Population dynamics and population control of *Galium aparine* L.

Promotoren: dr. ir. R. Rabbinge,
hoogleraar in de theoretische produktie ecologie

dr. P. Zonderwijk,
oud hoogleraar in de vegetatiekunde, plantenoecologie en onkruidkunde

Co-promotor: dr. J.M. van Groenendael,
universitair docent in de vegetatiekunde, plantenoecologie en onkruidkunde

R.Y. van der Weide

Population dynamics and population control of *Galium aparine* L.

Proefschrift

ter verkrijging van de graad van
doctor in de landbouw- en milieuwetenschappen,
op gezag van de rector magnificus,
dr. H.C. van der Plas,
in het openbaar te verdedigen
op vrijdag 4 juni 1993
des namiddags te vier uur in de aula
van de Landbouwuniversiteit te Wageningen

CIP-DATA KONINKLIJKE BIBLIOTHEEK, DEN HAAG

Weide, R.Y. van der

Population dynamics and population control of *Galium aparine* L. /
R.Y. van der Weide. - [S.l. : s.n.]
Thesis Wageningen. - With ref. - With summary in Dutch.
ISBN 90-5485-115-5
Subject leadings: weeds / *Galium aparine* L.

This thesis contains results of a research project of the Agricultural University in Wageningen, Department of Vegetation Science, Plant Ecology and Weed Science, Bornsesteeg 69, NL-6708 PD Wageningen, The Netherlands and Department of Theoretical Production Ecology, Bornsesteeg 65, NL-6708 PD Wageningen, The Netherlands.

The author's present address is:
Research Station for Arable Farming and Field Production of Vegetables (PAGV),
Postbox 430, NL-8200 AK Lelystad, The Netherlands.

Abstract

The population biology of *Galium aparine* L. needs to be better understood, in order to be able to rationalize decisions about the short- and long-term control of this weed species for different cropping practices.

A population dynamics model was developed to simulate the basic processes of the life cycle of *G. aparine* as influenced by environmental conditions. The effect of temperature, light, moisture, nitrate supply and soil structure on germination and emergence and on growth and seed production were investigated. Data were integrated in a model simulating field emergence and an ecophysiological model on crop-weed competition. The information was used to evaluate the effects of crop rotations, control levels, cultural measures and timing and choice of soil cultivation practices on the population dynamics of *G. aparine*. The ecophysiological model of competition between *G. aparine* and sugar beet was extended to predict reductions in crop yield reduction and increases or decreases in the weed population on the basis of the actual situation in the field. The variation caused by weather conditions appeared to be small.

The results of simulations demonstrate the possibilities of reducing herbicide use to control *G. aparine* in both the short and long term, by adapting crop rotation and cropping practice, increasing mechanical control in cereals and not controlling late-emerging *G. aparine* plants in sugar beet.

additional index words: weeds, population biology, *Galium aparine* L., germination, growth, seed production, weather, cultural measures, crop, control, model.

Stellingen

1. "Wie één jaar zijn roet laat staan, moet zeven jaar uit wieden gaan" is in z'n algemeenheid een onjuist spreekwoord met milieu-onvriendelijke implicaties.
Dit proefschrift.

2. Kennis van de strekkingssnelheden en de afsterving van gekiemde zaden op verschillende diepten is onmisbaar voor de voorspelling van de veldopkomst van grootzadige onkruiden.
Dit proefschrift.

3. Voor onkruiden met een variabel zaadgewicht is een éénvoudige allometrische maat, zoals de verhouding tussen zaadgewicht en plantgewicht, onbruikbaar voor de schatting van het aantal geproduceerde zaden.
Dit proefschrift.

4. Het waargenomen effect van het weer op de door kleefkruid veroorzaakte opbrengstreduktie van suikerbiet komt vooral tot stand door de weersinvloed op de opkomstpatronen van gewas en onkruid en niet door de invloed van het weer tijdens het eigenlijke concurrentieproces.
Dit proefschrift.

5. Om een soort als kleefkruid in het bouwplan te beheersen met zo weinig mogelijk gebruik van herbicide biedt mechanische onkruidbestrijding en de optimalisering van keuze, dosering en toedieningstijdstip van de herbiciden meer perspektief dan het gebruik van dynamische schadedrempels gedurende het groeiseizoen.
Dit proefschrift.

6. Een afname van het aantal typen pesticiden als gevolg van het zogenaamde stoffenbeleid, werkt risicomijdend gedrag in de hand en is contraproduktief ten aanzien van de vermindering van het herbicidengebruik.

7. Gezien de hoge energiebehoefte voor de produktie van herbiciden, kan mechanische onkruidbestrijding ook uit het oogpunt van zuinig energiegebruik wenselijk zijn.
Energiebehoeften uit S.J. Clarke and W.H. Wilson (1974) Evaluating crop production systems by energy used. SAE paper 740647, 6 pag.

8. Het is niet juist om een aardappelras, zoals recent de Bildstar, gifpieper te noemen.

9. Naarmate meer agrarische gronden uit produktie worden genomen en ter beschikking voor natuurontwikkeling worden gesteld is het noodzakelijk om onkruidkundigen bij het vegetatiebeheer te betrekken.

10. Ter vermindering van de uitstoot van roetachtige deeltjes door dieselvoertuigen is het belangrijker de bandenslijtage te reduceren dan de motor verder te verbeteren.
Meetgegevens I.W.-T.N.O.

11. Uitgangspunt in de ruitersport is dat de ruiter het paard dresseert; in de praktijk gebeurt het ook andersom.

12 Het salaris, dat AIO's bij hun aanstelling moeten inleveren ten behoeve van zelfontplooiing, is alleen terecht indien andere onderzoekers tijdens hun werk niets leren.

Stellingen behorende bij het proefschrift van Rommie van der Weide: 'Population dynamics and population control of *Galium aparine* L.'.

Wageningen, 4 juni 1993.

Dankwoord

Hoewel de verantwoordelijkheid voor dit proefschrift bij mij ligt, representeert het tevens de verdiensten van vele anderen. Graag wil ik van deze gelegenheid gebruik maken om een ieder te bedanken die direct of indirect bijgedragen heeft aan de tot stand koming van dit proefschrift.

Allereerst bedank ik Jan van Groenendael die mij begeleid heeft bij de vakgroep Vegetatiekunde, Plantenoecologie en Onkruidkunde. Toen ik startte met het onderzoek, vond je dat een promotieonderzoeker moest bewijzen zelfstandig onderzoek te kunnen uitvoeren. Ik heb het heerlijk gevonden dat je naast de vrijheid die je me gaf, altijd openstond om mee te denken als ik daar behoefte toe voelde. Als reflectiepunt voor mijn ideeën, maar zeker ook als warm menselijk steunpunt, kon ik me geen beter begeleider wensen. Prof. dr. P. Zonderwijk bedankt voor de belangstelling, ideeën en discussies over de manier waarop wij onze akker en ons landschap zouden moeten inrichten en beheren. Zeer veel waardering heb ik voor prof. dr. ir. R. Rabbinge, die ondanks zijn vele bezigheden, steeds weer tijd wist te maken om versies van de hoofdstukken in wording van waardevolle, kritische kanttekeningen te voorzien. Zijn team van promotiekandidaten (Bert Schnieders, Harrie Lövenstein, Tjeerd Bouma, Barbara Habekotté, Leo Vleeshouwers, Lammert Bastiaans, Pascal Deneroy, Koen Kramers, Wouter Gerritsma, Robert van Loo, Anita Linneman, Peter Kooman, Nico Stutterheim, Bjorn Dirks en anderen) bleken een goed platform voor wetenschappelijke discussie, lering en stimulans. Naast hun suggesties hoe concepten te verbeteren, hebben ook Bert Lotz, Jacco Wallinga en Harro Bouwmeester hierin bijgedragen. Mevr. J. Burrough-Boenisch corrigeerde delen van dit proef-schrift op correct Engels taalgebruik en Herman Klees verfraaide sommige figuren. Bärbel Gerowitt (Göttingen, Germany), Svend Christenssen (Flakkebjerg, Denmark) and Bernard Wilson (Long Ashton, England) thanks for the stimulating discussions.

In dit proefschrift wordt verslag gedaan van 6 experimenten in de kas, 18 experimenten in klimaatcellen en 9 experimenten op het veld. Zonder de inzet van vele stagiaires en mensen met een afstudeeropdracht was dat niet mogelijk geweest. Martzen ten Klooster, Sonja Honders, Marnetta van Asseldonk, Marleen Esmeijer, Wim Snijders, Marjolein Maters, Jan de Rooy, Frans van Dun, Carlo van der Weert, Fred Bruins en Wouter Strietman heel veel dank hiervoor. Bij de inzet van proeven en bij arbeidsintensieve oogsten heb ik vaak hulp gekregen van Aad van Ast, Jaap Blijenberg, Monte Gardeniers, Eugene van Bergen Henegouwen, Wim de Jager, Johan Hartholt, Miriam Albers en Felix de Becker. Maar ook andere medewerkers van o.a. VPO, TPE, CABO, IOO (Frans

Zoon), PAGV (de heer van den Brand), LU vakgroep experimentele plantenfysiologie en LU vakgroep grondbewerking (de heer Kroesbergen) waren vaak behulpzaam en zelfs Jan van Groenendael heeft zijn rug een keer geforceerd toen hij hielp met het handmatig oogsten van suikerbieten.

Vele collega's bij VPO, later bij het CABO en de laatste tijd bij het PAGV toonden belangstelling, stimuleerden en/of fungeerden als praatpaal. Met name Barbara Habekotté, Aad van Ast, Sini ter Borg, Ali Ormel, Frans Aarts (ook voor de foto op de omslag), Bert Schnieders, Roel Groeneveld, Bert Lotz, Meindert Hoogerkamp, Jan Jonkers, Piet Spoorenberg, Wijnand Sukkel, Annette Zweep en Ton Rotteveel (PD) bedankt. Met veel enthousiasme initieerde Gert Liefstingh dit onderzoek dat aanvankelijk als een dokteraalonderwerp bij Fytoconsult gestart was. De heer Riemens en Piet Spoorenberg tevens bedankt voor de geboden mogelijkheid om dit proefschrift gedeeltelijk in PAGV tijd af te ronden.

Inspanning is alleen maar mogelijk naast ontspanning. Fanny en vrienden bij manege Blauwendraad zorgden voor de broodnodige afleiding en veel plezier. Familie en verdere vrienden bedankt voor de gezelligheid en het begrip dat ik daar soms wel wat weinig tijd voor had. Tenslotte een speciaal woord van dank voor Ron, die me de vrijheid laat maar er is als ik hem nodig heb, en mijn ouders, die me altijd met veel liefde en vertrouwen in mijn kunnen omringen. Ik draag dit proefschrift op aan mijn vader, die gedreven door zijn eigen ervaring bijzondere waarde hecht aan het behalen van deze titel.

Contents

Account

Parts of this thesis have been included into the following publications:

Chapter 2	Van der Weide, R.Y. & Van Groenendael, J.M. (1990) How useful are population dynamical models: an example from *Galium aparine* L. Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz Sonderheft 12, 147-155.
Chapter 3	Van der Weide, R.Y. (submitted) The influence of microclimate and soil conditions on dormancy and germination of *Galium aparine* L. in the field.
Chapter 4	Van der Weide, R.Y. & Dannenburg, M. (submitted) The importance of temperature, moisture and soil structure for emergence of *Galium aparine* L. from different depths.
Chapter 5	Van der Weide, R.Y. (submitted) Modelling the field emergence of *Galium aparine* L..
Chapter 6	Van der Weide, R.Y. (1992) Phenology of arable and hedgerow populations of *Galium aparine* L. in relation to climate and soil conditions. Weed Research, 32, 249-258.
Chapter 7	Van der Weide, R.Y. (submitted) Towards predicting the seed production of *Galium aparine* L. in five crops.
Chapter 8	Van der Weide, R.Y. & Lotz, L.A.P. (submitted) Effects of weather on competition between *Galium aparine* L. and sugar beet analysed with a simulation model.

Chapter 1

General introduction

1.1 Background

Increasing concern about the environment has resulted in legislation requiring a reduction in the amount of pesticides used in the Netherlands. The aim is stepwise reduce the annual use of herbicides in relation to the mean annual amount for the years 1984-1988; 30 % by 1995, 45 % by 2000 and 55 % by 2010 (Ministry of Agriculture, Nature Management and Fisheries, 1990). Similar restrictions have already been introduced in other countries (Kudsk, 1989).

Weeds can cause considerable losses to crop yield, both in quantity and quality, and can interfere with harvest operations (Auld *et al.*, 1987). Although there are several methods of managing weed populations, weeds are frequently controlled by the use of herbicides. During the period 1984 - 1988 yearly application of active ingredient of herbicides per hectare in the Netherlands was 4.3 kg for sugar beet, 1.0 kg for potato, 1.8 kg for maize and 1.5 kg for the other cereals (Ministry of Agriculture, Nature Management and Fisheries, 1990). Ways of reducing this herbicide use can be found in increasing the use of mechanical weed control and in adjusting the type of herbicides used, their dosage and the method of application. Furthermore, weeds should only be controlled when they exceed a density at which the costs of no control equal the costs of the control measure (economic threshold). Improvement of farm hygiene and a deliberate choice of crop rotation, cultivar, sowing date and density, row distance and fertilization level can be helpful. Systems of integrated weed control use a combination of these measures. Introduction of some measures is hampered by a lack of quantitative information. Economic thresholds are not always available or are unreliable for different situations. Furthermore, the old British adage "One year's seeding means seven years' weeding" or its Dutch equivalent "Wie één jaar zijn roet laat staan, kan zeven jaar uit wieden gaan" is well known to farmers. However, it is not known whether this rule is valid for different situations. Anyhow thresholds should emphasize the future consequences of not controlling weeds too. There are also questions on the importance of various cultural measures, how weed populations can be kept at a certain level and how risks are affected by factors such as the weather. Information on weed biology, ecology and control is needed to answer such questions. Each weed species behaves differently and studies are necessary to quantify at least some common traits in comparable weeds. In the Netherlands the weed species *Chenopodium album* L., *Galium aparine* L., *Polygonum persicaria* L. and *Solanum nigrum* L. are very abundant and greatly determine the success of control (Ministry of Agriculture, Nature Management and Fisheries, 1990). *G. aparine* is exceptional among these species, because it can cause problems in both autumn and spring sown crops in the crop rotations popular today. Therefore *G. aparine* was chosen as a target species for a study on integrated weed control based on sound knowledge of its biology.

1.2 *Galium aparine L.*

Distribution and habitat

G. aparine is found in the temperate zones throughout the world and at higher altitudes in the tropics. It has been reported as a weed in 19 crops in 31 countries, and is still increasing in importance (Holm *et al.*, 1977). Its increase is caused by the use of soil-applied or phenoxyacetic herbicides which are not effective against this species, the decrease of mechanical control, the larger doses of nitrogen applied, the earlier sowing of crops in spring and later harvesting of cereals, the trend towards cereals with shorter stalks, the use of contaminated crop seed, and its ability to grow in both autumn and spring sown crops (Röttele, 1980; Van den Brand, 1984). Beside its occurrence as a weed in many crops, *G. aparine* is also frequently found in moist woodlands, waste ground and hedgerows. *G. aparine* plants of arable origin differ slightly in their morphology and ecological behaviour from those from hedgerows (Groll & Mahn, 1986; Auge & Mahn, 1988; Berkefeld, 1988; Niemann, 1988; Froud-Williams & Ferris-Kaan, 1991).

Morphology and biology

The species is a strictly annual and predominantly self-pollinating member of the family of Rubiaceae. Moore (1975) and Malik & Vanden Born (1988) described the morphology of *G. aparine* and its differences from the closely related *G. spurium* (not important in the Netherlands). A characteristic of both species is their square stems which have short downward-pointing hooked bristles on the angles, their whorled leaves, and the paired spherical fruits with stiff hooked bristles, borne on straight stalks. The recurved spines on stems and leaves enable them to become attached to other weeds or crop plants and to penetrate the crop canopy. The bristles on the seeds ensure the dispersion by animals. *G. aparine* has been reported as one of the most winterhardy weeds. More information on the biology of *G. aparine* can be found in the references mentioned earlier and in the other chapters of this thesis.

Control

G. aparine is resistant to phenoxyacetic herbicides (Malik & vanden Born, 1988), hardly sensitive to triazines (Sieberhein & Seever, 1974) and escapes many soil-applied herbicides because it germinates from relatively deep in the soil (Holm *et al.*, 1977). In areas used as catchments for drinking water, mechanical control of this species by harrowing in cereals is advocated (Gerowitt, 1992). But in practice, *G. aparine* is still mainly controlled by applying herbicides (e.g. fluroxypyr, fenoxapropionacetic herbicides). Which herbicide is chosen for a crop is often determined by the occurrence of this species and sometimes special additional applications or measures are taken for the solely to control *G. aparine*.

The effects of *G. aparine* on crop production are significant and are economically important. It competes with the crop, delays harvest in cereals, increases drying costs and contaminates harvested seeds. Examples of significant sugar beet, winter wheat and maize yield reduction caused by *G. aparine* have been reported to occur already at densities of 0.3 to 5 plants per m^2 (Aarts & Dekkers, 1985; Neururer, 1987). In some situations densities of 1 *G. aparine* plant per m^2 are sufficient to interfere with the harvesting of cereals (Wahmhoff, 1986). Furthermore, the reduction of crop yield reduction can vary considerably between years and locations (Wilson & Wright, 1987). Because of this and the unknown risk of population increase in the crop rotation, the introduction of thresholds for *G. aparine* has been considered as unrealistic (Wilson & Wright, 1987), or low thresholds have been set (in winter wheat 0.5 plants/m^2 by Wahmhoff in 1986, 0.01 plants/m^2 by Aarts in 1985). Such extremely low thresholds compared with other weed species (20-30 grass weeds and 40-50 broadleaf weeds/m^2 by Wahmhof, 1986), restrict the possibilities of reducing herbicide usage if *G. aparine* is present. More realistic thresholds are needed to improve this situation. To set realistic thresholds, the background for differences found in crop yield reduction caused by *G. aparine* between years and locations and the risk of population increase in the crop rotation should be known for different cropping practices.

1.3 Objectives

The aim of the research described in this thesis was to integrate existing knowledge on the population biology of *G. aparine* in models, to identify and fill in important gaps in knowledge for improving the models and to use the models to evaluate the effects of different management strategies both within and over years.

1.4 Outline of the thesis

In chapter 2 the use of population dynamic models with different levels of complexity for integrating knowledge on population biology is discussed. A preliminary model of population dynamics of *G. aparine* is introduced, based on literature data. Simulations using this model stress the need for more reliable knowledge of the values of parameters used in the model and their variation caused by differences in management and environment. Chapters 3 to 8 answer questions concerning the estimation of parameters for the model.

Additional data were collected on germination and emergence. In chapter 3 research on the dormancy patterns of *G. aparine* and the influence of temperature, light, nitrogen, moisture, and bulk density of the soil on the actual germination process, is presented. Chapter 4 reports on laboratory experiments on the effects of temperature, soil moisture and soil resistance on the percentage and rate of seeds emerging after germination at different depths in the soil. The information obtained on germination and emergence is integrated and validated in a model of field emergence in chapter 5. This model was used to predict emergence patterns in the field as influenced by the vertical distribution of the seeds in the soil, the timing of seedbed preparation, the soil resistance and the differences caused by weather.

To predict differences in growth, competition and seed production, additional research on phenology, growth and seed production was needed. Chapter 6 reports on the findings of this research on influence of temperature and day length on the phenology of *G. aparine*. A developmental scale was constructed to predict development of the first 4 whorls of leaves, the flowering date and shifts in dry matter distribution patterns in relation to the day length and temperatures experienced. Predictions of flowering dates of *G. aparine* plants with different emergence dates were compared with independent field observations in the Netherlands and England. In chapter 7 research on the growth and seed production of *G. aparine* with different densities and emergence dates in spring barley, winter wheat, oilseed rape, potato and sugar beet in 1988 and 1989 is presented. Data were used to relate the seed production of *G. aparine* to its mature dry weight without seeds. Variability in growth and competitiveness of *G. aparine* caused by weather conditions, level of nitrogen supply and differences in emergence times and densities of both crop and *G. aparine*, are analysed for a sugar beet crop in chapter 8.

Furthermore in chapter 8 a more detailed model is presented which predicts both crop yield reduction and weed population increase or decrease, based on the findings of the preceding chapters. The feasibility of reducing herbicide applications for *G. aparine* control in sugar beet is discussed.

The final chapter is devoted to a discussion on the questions that arose during the research in relation to the original goals of the research programme and the future research needs.

Chapter 2

How useful are population dynamical models: an example from *Galium aparine* L.

Abstract Goals for modelling the population dynamics of weeds are prediction of a future infestation, evaluation of different (integrated) control strategies (system level) or evaluation of the possibilities to control a problem weed species (population level). Methods for modelling the population dynamics of plant species differ in the level at which they describe and at which they explain. They differ in detail, in time interval and in the mathematical method used. This paper deals with a problem weed species (*Galium aparine* L.). By simulating the population dynamics with an extended demographic model, the necessary complexity of the model is investigated and the parameters that need further specification are identified.

The annual rate of increase of a weed population can vary considerably depending on agronomical practices, but also on the vertical distribution of the seeds in the soil (and in case of high densities of weeds on density and spatial heterogeneity). More detailled demographic models using time steps of one year are also too simple for evaluating the effects of various (integrated) control strategies. Changes in sowing time or time of herbicide application can cause important differences in the population dynamics of a species. In such cases a model is needed that describes the processes during the year in connection with relevant agronomic practices. For accurate predictions, the most important parameters have to be examined carefully and unexplained variation in these parameters has to be small. In the case of large variation, more explicit models based on physiological principles are needed, that have the advantage of making better predictions. These models also offer the possibility to predict the effect of new aspects (e.g. changes in crop density). If different and unpredictable weather conditions are the cause of important variation, physiological models are best suited for dealing with such conditions on the process level, which is necessary for risk analyses.

2.1 Introduction

The purpose of using models in plant population biology is to increase our understanding of the dynamics of populations on the basis of the underlying processes that determine life-history phenomena (Blom, 1988). Specifically in the study of the population dynamics of weed species in crops there are at least two related goals:

1) Current thresholds set in integrated weed control are based on annual damage to the crop. Allowance has to be made, however, for the fact that in cases where weeds are capable of forming an important seedbank, problems may arise in subsequent years. At least for *Alopecurus myosuroides* Huds. (Doyle *et al.*, 1986), *Avena fatua* L. (Cousens *et al.*, 1986; Vleeshouwers & Streibig, 1986), *Viola arvensis* Murray (Holzmann & Niemann, 1988) and *Abutilon theophrasti* Med. (Zanin & Sattin, 1988) it has been calculated that long term economic thresholds are substantially lower than thresholds set for a single year. Therefore, besides knowledge of future agricultural practices (especially crop rotation and cultivation), information is needed on the population dynamics of weeds in relation to agricultural measures, soil type and weather conditions.

2) Despite the availability of many herbicides and rigorous management practices, particular species remain a problem or are even increasing in arable crop production. Studies of the population dynamics of problem weed species can be useful in understanding their dynamic behaviour and in identifying the stages and processes that are important for their regulation. Models help to identify information gaps, to set research priorities and to develop control strategies. As a part of an integrated control strategy, besides reduction of chemical and increase of physical control, several biological measures (alone or in combination) are proposed, like for example the use of cultivars which rapidly cover the soil and produce abundant leaf area ; the use of green manure to suppress weeds in the stubble; late sowing to combine seed bed preparation with weed control; proper crop rotation and adapted nitrogen fertilization (Vereijken, 1989). With the help of population dynamic models that take into account different integrated control measures, the overall effect of several control strategies can be compared. In such cases the model is used for strategic evaluation on the population or system level.

