormancy like the one used in this study, or the ones presented by Spitters (1989), Benech-Arnold *et al.* (1990), Forcella (1992), Van der Weide (1993) and Forcella *et al.* (1996) may be used. The problem of modelling changes in dormancy does not occur in predictions of field emergence of non-dormant seeds of many crop species. Finch-Savage and Phelps (1993), however, showed that even for crop seed of uniform quality sown at a uniform depth, the emergence level may vary considerably as a result of soil conditions, which urged them to also constrain the model to maximum emergence observed in the field. This study shows that soil penetration resistance may be an important soil condition affecting emergence levels. The present model allows a quantification of the effect of soil penetration resistance on the level of field emergence.

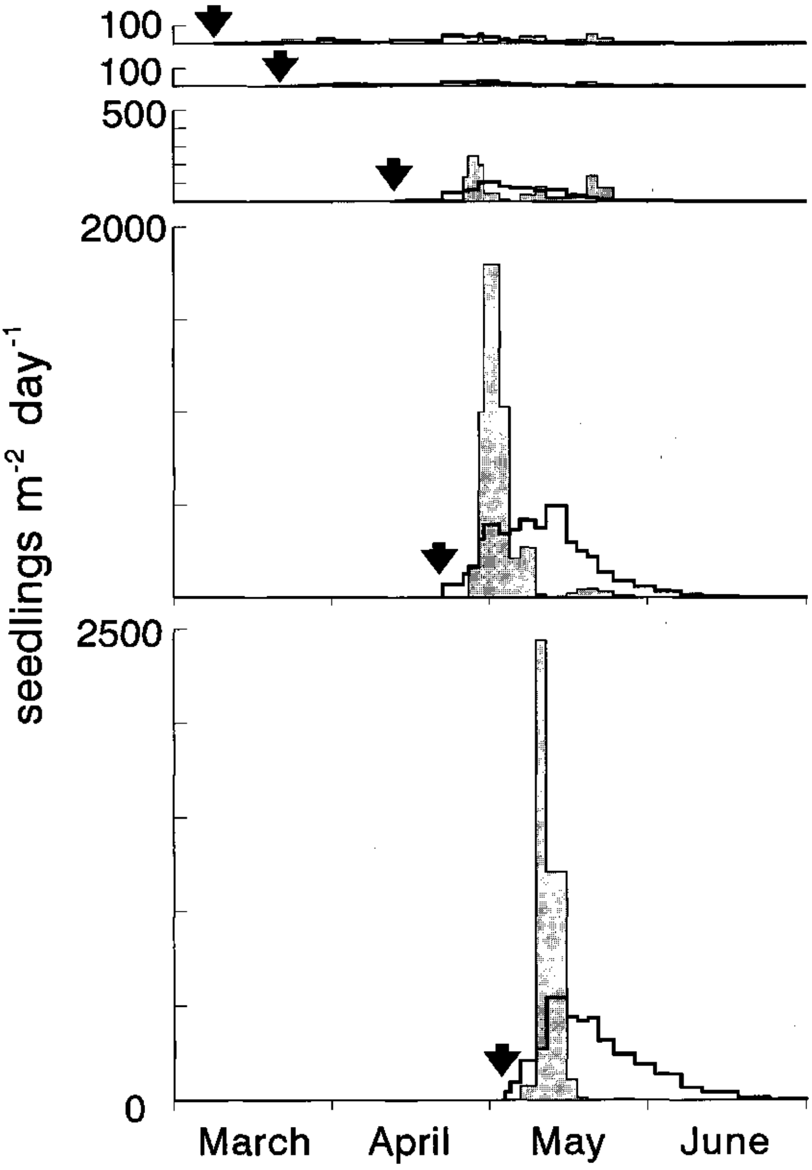

Fig. 6.9 Observed (▨) and simulated (□) weed seedling emergence (seedlings m^{-2}day^{-1}) of *Chenopodium album* following soil cultivation in 1994. Simulation was done by the model by Harvey and Forcella (1993). Arrows indicate the dates of soil cultivation. *Cf.* Fig. 6.7b.

6.3.6 Application

The main objective of the model described in this chapter was to increase understanding of the effects of environmental factors on field emergence patterns. For this purpose, itwas attempted to include the physiological mechanisms of dormancy release, germination and emergence in the model. At the present level of knowledge, however, simulation of these processes will inevitably be based on a mixture of empirical correlations and physiologically based relationships. The attempt to maximize the use of relationships that are based on physiological mechanisms in the simulation of weed emergence patterns was very useful for detecting gaps in physiological knowledge, and may be used as a guide-line for the research in this field.

The mechanisms of the processes that determine weed emergence are still partly hypothetical, and few quantitative data exist to model the physiological processes. This implies that descriptive models that are not based on physiological principles but on empirical relationships may give a better description of field emergence curves than physiological models. However, descriptive approaches to predict seedling numbers and the timing of their emergence have the disadvantage that extrapolation to environmental conditions outside the range tested is perilous, and, therefore, their predictive value is limited. In the long term, modelling the physiological mechanisms that result in seedling emergence may lead to a prediction that is reliable in a large range of conditions. For example, in this study a simple linear relationship with seed-bed temperature offered a better description of seedling numbers in flushes following soil cultivation at different times in spring than the more physiologically based model. The difference between such a relationship and a simulation model is that the former has no predictive value, while the latter has. Analysis with the simulation model even showed that in reality seed-bed temperature hardly affected the extent of the seedling flush.

For a prediction of the competitiveness of the weed population relative to that of the crop, the timing and extent of the first emergence is most important (Kropff and Van Laar, 1993; Leblanc and Cloutier, 1997). Kropff and Van Laar (1993) simulated yield loss curves of sugar-beet in competition with *Chenopodium album* populations differing in plant density, time of emergence relative to that of sugar-beet, and plant height. From these curves it can inferred that, at present, no emergence models are precise enough to allow an accurate estimation of crop yield loss from weed interference. Ideally, weed density should be predicted with an accuracy of one plant per square meter and the time between crop and weed emergence with an accuracy of one day.

For a better timing of seed-bed preparation, after having prepared a stale seed-bed, a prediction of the timing of the end of the emergence flush is important. Harvey and Forcella (1993) pointed out that also in this respect knowledge on the absolute number of seedlings in the flush is important, in order to assess, for example, whether the final 10% of the emergence flush that will emerge after seed-bed preparation comprises 2 or 100 seedlings per square meter. Again, this stresses the importance of quantitative assessment of seed dormancy and of seed numbers in the seed bank.