Different methods for studying and modelling the population dynamics of plants are available. The next part of this paper distinguishes several models. Secondly, an extended version of a model of the population dynamics of *Galium aparine* L. is proposed. Thereupon special attention will be given to the necessary level of complexity of the model in relation to the goals mentioned in the introduction. This will be illustrated with simulation results obtained with the proposed model for *G. aparine*.

2.1 Models of the population dynamics of plant species

Several methods for modelling the population dynamics of plant species have been used (Mortimer, 1983; Fernandez-Quitanilla, 1988; Van Groenendael, 1988). It is possible to categorize these models on the level at which they describe and at which they explain.

A model that is **descriptive on the population level** consists of annual monitoring of a single component of the population over several years and calculating the annual rate of growth of the population (lambda). The annual growth rate however, strongly depends upon the density of the species involved, the cropping system, soil type and climate (Mortimer, 1987; Fernandez-Quintanilla, 1988; Mortimer *et al.*, 1989). Its predictive value is limited and for every 'new' situation several years of monitoring in the field will be necessary.

The next category models are **explanatory on the population level and descriptive on the plant level.** Demographic models as reviewed by Mortimer (1983) belong to this category and are at the moment most commonly used. Basis for this approach is the life cycle of the species. The several stages in which the species can occur, are separated. Transitions between these stages are described with mathematical formulas. For a 'new' situation only the relevant transitions have to be reconsidered.

Modelling studies following this demographic approach differ a lot in detail, in time interval and in the mathematical method used:

1) In some research mainly in Germany the seed, seedling and seed producing plant stage are distinguished: Röttele (1980); Holzmann & Niemann (1988); Zwerger & Hurle (1988). In one formula the future number of seeds is calculated using a) the present number of seeds, b) a mortality ratio of seeds in the seedbank, c) an emergence ratio of seeds in the seedbank, d) a mortality ratio of emerged plants and e) the number of seeds produced by a surviving plant. Parameter values vary for different weeds and different crops. The time interval used is a year.

2) In extended demographic models more stages and parameters are used. Sometimes the plant population is divided into differently behaving cohorts of plants which for instance emerge in different periods (Mortimer, 1983). The seed stage often is divided into a) newly produced seeds on the plant, b) fresh seeds in the ground and c) old seeds in the ground (Cousens *et al.*, 1986) or a) deep and b) shallow seeds in the seedbank (Doyle *et al.*, 1986). Pollard (1982) divided the above ground plant population in five different morphological stages, using circa 35 parameters and considering 16 factors (e.g. date of drilling, seedbed preparation and harvest; weather in September; crop species and crop density, pre-harvest use of glyphosate). For every transition at least one formula is used. In cases where density dependence is important,a patchy distribution of a species can influence its population dynamics (Van Groenendael, 1988). For accurate modelling it can be necessary to account for heterogeneity in space and changes in the horizontal distribution of seeds and plants as a result of for example local dispersion. A spatial scale can be added to the demographic approach by simulating population dynamics for small plots separately and specifying dispersion as a function of for example the direction of operation of the combine harvester (Ballaré *et al.*, 1987). Neighbourhood models (Pacala, 1986) which formulate the population dynamics (including dispersion) of one individual as influenced by its surrounding plants, can also account for spatial

heterogeneity.

3) For more complex life cycles as with perennial weeds (e.g. *Agropyron repens* (L.) Beauv., Mortimer, 1983; *Euphorbia esula* L., Maxwell *et al.*, 1988), projection matrix models are often used. Good descriptions of these models and their special merits are reviewed by Van Groenendael *et al.* (1988) and Caswell (1989). The mathematical properties of such models correspond to specific life history characteristics like population growth rate, stable age distribution or reproductive value.

4) Most models referred to in the preceding text have a time span of one year. For evaluating the effect of timing of for example a herbicide spraying (often stage dependent control), it can be advantageous to work with very small time spans, like days or weeks. This is possible with matrix models (Mortimer et al., 1978) but for every time step a projection matrix has to be constructed. Aarts (1986) simulated the process during the year differently, using the boxcartrain method to mimic growth and development through the several growing stages that were recognized. This method which was already used by Janssen in 1974 for simulation of germination, is developed and reviewed by Goudriaan (1986).

Models that are **explanatory on the plant level** can be obtained by basing the transitions between the various plant stages on physiological principles (De Wit *et al.*, 1978). Until now this has only been done for parts of the life cycle. Spitters and Aerts (1983), Kropff (1988) and Spitters (1989) describe the growing process of crop weed ecosystems based upon photosynthesis, respiration and allocation of resources between competing organisms as influenced by light, water and temperature. If it is possible to convert biomass into numbers of seeds, their model can be used as a part of a population dynamic model. Janssen (1974) and Spitters (1989) show how to model the germination process as a function of for example dormancy, temperature and moisture.

These models offer a good base for explanation and prediction and make it possible to account for the weather conditions in risk analyses. Because the time span of these models is also very small, they can be used to evaluate effects of timing of treatments too.

The models mentioned above increase in complexity, but even the most complex models are a simplification of the real biological system. For managerial purposes however redundant precision is a nuisance rather than an advantage. The goals of the study therefore determine which level of complexity is needed (Zadoks & Rabbinge, 1985; see also below).

2.3 A population dynamic model of *G. aparine* L.

Despite very low thresholds used for the control of *G. aparine*, the agronomic significance of this species has increased during the past decade in Germany (Röttele, 1980; Niemann, 1981), the Netherlands (Aarts 1986) and The United Kingdom (Wilson & Froud-Williams, 1988). *G. aparine* is an economically important weed. It competes effectively with cereals, rapeseed and sugar beet, causes lodging of cereals, interferes with combine harvest operations and contaminates grain and rapeseed with its seeds (Malik & Vanden Born, 1988). Some herbicides (e.g. fluroxypyr and mecoprop) have been developed mainly for the control of *G. aparine.*

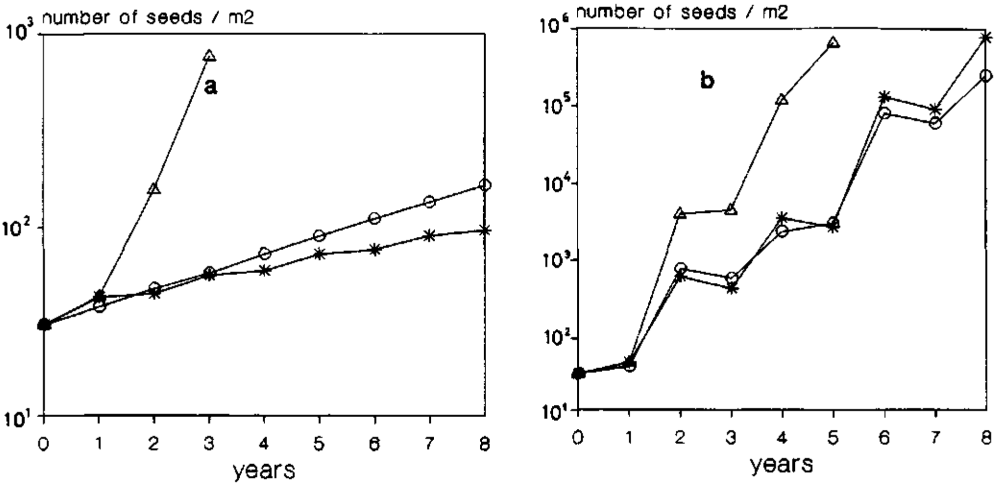
Biology and population dynamics of *G. aparine* have been studied and modelled by Röttele (1980) and Aarts (1986). Based basically on their data, it was possible to construct an extended version of the latter model (Van der Weide, 1987). This model can calculate on a day to day basis during several years, the amount of seeds and germinated seeds in several layers in the soil, the number of seedlings and plants in the one whorl, two- to four- whorl and more than four- whorl stage and the quantity of seeds on the plant and in the harvested product. By using the boxcartrain method (see chapter 2.1) growth and development during early plant stages are calculated depending on time in the year and plant stage. Germination and emergence are functions of the depth of the seed, time and method of cultivation and the time in the year. Depending on the surrounding crop, time in the year and the emergence time relative to the crop for summercrops or in absolute emergence time for wintercrops, plants suffer natural mortality and produce seeds. Normally *G. aparine* is only tolerated at very low densities. Therefore density dependence is not part of the model yet. Artificial mortality is dependent upon control method and stage of the plant or depth of the seed or germinated seed. The timing of seed production and seedfall is determined by time of emergence. Furthermore, seeds can be imported with low quality crop seed or exported during combine harvest operations. The vertical distribution of the seeds in the soil can be changed by tillage.

2.4 The level of complexity needed

With the detailed model introduced above it is possible to look at the consequences of simplification. It is possible for example to neglect the vertical distribution of the seeds by taking a mean value for germination and a mean value for mortality of germinated seeds over different depths in the soil. Simulation, if necessary with estimated parameter values, makes it clear to what detail a model has to be worked out to clarify the problem at hand.

Simulation results confirm that the explanatory and predictive value of a model **descriptive on population level** is very low. The annual rate of increase of the population varies with crop and growing practices, but also within the same cropping practices (Fig. 2.1 and 2.2). Simulation gave an annual growth rate of *G. aparine* in winter wheat of 1.4 and 0.8 and in sugar beet of 13.6 and 37.6 for the first and second time in a subsequent rotation with ploughing respectively (Fig. 2.1), dependent on the pattern of vertical distribution of the seeds in the soil. Dependent on timing sowing of sugar beet, timing of herbicide application and choice of herbicide, the annual growth rate of the population, lambda, is between 2 and 26 (Fig. 2.2).

Fig. 2.1 Population dynamics of *Galium aparine* L. taking into account or neglecting the vertical distribution of the seeds in two crop rotations with shallow cultivation or ploughing.



a) Simulation results for a continuous culture of winter wheat.

b) Simulation results for a rotation of winter wheat; sugar beet; spring barley and potato.

In both cases seeds emerged directly following seedbed preparation.

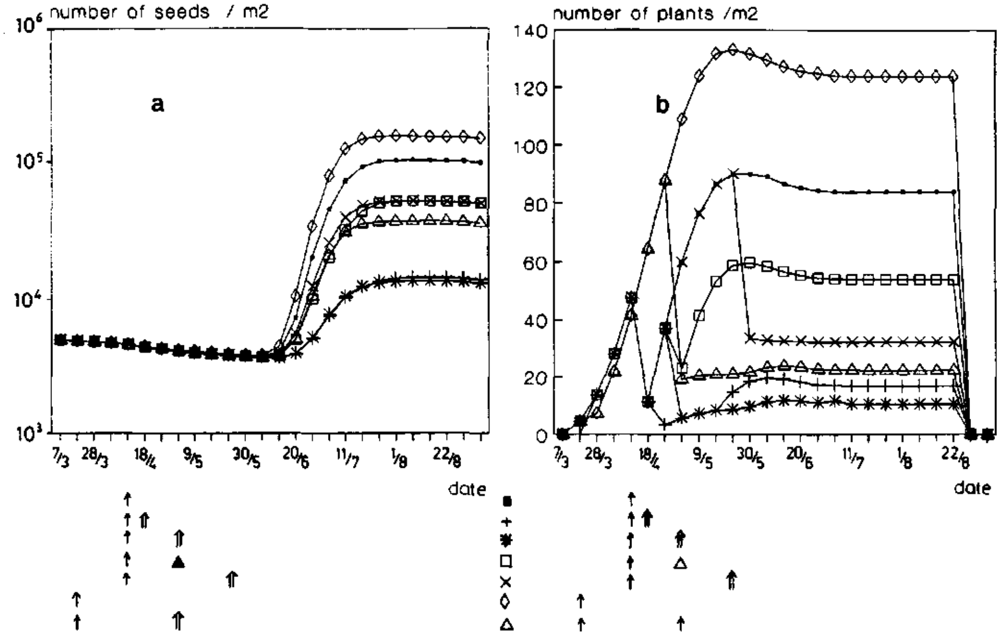
△ with vertical distribution of the seeds and shallow cultivation,
✳ with vertical distribution of the seeds and ploughing,
○ neglecting the vertical distribution of the seeds.

Many models which are **explanatory on the population level and descriptive on the plant level** mentioned under chapter 2.2 point 1, neglect the vertical distribution of the seeds in the soil. Simulation learns that this can give considerable deviations (Fig. 2.1). Starting with a homogeneous vertical distribution under ploughing and a monoculture of winter wheat, there were two times more seeds after eight years in simulations when this distribution was not taken into consideration. This is due to an underestimation of the natural mortality of the seeds caused by the negative effect of burial on survival. In contrast, after eight years of simulating a normal rotation of winter wheat, sugar beet, spring barley and potato, there were three times less seeds in simulations when this distribution was neglected. In open crops, many seeds are produced and buried by ploughing. If the vertical distribution of the seeds is neglected, this is leading to an overestimation of the amount of seedlings in the next year and an underestimation after two years. Open crops every other year intensify the multiplication, resulting in higher numbers after eight years taking into account the vertical distribution. After shallow cultivation newly produced seeds stay in the surface layer of the soil leading to a progressive increase in numbers. This is also known from field practice (Wilson & Froud-Williams, 1988). Neglecting the vertical distribution of the seeds in this case, causes enormous underestimations.

Many demographic models mentioned under chapter 2.2 point 2 contain density dependent regulation. In the model used here density dependence is neglected, leading to an unrealistic increase in numbers in some simulations. For more general predictive models and for species where intraspecific competition is an important factor in practice, density dependence but also a non-homogeneous horizontal distribution of the plants (Ballaré *et al.*, 1987) cannot be neglected.

Part of integrated control strategies is the optimisation of timing and method of cultivation as well as timing and method of control. If demographic models work on a year to year basis, for every variation for instance in treatment time, the mortality and the seed production of the remaining plants have to be determined again. Models that calculate the effect of these processes during the year (see chapter 2.2 point 4), are better suited for this purpose. If there are good estimates of the efficiency of a control method on the various plant stages and if it is possible to calculate the distribution over the various plant stages during the year, it is possible to calculate the overall effect of, for example, a control measure at different times of the year (Fig. 2.2). From the simulation results in Fig. 2.2 it can be learned that the lowest number of *G. aparine* in sugar beet can be obtained by late sowing of sugar beet (14/4 in stead of 22/3) and application of fenmedifam and ethofumesaat (Betanal Tandem) 16 days after sowing instead of 31 or 5 days after sowing. After a late herbicide application early emerged *G. aparine* plants escape. They produce the same amount of seeds as the, twice as many, late emerged *G. aparine* plants that escape a fenmedifam and chloridazon treatment. They also start their seed production earlier. This early seed production is important for crops that are harvested before August. The quick drop in numbers of plants in Fig. 2.2 b is caused by the assumption in the model that all outgrown plants die before 1 september or directly after crop harvest. Extension on this point can make the model more realistic, but does not affect the simulated population dynamics over the years. Dependent on timing sowing of sugar beet, timing of herbicide application and choice of herbicide, the annual growth rate of the population, lambda , is between 2 and 26.

Fig. 2.2 Simulation of the number of seeds a) and plants b) of *Galium aparine* L. during one season with different sowing times of the surrounding sugar beet crop, different herbicides and herbicide application times.



↑ sowing date of sugar beet

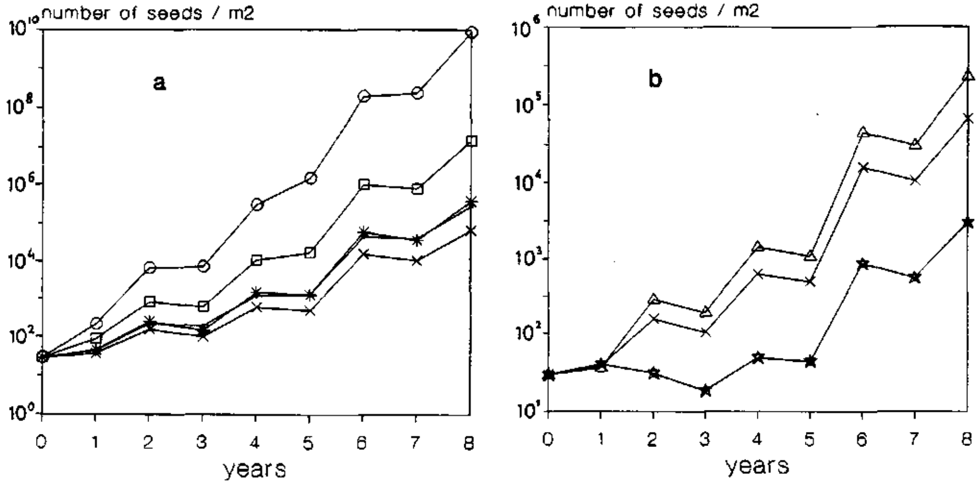
⇑ application of fenmedifam and ethofumesaat (0.5 and 0.3 kg/ha)

▲ application of fenmedifam and chloridazon (0.9 and 1.3 kg/ha)

It is very important to have reliable estimates of parameters, especially if the model is used for prediction. Simulation of a range of reasonable parameter values, can inform us whether more details are needed (Fig. 2.3). Fig. 2.3 a shows enormous differences in increase of *G. aparine* for simulations based on germination data of either Röttele (1980) or Aarts (1986). Especially a lower mortality of germinated seeds on different depths in the soil derived from Aarts (1986), is responsible for this. The year to year variation in the timing of emergence of *G. aparine* (Van den Brand, 1984) can cause quite different results as well. Multiplication of *G. aparine* in spring sown crops is stimulated by relatively more spring emergence and the opposite in winter crops (Fig. 2.3 b).

When the effect of the variation in a parameter remains too great it can be advantageous to replace this parameter by one based on the underlying (physiological) principles. At least part of the model will be **explanatory on the plant level** then. The effect of new crops, cultivars and/or crop densities on the relevant growth and seed production parameters has to be investi-gated and incorporated in the models before it is possible to account for these aspects. More explicit models based on physiological principles have the advantage of more precise predictions and sometimes of predictions of the effect of a new aspect. Physiologically based competition models for example have shown to give a good prediction of crop yield reduction caused by weeds under various conditions (Kropff, 1988). If different abiotic conditions are the cause of important variation, physiological models are necessary for competent risk analyses.

Fig. 2.3 Sensitivity of the population dynamics of *Galium aparine* L. in a crop rotation (winter wheat; sugar beet; spring barley and potato, with emergence following ploughing in autumn) for difference in germination and mortality of the seeds.



a) The effect of differences in depth dependent germination, depth dependent mortality after germination and for emergence and overall mortality of dormant seeds:

× parameters adapted from Röttele (1980)

o parameters adapted from Aarts (1986)

✱ parameters adapted from Röttele (1980) but depth dependent germination according to Aarts (1986)

• parameters adapted from Röttele (1980) but overall mortality of dormant seeds according to Aarts (1986)

□ parameters adapted from Röttele (1980) but depth dependent mortality of germinated seeds according to Aarts (1986)

b) The effect of differences in the timing of the germination and the emergence according to Van den Brand (1984):

× 70 % in autumn and 30 % in spring (mean of five years)

★ 95 % in autumn and 5 % in spring (as in 1979/1980)

△ 45 % in autumn and 55 % in spring (as in 1982/1983)

2.5 Conclusions from the model of *G. aparine* L

An extended demographic model describing the processes during the year and taking into account the vertical distribution of the seeds, is suited for strategic evaluation on the population or system level.

The first results obtained with such a model for *G. aparine* indicate that:

1) *G. aparine* infestation is strongly influenced by crop and growing practices. A strong increase especially occurs in open crops (sugar beet, potato) and after shallow cultivation.

2) Open crops every other year in a rotation with ploughing without sufficient control, intensify the problems with *G. aparine*.

3) The model can be used for optimisation of the timing of herbicide application and sowing of the crop.

4) Variation in germination and emergence parameters, especially depth dependent mortality of germinated seeds, strongly influences the population dynamics.

Several aspects like new crops, different cultivars and/or densities and changes in fertilization, form no part of the model yet. Additional research on the effects of these factors on the relevant parameters followed by extension of the model, is needed for evaluation of these aspects.

For accurate prediction of population increase at least some parameters especially those that strongly fluctuate as a result of variation in abiotic conditions, need to be based upon physiological principles.

Chapter 3

The influence of microclimate and soil conditions on dormancy and germination of *Galium aparine* L. in the field.

Abstract The effects of temperature, light, nitrate, soil moisture and soil compaction on the germination of different seed populations of *Galium aparine* L. were determined.

Primary dormancy occurred to various degrees, but always disappeared in one to three months depending on storage conditions. Seeds collected from plants which had emerged in autumn and seeds of plants which had emerged in spring were buried separately under natural conditions at 20 cm depth in the soil. Germination tests at a range of temperatures, after recovering part of the seeds every two months, showed that both origins could germinate in autumn as well as in spring. Seeds of *G. aparine* could not germinate in winter because their temperature requirements were higher than the actual field temperature (enforced dormancy). In summer germination was restricted to temperatures around 10 °C and secondary dormancy was induced. Secondary dormancy was induced by high temperatures but after this induction dormancy was released at high temperatures too.

The actual germination process was not influenced by fluctuations in temperature. The presence of light during twelve hours each day was inhibitory to germination. Nitrate and water availability needed for germination will be sufficient on the arable fields most of the time. Increasing the bulk density of a soil, considerably reduced germination. This explains the reduced germination of *G. aparine* at greater depths and the increased germination after soil cultivation.

In comparison with seeds from arable origin, seeds from *G. aparine* of hedgerow origin could germinate at a broader range of environmental conditions (temperature, light and nitrate).

Together with knowledge on the emergence phase, the collected data on dormancy patterns and germination can be used for modelling the field emergence of *G. aparine* on arable fields in relation to environmental conditions.

3.1 Introduction

To minimize environmental risks and to decrease costs, the development of integrated systems of weed control is promoted (Hoogerkamp, 1989). This requires better knowledge of the critical levels of weeds in crops and of the potential for increase in abundance on a longer time scale. This is especially true when dealing with weeds that cause problems in several crops, like *Galium aparine* L. (Holm et al., 1977).

Differences between weed and crop emergence date are responsible for differences in the relationships between crop yield and weed density (Joenje & Kropff, 1987). Furthermore the phases of germination and emergence are important for the population dynamics of annual weed species. Finally, knowledge on timing and levels of germination and subsequent emergence are expected to improve timing and choice of control measures.

The main environmental factors that determine weed seed germination under field conditions are reviewed by Koch (1969), Harper (1977), Karssen (1982), Egley (1986), Baskin & Baskin (1987) and Bouwmeester (1990). Whether a seed is able to germinate depends on its state of dormancy and the prevalent environmental conditions. Release of primary dormancy, induction and release of secondary dormancy and the actual germination process are regulated by environmental factors such as temperature, light, water potential, nitrate and levels of O2, CO2 and ethylene in the soil. These factors vary during the year as well as during the day depending on weather conditions, soil structure, soil layer, cultivation, choice of crop and application of fertilizers, thus providing the crucial stimuli that can initiate germination. Seeds originating from different plants or ecotypes can react differently (Baskin & Baskin, 1989; Bouwmeester, 1990).