6.4 Conclusions

A model simulating emergence patterns was developed and evaluated with regard to the extent and the timing of weed emergence in weed emergence patterns. Both extent and timing of emergence determine the degree of weed interference with crop growth. The model integrated simulation of changes in dormancy, germination and pre-emergence growth. The distinction of the three processes determining field emergence proved to be a crucial step in the quantitative understanding of weed emergence. It allows an accurate definition of the phases in the emergence process of which knowledge is lacking, and of the relative importance of the different environmental factors that affect the emergence process.

In existing models for emergence patterns, prediction of the extent of emergence remained relatively under-exposed. This study pointed out that differences in dormancy are a major cause of differences in the extent of emergence. Experimental assessment of the degree of dormancy of the buried seed population at the date of soil cultivation led to a good prediction of seedling numbers after soil cultivation. However, models simulating annual cycles in dormancy and germination of buried weed seeds (Bouwmeester and Karssen, 1992, 1993*a*,*b*; chapter 2), which might provide estimates of germination percentages resulting from soil cultivation, do not have the accuracy required for predictions in the field. Research aiming at improving the prediction of weed seedling emergence in the field should focus on improving the simulation of seasonal changes in dormancy and germination of buried weed seeds. The accurate prediction of seedling numbers once the germination percentage in the soil is known, suggests that the hampering effect of soil penetration resistance on pre-emergence growth is quantitatively well understood.

The timing of seedling emergence depends on the rates of germination and pre-emergence growth. If there is substantial emergence as a result of soil cultivation, a good estimate of the timing of the first emergence flush of the three species following soil cultivation can be given. In an agronomic perspective, therefore, model performance is satisfying. Prediction of the timing of emergence from compact soils may be improved by a quantification of underground shoot elongation rates at high soil penetration resistances. Prediction of the timing of emergence at the time of the season when the temperature hardly exceeds the minimum temperature for germination may be improved by a more accurate quantification of germination rates at low temperatures. Prediction of field emergence is limited to the first seedling flush following soil cultivation. Fluctuating environmental factors lead to emergence flushes, that do not depend on the date of soil cultivation with regard to their timing. For a prediction of complete emergence patterns, and of emergence patterns on undisturbed soil, these factors should be identified and quantified. In the perspective of crop-weed competition, however, prediction of the first weeds to emerge is far more important than prediction of the later flushes.

The two environmental factors that are reported in the literature to exert an overriding effect on seedling emergence, are temperature and soil moisture. Analysis by means of the simulation model shows that although correlations between seed-bed temperature and seedling numbers and the timing of emergence may be strong, they are only partly based on causal relationships. Temperature affects all three processes leading to weed emergence in the field. The degree of dormancy at the moment of soil cultivation can be calculated on the basis of temperature history. For the prediction of germination and pre-emergence growth after soil cultivation a temperature forecast must be used. An exact forecast of the temperature over the necessary time span is impossible. The present study points out that, within the range of temperatures occurring in spring in the Netherlands, the number of germinating seeds and the percentage of them which emerge as seedlings are not strongly affected by temperature. The rates of germination and pre-emergence growth are sensitive to temperature. However, a reliable risk analysis can be made based on the probability distribution of temperatures at the time of the year when emergence occurs. It is important that temperature is not only input as a daily average, but that also diurnal fluctuations are taken into account. In this study, the effect of soil moisture was not important in the period of the soil cultivations. However, for application of the model in a wider range of circumstances, quantification of the soil moisture effect is indispensable. Most likely, drying out of the seed-bed plays an important role in the triggering of later emergence flushes. The study showed that the effect of soil penetration resistance is quantitatively important, with respect to both seedling numbers and their time of emergence. This stresses the importance of the phase of pre-emergence growth in the emergence patterns of weeds.

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7 GENERAL DISCUSSION

7.1 Modelling weed emergence patterns

Arable weeds do not emerge at random over the year, but in clearly defined species-specific seasonal patterns, that are modulated by environmental factors and cultivation measures. Emergence patterns have been documented for more than 180 arable weed species in the temperate regions of the world. Quantitative understanding of the factors that determine weed emergence patterns may facilitate more precise *a priori* evaluations of weed control measures, and may thus support decisions to be made in weed control. However, most studies in the literature have provided only qualitative descriptions of seasonal distributions of weed seedling emergence. These studies have increased the general understanding of the factors that affect field emergence, but not the predictability of the patterns at the level of detail that is required for application in practice. For seven weed species only, quantitative models have been developed (Takayanagi and Kusinagi, 1989; Benech-Arnold *et al.*, 1990; Alm *et al.*, 1993; Forcella, 1993; Harvey and Forcella, 1993; Van der Weide, 1993; King and Oliver, 1994). The state of the art with respect to the understanding of emergence patterns is reflected in these models being mixtures of empirical correlations and physiological mechanisms. Only a quantification of the physiological processes that determine field emergence of weeds may lead to a mechanistic understanding of weed emergence patterns. Eventually, from such detailed mechanistic models, simple models for prediction may be derived.

The current study is one of the first steps towards a mechanistic model for weed emergence. To my knowledge, it is the first attempt at a general model for weed seedling emergence that includes predictions of both seedling numbers and the distribution in time of their emergence. Existing models use general descriptions of germination and emergence rates, *e.g.* thermal time, but do not include the extent of the flushes (Takayanagi and Kusinagi, 1989; Alm *et al.*, 1993; Forcella, 1993; Harvey and Forcella, 1993; King and Oliver, 1994), or simulate both emergence rate and emergence percentage, but in such a way that the model specifically applies to a certain species (*Sorghum halepense*, Benech-Arnold *et al.*, 1990; *Galium aparine*, Van der Weide, 1993). The present model applies to the large group of weed species from temperate regions that require light for germination. It was tested for three summer annual weed species, but adaptation to other species including winter annuals is only a matter of parameterization.

In this study, the combination of experimental work and analysis with help of computer simulation proved to be an effective tool in gaining insight in the relationships between the processes and environmental factors determining weed emergence patterns. Gaps in the existing knowledge have been identified and filled in. The distinction between changes in dormancy, germination and pre-emergence growth appeared to be crucial for an improved understanding of field emergence patterns of weeds (*cf.* Cousens and Peters, 1993). Separate submodels were developed for changes in dormancy, germination and pre-emergence growth, in which the effects of the most relevant environmental factors on these processes were quantified. Both the relevant factors and their quantitative effects differed between the processes. The model simulating field emergence, that is presented in this study, is an integration of the submodels. The model was evaluated with help of field observations. Substantial emergence flushes following soil cultivation, especially later in spring, can be simulated well, using an experimental method for estimating the degree of dormancy at the moment of soil cultivation. Evaluation of the model led to an assessment of the relative importance of the different processes and environmental factors, to the identification of lacks of knowledge and, as far as gaps in the knowledge could not be filled in within the current study, to specific recommendations for further research in all three processes. Here the current state of development with respect to the simulation of dormancy, germination and pre-emergence growth will be summarized, and options for improvement will be discussed.

7.1.1 Annual cycles in dormancy and germination

To my knowledge, the simulation model for annual cycles in dormancy and germination that is presented in this study is the first attempt at a quantification of these cycles that is based on a hypothesis about the underlying mechanism. It integrates the biochemical concept of dormancy hypothesized by Hilhorst (1993), in which dormancy is related to the amount of a phytochrome receptor, and the ecophysiological concept presented by Karssen (1982), in which dormancy is related to the temperature range over which seeds germinate. Evaluation of field and laboratory experiments pointed out that annual changes in seed dormancy and germination can be simulated with reasonable accuracy (chapter 2), but not at a time scale that is required for predicting field emergence (chapter 6).

In the model simulating seasonal changes in dormancy and germination, a submodel for dormancy and a subroutine for the extent of germination were integrated. At present, the model was parameterized by a calibration procedure, using data from a three years' burial experiment. Parameterization of the model may be improved by storing seeds in different temperature regimes in artificial conditions, by testing samples of the stored seeds for germination at regular time intervals in a range of temperatures, and thus estimate more exactly the temperature relationships of dormancy release, dormancy induction and germination. The most significant progress in the simulation of annual cycles in dormancy and germination, however, is to be expected from research at a molecular physiological level. The dormancy submodel reflects a highly hypothetical system. Dormancy is related to the availability of a hypothetical membrane protein acting as a phytochrome receptor (chapters 1 and 2). The receptor protein has not been identified yet, implying that direct measurement of the degree of dormancy in seeds is not possible. The subroutine for the extent of germination uses the amount of available phytochrome receptor, simulated by the dormancy submodel, as an input for simulating germination percentages in the seed population (chapter 2). For that purpose, it quantifies the kinetics of the interaction between phytochrome and its tentative receptor. The hypothetical nature of the receptor implies that only indirect measurements on the mechanisms comprised in both the dormancy submodel and the germination subroutine are possible. For an improved evaluation of the simulation of seasonal changes in dormancy and germination, more knowledge is needed on the physiological mechanism that causes changes in the width of the temperature range for germination, and in the sensitivity for germination stimulants like light and nitrate. Research into gene expression during annual dormancy cycling, in relation to simultaneous changes in responsiveness to temperature, light and nitrate is envisaged by the Department of Plant Physiology of Wageningen Agricultural University (Hilhorst, pers. comm.). The eventual possibility to measure seed dormancy directly, without the necessity of conducting a germination test, allows a more detailed evaluation of the model structure of the dormancy submodel and a more exact estimation of parameters. Such a progress in physiological research would also imply that simulation of the interaction between phytochrome and its receptor can be evaluated separately from simulation of dormancy, which may lead to a refinement of the model structure and improvement of parameter estimation in the germination subroutine.

7.1.2 The effect of desiccation on dormancy

Prediction of field emergence by the model is limited to the first seedling flush following soil cultivation. Especially in *C. album* and *S. arvensis*, fluctuating environmental factors led to emergence flushes later in the season that did not depend on soil cultivation (chapters 5 and 6). Desiccation may play an important role in the triggering of these late season emergence flushes. In *C. album* and *S. arvensis*, desiccation to a seed moisture content of 6-9% breaks dormancy, in addition to the changes in dormancy occurring during burial in moist soil (Bouwmeester and Karssen, 1989; Bouwmeester, 1990). Results by Bouwmeester (1990) indicate that the effect of desiccation may increase with burial time over years, implying that in an natural seed bank the effect may even be larger than observed in the one-season field experiment reported in chapters 5 and 6. Quantification of the dormancy breaking effect of desiccation, and its interaction with other environmental factors may be the first and most important step towards quantifying weed emergence flushes later in the season.

7.1.3 Germination

The germination process is simulated in two separate subroutines (chapter 6). The first subroutine simulates the percentage of seeds germinating, and is closely integrated with the dormancy submodel. The model in which the subroutine simulating germination percentages and the dormancy submodel are integrated, is evaluated in a previous section. The second subroutine simulates the distribution of germination times.

Germination percentage

In the present germination subroutine, the effect of temperature is quantified on a gradual scale, while light and nitrate are treated as all-or-nothing factors. For the simulation of weed seed germination in most field situations, including those in the current study (chapter 6), this is appropriate. If the model would be used to evaluate weed emergence in relation to the amount of nitrogen fertilizer, and after soil cultivation in reduced light conditions, *e.g.* at night or using covered implements, the quantitative effects of light intensity and nitrate concentration on germination should be included. Data like those presented by Derkx and Karssen (1993) may be used for this purpose.

As yet, the germination tests that were used to parameterize the subroutine for the extent of germination were conducted at constant temperatures. Assessment of germination at fluctuating temperatures may increase the insight in the temperature relationships for germination, and may also lead to improved predictions in fluctuating field situations. An invaluable data set may be found in the articles by Baskin and Baskin (see Baskin and Baskin, 1985).

Timing of germination

In the subroutine simulating the timing of germination, irradiation of the seeds triggers the germination process, and temperature determines the rate at which the germination process proceeds. In the field, irradiation of seeds in the seed bank occurs as a result of soil cultivation. In the field experiment in this study soil cultivation proved to be the major trigger for seedling emergence flushes (chapter 5). The effect of temperature on the rate of germination was quantified by the thermal time concept, which provided a good description in both laboratory and field situations (chapter 6). Water stress periods occurring during the field experiment reported in this study were too short to successfully introduce the effect of reduced soil moisture on the timing of germination. When applying the model to spring germinating weeds in the Netherlands, omitting the effect of soil moisture on germination rate may be adequate, since in Dutch springtime conditions moisture is seldom an impediment to seed germination. For a prediction of weed emergence patterns in a larger range of conditions it may be important to include the effect of soil moisture on the rate of germination. A method to include the effect of soil moisture on germination may be the hydrotime concept, that is analogous to the thermal time concept (see Bradford, 1995). In the hydrotime concept, the rate of germination in relation to the water potential of the environment is proportional to the difference between the current water potential and a base water potential. Interaction between temperature and soil moisture effects are quite large, but for prediction of germination under field conditions, combination of thermal time and hydrotime into one hydrothermal time may give sufficiently accurate description of the germination process (Bradford, 1995).