Germination of *G. aparine* under field conditions is very variable. In some years more seeds germinate in autumn and in other years more seeds germinate in spring (Van den Brand, 1984). Percentage germination differs with depth and between locations (Röttele, 1980; Aarts, 1986). Differences between years and locations can have a considerable effect on the population dynamics of *G. aparine* (Chapter 2).

To predict germination of *G. aparine* for different climatic conditions, for distinct soils and for various agricultural practices, detailed knowledge of the factors that regulate dormancy and germination is required. Therefore dormancy patterns during burial in the soil, the effect of temperature on dormancy patterns under controlled conditions and the effects of temperature, light, nitrate, soil moisture and soil structure on the actual germination process, were studied. Also differences in germination behaviour between *G. aparine* seeds of different origin (collected in hedgerows, at arable fields from autumn germinated plants or at arable fields from spring germinated plants) were studied to evaluate whether these differences are important for the prediction of germination.

3.2 Material and methods

General information on the germination tests

Unless stated otherwise in the other paragraphs, the next conditions were used for the different germination tests. Observations were done with 'safe green' light at 25 seeds on a filter paper soaked with 12.5 mmol/l KNO3 at the start of the experiment and keep moist with destilled water afterwards. Filter papers were placed in Petri dishes with aeration possibilities. During the experiment seeds were placed in dark conditions at a constant temperature of 8 °C. In the experiments which did not involve dormancy patterns, dry stored seeds that were able to germinate at optimal conditions were used.

Seeds in the petridishes were considered germinated when the radicles were just visible. To assess the time required for germination (mean and standard deviation of the population), germination was recorded at least every other day during peak germination and once a week afterwards. At the end of the experiments (after at least 21 days) the vitality of the remaining seeds was determined using tetrazolium (Moore,1970). Percentages germination were corrected for dead seeds. Seeds that were buried in soil were considered germinated if they could not be recovered in the soil after sieving at the end of the experiment. In this way germinated seeds that died during emergence were included.

Means and standard deviations of 4 (unless stated otherwise) replicates were calculated and analysis of variance were performed after arcsin square root transformation of the percentages. Effects called significant had a unreliability less then 0.05. The data of the influence of lightflashes on the germination were analyzed using the distribution-free sign test. The data on primary dormancy were analyzed using regression analyses with generalized linear models for binomials (Genstat, 1988).

Research on primary dormancy

In the summer and autumn of 1988, 1989 and 1990 bulk samples of mericarps (hereafter referred to as seeds) with different degree of ripeness, were collected by hand from plants of G. aparine growing in different crops in the vicinity of Wageningen (oilseed rape, winter wheat, sugar beet and potato) or in the north of the Netherlands (sugar beet) and in hedgerows in the vicinity of Wageningen. The level of primary dormancy was investigated by scoring the percentage of not germinated and viable seeds after at least 21 days under conditions adequate for germination (in preceding paragraph). Seeds were put under these conditions immediately after collection in the field and in three replicates.

Release of primary dormancy was studied with green seeds of *G. aparine* collected in a sugar beet crop in 1988. Seeds were stored dry at room temperature in light or darkness and at 5 °C in darkness during 0, 6, 17, 30 and 100 days. Release of primary dormancy was also registered in the research on dormancy patterns during burial in the soil.

Research on secondary dormancy patterns

The induction and release of secondary dormancy during natural storage was investigated with three collections of seeds of *G. aparine*: A) collected in summer 1987 in winter barley, B) collected in summer 1988 in oilseed rape and C) collected in autumn 1988 in sugar beet. Lots A and B originated of plants that emerged in autumn, lot C originated of plants that emerged in spring. The seeds were buried immediately after collection at 20 cm in compacted clay soil in pots buried in the field. Seeds were exhumed to test germination at 8-8-1988 (A,B); 27-10-1988 (B,C); 6-1-1988 (B,C); 11-4-1989 (A,B,C); 20-6-1989 (B;C) and 4-9-1989 (A,B,C). Germination was tested at ten different constant temperatures between 0 and 22 °C at a thermos-gradient bar (Grime and Thompson, 1976) in three replicates.

In an additional experiment the influence of temperature during storage under controlled conditions on changes in dormancy was tested. Therefore seeds were stored under moist conditions at 5, 10, 15 and 20 °C in incubators during 0, 2, 4, 6 and 10 weeks and subsequently placed to germinate at 5, 10, 15 and 20 °C. During storage at 15 and 20 °C without nitrate in the filter papers, seeds did not germinate. Germination was only possible after placing the seeds at the different temperatures with nitrogen. However during storage at 5 °C after 4 weeks and at 10 °C seeds partly germinated. Further investigations on the not germinated seeds after storage at these lower temperatures were not used because of possible effects of a selection of the population.

Experiments on the effect of environmental factors on the actual germination process

Seeds of arable and hedgerow origin were placed at a thermos-gradient bar (Grime and Thomp-son, 1976) at constant temperatures ranging from 0 to 20 °C (in ten almost equal steps) or at a fluctuating temperature with a mean of 12.5 °C and an amplitude increasing from 0.5 to 9 °C (in five steps). In this experiment treatments were in duplicate.

The influence of light was investigated by eliminating light or varying the light quantity between 0.1 and 6.8 $\mu E^{*}m^{-2}s^{-1}$ with a correlated light quality in terms of a red/far red ratio from 0.02 to 2.0 (in five steps) during twelve hours each day (Corré, 1983). Germination of two origins (hedgerow and arable) were tested in 5 replicates. The potassium nitrate concentration used was 25 mmol/l.

In addition the effect of a weekly illumination period (± 5 minutes daylight) compared to absolute darkness on germination of 9 collections of freshly harvested seeds (6 harvested before half august and 3 later than half august) was investigated with two to fifteen replicates per collection.

The effect of potassium nitrate (0, 0.25 or 25 mmol/l) on the germination of an arable or a hedgerow population was investigated in 5 replicates. The effect of the nitrate concentration (0, 0.25, 0.625, 1.25, 2.5, 6.25, 12.5, 25 or 50 mmol/l) on the germination of the arable population was studied again in more detail.

The influence of moisture on germination was studied comparing an arable and a hedgerow population in an open greenhouse in autumn 1988 (5 replicates) and repeated for the arable population at constant temperatures of 8 or 14 oC. Seeds were buried at two cm in a clay soil. Soil suctions (pF) from ± 4 to 2 in five equal steps were installed using previous determined pF curves for the used soils (regulating the gravimetric moisture content accordingly from 15.5 to 34.0 % for the clay used first; 9.3 to 28.9 % for the clay used secondly).

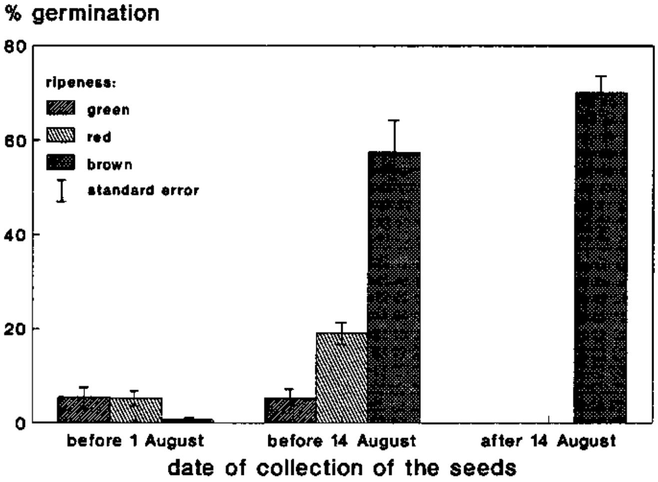
Seeds (only arable origin) were also buried at 2 cm in soil with different compactions. Soil structure was influenced by compressing the sandy soil with 11 % gravimetric moisture content (± pF 2.7 uncompressed) in cylinders. Measured penetration resistances were 1.6, 4.9, 6.6, 9.5, 13.7, 18.3 and 23.3 kg/cm2 (1.16 to 1.60 g dry soil/cm3).

3.3 Results

Primary dormancy

There was a significant interaction between the date of collection within a year and the ripeness of the collected seeds on the degree of primary dormancy (Fig. 3.1). Differences in primary dormancy between years were also significant but less important (standard errors in Fig. 3.1 are mainly determined by the differences between years).

Fig. 3.1 Primary dormancy as observed immediately after collection of *Galium aparine* L. seeds of varying ripeness at different times.



Primary dormancy was released during dry storage of the seeds (Fig. 3.2). Initially, relief of primary dormancy occurred best at 20 °C in the light, but after 100 days storage remaining primary dormancy did not differ significantly anymore. Under natural storage conditions (buried in the soil outdoor) primary dormancy also decreased. Germination increased from 60 to 95% within a few months (Fig. 3.3).

Fig. 3.2 Release of primary dormancy (percentage seeds which can germinate) of *Galium aparine* L. as influenced by the duration and method of dry storage.

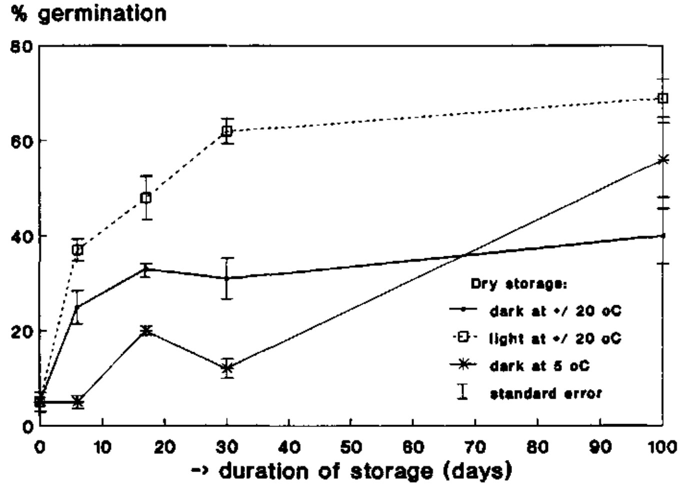
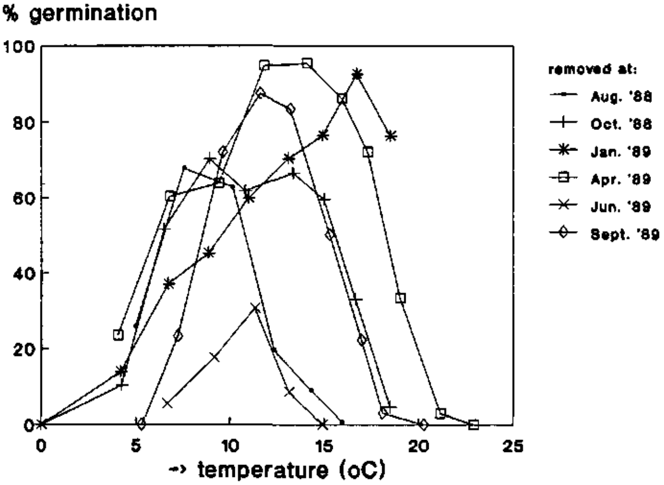


Fig. 3.3 Temperature requirements for germination of *Galium aparine* L. collected in oilseed rape in August 1988 and retrieved at different times after burial under natural conditions.

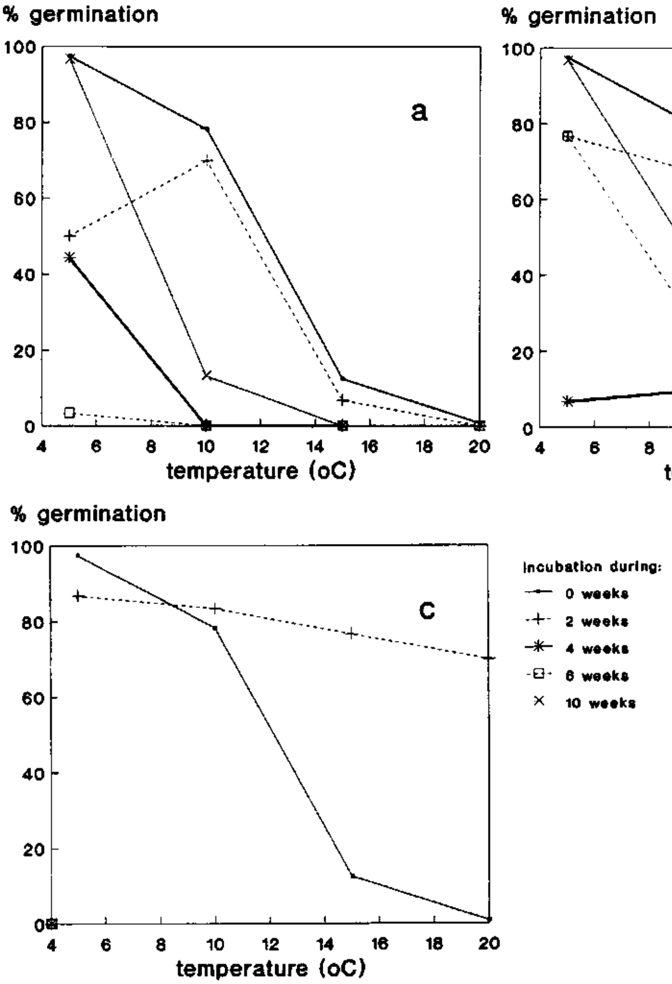


Secondary dormancy patterns

The temperature requirements for germination (temperature window) of *G. aparine* seeds changed with the duration of their stay in the soil. Seeds from autumn-germinated (Fig. 3.3) as well as from spring-germinated plants (arable origin) could germinate in autumn as well as in spring. (Data on seeds from spring-germinated plants were not presented in this papar, but a model description of the data of both collections is in chapter 5.) In winter seeds were able to germinate but only at the higher temperatures which do not occur under natural conditions at that time. In summer, secondary dormancy was induced. Only few seeds could germinate at temperatures around 10 °C only.

Changes in temperature requirements for germination as observed during burial under natural conditions, were also recorded during incubation at different temperatures under controlled conditions. Incubation at 5 °C during 2 weeks resulted in increased germination at higher temperatures than before this incubation (Fig. 3.4c). During incubation at higher temperatures (15 and 20 °C) secondary dormancy was induced (Fig. 3.4a and b). After longer duration of the incubation at the same temperature, secondary dormancy was also released again.

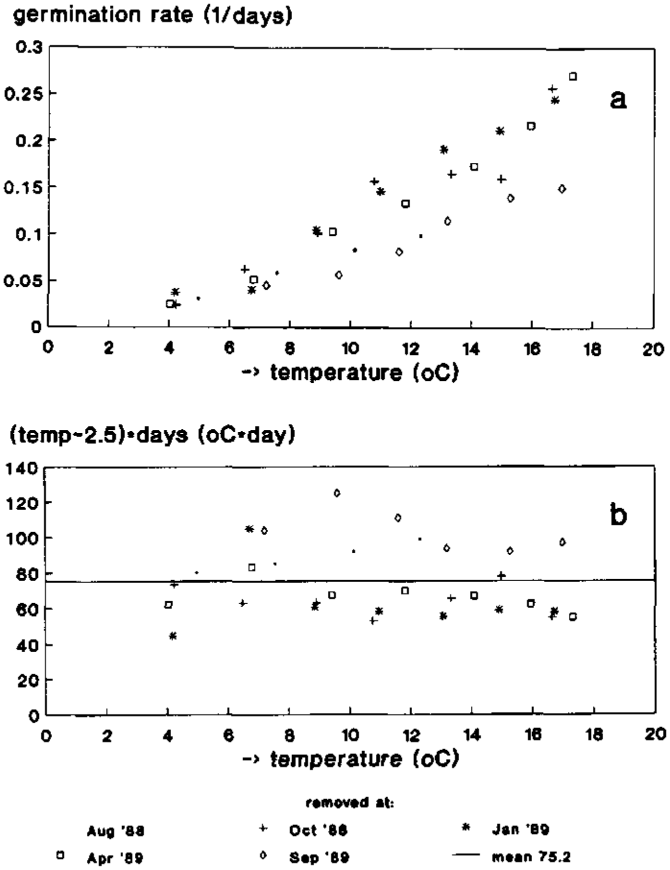
Fig. 3.4 Changes in temperatuur dependent germination behaviour of *Galium aparine* L. after incubation at 20 °C (a), 15 °C (b) and 5 °C (c) during 0, 2, 4, 6 or 10 weeks.



The effect of environmental factors on the actual germination process

The actual environmental temperature determined whether a seed did germinate or not (Fig. 3.3 and Fig. 3.4). Seeds from a field population had a more restricited range of temperatures suitable for germination than seeds from the hedgerow population ($P<0.01$, data not shown). Daily fluctuation in temperature did not have any significant influence on the actual germination process (data not shown). The temperature dependent rate of germination varied significantly between the different dates of exhumation (see Fig. 3.5 a). Neglecting the effect of removal date, a mean (for the individual seeds to germinate) thermal time requirement of 75.2 °C day above a base temperature of 2.5 °C gave the best fit with the experimental data (Fig. 3.5 b). The standard deviation in duration of germination of the individual seeds was 12.5 % of the mean duration.

Fig. 3.5 The influence of temperature on germination rate (a) and mean thermal time required for germination (b) of *Galium aparine* L. seeds collected in oilseed rape in August 1988 and retrieved at different times after burial.



Light during 12 hours each day reduced the germination of seeds of G. aparine (Fig. 3.6). Especially far red light had a strong influence on the germination. Seeds collected in hedgerows were significantly less sensitive to light than seeds of arable origin. Fresh seeds harvested after the 15th of August were significantly stimulated by short periods of illumination (83.7 % germination compared to 53.5 % germination in absolute darkness). Fresh seeds harvested before the 15th of august were not affected.

Fig. 3.6 Germination of *Galium aparine* L. seeds collected at a arable field and in a hedgerow as influenced by different light quantities and qualities.

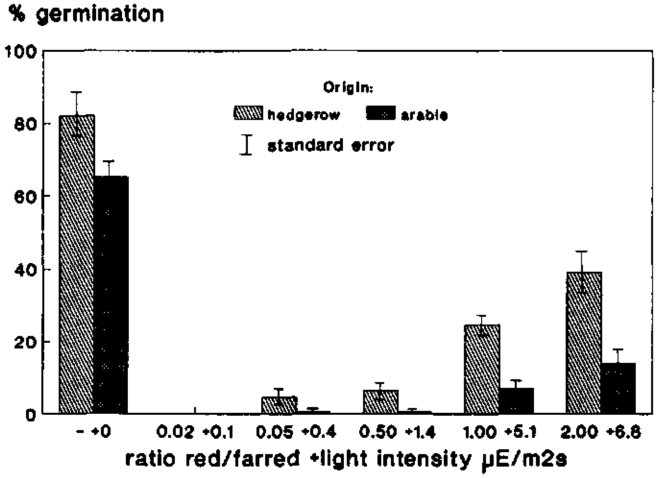
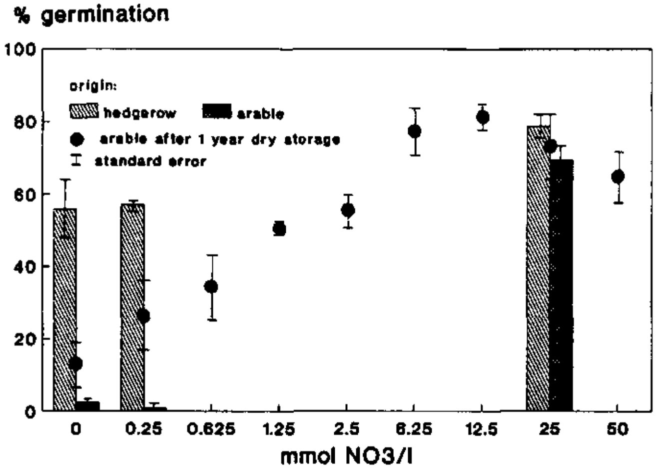


Fig. 3.7 Germination of *Galium aparine* L. seeds collected at a arable field and in a hedgerow as influenced by nitrate availability.



Seeds from arable origin required nitrate for their germination (Fig. 3.7). Germination was optimal at KNO3 concentrations between 6.25 and 25 mmol/l. The reduction of the germination of seeds of arable origin at suboptimal KNO3 concentrations was less pronounced for older dry stored seeds. Germination of seeds of hedgerow origin was significantly less influenced by nitrate availability then seeds of arable origin (Fig. 3.7).

Fig. 3.8 Germination of *Galium aparine* L. seeds in a clay soil with different moisture availability at two temperatures.

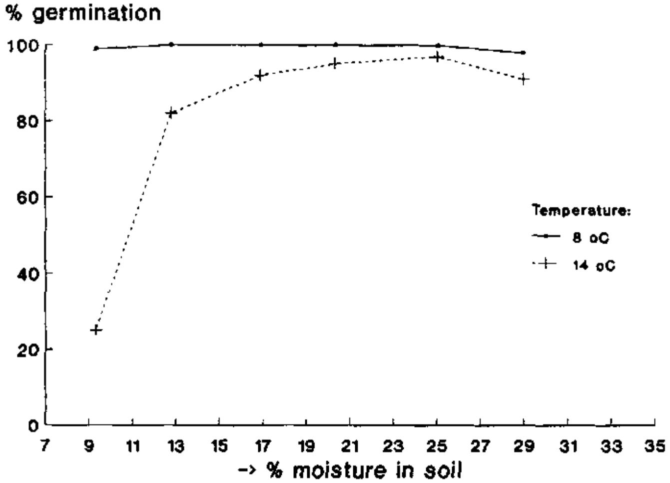
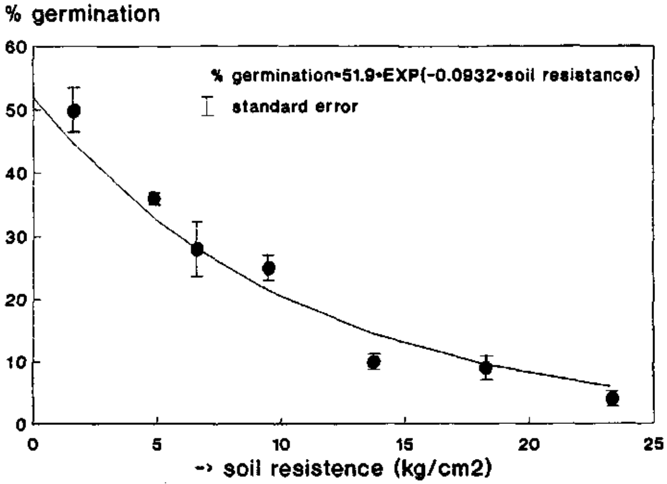


Fig. 3.9 The influence of soil structure on germination of *Galium aparine* L.



Reduced moisture availability (pF ± 2 to 4) decreased germination at 14 °C but not at 8 °C (Fig. 3.8, interaction $P<0.05$). Availability of moisture under natural temperature conditions during autumn, influenced the germination of seeds to a small degree (80 % at pF ± 2 to 65 % at pF ± 4). It was not possible to discriminate moisture related differences in germination between hedgerow and arable collections of *G. aparine* (data not shown).

Soil structure clearly influenced germination of seeds at a temperature of 8 °C and adequate moisture availability (Fig. 3.9). Increasing compaction of the soil influenced the aeration of the soil (43 to 21 volume % of air in the soil) as well as the mechanical resistance the seeds experienced (1.6 to 23.3 kg/cm2).