In *P. persicaria*, it was observed that an increasing degree of dormancy resulted in lower germination percentages and lower germination rates (chapter 3). Similar experiments with *C. album* and *S. arvensis* have not been done yet. In the present simulation model, the effect of dormancy on the germination rate has not been included (chapter 6). An exploratory calculation for *P. persicaria* in competition with sugar-beet, pointed out that, quantitatively, the effect of dormancy through reduction of the germination percentage is more important, but its effect through reduction of the germination rate may not be negligible. A further step in refining the model may therefore be the inclusion of a quantification of the effect of dormancy on the rate of germination.

7.1.4 Pre-emergence growth

Pre-emergence growth of weed seedlings in the laboratory was described well by a physiologically based model (chapter 4). The pre-emergence growth submodel was successfully used in the simulation of weed emergence patterns in the field (chapter 6). Compared to the importance of pre-emergence growth in the overall process of field emergence of weeds, this phase is strongly under-exposed in the literature. Hardly any quantitative information on underground seedling growth is available. A few data from this study are presented to indicate the quantitative importance of pre-emergence growth, with respect to both seedling numbers and their time of emergence. For example, in the field experiment, the estimated percentage unsuccessful emergence resulting from seedling mortality in the upper 15 cm of the soil ranged from 9 to 66%, depending on species and cultivation date. The average percentage was 35% (chapter 5). Evaluation with help of the model showed that in the field experiment increased soil penetration resistance reduced the fraction germinated seeds giving rise to emerged seedlings by a factor 2 to 3. Pre-emergence growth takes 19 to 73% of the time between soil cultivation and seedling emergence, dependent on species, temperature and soil penetration resistance (chapter 6).

Periods of water stress during the field experiment in this study were too short to successfully introduce the effect of reduced soil moisture on pre-emergence growth. For a prediction of weed emergence patterns in a large range of conditions it may be important to include the effect of soil moisture on pre-emergence growth. There is likely to be a direct effect of reduced soil moisture on pre-emergence growth, and an indirect effect via soil penetration resistance, which increases with decreasing soil water content (Kroesbergen, pers. comm.). The scientific challenge with respect to pre-emergence growth is to develop a more mechanistic model for underground seedling growth by studying and quantifying the processes in the soil.

7.1.5 Conclusion

Overall evaluation showed that, in the prediction of weed emergence in the field, modelling annual cycles in dormancy and germination was the weak spot. Therefore, research to improve the simulation of weed emergence patterns should focus on the simulation of these cycles. Seasonal changes in dormancy and germination relate mainly to changes in the extent of germination. This implies that the timing of weed seedling emergence is easier to predict than the numbers of seedlings in the emergence flushes. This conclusion is confirmed by the success of the weed emergence models by Takayanagi and Kusinagi (1989), Forcella (1993), Harvey and Forcella (1993) and King and Oliver (1994), that use *proportional* extent in the model, and thus exclude differences in seedling numbers of the flushes that are predicted. It also implies that predicting crop emergence from non-dormant seeds is feasible.

7.2 Environment

Irrespective of our understanding of weed population biology, forecasting future weed infestations is bound up with error margins, since the forecasting of future weather conditions always involves uncertainty. A simulation model may be used to generate predictions of the weed vegetation for different weather scenarios, and analyse the risks that are related to the uncertainty of the weather forecast. Simulation of seed-bed microclimate, and the way it is being affected by soil cultivation measures, may be combined with the emergence model to explore possibilities to manipulate the seed-bed in such a way that weed emergence is suppressed, or can be controlled easily.

7.3 Practical application

In this thesis, the scientific objective of the model prevailed. However, the ultimate objective of this and related work is to make weed control more efficient, and to reduce its negative side effects on the environment, by predicting weed emergence patterns. In this section, the future role of the model in achieving this goal will be evaluated. The general concept is that by predicting weed emergence patterns, control measures can be attuned to expected weed emergence, which may save time and resources (Leblanc and Cloutier, 1997). Effective weed control relies on precise timing in relation to the flush of weed seedling emergence that follows seed-bed preparation. For example, if weed control is too early in relation to this flush, seedlings will continue to emerge and compel additional control measures. If removal is too late, early emerged weeds will have passed the plant stage at which effective weed control is feasible, and compel alternative control measures, that may be more expensive and less environmentally friendly. In extreme cases, early emerged weeds may already have exerted an irreparable effect on crop yield and crop quality. A better understanding of the factors that affect the pattern of weed seedling emergence may be used to optimize the timing of weed removal, or adjust the applied measures to the plant stage of the weeds.

Several authors have given practical examples on how a prediction of weed seedling emergence can be used in weed control. Benech-Arnold *et al.* (1990) presented a simulation model for predicting seedling recruitment of *Sorghum halepense* from the seed bank. They mention that the model may be used to calculate which proportion of the population has already germinated at a certain time, thus conferring an advantage in deciding when a post-emergence herbicide should be applied. Bond and Baker (1990) stated that in some crops a single weeding at the ideal time will be enough to prevent loss of yield. The ideal timing of weeding depends on when the weeds emerge in relation to the crop. The problem of putting this into practice has always been the difficulty of defining in advance the optimum stage to remove weeds from the crop, mostly due to variation in the pattern of weed emergence. Similarly, they mention that the success of the stale seed-bed technique in reducing weed numbers depends upon delaying the destruction of emerged weeds until after the main flush of seedlings has appeared. Forcella *et al.* (1993) gave an example on how a prediction of weed seedling emergence may be used to optimize the time of crop seed-bed preparation. In the agricultural system that they are working in, seed-bed preparation also acts as a weed control measure. The later the seed-bed is prepared, the higher the number of seedlings that have emerged prior to seed-bed preparation, and the lower the number of weeds that will emerge in the crop, and the lower the yield loss owing to weeds. However, waiting for maximum weed seedling emergence prior to seed-bed preparation results in a delay in crop sowing, and thus in a shorter growing season, which also reduces crop yield. Using a fixed relationship between calendar date and the extent of weed emergence, Forcella *et al.* (1993) calculated the optimum trade-off between reduction of weed emergence in the crop and shortening of the growing season.

Here, I will elaborate on the question whether and how present and future research into predicting weed emergence patterns may be used in practice, in the context of arable farming in the Netherlands. Concern about the adverse environmental effects of chemical control has resulted in legislation that restricts the amount of pesticides used in Dutch agriculture. In arable farming, the annual use of herbicides should be reduced by 30% in 1995 and by 45% in 2000, compared to the reference period 1984-1988 (Anonymous, 1991*a*). Research into integrated weed control at 38 arable farms (the 'innovation farms') indicated that these objectives can be reached amply by an increased use of mechanical weed control, by reduced dosage spraying and row application of herbicides, without losing profitability. In 1991, after two years of practical research, these farms already exceeded the requirement for 2000, by effecting a reduction of 54% (Wijnands *et al.*, 1993).

The development at the innovation farms proves that the first step towards integrated weed control was not hampered by a lack of scientific knowledge. The reduction in the use of herbicides at these farms has been achieved by developing alternative weed control methods

(Van der Weide and Wijnands, 1993), which were already successful at a time when scientific research projects that had been initiated as a reaction to the change in government policy were not generating results yet. This seems to contradict the statement in the general introduction of this thesis, namely that the development of integrated weed management lags behind that of other pests since detailed understanding of weed biology in relation to cropping practices is lacking. Apparently, the incentive to apply alternative control methods was lacking, and still is, in conventional Dutch arable farming. Conventional farmers fear the risk and time consumption related to adopting the newly developed or improved techniques. In conventional arable farming the use of herbicides has decreased as a result of an increased use of mechanical control, a substitution of herbicides by others with a lower amount of active ingredient, and probably also by a temporary downward trend in the market, but this has not been enough to achieve the 1995 target, neither is it expected that the 2000 requirement will be met (Rotteveel, pers. comm.).

As to weed control in arable farming, attention has been directed mainly to the reduction of the use of herbicides, expressed in kg active ingredient per hectare. However, the Dutch governmental policy also included objectives related to reductions of the dependence on pesticides and the emission of pesticides to the environment (Anonymous, 1991*a*,*b*). Apart from the difficulty in quantifying dependence and emission, meeting these objectives may necessitate additional efforts in agricultural practice.

Even if the objectives stated by the Dutch government (Anonymous, 1991*a*,*b*) will eventually be achieved, it is unlikely that the success will lead to a lasting complacency. More likely, initiatives will be taken to further reduce the amount of herbicides used. The board advising the government on the herbicide reduction that may be achieved in arable farming, already added a reduction percentage of 55% as a target for 2010 (Anonymous, 1990). Societal aversion against chemical control is likely to last, and may even increase by the gradually growing concern about long time exposure to low concentrations of chemical components in the environment. A further reduction of pesticide use is likely to have important consequences for weed control. On ecological farms it shows that the problems in crop protection resulting from complete abandoning of pesticide use, particularly relate to the control of weeds (Vereijken and Kropff, 1996). It is questionable whether a reduction in the use of herbicides that goes further than the present objectives set by the Dutch government can be achieved within conventional arable farming systems. At the innovation farms, reductions achieved in the first three years of the project were 37%, 54% and 58%, respectively (Wijnands *et al.*, 1993), suggesting that within the system that was investigated, the maximum reduction in herbicide use based on existing technology may have been reached. The results may indicate that a further reduction in herbicide use while maintaining an economically sound weed management may require drastic changes in arable farming systems. The development of new systems requires extensive input of knowledge from both scientific and applied research (Van der Weide and Wijnands, 1993).

Although the results obtained by the innovation farms showed that the first step in the development of integrated weed control was not hampered by a lack of scientific knowledge, additional scientific research may play a role in achieving the intended reduction of herbicide use by Dutch arable farming. Attention of the research may be directed to taking away the disadvantages that prevent conventional farmers from using the newly developed and improved weed control techniques, and to meeting the objectives with respect to reduction of herbicide emission and dependence on chemical control that were set by the Dutch government. On the long term, scientific research may contribute to developing farming systems in which weeds are controlled with a very low, or without input of herbicides.

As yet, studies into weed biology and ecology, and more specifically the development of modelling frameworks for weed population dynamics and crop-weed interactions have hardly been used to improve weed management systems (Norris, 1992; Kropff *et al.*, 1996). However, in my view, the necessity to increasingly abandon herbicide use from weed control will force practical researchers to develop, and farmers to apply, solutions to weed problems, that stem from outside the range of options from which they were used to choose. The task of science in this is to ensure that enough biological and ecological knowledge of weeds is available, so that also weed biology and ecology may provide ingredients to practical researchers in developing new weed management systems. This is not likely to be achieved by providing tailor-made solutions, but it may be achieved by providing basic knowledge and insight, and communicating these, and possible options for usage to practical researchers. I will give some examples on how the current study, or its continuation in the future, may contribute to the solution of problems related to the above-mentioned three issues.

Stale seed-bed. In conventional farming the shortening of the growing season as a result of preparing a stale seed-bed is considered to be a large drawback. In ecological farming, where time-consuming harrowing and hand-weeding are used extensively, it may be a realistic option. A prediction of emergence may indicate at what time of the season the making of a stale seed-bed will be most effective, and at what day the majority of weed seedlings in the flush has emerged so that a seed-bed for the crop can be prepared.

Optimizing effectiveness of control. The effectiveness of harrowing and reduced dosage herbicide application, which make up an important part of the weed control measures in integrated weed management, relies on application in a early plant stage of the weeds, even more than that of conventional herbicide application. In some instances, harrowing is most effective on weed seedlings just before emergence. Since time margins for a successful application are narrow, prediction of weed germination and emergence may be helpful for planning these control measures.

Time saving. As a result of harrowing and reduced dosage application of herbicides, the number of applications has increased considerably compared to standard agricultural practice in arable farming. A bottleneck on the innovation farms, and a barrier to the adoption of integrated weed management by conventional farming is labour availability, especially during some periods of the season. Prediction of the later emergence flushes in the season, that may also be triggered by harrowing, may make the applications more effective, so that less applications are necessary, or may indicate moments of the season when control is not necessary, so that the number of applications may be reduced.

Risk reduction. One of the reasons why conventional arable farming is reluctant to adopt the techniques used at the innovation farms, is the conception that the risk involved in integrated weed management is too high. A prediction of weed problems may help farmers in weighing where and when they want to apply chemical control, and where and when, for example, mechanical control is possible. In this way, the risk of using mechanical control may be reduced.

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SUMMARY

Anticipating weed pressure may be important in selecting and timing weed control measures in order to optimize their effectiveness, and thus reduce herbicide use. Therefore, a predictive model of the time of emergence and the numbers of seedling emerging (the weed emergence pattern) after soil cultivation may be a useful tool in integrated weed management. In this study, a simulation model was developed in order to increase the quantitative understanding of weed emergence in the field in relation to weather, soil and cultivation measures. In the model, three phases were distinguished in the process of weed emergence in the field, and modelled in separate modules: annual changes in dormancy of buried seeds, seed germination, and pre-emergence growth of seedlings. The model was parameterized and tested for three arable weed species: *Polygonum persicaria, Chenopodium album* and *Spergula arvensis*.