3.4 Discussion

Primary dormancy

Literature data on primary dormancy in seeds of *G. aparine* are contradictory. Many research workers found no primary dormancy in seeds of *G. aparine* (Sjöstedt, 1959; Webster, 1979; Håkansson, 1983 and Froud-Williams et. al., 1984), but others did report on primary dormancy (Grime et. al., 1981 and Hilton and Owen, 1985) and some found both, seed lots with or without primary dormancy (Froud-Williams, 1985 and Hilton and Thomas, 1987). This is not surprising given the variation in primary dormancy for seeds collected at different dates and with varying ripeness and the speed with which dormancy was broken during dry storage. Since seeds of *G. aparine* which mature before the 15th of August were more dormant then later matured seeds, primary dormancy was possibly influenced by environmental conditions during maturation (Gutterman, 1973 and Creswell and Grime, 1981). Primary dormancy of relatively late maturing cleaver seeds decreased during their maturation on the plant, but not for early in the season maturing seeds. Moreover primary dormancy of late maturing seeds was overestimated because part of the assumed primary dormancy was overcome by short periods of illumination. These observations suggest that the seed coat is impermeable for red light which may be one of causes of primary dormancy. Froud-Williams (1985) reported that seeds which passed through a combine harvester lost their dormancy more rapidly. This indicates a seed coat as barrier for stimulants coming into the seed or inhibitors going out. Additional research on the physiological backgrounds of primary dormancy in *G. aparine* seeds is needed to understand the observed differences and to predict remaining primary dormancy more accurately. However prediction of primary dormancy as an aspect of predicting field emergence, is only important for situations in which the soil is not ploughed. Most arable fields however are still ploughed yearly, and most fresh seeds buried during the first year to soil layers where they can not germinate anyhow. Primary dormancy will have been released by the time the seeds return to the upper soil layers. In these cases predicting primary dormancy is not required.

Secondary dormancy patterns

The changes in the range of temperatures suitable for germination and the induction of secondary dormancy are fundamental for understanding germination patterns in the field.

Low temperatures induced a shift in the temperature interval towards higher temperatures. High temperatures induced a reduction of the appropriate interval at low temperatures and secondary dormancy. Secondary dormancy however was also released during storage at high temperatures. It seems that changes in temperature reaction are induced by the temperatures previously experienced. Under natural conditions this leads to enforced dormancy during winter (the actual temperature is too low), secondary dormancy in summer and germination in autumn and spring for seeds originated from *G. aparine* emerged in both spring and autumn.

The influence of environmental factors on the actual germination process

Under otherwise optimal conditions, soil moisture is not important for the germination of *G. aparine* and even under sub optimal conditions it only influences germination at very low moisture values. Hanf (1941), Sjöstedt (1959) and Hirdina (1959) also stated that *G. aparine* was not very sensible for moisture shortage.

Germination of *G. aparine* of field origin was optimal at a nitrate concentration of approximately 6.25 to 25 mmol/l. This concentration range is found in arable fields. Fitter & Hay (1981) reported a mean concentration of 9.1 mmol/l in soil solutions. So nitrate seem hardly important for prediction of germination in the field.

Light and especially far-red light during several hours each day inhibits germination of *G. aparine* and as such prevents germination at the soil surface. This is also reported by Hirdina (1959), Sjöstedt (1959) and for the closely related *G. spurium* by Malik and Vanden Born (1987). Physiologically and ecologically significant amounts of light rarely penetrate more than 4-5 mm through the soil and often even less (Tester and Morris, 1987). Depths at which *G. aparine* germinate range from 0 to 10 cm, with an optimum around 2 to 3 cm (Röttele, 1980). So, most seeds germinate in complete darkness. The stimulation of germination of *G. aparine* by short periods of illumination was also reported by Hilton and Owen (1985). The light flashes seeds receive during soil cultivation may stimulate their germination. This was also suggested by Hartman and Nezadal (1990), who cultivated the soil in the dark and found among others less emergence of *G. aparine*.

Many weed species germinate at suitable depths in the soil or in gaps because they respond to daily fluctuations in temperature and to light quantity and quality. Germination of *G. aparine* is also reduced at greater depths (Röttele, 1980). But reduced daily fluctuations in temperature at greater depths do not limit the germination of *G. aparine*, because it is not stimulated by temperature fluctuations. The absence of light does not cause reduction of germination at greater depths either, because germination of *G. aparine* is not stimulated and even inhibited by light during several hours each day. However, it seems that soil structure and the related aeration of the soil limits the germination of *G. aparine* to certain depths. *G. aparine* require much oxygen for their germination (Müllverstedt, 1963) and carbondioxide and ethylene can inhibit the germination process. The oxygen concentration decreases with depth and the carbondioxide and ethylene concentration increases with depth. Levels vary also with soil moisture, season of the year and the presence of organic material and organisms (Egley, 1986). Gas diffusion depends on the aeration of the soil. Bulk density of the soil increases with depth, decreases after soil cultivation and differs between different soil types (Locher & Bakker, 1990). Soil resistance increases with the bulk density, so germination decreases with depth or with compaction of the soil. Relatively less emergence of *G. aparine* on badly aerated soil in the field is reported by Hanf (1941) and Noda (cited by Froud-Williams, 1985). For reliable extrapolation, additional research is needed to determine whether cleaver germination at greater depths in the soil is reduced because of physical impediment or impeding concentrations of oxygen, carbondioxide or ethylene or a combination of these factors.

Differences between origins of the seeds

Seeds collected in hedgerows were less sensitive to the presence of light. This was also expected because in this habitat seeds are not buried to the same extent as seeds of arable origin (by soil cultivation). The difference in germination response to nitrate of hedgerow and arable origin of *G. aparine* was also reported by Froud-Williams (1985) and Groll and Mahn (1986). The potential of hedgerow- originated seeds to germinate in absence of nitrate also fits with their non-arable habitat. Maturation on the plant in a hedgerow will not be terminated artificially by harvest. By the time the seeds of hedgerow origin tumble, they lack primary dormancy. The range of temperatures suitable for germination is broader than for arable origins. Germination of seeds in the hedgerows is less restricted by the environmental factors that regulate the germination of seeds of an arable population. Germination of seeds in the surface soil layers in hedgerows is probably more influenced by moisture availability and the experienced light quality.

The provided data on dormancy patterns and germination and the data on the subsequent emergence phase (chapter 4) are used for a simulation model of field emergence of *G. aparine* as influenced by environmental conditions (chapter 5).

3.5 Conclusions

Primary dormancy is of secondary importance for predicting germination on ploughed arable soils.

The temperature requirements for germination of seeds stored under natural conditions, change during the year (dormancy patterns). Seeds from *G. aparine* that emerged in autumn and seeds from *G. aparine* that emerged in spring can both germinate in autumn as well as in spring.

Light inhibits the actual germination of *G. aparine* <u>on</u> the soil. Temperature and soil structure are of primary importance for the actual germination of *G. aparine* <u>in</u> the soil.

In comparison with seeds from arable origin, seeds from *G. aparine* of hedgerow origin can germinate at a broader range of environmental conditions.

Chapter 4

The effect of temperature, moisture and soil structure on emergence of *Galium aparine* L. from different depths.

Abstract Knowledge of germination has to be supplemented with data on the emergence phase to understand emergence patterns in the field.

In several experiments in climate chambers and in an open greenhouse, the duration and percentage of emergence of germinated seeds were investigated. Germinated seeds were planted at different depths, in two soil types, with various compactions and/or moisture availability at distinct temperature regimes. The difference in emergence percentage between laboratory germinated seeds and naturally germinated seeds was examined in another experiment.

The most important factors determining emergence rate were the temperature and the depth of the seeds in the soil. Summation of temperature above a base temperature of 2.5 °C characterized the duration of half of the seeds emerging as influenced by depth, soil compaction and moisture availability (60 degreedays for germinated seeds to overcome 1 cm of soil and 300 degreedays to overcome 5 cm).

Under otherwise optimal conditions *Galium aparine* L. emerged over a wide range of soil moisture contents even at very low ones. Under less favourable conditions, for instance high soil resistance, low soil moisture became more limiting. Soil type appeared to have no effect on percentage or rate of emergence in this study. This was probably due to the fact that in the field factors related to soil type were variable, whereas in the experiment these factors were controlled. The most important factors determining percentage of emergence were the soil resistance and the depth of the seeds in the soil (0 to 100 % emergence). It was possible to fit an equation for percentage of emergence in dependence of soil resistance and depth ($r=0.911$). This equation and the temperature sums are needed for modelling the field emergence of *G. aparine*.

4.1 Introduction

An increased understanding of the field emergence of weed species is needed to improve timing and choice of weed control measures and to evaluate the necessity of control. Germination of weed species as influenced by environmental factors is reviewed by Egley

(1986). Germination under field conditions however, can not be recorded until the seedlings have grown to the soil surface. This emergence phase in the life cycle of species is time consuming and brings about loss of individuals by mortality. To comprehend emergence patterns in the field, knowledge on the emergence phase has to be added to data on germination requirements.

Two aspects of the emergence phase are important: the percentage of germinated seeds which succeed in reaching the soil surface and the duration of the emergence. The troublesome weed species *Galium aparine* L. is able to emergence from at least 9.5 cm depth (Röttele,1980). Data on mortality of germinated *G. aparine* seeds under arable field conditions (Röttele, 1980 and Aarts, 1986) show large differences. These unexplained differences are responsible for great variation in the population dynamics of *G. aparine* (chapter 5). Because of the ability of *G. aparine* to emerge from a range of depths, duration of emergence may show a considerable variation, causing an emergence wave extending over a long period. This will have consequences for the control of *G. aparine*. One herbicide treatment often may not be sufficient to kill all *G. aparine* plants. Furthermore the timing of emergence of weeds relative to emergence of the crop largely influences crop yield reduction by the presence of weeds (Håkansson, 1986; Joenje and Kropff, 1987).

Only few studies on emergence discriminated between the germination and the emergence phase. During emergence the coleoptile is elongating. In this process temperature and the distance to the soil surface are of primary importance (Morrow *et al.*, 1982; Carberry and Campbell, 1989; Boydston, 1989). Soil structure (Hanf, 1941; Terpstra, 1986) and moisture availability (Hanf, 1941; Finch-Savage, 1987) are also important factors during the emergence phase.

To model and to understand field emergence of *G. aparine* in relation to environmental factors (chapter 5), germination (chapter 3) and emergence were investigated. In the study for this paper the influence of planting depth, temperature, soil structure and moisture availability on rate and percentage of emergence of germinated seeds was determined.

4.2 Material and methods

To examine the influence of several environmental conditions on the emergence of Galium aparine, several experiments were carried out in 1989 and 1990 in greenhouse or climate chambers.

Experimental conditions

Experimental units were soil filled PVC tubes with a diameter of 5.5 cm, containing 10 germinated or 25 ungerminated seeds of arable origin. Pre-germinated seeds were obtained by incubation on filter-paper in petri-dishes with 5 ml 12.5 mM KNO3 solution, and putting them in a climate chamber at 8°C in complete darkness. Relationships between soil compaction and soil resistance and relationships between gravimetric moisture content and soil suction were determined for the different soils used. These relationships were determine soil moisture content and soil compaction required for the desired soil suctions and soil resistances. Moisture contents were achieved by drying or adding water and mixing the soil before compaction. Compactions were achieved by compressing the calculated amount of soil in layers of 2 cm into the tubes. Before adding a new layer of soil, the surface of the previous layer was superficially raked with a fork and if appropriate (un)germinated seeds were placed on this layer. Soil resistance was measured with a penetrometer. Evaporation was minimized by covering the tubes with punctuated parafilm (experiment 1, 3 and 4) or saturating the environmental air with moisture by covering tubes with wet paper (experiment 2). This was done to minimize the necessity of water to be added during the experiment thus preventing sagging of the soil. Emerged seedlings were counted and carefully cut away daily during flushes of emergence and once every three days afterwards. Seeds that did not germinate during the experiment were recovered by sieving. The results were compared using analyses of variance or regression analyses. Significance is indicated at the 5 % level.

Experimental factors

The influence of depth and temperature was tested in 1989 in an experiment with all combinations of 4 planting depths (1, 3, 5 and 7 cm) and 5 temperatures (8, 10, 15, 20 and 30°C), with 4 replicates. The soil used was a humus-rich sandy soil with a moisture content of 13 % (pF ± 2.7). Pre-germinated seeds were used. The soil resistance was 5.0 kg/cm^2 (experiment 1a). The experiment was repeated with a soil resistance of 2.6 kg/cm^2 (experiment 1b).

The effects of depth and soil resistance on emergence of pre-germinated seeds were examined in 1989 in an unheated greenhouse (experiment 2). All combinations of three soil resistances (1.6, 5.0, 10.0 kg/cm^2) and 8 depths (1, 2, 3, 4, 5, 7, 10, 15 cm) were tested, with 5 replicates. Soil type and moisture content were the same as in experiment 1.

At two temperatures (8 and 14 °C), the impact of soil suction (pF ± 2.0, 2.3, 2.7, 3.0, 3.5 and 4.0) during emergence was determined (experiment 3). The 12 treatments each had 4 replicates. Pre-germinated seeds were buried at 2 cm depth in a clay soil with a soil resistance of 2 kg/cm^2.

The influence of soil suction, soil type, soil resistance, temperature and their interactions were tested in 1990 in an experiment with 2 soil types (humus-rich sand and clay), 2 soil suctions (pF ± 2 and 2.7), 3 soil resistances (± 2.0, 6.0 and 10.0 kg/cm^2)

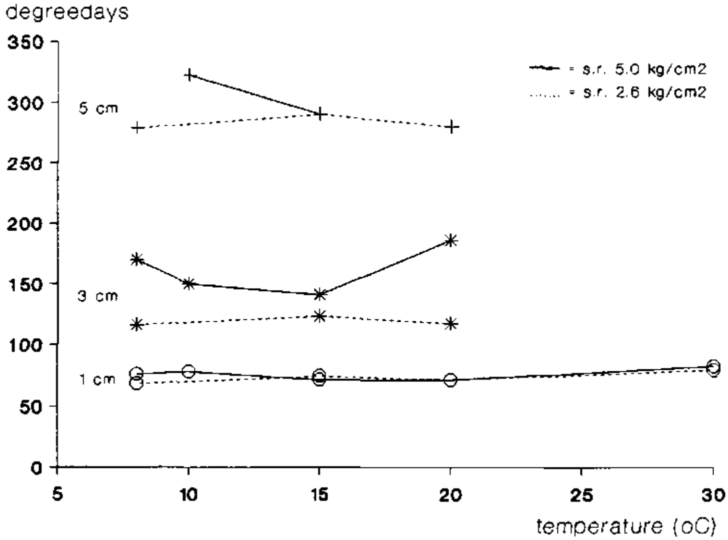
and 2 temperatures (8 and 14°C). Thus there were 24 combinations of factors with 4 replicates. Planting depth was 2 cm. In the experiment (4 a) pre-germinated seeds were used. In an similar experiment (4 b) ungerminated seeds were used to be able to determine the effect of using pre-germinated seeds.

4.3 Results

Emergence rate

Emergence rate or its opposite the mean duration of the time period between germination and plants emerging was clearly influenced by temperature as could be expected. Duration of emergence can be expressed as a thermal time in degreedays (°C*day) needed for 50 % emergence. Thermal times have constant values independently of the temperatures experienced. Such termal times are calculated by multiplying time in days with the daily temperature minus a base temperature. When temperatures exceed a maximum, rate of emergence does not increase anymore and may even decrease again. This maximum temperature was calculated too. By least X square analysis on the data of experiment 1 an average minimum and maximum were calculated, being 2.5°C and 18.0°C respectively.

Fig. 4.1 The influence of temperature on the duration of emergence (mean temperature summation above a base temperature of 2.5 oC and a maximum effective temperature of 18 oC for the time period between germination and emergence) of *Galium aparine* L. from different depths under different soil resistances.

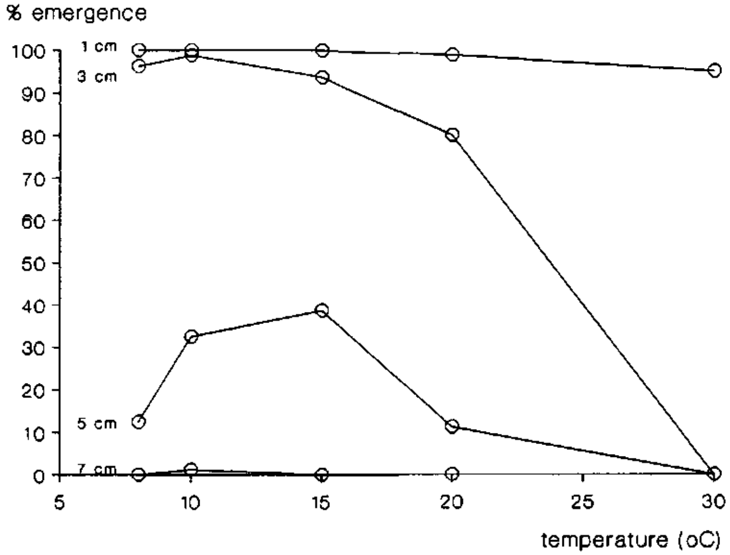


The mean temperature sum for germinated seeds emerging was clearly influenced by both the depth and the soil resistance. At a depth of 1 cm duration of emergence was about 70 - 75 degreedays, at 3 cm 120 - 160 degreedays and at 5 cm 280 - 300 degreedays at a soil moisture content of pF 2.7 and soil resistances 2.6 and 5.0 kg/cm² (Experiment 1, Fig. 4.1). At a depth of 2 cm duration varied between 70 and 120 degreedays for soil resistances between 1.5 and 10 kg/cm² (experiment 4a, Fig. 4.4b). Standard deviation of the duration of emergence was circa 12.5 percent of the mean (of the individual seeds) duration of emergence.

Mortality during emergence

There was a significant interaction between the effects of depth and temperature on the percentage emergence (experiment 1, Fig. 4.2). The negative effect of greater planting depths was especially large at temperatures beneath or above the optimum (10 - 15°C). At increasing depth emergence was more and more restricted to the optimal temperature.

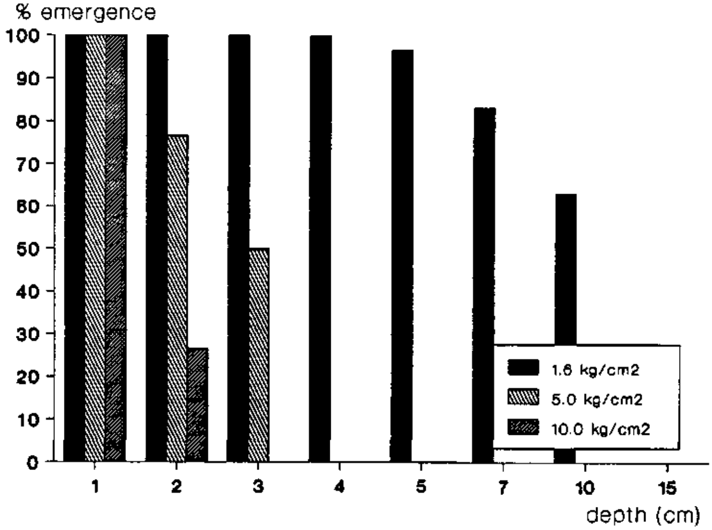
Fig. 4.2 The influence of temperature on the percentage of emergence of *Galium aparine* L. from different depths.



Data points are mean results from both soil resistances.

The interaction between the effects of depth and soil resistance was also highly significant (experiment 2, Fig. 4.3). Emergence was possible from great depth (to 10 cm) at low soil resistance (1.6 kg/cm²) but emergence was restricted to superficially germinated seeds at high soil resistance (10.0 kg/cm²).

Fig. 4.3 The influence of soil resistance on the percentage of emergence of *Galium aparine* L. from different depths.



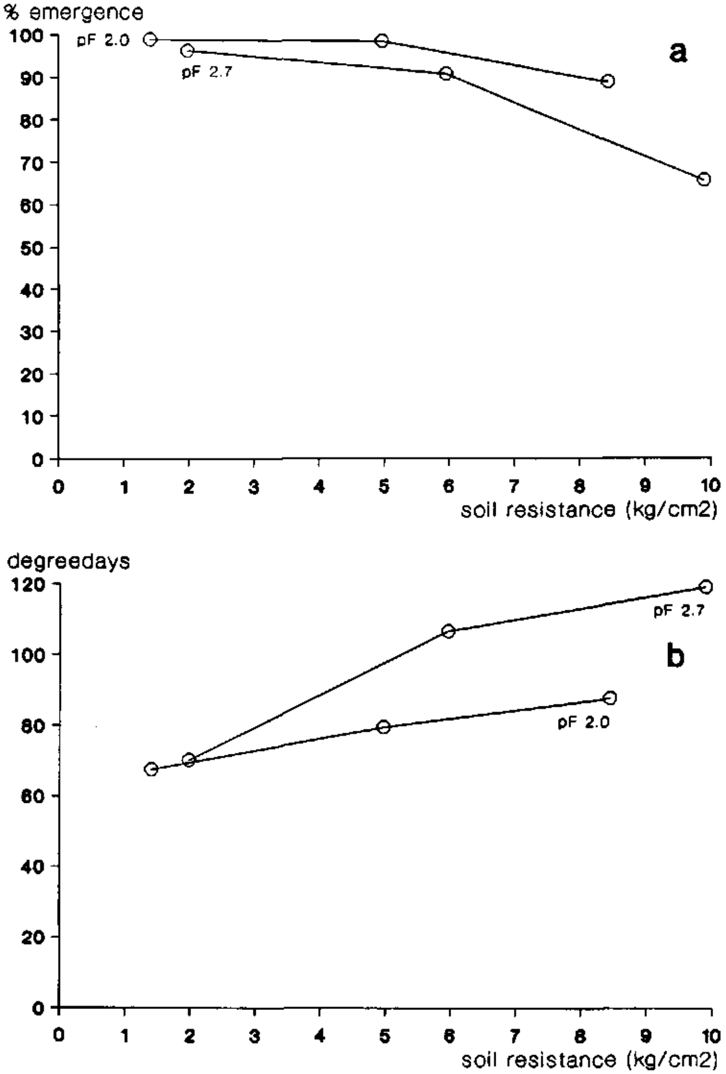
Boydston (1989), working with pregerminated seeds of *Cenchrus longispinus* from depths up to 11 cm, found the percentage emergence decreasing with depth following a sigmoid curve (%emergence = 100 + b1*depth + b2*depth*depth). According to the data collected, such a curve will also fit the emergence of *G. aparine*. The values of the parameters in this equation however will differ with the environmental conditions experienced. Regression analyses on all data of the experiments 1 and 2 resulted in the highest correlation coefficient, when the parameters b1 and b2 were corrected for both soil resistance and deviations from the optimal temperature of 12.5 °C. Temperature, although a significant factor in the regression analyses, hardly improved the correlation coefficient (r=0.912 in stead of r=0.911). Moreover the temperature range over which seeds may germinate under field conditions is much smaller (chapter 3) than the temperature range investigated here. Therefore the effect of temperature on the percentage of emergence was neglected. This resulted in the next equation (r=0.911) for conditions with adequate moisture availability:

%emergence=100-6.828*D-2.342*R*D+0.16192*R*D*D,

with R is soil resistance in kg/cm2 and D is depth in cm.

Percentages of emergence varied only between 92.5 and 100 % irrespective of the soil suctions between ± 2 to 4 and the temperature of 8 or 14 °C at a low soil resistance in experiment 3. At high soil resistances soil suction became more important (experiment 4a, Fig. 4.4). The effect of soil type with soil suction and soil resistance set comparable (experiment 4, Fig. 4.5) on the emergence was not significant.