In chapter 2, a model is described simulating the annual dormancy cycle of seeds in the seed bank, and the germination of exhumed seeds in the laboratory. Simulation of dormancy and germination is based on a physiological model concerning the action of phytochrome in the seed. Dormancy is related to the amount of an hypothetical phytochrome receptor, that fluctuates in an annual pattern. Relief of dormancy is equivalent to an increase in the amount of receptor, and results in a widening of the range of temperatures over which germination can occur. Induction of dormancy is equivalent to a decrease in the amount of receptor, and results in a narrowing of this range. Annual changes in temperature are the driving force for annual changes in the amount of phytochrome receptor in seeds that are buried in the seed bank. From the average amount of phytochrome receptor in the seeds of a population, the model calculates the germination percentage that is reached, when a seed sample from the population is exhumed, irradiated, and germinated at a given temperature in darkness. The model assumes that germination is triggered by light. The active phytochrome (Pfr) that is generated by a short irradiation of the seed, will bind to the receptor, from which it will subsequently gradually disappear by dark reversion. The seed will germinate when the residence time of Pfr to its receptor exceeds a certain period, called the escape time. The model derives the germination percentage from a comparison of the period Pfr is receptor-bound and the escape time. The outcome of the comparison depends on the temperature, which affects both dark reversion and escape time, and on the amount of phytochrome receptor present (and thus on the level of dormancy).

The dormancy model was tested in a burial experiment with seeds of *P. persicaria, C. album* and *S. arvensis* that were buried in envelopes in the field. At regular time intervals during three years, subsamples of these seeds were exhumed. The dormancy of these subsamples was assessed by irradiating them and testing their germination over a range of temperatures in darkness. The simulation model gave a reasonably accurate description of the observed cyclic changes in germinability of exhumed seeds.

Chapter 3 describes an experimental quantification of changes in the germination percentage and germination rate of *P. persicaria* resulting from loss of primary dormancy during chilling of imbibed seeds. Both percentage and rate of germination increased with increasing loss of dormancy. When evaluated in relation to competition between sugar-beet and *P. persicaria*, the effect of dormancy on the germination percentage was more important than the effect on germination rate, but for an accurate prediction of yield loss, the latter effect may not be negligible.

A physiologically based model describing the effects of temperature, soil penetration resistance, burial depth and seed weight on pre-emergence growth of seedlings is presented

in chapter 4. In the model, cumulative emergence is described by a Gompertz curve. The parameters in the curve are related to environmental factors and seed characteristics. The central process in the model is the conversion of seed reserves into seedling material. The ability of a seedling to emerge depends on whether it can convert its seed reserves into a seedling with a shoot that has sufficient length to reach the soil surface. Consequently, this ability depends on seed weight and burial depth. In addition, the conversion efficiency from seed reserves into shoot length and the shoot elongation rate depend on soil penetration resistance and temperature.

The model was tested with emergence data of *P. persicaria*, *C. album* and *S. arvensis* that were obtained by burial of pre-germinated seeds at different depths in soil with different penetration resistances at a range of constant temperatures in the laboratory. The model was used to analyse the experimental data in order to obtain insight into the effects of these factors on seedling emergence. The model provided a good description of the trends observed in the experiment.

In chapter 5, an experiment is described in which emergence of *P. persicaria*, *C. album* and *S. arvensis* was monitored in the field. Field plots were sterilized and seeds of the three species were mixed through the soil in winter. Separate field plots were cultivated once only during spring, and seedling emergence was monitored regularly. Seedling emergence was also monitored in undisturbed plots. Simultaneously, seasonal changes in seed dormancy of the buried weed seeds were assessed by exhuming seed lots buried in envelopes, and testing their germination in the laboratory. Seed survival at the end of the period of field observations was assessed by sampling the soil in the plots.

The date of soil cultivation had a strong effect on seedling numbers in the spring emergence flushes, and on the timing of these flushes. A high correlation existed between mean seed-bed temperature in the week after soil cultivation and the number of seedlings in the spring emergence flush. The onset of the spring flushes could be described well by a temperature sum. Summer emergence flushes in *C. album* and *S. arvensis* resulted from remoistening of the seed-bed by rainfall after periods of drought. Like seedling emergence, seed survival was affected by the date of soil cultivation. The correlation between emergence and depletion of the seed bank, however, is slight.

In chapter 6, a model is presented simulating weed emergence patterns after soil cultivation. In the model, separate modules simulating the consecutive processes of dormancy release (chapter 2), germination (data from literature) and pre-emergence growth (chapter 4) were linked. Input variables of the model are the date and method of soil cultivation, soil temperature and soil penetration resistance. Output of the model is seedling density and the timing of seedling emergence. The model was parameterized for *P. persicaria*, *C. album* and *S. arvensis* with help of previous field and laboratory experiments. The model was evaluated with data from the field experiment described in chapter 5. When using the germination results of the exhumed seed lots to estimate the degree of dormancy at the time of soil cultivation, the extent of the emergence flushes following soil cultivation could be described well. Although the dormancy model gave a good description of annual cycles in dormancy (chapter 2), the quantitative prediction of seasonal changes in dormancy and germination was not accurate enough for predicting field emergence, and appeared to be the weak point in predicting weed emergence patterns. When there was substantial emergence as a result of soil cultivation, the timing of emergence could be predicted accurately. Analysis with the simulation model revealed that the high correlations between seed-bed temperature and both extent and rate of emergence (chapter 5) were only partly based on causal relationships.

The general discussion (chapter 7) describes the state of the art in modelling emergence patterns. In the literature considerably more attention has been given to the simulation of the timing of emergence than to the simulation of seedling numbers in the emergence flushes. The present model aims at predictions of both aspects of emergence patterns: timing and extent. Comparing the 'standard' analysis in chapter 5 and the system analysis by means of simulation in chapter 6, it was concluded that a combination of experimental work and analysis with help of computer simulation proves to be an effective tool in gaining insight in the relationships between the processes and environmental factors determining weed emergence. Recommendations are given to direct the improvement of the present modelling approach. Improvement of simulation of annual cycles in dormancy and germination is most likely to take place via molecular physiological research into mechanisms of dormancy. Finally, the use of weed emergence predictions in arable farming is discussed against the background of ongoing and anticipated reductions in herbicide use in Dutch arable farming.

SAMENVATTING

Het terugdringen van de hoeveelheid gebruikte chemische bestrijdingsmiddelen is een van de prioriteiten binnen het Nederlandse landbouwbeleid. Indien men vroeg in het seizoen een voorspelling kan maken van te verwachten onkruidproblemen, kan men daarop de keuze van de bestrijdingsmethode en het tijdstip van toepassing baseren. Dit kan leiden tot een grotere effectiviteit van de bestrijdingsmaatregelen, waardoor het bijvoorbeeld mogelijk is een lagere dosis chemische bestrijdingsmiddelen in te zetten of gebruik te maken van alternatieve methoden, zoals mechanische onkruidbestrijding. Een model dat een voorspelling maakt van het aantal onkruidplanten en het tijdstip van hun opkomst (kort gezegd: van het opkomstpatroon) kan daarom toepassing vinden in de geïntegreerde onkruidbestrijding. In het onderzoek dat beschreven wordt in dit proefschrift werd een simulatiemodel ontwikkeld dat tot doel had inzicht te verschaffen in opkomstpatronen van onkruiden in het veld, en verbanden te leggen met weersomstandigheden, bodemeigenschappen en grondbewerkingsmaatregelen. In het model worden drie processen onderscheiden die een rol spelen bij de opkomst van onkruiden in het veld: (1) jaarlijkse cycli in kiemrust van onkruidzaden in de zaadbank, (2) zaadkieming en (3) voor-opkomstgroei van kiemplanten. De processen werden gekwantificeerd in drie afzonderlijke submodellen. De parameters in het model werden geschat en het model werd vervolgens getoetst voor drie akkeronkruidsoorten: *Polygonum persicaria* (perzikkruid), *Chenopodium album* (melganzevoet) en *Spergula arvensis* (spurrie).

In hoofdstuk 2 wordt een simulatiemodel beschreven van (1) de jaarlijkse kiemrustcyclus van zaden onder veldomstandigheden en (2) de kieming van opgegraven zaden in het laboratorium. De simulatie van kiemrust en kieming is gebaseerd op een fysiologisch model van de werking van fytochroom in het zaad. Kiemrust houdt verband met de hoeveelheid van een hypothetische fytochroomreceptor die toe- en afneemt in een jaarlijkse cyclus. Toename van de hoeveelheid receptor komt overeen met breking van kiemrust en resulteert in een verbreding van het temperatuurtraject waarbinnen kieming mogelijk is. Afname van de hoeveelheid receptor komt overeen met inductie van kiemrust en leidt tot een versmalling van dit temperatuurtraject. Het jaarlijkse verloop van de omgevingstemperatuur veroorzaakt de jaarlijkse cyclus van de hoeveelheid fytochroomreceptor in zaden die in de bodem begraven zijn. Op basis van de gemiddelde hoeveelheid fytochroomreceptor in een zaadpopulatie berekent het model het kiemingspercentage dat wordt bereikt wanneer een zaadmonster uit de populatie wordt opgegraven, belicht, en vervolgens te kiemen gelegd bij een bepaalde temperatuur in het donker. Kieming wordt in gang gezet door een korte belichting van het zaad. Het actieve fytochroom (Pfr) dat gevormd wordt tijdens deze belichting, vormt een verbinding met de receptor, die vervolgens geleidelijk weer verbroken wordt als gevolg van *dark reversion*, het proces waarbij actief fytochroom in het donker terugvalt in zijn inactieve vorm (Pr). Het zaad kiemt indien de verblijfstijd van Pfr aan de receptor een bepaalde tijdsduur, de *escape time*, overschrijdt. In het model wordt het kiemingspercentage afgeleid uit een vergelijking van de tijd dat Pfr aan de receptor gebonden is en de *escape time*. Het resultaat van deze vergelijking is afhankelijk van de temperatuur en van de hoeveelheid fytochroomreceptor (en dus van de mate van kiemrust).

Het kiemrustmodel werd getoetst met gegevens uit een begraafexperiment met zaden van *P. persicaria*, *C. album* en *S. arvensis*. Vitrage-zakjes met zaden van de drie soorten werden in het veld begraven en met regelmatige tussenpozen gedurende drie achtereenvolgende jaren weer opgegraven. De kiemrust van de zaden werd bepaald door de zaden kort te belichten en vervolgens te kiemen te leggen bij een aantal verschillende temperaturen in het donker. Het simulatiemodel gaf een goede beschrijving van de waargenomen cyclische veranderingen in kiemingsbereidheid van de opgegraven zaden.

Hoofdstuk 3 beschrijft een experiment waarin onderzocht werd hoe het kiemingspercentage en de kiemingssnelheid van *P. persicaria* veranderen gedurende breking van primaire kiemrust. Breking van rust vond plaats door bewaring van geïmbibeerde zaden bij een temperatuur van 2°C. Zowel het percentage als de snelheid van kieming nam toe als gevolg van breking van kiemrust. Als men deze gegevens betrekt op de concurrentie tussen suikerbiet en *P. persicaria*, dan blijkt kiemrust meer effect op de opbrengst van suikerbiet te hebben via de invloed op het kiemingspercentage dan via de invloed op de kiemingssnelheid. Het effect van kiemrust op de kiemingssnelheid is echter nog steeds zo groot dat men dit voor een nauwkeurige schatting van het opbrengstverlies niet kan verwaarlozen.

Een model dat de invloed van temperatuur, bodemverdichting, begraafdiepte en zaadgewicht op de voor-opkomstgroei van onkruiden beschrijft, wordt gepresenteerd in hoofdstuk 4. In het model wordt cumulatieve opkomst beschreven met een Gompertz-curve. De parameters in de curve zijn afhankelijk van omgevingsfactoren en zaadeigenschappen. Het centrale proces in het model is de omzetting van in het zaad aanwezige reservestoffen in kiemplantmateriaal. Of een kiemplant al dan niet opkomt is afhankelijk van de vraag of hij uit de reserves in het zaad een spruit kan vormen die genoeg lengte heeft om het grondoppervlak te bereiken. Als gevolg daarvan is opkomst afhankelijk van zaadgewicht en begraafdiepte. Daarnaast zijn de omzettingsefficiëntie van zaadreserves in spruitlengte en de groeisnelheid van de spruit afhankelijk van de doordringingsweerstand van de bodem en de temperatuur.

Het voor-opkomstgroeimodel werd getoetst met opkomstgegevens van *P. persicaria*, *C. album* en *S. arvensis*. In het laboratorium werden voorgekiemde zaden begraven op verschillende diepten in grond met verschillende doordringingsweerstanden en werd vervolgens de opkomst van kiemplanten waargenomen bij een aantal constante temperaturen. Het model werd gebruikt om de experimentele gegevens te analyseren en inzicht te verkrijgen in het effect van deze factoren op kiemplant-opkomst. Het model gaf een goede beschrijving van de experimentele waarnemingen.