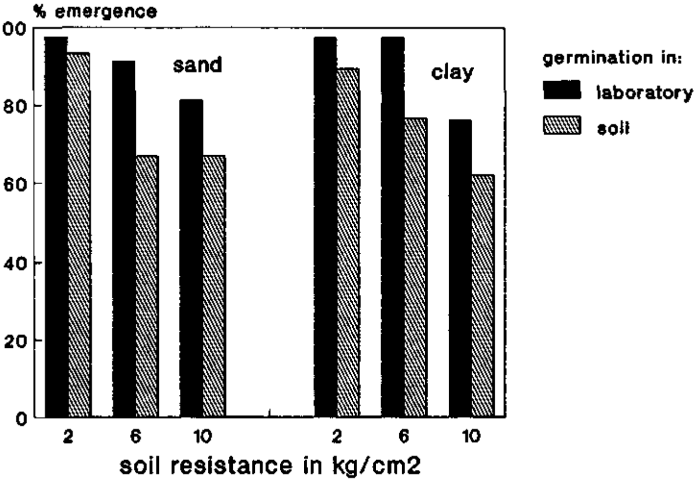
Fig. 4.4 The influence of soil resistance and moisture availability on a) the percentage of emergence and b) the duration of emergence (see also Fig. 4.1) of *Galium aparine* L.



Data points are mean results from both soil types.

Figure 4.5 shows the percentages of emergence found with pre-germinated seed (experiment 4a) and with seed germinated in the soil (experiment 4b), respectively. The percentages in figure 4.5 are corrected for non-germinated seeds (0 to 20 %): only seeds which had disappeared (mortality possibly caused by unsuccessful germination and emergence) or germinated were taken into account. Pre-germinated seedlings appeared to emerge in slightly higher percentages than seedlings germinated in the ground. This holds for almost every combination of experimental factors, but seems to be more apparent under unfavourable conditions, such as high soil resistance.

Fig. 4.5 The influence of soil type and soil resistance on the percentage of emergence of pregerminated seeds of *Galium aparine* L. in comparison with germination *in situ*.



Data points are mean results from both soil suctions.

4.4 Discussion

The long emergence time of *G. aparine* causes the escape of this weed species from several control methods. The present study showed that the long emergence period of *G. aparine* in the field is mainly caused by the duration of emergence of germinated seeds at different depths in the soil. Although higher soil resistances and low moisture availability could slightly decrease the emergence rate, temperature and the distance to bridge to the surface were much more important. The wave in emergence spanned 6 to 36 days at 12 °C or 10 to 61 days at 8 °C after germination at one date of seeds at a depth of 1 to 5 cm, respectively. In reality all seeds do not germinate at one date. Duration of germination is 7 to 9 days at 12 °C and 12 to 15 days at 8 °C. Initiation of germination is strongly regulated to one date by the timing of soil cultivation in autumn or spring. Soil cultivation in autumn and spring is quite appropriate for Dutch farming practices. Initiation of germination after cultivation in winter and summer however, is more diffuse because then initiation of germination is regulated by slowly changing dormancy patterns (chapter 5).

Soil type appeared not to have an effect on percentage or rate of emergence in this study. This is probably due to the fact that soil suction and soil resistance were controlled in the experiments, only percentage air in the two soil types were differing. Soil type may have a great influence in field situations however, because soil resistance and soil moisture content are related to soil type.

In addition to the depth of the seeds, the resistance of the soil is the most important factor influencing the percentage of emergence. This is especially true because seeds are still germinating (although reduced, chapter 3) at soil resistances clearly reducing the percentage of emergence. Differences in mortality of the germinated *G. aparine* seeds under field conditions can be found in the literature:

- 72 or 96 % mortality of germinated seeds between 0 and 5 cm or between 5 and 10 cm depth in the soil respectively, according to Röttele (1980),
- 22 or 33 % mortality of germinated seeds between 0 and 5 cm or between 5 and 10 cm depth in the soil respectively, according to Aarts (1986).

Aarts however investigated the emergence in a fine-structured cultivated soil. It seems quite reasonable to assume that these differences are substantially caused by differences in soil resistance. Nevertheless it will be difficult to characterize soil resistances in the field. Soil resistance is correlated with the bulk density of the soil. Resistance and density increase with depth, decrease during soil cultivation, increase again after soil cultivation and differ between different soil types (Hielkema, 1974; Smith, 1987; Locher and Bakker, 1990). Furthermore they also varie in the horizontal area within a field (own measurements, data not shown) or within the clods of a soil (Terpstra, 1986).

Together with data on germination (chapter 3), the equation for the calculation of the percentage of emergence of germinated seeds and the temperature summations for the duration of emergence, will be used in a simulation model of the field emergence of *G. aparine* (chapter 5). Using the emergence of laboratory germinated seeds for extrapolation to the field will result in a slight underestimation of the effect of limiting factors. *In situ* germinated seeds have not been selected for rapid germination within two weeks at 10 °C and possibly contain also some weaker individuals. Although soil suction was not important at temperatures between 8 and 14 °C and low soil resistances, this factor can gain influence when other conditions become less favourable. Nevertheless not all unfavourable conditions will be important for field situations. At some inconvenient circumstances the individuals will be protected from mortality during emergence because seeds just do not germinate at these conditions (for example high temperatures for *G. aparine*). This protection however is not absolute. Morrow *et al.* (1982) and Terpstra (1986) reported germination with unsuccessful emergence for several weed species, thereby confirmed the importance of the emergence phase.

Chapter 5

Modelling the field emergence of *Galium aparine* L.

Abstract A dynamic model which simulates germination and field emergence of *Galium aparine* L. in relation to weather and soil conditions was developed. The model is based on detailed knowledge of the basic processes involved.

Because of its fast disappearance primary dormancy is neglected. Germination is not possible before cultivation of the soil. Maximum percentage germination during a year depends on mechanical resistance of the soil after cultivation. The fraction of seeds which will start to germinate at a particular time depends on the actual temperature in comparison with a low and an upper temperature limit for germination. These temperature limits change during the year, depending on the induction and release of secondary dormancy. The depth of the seeds in the soil, the daily average temperature above a base temperature of 2.5 °C and the mechanical resistance of the soil determine the rate of germination and emergence. Mortality of germinated seeds is a function of the mechanical resistance of the soil and the depth of the seeds.

Simulation results were compared with observations in three experiments. Predictions were good, although primary dormancy could only be neglected at soils which were ploughed. The depth of the seeds in the soil, the date of seedbed preparation, the actual field temperature and the soil resistance all clearly influenced the period during which *G. aparine* emerged. Model predictions were little affected by differences between collections of the seeds or differences in their secondary dormancy patterns. Especially the effect of environmental factors on the emergence rate proved to be of great importance for understanding patterns of emergence in the field.

5.1 Introduction

Knowledge of timing and extent of field emergence of weed species is necessary:

- to develop a better timing and choice of control measures,
- to acquire an increased insight in the differences in competivability of weed species under different field and weather conditions,
- to obtain a more thorough understanding of the population dynamics of the weed species and the of risks of future infestations.

To understand the emergence of *Galium aparine* L. under field conditions, the influence of temperature, light, nitrogen, moisture and soil structure on dormancy patterns, germination and emergence of seeds at different depths in the soil were investigated in laboratory experiments (chapter 3 and 4). The distinct processes that determine field emergence are influenced differently by these environmental conditions (Table 5.1). A simulation model is a useful tool to combine the effects of various factors and to evaluate the importance of these factors. At least all factors with moderate or big effects in Table 5.1 should be considered in such a simulation model of the field emergence of *G. aparine.*

Table 5.1 The importance of environmental factors for the processes which determine germination and field emergence of *Galium aparine* L.

Process:	origin	depth	temperature	light	moisture	nutrients	soil structure
Shifts in dormancy of the seeds	**		***				
Actual germination	*		***	**	*	*	**
Germination rate	_		***	-	*	-	*
Mortality during emergence	-	***	*		*		***
Emergence rate	*	***	***		**		**

blank: not investigated
- : not significant in experiments
* : significant ($P < 0.05$), but rather small effects
** : significant, intermediate effects
*** : very significant and important

Most studies of germination are based on laboratory investigations at which the appearance of the radicle (germination) is recorded. These studies show that the cumulative number of germinated seeds progresses in time according to an S-shaped curve. The mean rate of germination is linearly related to the temperature above a base temperature (Carbery & Campbell, 1989). The variation in rate of germination is responsible for the S shape. To describe the process in time, the cumulative normal distribution function has been proposed by Janssen (1973), the negative exponential distribution by Spitters (1980,1986), the Richards function by Berry *et al.* (1988), the Weibull distribution by Brown & Mayer (1988) and Bridges *et al.* (1989). The advantages of these descriptive formulas are simplicity and clarity. However, using these formulas for the description of the emergence under field conditions causes problems. Firstly, the emergence phase between germination and the emergence of the cotyledons above the soil surface, is not included. Secondly, not all the seeds are initiated for germination at the same moment. Different groups of seeds start their germination at different times after release of dormancy. Thirdly, the environment is not constant. Under these conditions the approach of dynamic simulation (De Wit & Goudriaan, 1974; Janssen, 1974) is more useful. These flexible models mimic the germination process from the moment seeds are initiated to start the germination process onwards, thereby considering different starting positions. Rates with which seeds pass through the germination and the emergence processes depend on actual temperatures, thus slowing down in times with cold and accelerating in times with high temperatures. To start this dynamic simulation, the initiation of groups of seeds to start their germination has to be described. The initiation of a population of seeds to germinate depends on their state of dormancy and the actual temperature. Percentage of seeds able to germinate have been described as quadratic function of the actual temperature (Bouwmeester, 1990 and Bouwmeester & Karssen, 1992). This descriptive function differs with state of dormancy. Washitani (1987) based his description of the ability of a population of seeds to germinate on the qualitative respons of individual seeds. Each seed has a lower and a upper temperature limit for germination. For the response of a population of seeds, he assumed normal distribution functions around these temperature limits. The latter description is chosen because it is a more mechanistic approach than the first description. Furthermore the latter decription can easily be extended to account for secondary dormancy release and induction by simply varying the temperature limits.

In this paper a dynamic model, which simulates germination and field emergence of *G. aparine* in relation to weather and soil conditions is presented and validated. The model was then used to evaluate the importance of several environmental factors and the significance of the different aspects of germination and emergence for predicting field emergence.

Material and methods

The model

In general

In successive steps the model calculates the amount of seeds that are potentially capable of germination (maximum germination percentage during autumn and during the rest of the year), how many seeds actually start to germinate, the rate of germination and emergence and the mortality of seeds at different depths during emergence. The model was parameterised with data from laboratory experiments (chapter 3 and 4).

Potential for germination

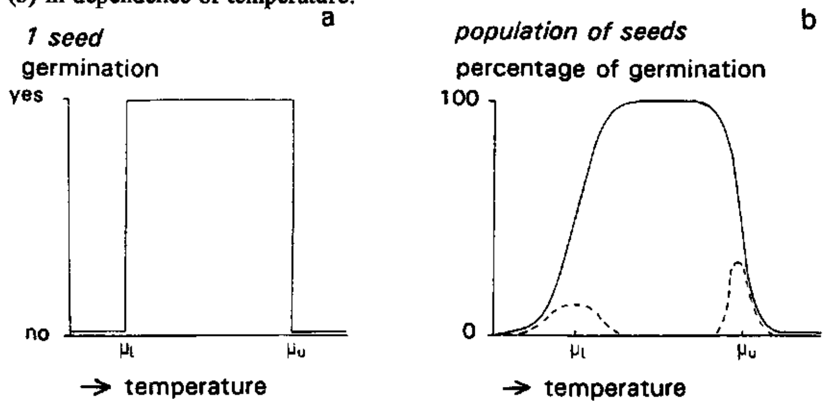
Primary dormancy in *G. aparine* is very variable (0 to 100 %) and not yet fully understood. Because release of primary dormancy takes place already during the first autumn and winter after burial and because fresh seeds are generally buried the first year as a result of ploughing to a depth were they can not germinate, primary dormancy is neglected in the model. For one situation where the soil was not ploughed (field experiment 1), assumptions on percentage primary dormancy were made.

The maximum yearly percentage of germination of seeds (MG) depends on the mechanical resistance (R in kg*cm^{-2}) of the soil after cultivation : MG=100*EXP(-0.09322*R).

Initiation of germination

An individual seed will react on its environment by germinating or not germinating. A stimulus-response curve of the type shown in Fig. 5.1a gives the relation between stimulus (environment) and response (initiation of germination or no initiation of germination) for one seed. The lower and upper temperature limit will differ for individual seeds in a population resulting in a probability distribution of the respons of a population of seeds around the limits (see broken lines in Fig. 5.1b).

Fig. 5.1 Scheme of the initiation of germination response of an individual seed (a) or a population of seeds (b) in dependence of temperature.



- - - - normal probability distributions for the lower and upper temperature limit for germination of a population seeds

The shape of the probability distribution is not known, but in most cases the normal distribution is an adequate approximation (Zadoks & Schein, 1979). Washitani (1987) used the normal distribution for the qualitative reaction of seeds to temperature. He calculated the germinable seed fraction at a given temperature (Gf(T)) as the product of the fraction (Fl(T)) that can germinate given the lower temperature limit and the fraction (Fu(T)) that can germinate given the upper temperature limit. Fl(T) and Fu(T) are given by cumulative normal distribution functions:

$$Fl(T) = \int_{-\infty}^{(T-\mu_l)/\sigma_l} (1/\sqrt{2\pi})\exp(-x^2/2)dx$$

$$\text{and } Fu(T) = \int_{(T-\mu_u)/\sigma_u}^{\infty} (1/\sqrt{2\pi})\exp(-x^2/2)dx \ .$$

in which μ_l and μ_u are the mean lower and upper temperature limit and σ_l and σ_u the standard deviations around these mean limits.

Induction and release of secondary dormancy can be expressed as shifts in temperature limits (μ_l and μ_u) and/or their standard deviations. Best fits of these formulas on the experimental data for different collections of *G. aparine* retrieved from the soil at different times of the year (chapter 3) are in Table 5.2.

Table 5.2 Changes in the temperature response for initiation of germination of different collections of *Galium aparine* L. seeds, recovered from the soil at several dates

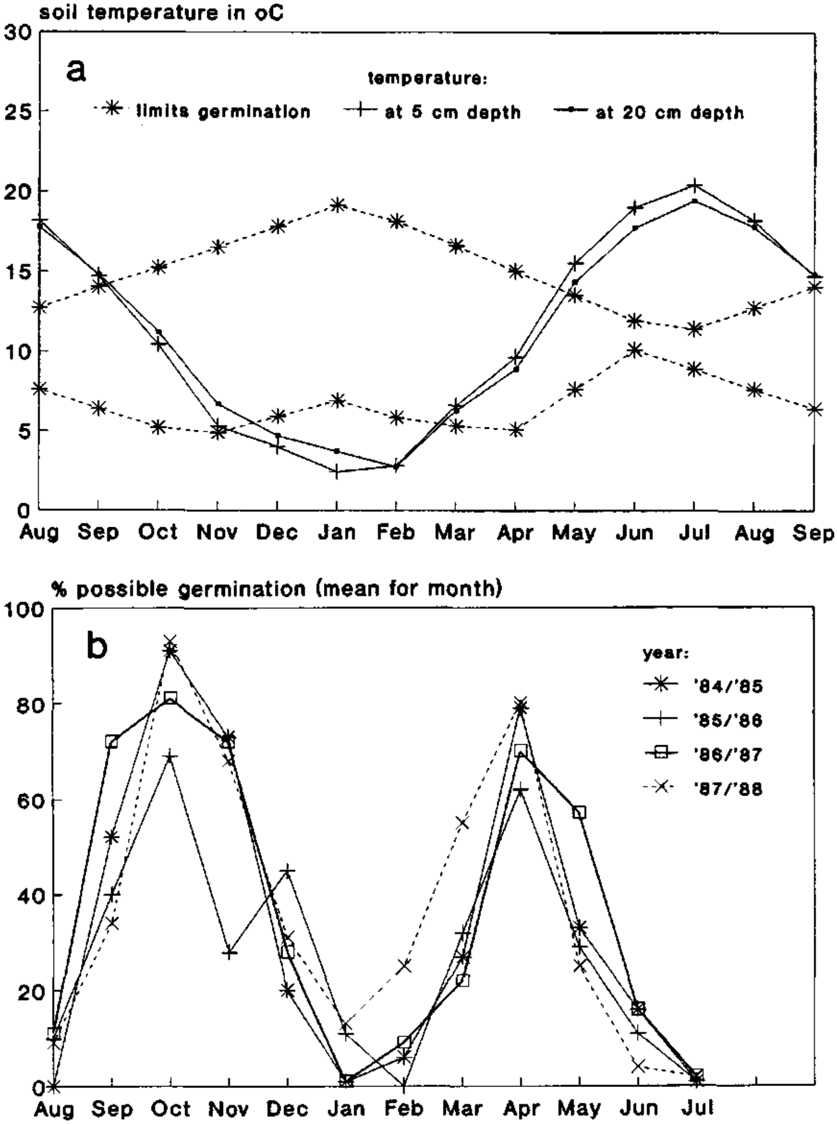
Seeds from:	plants that germinated in autumn			plants that germinated in spring			plants that germinated in autumn		
Buried at:	8-8-1988			27-10-1988			29-9-1987		
date:	max.	μ_l μ_u	σ_l σ_u	max.	μ_l μ_u	σ_l σ_u	max.	μ_l μ_u	σ_l σ_u
8-8	70%	6.3 10.9	2.1 2.2				100%	4.2 12.3	2.0 2.5
27-10	70%	7.1 15.0	2.6 2.4	85%	4.2 11.5	1.9 2.4			
6-1	100%	10.0 20.3	5.0 2.5	85%	4.2 18.4	2.0 3.4			
11-4	100%	6.6 18.1	3.7 2.0	100%	4.1 16.6	2.3 1.2	100%	3.6 15.5	2.2 1.5
20-6	100%	11.5 11.7	3.0 1.3	100%	9.7 9.8	1.4 3.8			
4-9	100%	8.6 15.1	2.1 2.0	100%	11.1 14.4	6.1 3.7	100%	5.7 14.8	2.5 2.7

max. : percentage of seeds without primary dormancy

μ_l and μ_u : Mean low and upper temperature limits for germination

σ_l and σ_u : standard deviations belonging to μ_l and μ_u

Fig. 5.2 The changes in the temperature limits (μ_l and μ_u) for germination of *Galium aparine* L. seeds during the year and the mean soil temperature during several years (a) and the possible germination as influenced by the actual temperatures in several years (b).



Mean limits are in Fig. 5.2a and the standard deviations were assumed to be constant (σ_l=2.5 and σ_u=2.2). The effect of the mean daily soil temperature on the percentage of seeds which can be initiated to germinate varies in and between years (Fig. 5.2b). After soil cultivation and release of primary dormancy seeds are initiated to germinate according to the calculation above given the actual day temperature and the limits belonging to that day. Every time the calculated percentage of seeds able to start germination has increased a new group of seeds is initiated to germinate. The size of the group corresponds with the difference in the calculated percentages.

Rates of emergence

The model dynamically simulates the emergence of batches of simultaneously initiated seeds, resulting in a normal probability distribution of emergence (Goudriaan, 1986). Normal distribution functions used are characterized by:

- a mean temperature sum (above the base temperature of 2.5 °C and with a maximum effective temperature of 18 °C) of 75, 146, 195 or 360 degreedays for seeds emerging from 0, 1 , 3 or 5 cm depth respectively in a loose soil (2.0 kg/cm^2) or 285 degreedays for seeds emerging from 2.5 cm in a soil with resistance 6.6 kg/cm^2,
- a standard deviation which is 12.5 % of the mean temperature sum for emergence.

Shortage of moisture may have effects on emergence rates in the same order of importance as an increased soil resistance. Important moisture shortages however seldomly occur during several weeks in autumn or spring in the Netherlands. Therefore moisture shortage was neglected in the presented simulations.

Mortality of germinated seeds

Percentage mortality of seeds once germinated (M) depends on soil resistance (R in kg/cm^2) and depth of the seeds (D in cm): $M=6.828*D+2.342*R*D-0.16192*R*D*D$.

Field data for evaluation of the model

Three independent sets of field data have been used to evaluate the model performance. The data sets differ in time span and detail of the observations.

Experiment 1

Van den Brand (1986) reported on the emergence of *G. aparine* from August 1978 to August 1983. Fresh partly dormant seeds were homogenously distributed over the tilth by mixing the soil. Dates of mixing and loosening the soil were 18-8-1978, 26-9-1979, 9-9-1980, 28-7-1981 and 6-8-1982. Emergence was recorded once or twice a month. Emergence was expressed as monthly percentages of the total annual emergence (August till August). The soil structure after the seedbed preparation was assumed to be loose. Soil temperatures were approximated using data from the Meteorological station in Wageningen.

Experiment 2

Field emergence of *G. aparine* in winter wheat with two different sowing dates was recorded weekly during autumn and twice a month thereafter to the end of the growing season. Seedbed preparation and sowing of the winter wheat (at the same day) occurred on 16-9-1987 and 4-11-1987, respectively. Observation areas were 37.5 m^2 in duplicate. Density of *G. aparine* plants emerging during the experiment was 7.2 plants per m^2. The experiment was located at an experimental farm near Wageningen. The soil structure after the seedbed preparation was assumed to be loose. Soil temperature data measured at 5 cm beneath a canopy by the Meteorological station in Wageningen were used.

Experiment 3

At 29-9-1987 non-dormant *G. aparine* seeds were buried at an arable field near Wageningen. Fifty seeds were placed at the bottom of a hole (8 cm diameter, 2.5 cm depth) and the soil core was placed back, leaving the soil almost undisturbed. Emerged plants were counted in 20 replicates weekly during the peak emergence and less frequently afterwards. Emerged plants were carefully removed so the soil would not be disturbed. After one year the soil at the places of burial was collected and the remaining seeds washed out to calculate the percentage germination. The temperature at 2.5 cm depth was recorded every hour with a data recorder. Penetration resistance of the soil was measured in October with a penetrometer (mean resistance: 6.6 kg/cm^2 at 2.5 cm depth).

5.3 Results

Emergence of *G. aparine* in the field in experiment 1 was distributed over both autumn and spring in four of the five years (Fig. 5.3). In 1979/1980 seeds were collected and buried late in autumn, therefore (chapter 3) these seeds lacked primary dormancy and mainly emerged during that same autumn. If primary dormancy was neglected, simulated emergence only occurred in autumn (Fig. 5.3a). With the experimental conditions in four of the five years in experiment 1 (freshly produced seeds remained in superficial soil layers and were buried early in autumn) primary dormancy should not be neglected, as is the case with the other experiments. If primary dormancy is taken into account, simulation of the variation in emergence patterns based on the actual temperatures and cultivation date in different years compares well with the actually observed emergence patterns (Fig. 5.3b). A simulated depth of the seeds of 3 cm was chosen, because most of the germinating seeds will be around in superficial soil layers after hand mixing and mean germination depth of *G. aparine* under field conditions is reported to be 2 to 3 cm (Röttele, 1980).