In hoofdstuk 5 wordt een experiment beschreven waarin opkomst van *P. persicaria*, *C. album* en *S. arvensis* werd waargenomen in het veld. De grond in een aantal proefveldjes werd gesteriliseerd en in de winter werden zaden van de drie betreffende soorten door de bovenlaag gemengd. De proefveldjes werden elk eenmalig bewerkt in de loop van het voorjaar en kiemplantopkomst werd met regelmatige tussenpozen waargenomen. Daarnaast werd de opkomst van kiemplanten in onbewerkte proefveldjes geregistreerd. Gelijktijdig werden seizoensveranderingen in kiemrust bepaald door zakjes met zaadmonsters op te graven en de kieming ervan in het lab te testen. Aan het einde van het veldexperiment werd de overleving van zaden in de proefveldjes bepaald door grondmonsters te nemen en de overgebleven zaden te tellen.

De datum van grondbewerking had een sterke invloed op het aantal kiemplanten in de opkomstgolf en op het tijdstip van de opkomstgolf. Er bestond een sterke correlatie tussen de gemiddelde bodemtemperatuur in het zaaibed in de week na grondbewerking en het aantal kiemplanten dat gedurende de lente opkwam. Het begin van de opkomstgolf na grondbewerking kon goed beschreven worden met behulp van een temperatuursom. Opkomstgolven van *C. album* en *S. arvensis* in de zomer waren het gevolg van een bevochtiging van de bodem door regenval na perioden van droogte. Net als kiemplantopkomst werd zaadoverleving beïnvloed door de datum van grondbewerking, maar desondanks was de correlatie tussen opkomst vanuit de bodem en afname van de zaadvoorraad in de bodem zwak.

In hoofdstuk 6 wordt een model gepresenteerd dat opkomstpatronen van onkruiden na grondbewerking simuleert. In het model worden afzonderlijke submodellen voor de simulatie van de opeenvolgende processen van kiemrustbreking (hoofdstuk 2), kieming (gegevens uit de literatuur) en voor-opkomstgroei (hoofdstuk 4) aan elkaar gekoppeld. Invoervariabelen zijn de datum en de methode van grondbewerking, bodemtemperatuur en bodemdoordringingsweerstand. Uitvoer van het model is kiemplantdichtheid en de verdeling van kiemplantopkomst in de tijd. Uit eerdere laboratorium- en veldexperimenten werden de modelparameters voor *P. persicaria*, *C. album* en *S. arvensis* bepaald. Het model werd getoetst met behulp van gegevens uit het veldexperiment dat beschreven wordt in hoofdstuk 5. Indien men de mate van kiemrust op het moment van grondbewerking bepaalt op grond van de kiemingsresultaten van de opgegraven zaadmonsters, kan men de omvang van de opkomstgolven na grondbewerking goed beschrijven. Hoewel het kiemrustmodel een goede beschrijving gaf van de jaarcycli in de kiemrust van de drie soorten (hoofdstuk 2), bleek de kwantitatieve voorspelling van seizoensveranderingen in kiemrust niet accuraat genoeg voor het voorspellen van veldopkomst en vormt derhalve de zwakke schakel in de voorspelling van opkomstpatronen van onkruiden. De substantiële opkomstgolven na grondbewerking kunnen ook qua tijdstip nauwkeurig voorspeld worden. Analyse met behulp van het simulatiemodel toonde aan dat de goede correlaties tussen zaaibedtemperatuur en zowel de omvang als het tijdstip van opkomst (hoofdstuk 5) slechts gedeeltelijk op causale verbanden berusten.

De algemene discussie (hoofdstuk 7) schetst de huidige stand van zaken met betrekking tot het modelleren van opkomstpatronen. In de literatuur is voornamelijk aandacht geschonken aan het voorspellen van het tijdstip van opkomst. Het model dat beschreven wordt in dit proefschrift heeft tot doel zowel het tijdstip als de omvang van opkomstgolven te voorspellen. Als men de 'conventionele' analyse uitgevoerd in hoofdstuk 5 vergelijkt met de systeemanalytische benadering in hoofdstuk 6, kan men concluderen dat de combinatie van experimenteel werk en analyse met behulp van computersimulatie een effectief middel is om inzicht te verkrijgen in de relaties tussen de processen en omgevingsfactoren die onkruidopkomst bepalen. Er wordt een aantal aanbevelingen tot verder onderzoek gedaan die tot verbetering van het huidige model kunnen leiden. Verbetering van de simulatie van kiemrust zal hoogstwaarschijnlijk alleen kunnen plaatsvinden via moleculair fysiologisch onderzoek naar kiemrustmechanismen. Tenslotte wordt het gebruik van opkomstvoorspellingen besproken tegen de achtergrond van de huidige en de te voorziene reducties in het gebruik van chemische onkruidbestrijdingsmiddelen in de Nederlandse akkerbouw.

CURRICULUM VITAE

Leo Vleeshouwers werd geboren op 17 december 1960 te Schaesberg (thans gemeente Landgraaf). Hij behaalde het VWO diploma (Gymnasium β) in mei 1979 aan het Coriovallum College te Heerlen. Aansluitend startte hij de studie Biologie aan de Landbouwuniversiteit in Wageningen. Tijdens de doctoraalstudie doorliep hij de vakken Vegetatiekunde, Theoretische Produktie-ecologie en Onkruidkunde. In juni 1987 behaalde hij het doctoraalexamen. Vervolgens werkte hij tot maart 1989 bij de afdeling Pers en Voorlichting van de Vrije Universiteit in Amsterdam, in het kader van zijn vervangende dienstplicht. In april 1989 begon hij zijn aanstelling als assistent in opleiding bij de toenmalige vakgroep Vegetatiekunde, Plantenoecologie en Onkruidkunde van de Landbouwuniversiteit in Wageningen. Na verplaatsing van de leerstoel Onkruidkunde naar de vakgroep Theoretische Produktie-ecologie in 1994 zette hij het onderzoek aan die vakgroep voort. Zijn onderzoek betrof het modelleren van opkomstpatronen van akkeronkruiden. De resultaten van dit onderzoek onder leiding van de promotoren prof. dr. M.J. Kropff en prof. dr. C.M. Karssen zijn vastgelegd in dit proefschrift. Sinds 1 april 1997 is hij bij de vakgroep Theoretische Produktie-ecologie werkzaam aan het schatten van opbrengstmogelijkheden van energiegewassen, binnen het Nationaal Onderzoekprogramma 'Mondiale luchtverontreiniging en klimaatverandering'.