In experiment 2 the differences in emergence after early (Fig. 5.4a) and late seedbed preparation (Fig. 5.4b) were correctly simulated. Simulated emergence after early seedbed preparation was slightly earlier than the observed values. Different depths of emergence were corresponding with the different peaks in emergence. In reality seeds will be distributed over these depths. Results for different vertical distributions of the seeds can be obtained by summing the products of emergence at a depth with the relative abundance of seeds at that depth. Results of such a calculation are not presented in Fig. 5.4 because the distribution of the seeds in the soil could not be determined (less then 1 seed per kg soil).

Fig. 5.3 Observed (Van den Brand, 1984) and simulated field emergence of *Galium aparine* L. during five years without (a) and with (b) primary dormancy.

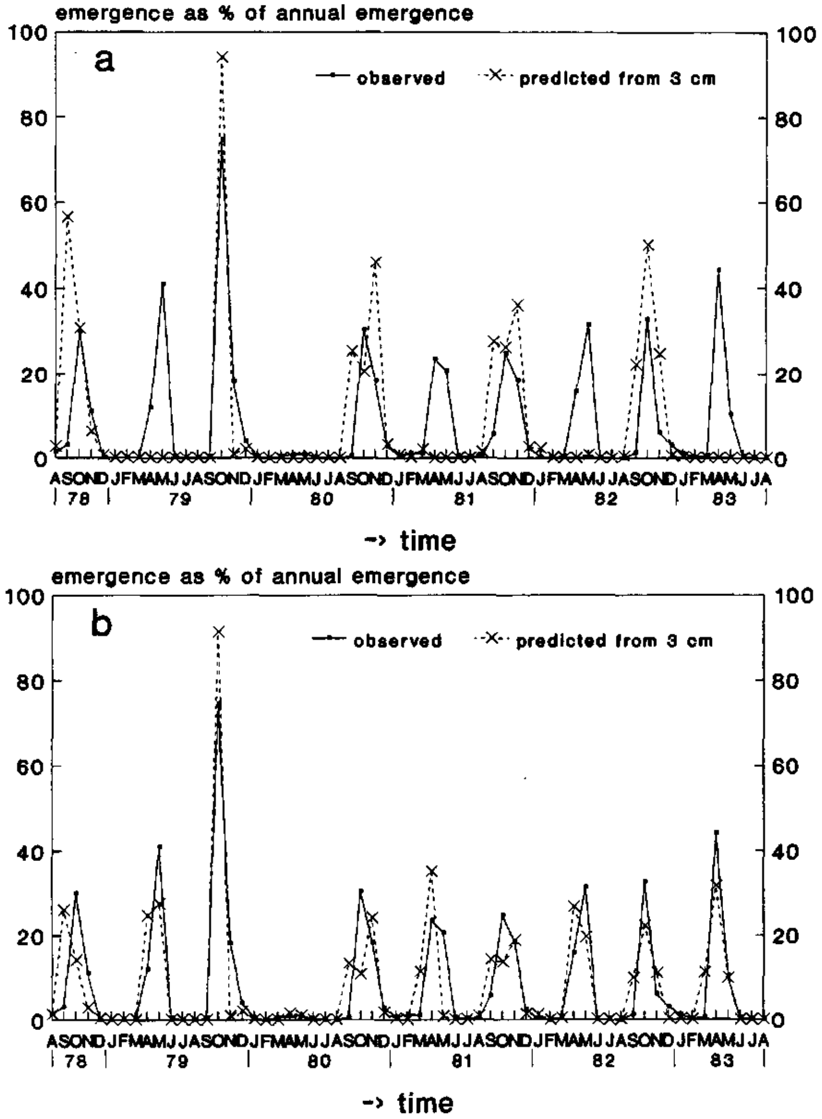
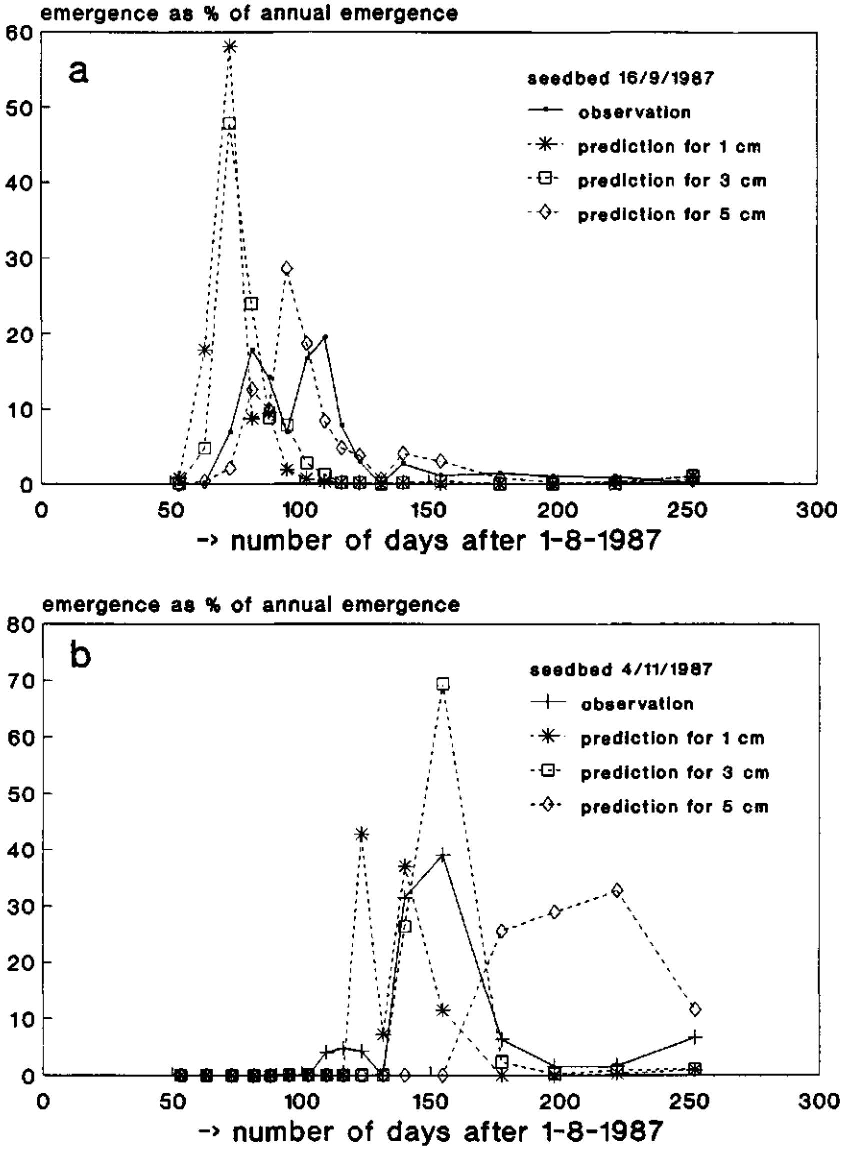
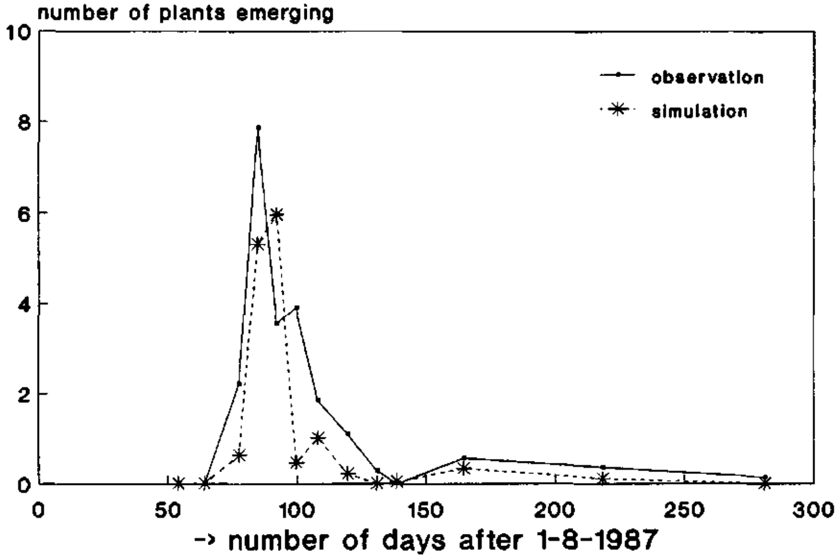


Fig. 5.4 Observed and simulated field emergence of *Galium aparine* L. from different depths in the soil after two dates of seedbed preparation.



In experiment 3, depth and number of seeds were known. Therefore it was possible to simulate not only the emergence pattern but also the actual numbers of plants emerging. Exact soil temperatures and the mechanical resistance of the soil were known in this experiment. The pattern of emergence was simulated well (Fig. 5.5). Simulated numbers of plants emerging were too high. Based on a soil penetration resistance of 6.6 kg/cm^2 only 54 % of the seeds should germinate. In reality 95.4 % of the seeds germinated, probably caused by the burial method used. Observed mortality of germinated seeds was 46 % and simulated mortality was 49%.

Fig. 5.5 Observed and simulated field emergence of *Galium aparine* L. buried at 2.5 cm depth in the soil.

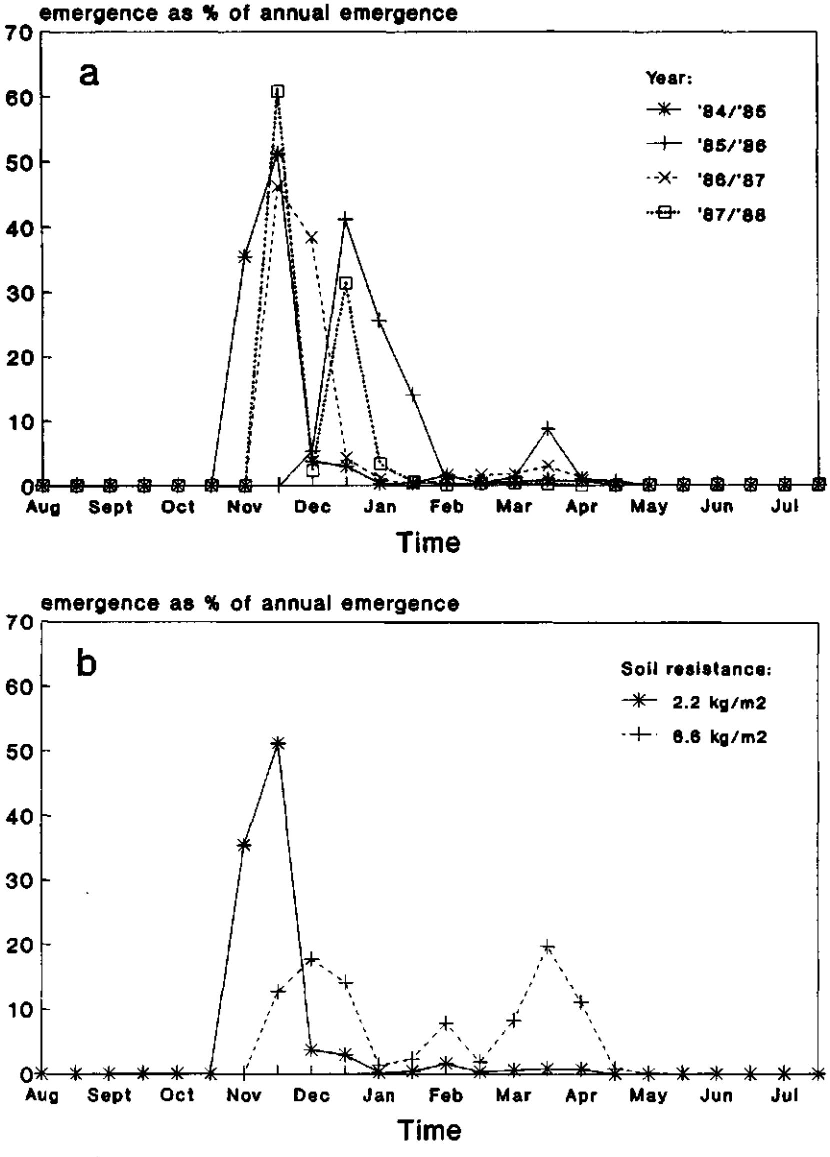


Simulation results showed that the depth of the seeds in the soil (Fig. 5.4), the date of seedbed preparation (Fig. 5.4 and 5.7), the actual temperatures during different years (Fig. 5.6a) and soil resistance (Fig. 5.6b) are important for field emergence of *G. aparine*. Differences in the secondary dormancy patterns (or the changes in temperature limits during the year) between origins were found and ignored (Table 5.2) as was also done for differences in the secondary dormancy patterns between years. Simulating variation in seconday dormancy patterns by reducing the former temperature limits for initiation of germination with 2 °C, showed that these neglections are justified, especially after seedbed preparation in October which is common for winter wheat (Fig. 5.7a). Ignoring secondary dormancy patterns at all by starting the germination of all seeds immediately after soil cultivation, gave large differences in emergence patterns especially after early seedbed preparation (Fig. 5.7b).

5.4 Discussion

It is possible to simulate emergence patterns and mortality during emergence of *G. aparine* in relation to weather and soil conditions. Differences in emergence pattern caused by different temperature conditions between years can be considerable, but the date of soil cultivation and the structure of the soil cause even more variation in emergence.

Fig. 5.6 The effect of temperature (a) and soil resistance (b) on the simulated emergence of *Galium aparine* L. at 2.5 cm depth .



In general the length of the period during which *G. aparine* emerges is relatively long. This is one of the reasons why this species at least partly escapes control. Many control methods depend on the stage of the weeds (e.g. large plants escape) or have a temporary effect (e.g. after germination). Knowledge on the emergence patterns can be used to optimize timing and type of cultural and control measures. The period during which G. *aparine* emerges can be shortened by soil cultivation at times with relatively high soil temperatures (early in autumn or late in spring) and by a good seedbed preparation. Two emergence flushes may occur in case of a high soil resistance, long periods of dry or relatively cold weather and/or after cultivation late in autumn. These flushes are located in late autumn / early winter and in late winter / early spring. Otherwise main emergence will be in autumn after cultivation in autumn or in spring after cultivation in spring. However, this is only true in situations where primary dormancy is not important. In case of yearly ploughing most of the seeds are buried the first year to a depth were they cannot germinate (Cousens & Moss, 1990). There primary dormancy is released and can be neglected for the future. If the soil is not turned, seeds which have primary dormancy will be initiated to germinate in spring in stead of autumn, causing two emergence peaks.

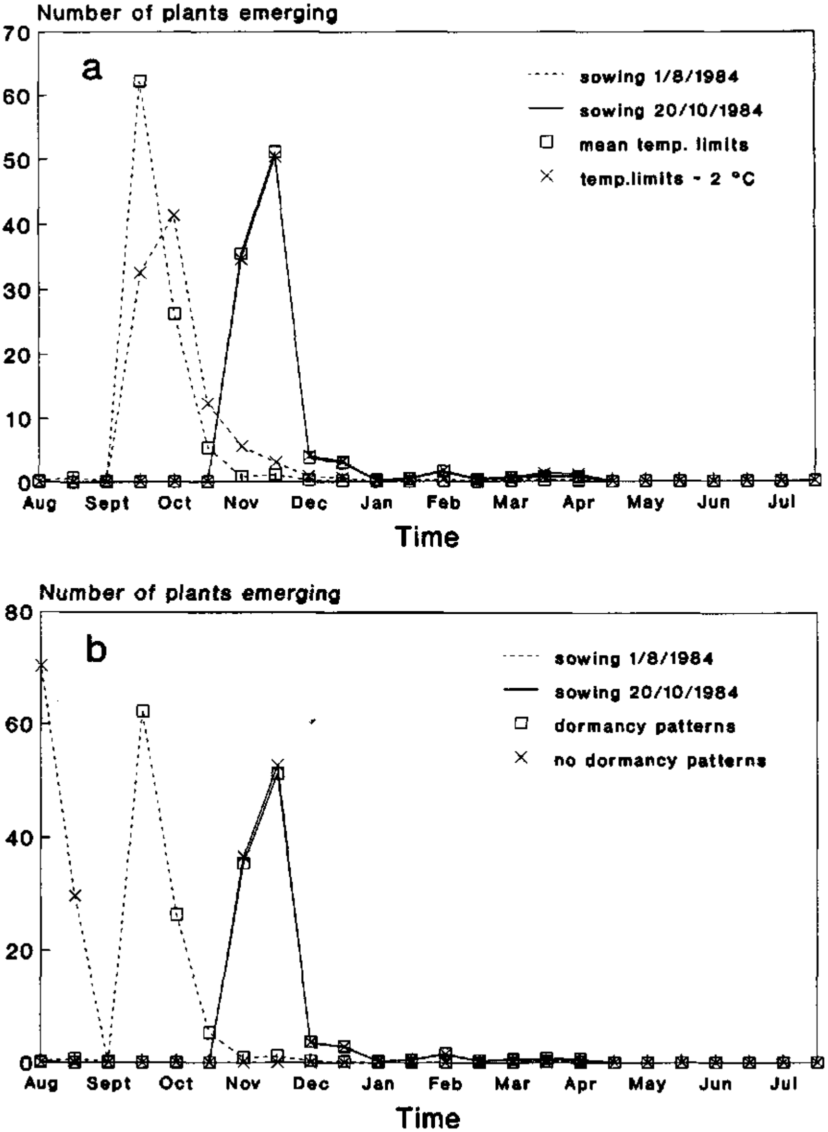
Differences between years and locations in crop yield losses due to G. *aparine*, are at least partly caused by differences in emergence patterns. Weed plants which emerge early relative to crop emergence are much more competitive than plants which emerge late in the crop. Economic weed control thresholds for different situations therefore should be adjusted for differences in expected emergence patterns. Risk analysis with the simulation model on e.g. different weather conditions, can then be used for advising timing and type of control methods based on adjusted thresholds.

Knowledge on the germination and emergence of G. *aparine* is necessary and very important for predictions of the population dynamics of this species. Consequences of for example the differences in mortality during emergence for the rate of infestation of the weed can be considerable as shown in simulations of the population dynamics of this weed (chapter 2). The yearly population growth rate of G. *aparine* in a monoculture of winter wheat was 6 or 38 if emergence parameter estimations were based on Röttele (1980) or on Aarts (1986), respectively. The increased insight in germination and emergence can be used to adjust values of the germination and emergence parameters used in the population dynamic model for different situations. The high mortality of germinated seeds in the experiments of Röttele (1980) indicate a heavy soil structure. In the Netherlands on arable fields with a good soil structure losses during emergence especially from superficial layers will be much smaller as indicated by Aarts (1986) and by this study.

The model presented here can be adjusted for other weed species with dormancy patterns depending on shifts in temperature requirements for germination during the year, such as *Chenopodium album* L., *Polygonum persicaria* L. and *Spergula arvensis* L. (Bouwmeester, 1990; Bouwmeester & Karssen, 1992; Bouwmeester & Karssen, in press), *Thlaspi arvense* L. (Baskin & Baskin, 1989) and *Poa annua* L. (Standifer & Wilson, 1988). In some cases as in *Solanum nigrum* L., a large daily temperature fluctuation is required for germination and the minimum required fluctuation can change during the year (Roberts &

Lockett, 1978). Other types of models can be more suited for species as e.g. *Sorghum halepense* (L.) Pers., were the release of overall dormancy is determining field emergence (Benech Arnold *et al.*, 1990 a and b).

Fig. 5.7 The effect of variation within the dormancy patterns (a) and the effect of neglecting dormancy patterns (b) on the results of simulation of the field emergence after sowing at different dates.



The influence of the temperature on the actual induction of germination and on the rate of germination and emergence is part of the presented simulation model. The effect of differences in temperature between years on the secondary dormancy patterns is not part of the model yet. The differences between different origins and dispersal dates of *G. aparine* were also neglected. Sensitivity analyses (Fig. 5.7) learned that these simplifications are acceptable. A great deal of research on germination of weeds is devoted to increasing insight in dormancy patterns, but hardly anything to the effect of environmental factors on the germination and emergence rates. However, to understand patterns of emergence in the field this latter factor proved to be of great importance.

Chapter 6

Phenology of arable and hedgerow populations of *Galium aparine* L. in relation to climate and soil conditions.

Abstract If the phenology of weeds is known, the timing of their control can be optimized. This knowledge also casts light on how the competition between crop and weed is influenced by the weather and enables possible future weed infestations to be evaluated in relation to crop management strategies.

Data collected in seven experiments in greenhouses or phytotrons were used to develop an empirical description of the phenology of populations of *Galium aparine* L.

G. aparine from a hedgerow population were found to differ from *G. aparine* from an arable population in their need for vernalization. Moisture regime and amount of light proved to be unimportant for the timing of flowering. Nutrition had some influence on the timing of flowering, but the day length and the maximum temperature were most important in this respect. Both can be involved by summation of the product of day length with the effective maximum temperature (°C above the base temperature of 5.3). The resulting descriptive formula enables relevant developmental rates of arable field populations to be predicted across a broad range of environmental conditions.

The flowering date in the field of *G. aparine* from an arable population could be correctly predicted for cohorts of plants emerging at different dates in two independent sets of data collected in England and the Netherlands, by using this summation (17300 °C*hour between emergence and flowering).

The temperature sum divided by 17300 can also be used as a developmental scale that governs the changes in patterns of carbohydrate partitioning. Although the development of the first whorls on *G. aparine* is mainly related to the mean day temperature, the summation can also be used to describe the development of the first whorls.

6.1 Introduction

Phenology is the study of the cycle of sprouting, blooming, bearing of fruit and senescence in a plant, as affected by climatic changes (Larcher, 1975) or the development and timing of plant functions (Bannister, 1980). There are several good reasons for studying the phenology of weeds, in particular:

- The efficiency of many weed control methods (herbicides as well as mechanical control) depends on the developmental stages of weed and crop (Koch, 1970). It would be useful to be able to predict the development of weed and crop, so that the weed control could be timed accurately (Cudney *et al.*, 1989; Ghersa *et al.*, 1990).
- The distribution of carbohydrates to different plant organs mainly depends on the developmental stage of the plant (Orwick, Schreiber & Holt, 1978; Spitters *et al.*, 1989; Wall & Morrison, 1990). Data on phenology and distribution are used in eco-physiological models that simulate how competition between crop and weeds is influenced by weather conditions (Kropff, 1988; Spitters, 1989).
- Knowledge about phenology is needed to understand and calculate future infestations of weeds in relation to crop management (Aarts, 1986; chapter 2). For example, the timing of seed production and seed release of *Galium aparine* L. is important in crops such as spring barley and oilseed rape, which are harvested early (chapter 7).

For phenological studies the relevant developmental stages must be clearly distinguishable. In many cases the first distinction is between vegetative and reproductive growth, followed by subscales related to, for example, the number of leaves (or in this case whorls) and the maturation process (Gepts, 1987). The timing of the appearance of these stages then has to be characterized. Usually phenological stages cannot be ordered simply by calendar timing (days after emergence or dates) because environmental factors as for example temperature will influence the rate of development. The switch from vegetative to reproductive growth or the onset of flowering can be influenced by temperature, light (photoperiod, quantity and quality), moisture, nutrition, added growth regulators and genotype (Dennis, 1984; Gepts, 1987; Van Keulen *et al.*, 1988; Porter & Delecolle, 1988). Genotype can be a major source of variability in phenology, especially between crop cultivars bred for different climates or within and between natural populations. In most cases temperature (also for vernalization) and photoperiod are the most critical factors influencing plant development.

Phenological development has therefore often been related to a temperature sum. These empirical functions have been very successful in predicting phenological stages for various plant species (Rimmington & Charles-Edwards, 1987).

The objective of this study was to develop an empirical description of the phenology of different populations of *G. aparine* and to predict relevant developmental rates across a broad range of environmental conditions.

The most important event in the phenology of annual plants is the switch from vegetative to reproductive growth. Therefore the timing of flowering in relation to the environmental conditions experienced is crucial for the development of a phenological scale. Firstly the importance of photoperiod, temperature, amount of light, nutrition and moisture for the timing of flowering of populations of *G. aparine* will be examined.

Secondly a phenological scale will be constructed. Thirdly the utility of this scale will be evaluated.

6.2 Materials and methods

Greenhouse and phytotron experiments

The phenology of *G. aparine* was observed in seven experiments in greenhouse and phytotron. Plants from different *G. aparine* populations were subjected to treatments in which temperature, photoperiod, amount of light, nutrition and moisture regime were varied (Table 6.1). Some of the experiments had been designed for other purposes, but could also be used to provide data on development at new combinations of photoperiod and temperature. Differences in durations of photoperiods (8 to 16 hours) and temperatures (8 to 23 °C) corresponded with the variation at the field in the Netherlands, with exception of the low temperatures during winter. Furthermore to evaluate the importance of light quantity, nutrition and moisture for development, treatments varied from optimal for arable field situations to bad (20 % of light quantity, no nutrients in poor soil, pF ± 4). In experiments 1 to 6, the onset of flowering was recorded weekly for every pot (each pot contained one plant). The development of the first five whorls was noted once or twice a week in experiments 2, 3 and 7. Data collected during several harvests in experiment 4 (dry weight of roots, stalks, leaves, and seeds), provided information about the changes in distribution pattern of newly produced dry weight during development. For information on the treatments in the experiments and the experimental conditions, see Table 6.1. The results of experiments 2, 4, 5 and 6 have been subjected to analysis of variance. Data from all the experiments were subjected to (multiple) linear regression analyses. The program package used was SPSS.

The data from the greenhouse and phytotron experiments were used to construct a phenological scale which was compared with independent field data to asses its usefulness for:

1) characterizing the changes in the distribution pattern of newly produced dry weight,
2) predicting the flowering dates of *G. aparine* that emerge in different cohorts,
3) predicting the course of development of the first 5 whorls of leaves.

Field experiments

The experiments which provided independent field data for evaluation of the phenological scale are described in detail by Ferris (1988) and in chapter 7.

Table 6.1 Experimental conditions in 7 experiments used for observations on the phenology of *Galium aparine* of different origin.

Experiment	1	2	3	4	5	6	7
Treatment:							
origin &1		x	x	x			
temperature		x	x	(x)	(x)		x
photoperiod (hours)	x		x				
light quantity				x	x		
nutrients					x	x	
moisture						x	
Conditions:							
greenhouse	x			x	x	x	
phytotron		x	x				x
size of pot (l)	3.5	3	3	3.5	3	0.5	6
soil medium	potting compost			sandy arable			sand
day/night temperature in °C	17/16	13/13 23/23 &2	18/12+14h 20/20+14h 25/25+8h	21/15 19/13 17/12 &3	24/17 21/16 &3	22/14	8/8;12/12; 16/16; 20/20
photoperiod (hours)	8;12;16	14		12+&4	16	14+&5	12
amount of light in μE/m^{2}s PAR (+70% daylight)	8h day + 4 or 8h 10	240	400-550	150+100;4 5;20%day	150+ 100; 20% day	200	550
nutrition	optimal in nutrient rich compost			40kgN/ha =16mg/l	no;1* or 2* 40kgN/ha; 4 g/l &6	no; 4g/l &6	250 ml Steiner (1968) weekly
moisture	optimal by daily watering					&7	opti.
Replicates	18	4 or 8	10	4	6	5	25

&1 The populations used were collected from arable fields (all experiments) or as contrast from hedgerows (experiments with a comparison of origin).

&2 After 2; 5; 8; 12; and 16 weeks, 4 plants of each origin were changed from 13 to 23 oC and vice versa. Eight replicates were not moved.

&3 Light quantity in the 12 compartments was manipulated by covering with none, one or two layers of small-mesh netting. This also had consequences for the temperature in the compartments. The design of the experiments was split-plot: light level/ nutrition regime and light level/origin*harvest time (0; 11; 25; 39; 52; 67; 88; 124; 178 days after emergence).

&4 The photoperiod was at least 12 hours but after 21 March (17 days after emergence) followed the natural course.

&5 The photoperiod was at least 14 hours but after 20 April (29 days after emergence) followed the natural course.

&6 Slow release nutrition with 15% N, 11 % P_2O_5, 13% K_2O and 2% MgO (Osmocote).

&7 Soil moisture percentage continuously at 34; 27; 20 or 16 % (pF 2 to 4) or with fluctuations of 4 % or 9 % around 20 % and 27 % moisture regimes. The latter conditions only with supply of nutrients. Moisture regimes were adjusted continuously by using the watering robot of Zoon et al. (1990), which weighs the pots during daytime at least every hour, and waters them accordingly.

Ferris (1988) sowed eight populations of *G. aparine*, 4 field populations and 4 hedgerow populations, every three weeks starting on 27-9-1985 in an arable field at Reading (UK) in four replicates. He recorded the number of days between sowing and flowering. I obtained field-temperature data at 150 cm above the soil level for the period of the experiment from the Department of Meteorology of the University of Reading. These data were corrected for 10 cm above soil, using the mean difference between maximum temperature at 150 cm and at 10 cm for every month in the Netherlands. The plants were assumed to emerge two weeks after sowing.

In experiments in the Netherlands *G. aparine* was planted on several dates and at several densities in oilseed rape, winter wheat, summer barley, potato and sugarbeet near Wageningen (chapter 7). Every two weeks the exact developmental stage of the individual plants was recorded. These data were used to calculate the exact number of days between emergence and the appearance of the first whorls or the onset of flowering. Weather data were obtained from the Department of Meteorology of the Agricultural University in Wageningen.

Results and discussion

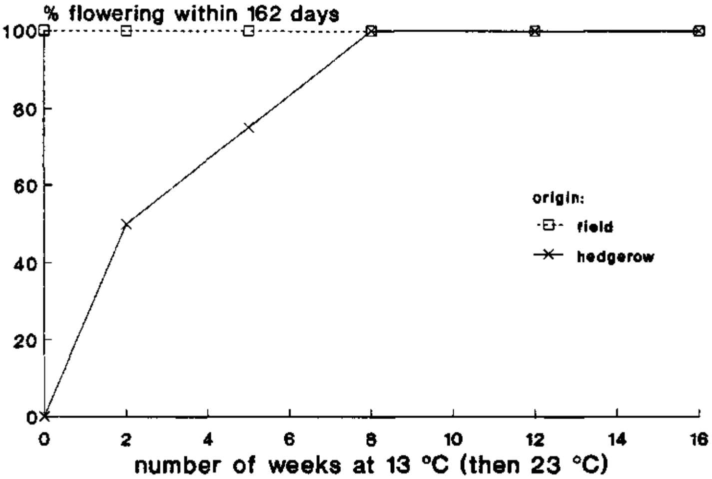
The influence of photoperiod, temperature, light quantity, nutrition and moisture on development

The time between emergence and flowering of *G. aparine* in experiment 1 with a photoperiod of 8 hours was more than twice that with a photoperiod of 16 hours.

In experiment 2 the plants did not flower while the temperature remained 13 °C. If plants were moved from 13 °C to 23 °C after different periods of time, there was a significant interaction ($p<0.001$) between the length of time spent at 13 °C and the origin of the population. The hedgerow population needed vernalization in order to flower within 162 days (Fig. 6.1) but the arable population did not. In experiment 3 the hedgerow population did not flower within 162 days either. The shorter the length of time the arable population spent at 13 °C (i.e. the higher the overall temperature), the shorter the period between emergence and flowering (Fig. 6.2b, data points experiment 2).

In both experiments 4 (arable field population) and 5, a higher amount of light significantly ($p<0.005$) prolonged the period between emergence and flowering. The differences in temperature corresponding with the shading, however, did explain the differences observed (Fig. 6.2b, d and f data points experiments 4 and 5). In experiment 5 the interaction between shade/temperature and nutrition was significant ($p<0.05$). Without shading, there were no differences between the different nutrition regimes, possibly because there were fewer days before flowering. With shading, the number of days before flowering decreased with increasing (especially slow-release) N nutrition (78, 77, 75 and 67 days for the 4 nutrition regimes respectively). This was also observed in experiment 6: 63 days with no additional N nutrition compared with 54 days with additional slow release N nutrition, independent of moisture level ($p<0.05$). Variation in nutrient supply on arable fields will be very small compared with the variation in these experiments and therefore will probably not be an important factor in an arable field situation. In Fig. 6.2 and 6.3 nutrition has been ignored. The different moisture regimes in experiment 6 did not have any effect on the timing of flowering.

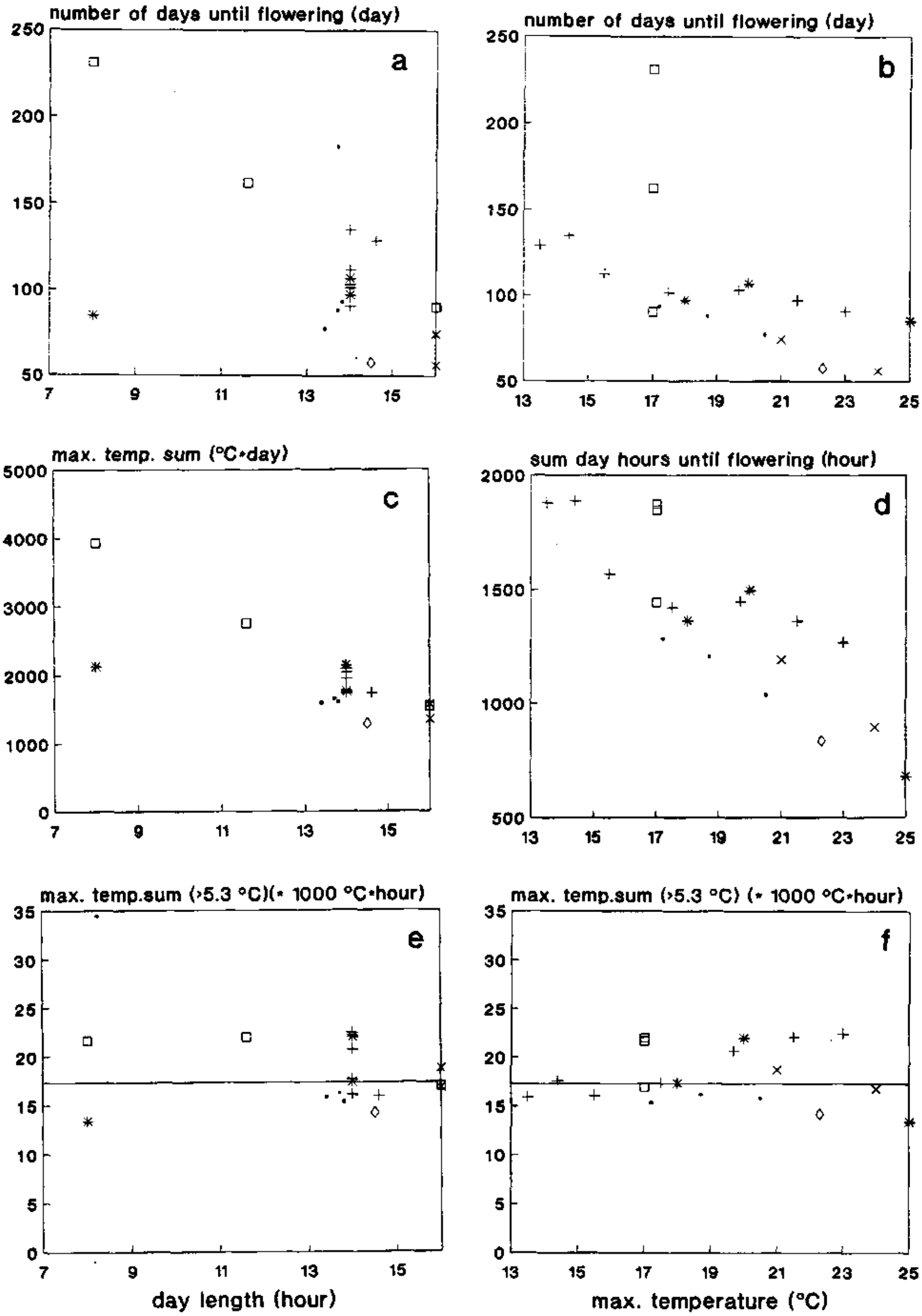
Fig. 6.1 The influence of vernalization on flowering of a hedgerow and a field population of *Galium aparine* L.



Phenological scale

In Fig. 6.2 the average flowering rate of the arable field population for the different treatments in six experiments (except differences in nutrition) are plotted against the day length (a, c and e) and against the maximum temperature (b, d and f). The length of the observation period was long enough to record the number of days until flowering (Fig. 6.2a and b) for all plants of the arable field population used at mean temperatures above 13 °C. Regression analyses showed that day length as well as temperature did correlate significantly with the number of days before flowering ($p<0.001$). Therefore an empirical description of the phenology must involve both temperature and day length. It is possible to relate the sum of temperatures until flowering to the day length or to relate the sum of hours of daylight until flowering to the temperature (Fig. 6.2c and d). The correlation between the sum of hours daylight until flowering and the maximum temperature (= temperature during the photoperiod in these experiments) was greater than the correlation between the sum of hours daylight until flowering and the mean diel (day and night) temperature (Fig. 6.3).

Fig. 6.2 The influence of day length and the maximum temperature in six phytotron or greenhouse experiments on flowering rate of *Galium aparine* L.



Average for all plants of the arable field population with the same treatment in experiment (Table 6.1):

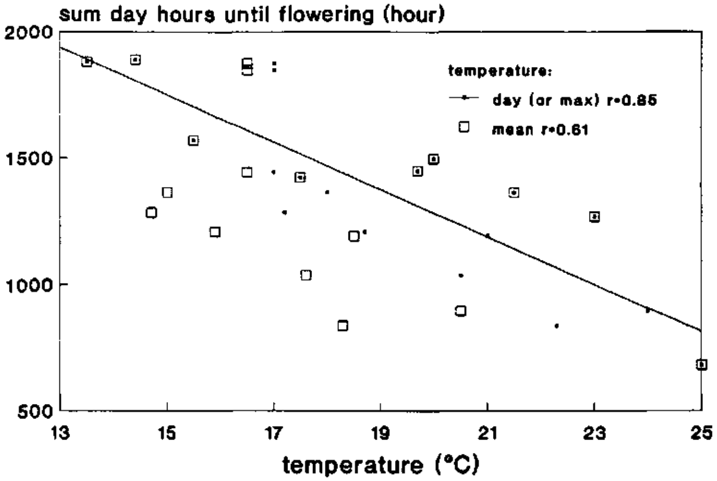
1 □ 2 + 3 ✳ 4 . 5 × 6 ◊

Dennis (1984) showed that it is possible to include day length in calculations of the required number of heat units from sowing to heading in winter wheat, by daily summation of the product of the heat units (temperature minus minimum temperature for development) and the day length. Such a summation seems reasonable for predicting the flowering of *G. aparine* too (Fig. 6.2e and f). Temperature daylength sums were calculated for all base temperatures between 0.0 and 10.0 °C. The best base temperature was chosen by comparing regression analyses of different calculated temperature daylength sums versus the temperature. The temperature daylength sum has to be independent of the temperature, thus the correlation coefficient between sum and temperature has to be zero. This was valid for a base temperature of 5.3 °C. The mean temperature daylength sum (weighted for the number of observations) until flowering was 17300 °C*hour (Development scale DVS=1). Hence the following phenological scale for development is proposed:

$$DVS(t)=(\sum_{x=1}^{t}(DT(x)-5.3)*DL(x))/17300$$

with x the number of days after emergence, DT(x) the mean diurnal temperature or the maximum diel temperature on day number x in °C (minimal 5.3) and DL(x) the length of the photoperiod on day number x in hours.

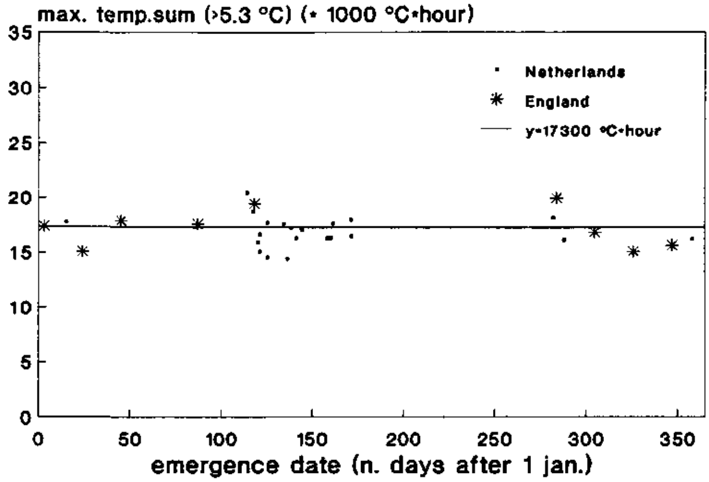
Fig. 6.3 The relation between duration until flowering of *Galium aparine* L. and the mean day temperature or the maximum day temperature.



Prediction of the flowering date

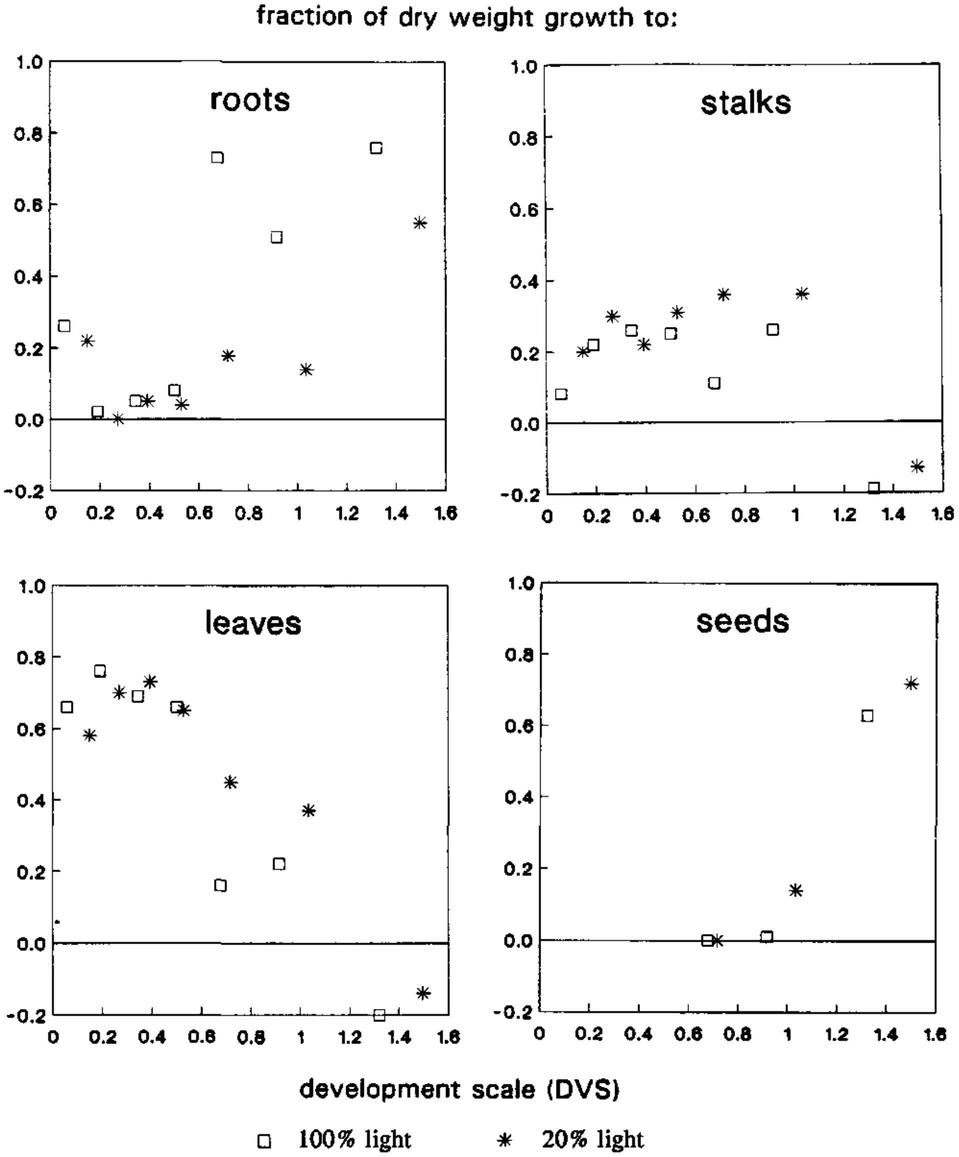
To find out whether flowering can be predicted by this summation obtained from phytotron and greenhouse experiments, the formula was applied to independent sets of field data from England and the Netherlands (Fig. 6.4). The summations until the date of flowering for the field observations varied around the suggested 17300 °C*hour using the maximum diel temperature and around 12600 °C*hour using the mean diurnal temperature. Although the mean diurnal temperature seemed a better parameter from a physiological point of view, the maximum diel temperature resulted in a better fit between phytotron/greenhouse experiment and field data. Further research is needed to reveal whether 1) maximum temperature is more important for the development of *G. aparine* than mean diurnal temperature or 2) maximum temperature at 10 cm above bare soil is better related to the temperature experienced in the plants during daylight on the field then the mean diurnal temperature at 10 cm above bare soil (reflection of sunlight). Until more is known, it seems justifiable to use maximum diel temperatures. It proved to be important to take the maximum temperature at 10 cm height instead of at 150 cm height, because at the latter height the maximum temperature was considerably less. No trend between emergence time on the field and the summation could be demonstrated using the usual times of emergence during autumn, winter and spring. The standard deviation around the level of 17300 °C*hour was 1500 °C*hour. This corresponds to 5 days with a day length of 16 hours and a maximum temperature of 22 °C, which are the prevailing day lengths and maximum temperatures during the start of flowering at the field. The difference between observed and predicted date of flowering is small compared with the 80 to 260 days the plants need between emergence and flowering in England.

Fig. 6.4 The correspondence between the suggested temperature day length sum for flowering of *Galium aparine* L. and field observations.



Differences among arable field populations were not important (Ferris (1988) and comparison between data from England and the Netherlands and between the phytotron and greenhouse experiments). When the hedgerow and arable populations were sown on the field before the end of March, the mean differences in flowering date between the origins did not exceed 5 days. Late emerging plants from a hedgerow population, however, are at least delayed by their need for low temperatures for vernalization (20 days for a sowing date of 9 April (Ferris, 1988)).

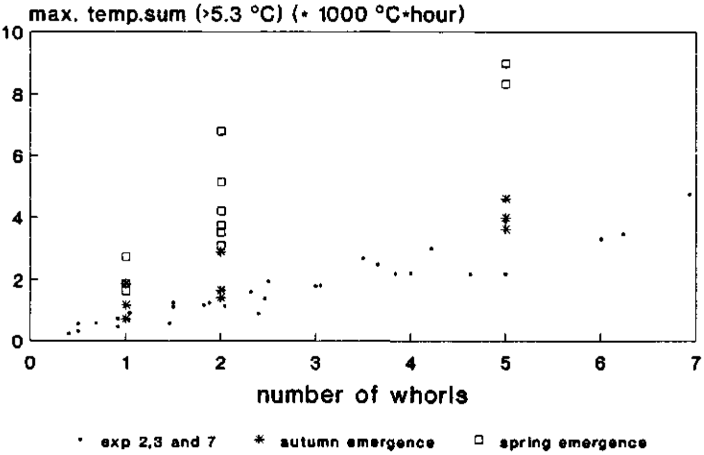
Fig. 6.5 The distribution of freshly produced dry weight of *Galium aparine* L. during its development at two light levels.



Dry weight distribution patterns

The phenological scale can also be used to describe the changes in distribution patterns of dry weight increment during development (see Fig. 6.5). The different light levels (experiment 4) correlated with different temperatures. Differences in the distribution of dry weight increment between the treatments as observed at one harvest time, can be explained by plotting this distribution against the phenological scale. This clearly shows the timing of changes in the distribution pattern: firstly investment mainly in the leaves, then in the roots and lastly in the seeds. Only the absolute amount of dry weight invested in the roots and in the leaves seemed to be influenced by the light level: at low light level relatively less is invested in the roots and more in the leaves. This adaptation mechanism to low light levels is seen in several plant species (Wilson, 1988).

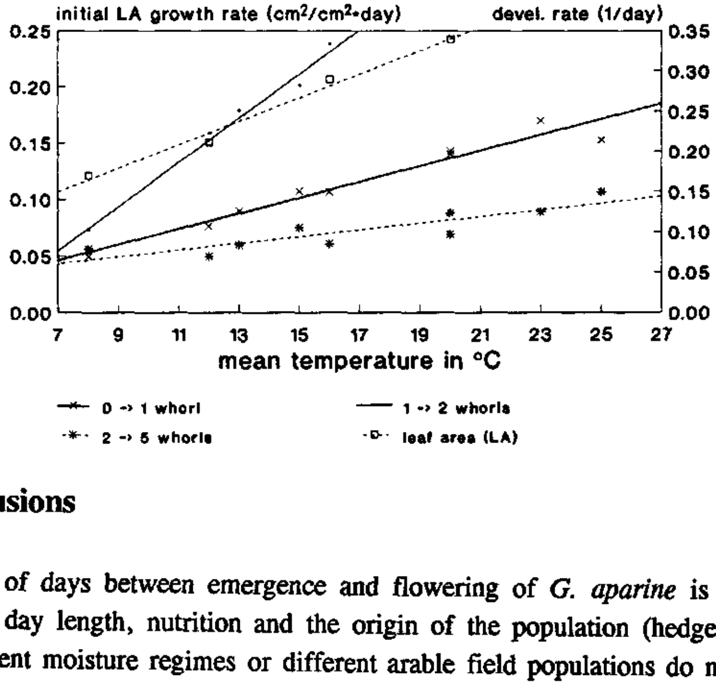
Fig. 6.6 The correspondence of the temperature day length sum for the course of development of the first whorls of *Galium aparine* L. as observed in phytotrons or for autumn and spring emergence in the field.



Development rate of the first whorls of leaves

The developmental stages of *G. aparine* that are important for the efficacy of weed control are seedling stage, plants with one whorl, plants with 2 up to and including 4 whorls and plants with more than 4 whorls (Aarts,1986). The development of the first whorls cannot completely be separated from growth. After 25 days of growth at 100 % light, a cleaver plant had, an average, 5.25 whorls, at 45 % light it had 4 whorls and at 20 % light it had 3.5 whorls. But environmental conditions that are less favourable for plant growth (such as the lower light levels in experiment 4), are much more important for the branching on the first node (6.25, 3 and 1.75 branches after 25 days at 100 %, 45 % and 20 % light respectively). Temperature is much more important than light for the development of whorls. Fig. 6.6 shows the developmental rates as observed in experiments 2, 3 and 7. The development of the first whorls relates better to the mean temperature than to the maximum temperature and is not related to the day length (data in Fig. 6.7 observed at different day lengths and 12/18 °C regime and in comparison with field data in Fig. 6.6). The validity of the suggested phenological scale for characterizing the timing of flowering and changes in dry matter partitioning is not undermined by this, because the onset of flowering does not depend on the availability of a certain number of whorls of leaves. Nevertheless the day length temperature summation can also be used to describe the development of the first whorls in the field (Fig. 6.6), but in that case an empirical relation has to be fitted to field data on the development of different cohorts.

Fig. 6.7 The influence of the mean temperature (in phytotrons) on the initial leaf area growth rate and the developmental rates of *Galium aparine* L.



6.4 Conclusions

The number of days between emergence and flowering of *G. aparine* is influenced by temperature, day length, nutrition and the origin of the population (hedgerow or arable field). Different moisture regimes or different arable field populations do not seem to be important.

For arable situations, the day length and the maximum diel temperature are especially important. Both can be involved by summation of the product of day length with the effective maximum temperature (°C above the base temperature of 5.3). These daylength temperature summations can be used for predicting the flowering date (17300 °C*hour between emergence and flowering).

The temperature sum divided by 17300 can also be used as a developmental scale that governs the partitioning of freshly produced dry weight during development.

The development of the first 5 whorls of *G. aparine* is not related to day length and depends on mean temperatures rather than on maximum temperatures.

Chapter 7

Towards predicting the seed production of *Galium aparine* L. in five crops.

Abstract To evaluate the risks of future weed infestations, it is necessary to predict the seed production of the surviving weeds and the flow of these seeds into the seedbank. Components of seed yield and seed fall in *Galium aparine* L. were measured on individual plants with different relative emergence times and different densities in spring barley, potato, oilseed rape, winter wheat and sugar beet during 1988 and 1989.

Shoot dry weight of *G. aparine* was clearly influenced by the crop within which it was growing and its relative emergence time and slightly by its density and the year of observation. A linear relationship was found between the number of flowers (nF) and the mature shoot dry weight without seeds in gram (mb) where nF=110*mb (r=0.97). This relationship was not influenced significantly by companion crop type, relative emergence time, year or weed density. The mean number of seeds per flower of mature *G. aparine* plants depended mainly on the companion crop (1.0, 1.1, 1.2, 1.6 and 1.8 for spring barley, winter wheat, oilseed rape, potato and sugar beet respectively). Viability of the mature seeds was high (> 95 %). Seed fall decreased with a late emergence time and increased with harvest time. The presented relationships can be used to extend an eco-physiological model on competition between a crop and *G. aparine* to predict not only crop yield reduction but also weed seed production.

7.1 Introduction

To reduce pesticide application, attempts have been made to develop integrated control methods for arable weeds. An important development is the use of economic damage thresholds whereby weeds are controlled only if the costs incurred through crop damage exceed those of herbicide control. Thresholds have been set indicating the period for which the weed can be tolerated or the densities of weed species that can be tolerated in the arable crop (Nieto *et al.*, 1968; Neururer, 1975; Ammon, 1978; Niemann, 1981; Wilson & Wright, 1990).

Current thresholds are based on annual damage to the crop. But allowance should be made for the fact that where weeds are capable of forming an important seedbank, problems may occur in subsequent years. When this aspect is taken into account, much smaller quantities of *Abutilon theophrasti* Med. (Zanin & Sattin, 1988), *Alopecurus myosuroides* Huds. and *Avena fatua* L. (Cussans *et al.*, 1986) can be tolerated than are acceptable during one growing season only. An over-years approach is also necessary for *Galium aparine* L. (Niemann, 1981; Cussans *et al.*, 1986). As well as knowing future farming practice (especially crop rotation and cultivation), information is required regarding the population dynamics of this weed. An important aspect is the seed production and the flow of seeds into the seedbank, provided that survival and germination of the seeds can be predicted with sufficient accuracy.

Components which determine the viable seed yield are plant biomass, number of flowers per unit of biomass, number of seeds per flower and the seed viability. These components depend on the resources available to the mother plant (Haig & Westoby, 1988; Charles-Edwards *et al.*, 1986). Competition between weed and crop is thus very important for the weed's seed production. Seed production differs with time of emergence, density of the weed plants, presence of other weed species and type of crop (Röttele, 1980; Aarts, 1986; Légère & Deschênes, 1986; Chaem, 1986). Seeds retained are often harvested together with the crop (Röttele,1980; McCanny & Cavers, 1988). Therefore seed fall, date of harvest and harvest method determine the seed flow into the soil weed seed bank.

The objective of this study was to develop a method for the prediction of the quantity of *G. aparine* seeds remaining in the field as influenced by weed density, relative emergence time and type of companion crop.

7.2 Material and methods

In 1988 and 1989 field experiments were set up to analyse the growth and seed production of *G. aparine* in a variety of crops: spring barley intercropped with ryegrass, potato, sugar beet, oilseed rape and winter wheat. The experimental plots were situated on a clay soil in Randwijk, the Netherlands. Production practices were as being standard for the region except weeds were removed by hand. Seedlings of *G. aparine* were transplanted into the crop at various times (at crop emergence up to 6 weeks after crop emergence for summer crops or up to spring for winter crops) and in different densities (1 to 30 plants per m^2). Emergence times in oilseed rape were late in comparison with the other crops because the natural emergence of *G. aparine* starts in October while the oilseed rape emergenced at the end of August. Additional information about crop cultivars, dates of sowing, relative emergence time and density of the different cohorts and harvest and plot size are presented in Table 7.1. In every crop all treatments were in twelve replicates in a completely randomized block design. In 1989 the sugar beet experiment was repeated with a slightly different statistical design in order to obtain further insight in the effects of cultivar choice and harvest time. The design of this experiment was split-plot with three different cultivars in four blocks, where crop and weeds were harvested at four different dates (block * cultivar / emergence time * density * harvest time). The cultivars chosen differed in soil coverage and therewith weed suppression (Lotz *et. al.*, 1991).

Table 7.1 Experimental conditions in field experiments used for observations on seed yield components of *Galium aparine L.*

crop:	spring barley	sugar-beet	potato	winter wheat	oilseed rape	sugar-beet
year:	'88	'88	'88	'88/'89	'88/'89	'89
cultivar:	Trumpf *1	Avativ	Bintje	Obelisk	Jet Neuf	*2
sowing date:	12-4	14-4	14-4	27-10	23-8	24-4
emergence date:	29-4	30-4	16-5	16-11	31-8	5-5
harvest date(s):	12-8	30-9	20-9	9-8	5-7	20-6, 9-8, 6-9, 11-10
yield (ton/ha):	6.5	58	58	8.6	3.9	
plot size (m2):	0.36	0.75	1.13	0.5	0.5	0.75
RET 1:	-2	<-30	-15			
RET 2:	+3	0	0	+7	+39	+7
RET 3:	+25	+21	+24	+28	+105	
RET 4:	+39	+42	+35	+180	+236	+43
DEN 1:	3	1	1			
DEN 2:	3 or 28	1, 7 or 33	1, 3 or 9	2, 10 or 30	2, 10 or 30	1, 7 or 20
DEN 3:	3	1	1	2	2	
DEN 4:	3	1	1	2	2	1, 7 or 20

RET =	Relative emergence time of a cohort *G. aparine* in days after crop emergence
DEN =	Density of *G. aparine* in a cohort in plants m^{-2}
*1	intercropped with English Rye cultivar Gambit, which was removed in an extra treatment for cohort 2 of the low density of *G. aparine*
*2	Cultivars Carla, Univers and Lucy

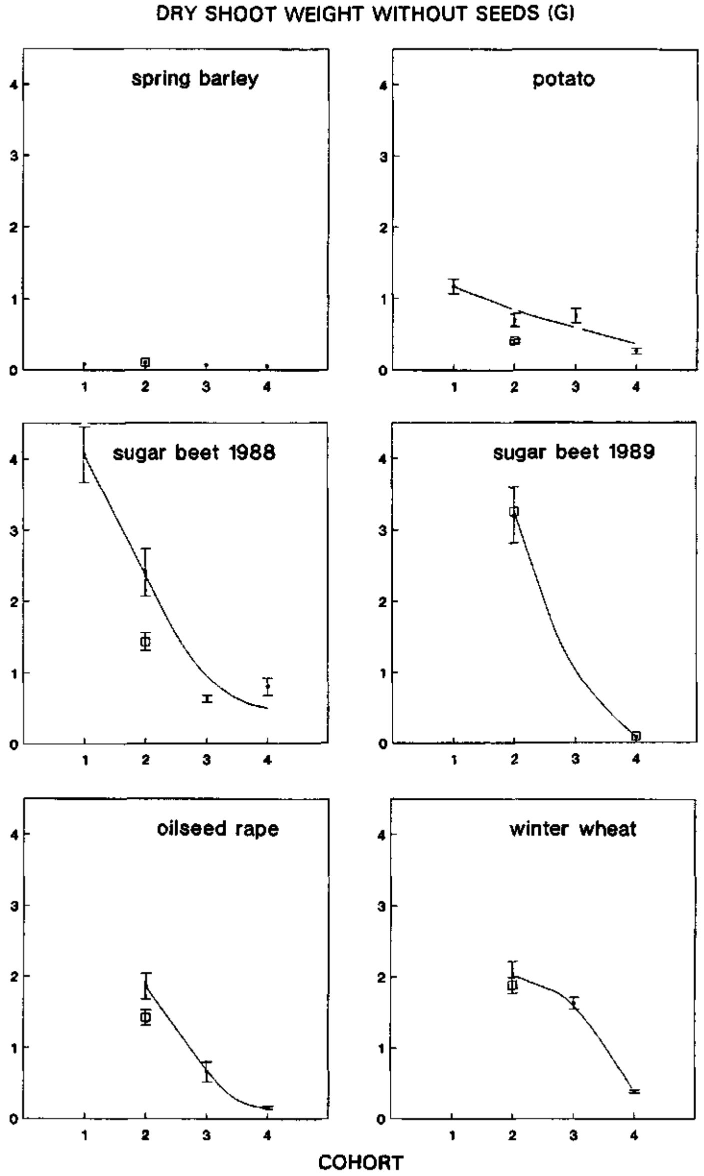
At harvest, at least one *G. aparine* plant was selected at random in every plot. The weight of the plants (minus seeds) after drying at 110 °C and the number of seed-producing tips (split into different categories: equally or unequally developed with different degree of ripeness as not yet developed, green, red, brown and dropped seed) were measured. Each seed-producing tip originally started as one flower. A maximum of two seeds per flower are able to develop. Mature seeds easily drop leaving a (half) empty tip. Undeveloped seeds do not drop and can be counted, even if the counterpart seed was mature and/or dropped. The number of seeds produced by the plant was estimated by doubling the number of complete empty tips (from which developed seeds had dropped) and the number of tips with two fully developed seeds and adding the number of tips with unevenly developed seeds. With these data it is possible to calculate the realisation of potential seed production (number of seeds per flower or tip) and the seed fall. Data on seed drop from Röttele (1980) were included for the regression analyses of seed fall in relation to harvest and emergence time. The viability of seeds with different degrees of ripeness was measured using the tetrazolium test of Moore (1970). The single seed weight $(n>=10)$ of *G. aparine* in every treatment was determined in four replicates. Data were subjected to analysis of variance or regression analyses as appropriate. The critical level of significance was set to $P<= 0.05$.

7.3 Results

Weed biomass

Biomass production of a *G. aparine* plant was hardly influenced by its own density and clearly influenced by both companion crop species and relative emergence time (Fig. 7.1). In spring barley intercropped with ryegrass, *G. aparine* hardly grew at all. Growth doubled when the ryegrass was removed (shoot weight without seeds 0.18 in stead of 0.08 gram, $P<0.05$). The *G. aparine* plants in sugar beet were up to forty times heavier than those in spring barley. No significant differences were observed between *G. aparine* growing in different sugar beet cultivars (data not presented). Shoot dry weights of *G. aparine* in winter wheat, oilseed rape and potato were intermediate in between the dry weights produced in sugar beet and in spring barley. The time of weed emergence influenced shoot biomass of *G. aparine* significantly in all the crops except for spring barley, where growth was so poor that hardly any difference could be measured. In the other crops, the dry weight of late emerged *G. aparine* plants was one-quarter to one-twentieth the dry weight of plants that emerged earlier. In relatively open crops such as sugar beet, plants that emerged early started to grow without crop competition, resulting in relatively high dry weights. In tall crops such as oilseed rape and winter wheat, plants that emerged late could not reach the top of the crop, in contrast to those that emerged

Fig. 7.1 Biomass production of *Galium aparine* L. with different emergence times and densities in different crops.



cohort 1: emergence before crop emergence
2: emergence within a week after crop emergence
3: emergence within a month after crop emergence
4: emergence more than a month after crop emergence
(except oilseed rape, Table 7.1)

density *G. aparine* low: + high: □ (Table 7.1)

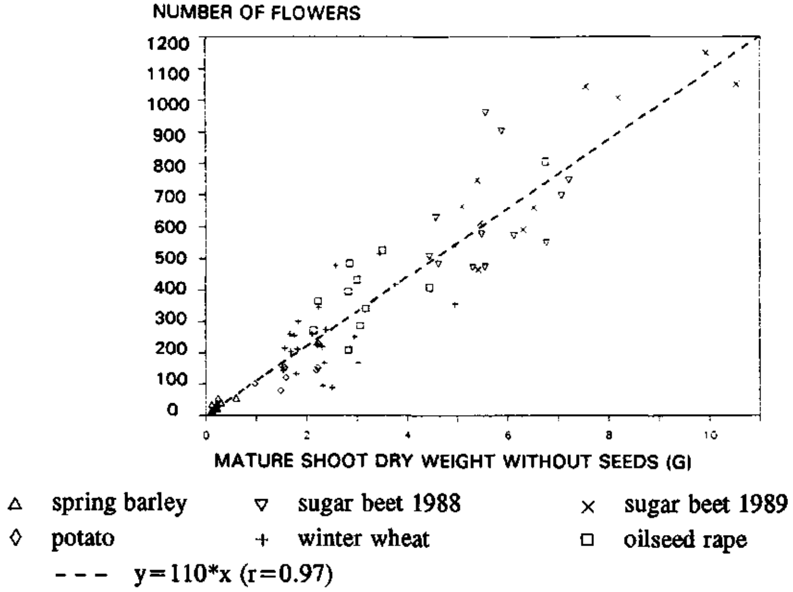
Standard error: I

early. The reduction in dry weight caused by late emergence was relatively large in these tall crops.

Number of seed producing tips per unit of biomass

At crop harvest, the *G. aparine* plants were mature (dead or dying), except for those that emerged in spring in the winter crops, the two latest emergence dates in potato and the latest emergence date in sugar beet in 1988. These latter (immature) plants produced fewer flowers per gram shoot dry weight (data not presented). The number of flowers (or seed producing tips) is closely related to the dry weight of mature *G. aparine* plants (Fig. 7.2). The following relationship was calculated from the data collected in the five crops for mature *G. aparine* plants: number of seed-producing tips = 110.0 * g dry shoot weight of the plant without the seeds (r=0.97). Regression analysis showed that type of crop, density of *G. aparine*, year or emergence time did not significantly affect this relationship.

Fig. 7.2 Relation between shoot dry weight (without seeds) and the flower number of mature *Galium aparine* L. plants grown in five crops in 1988 and 1989.

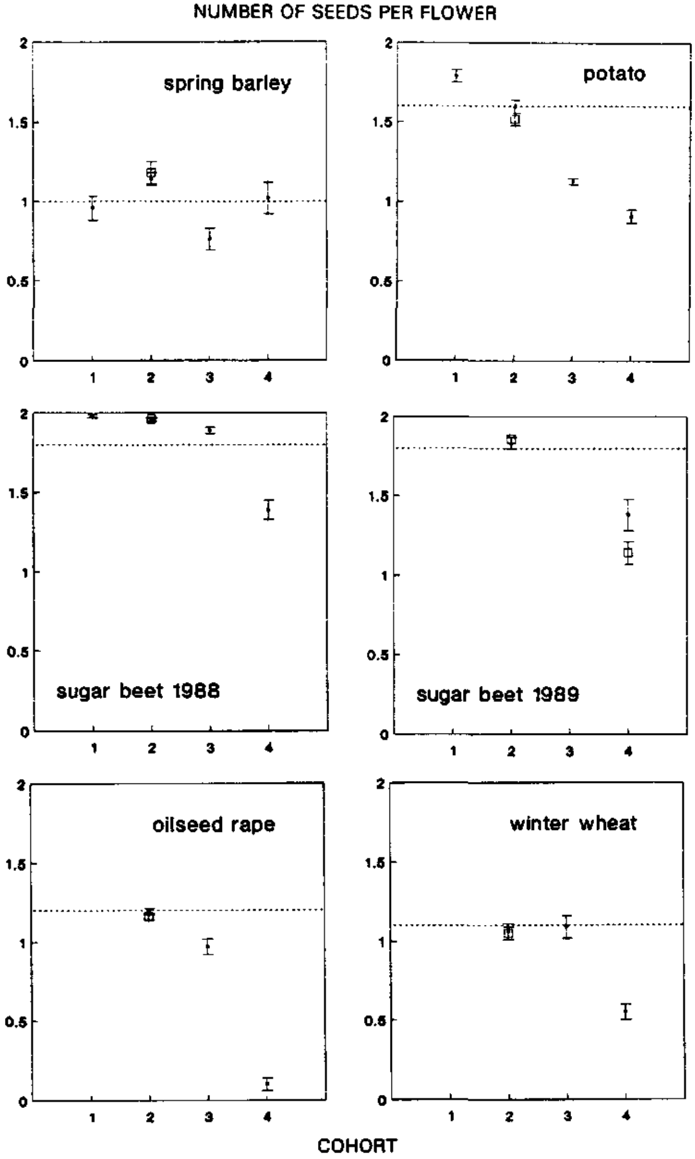


Number of seeds per seed producing tip

The realisation of seed production (of maximum 2 seeds per flower) differed with the crop (Fig. 7.3), relative emergence time (Fig. 7.3) and harvest time (Fig. 7.4). The density of *G. aparine* did not influence the number of seeds per flower (Fig. 7.3).

However compared with the variation in flower production (differences in the related mature biomass up to a factor 50), the variation in the realisation of potential seed production (differences up to a factor 2 at normal crop harvest time, except for plants that emerged very late in winter crops) was less important in magnitude.

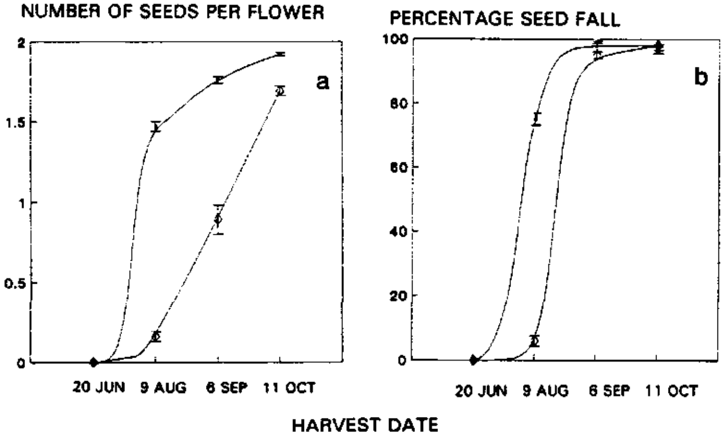
Fig. 7.3 Realisation of potential seed production of *Galium aparine* L. with different emergence times and densities in different crops.



See for legend Fig. 7.1

The mean number of actually produced seeds per flower was 1.0, 1.1, 1.2, 1.6 and 1.8 for mature *G. aparine* plants growing in spring barley, winter wheat, oilseed rape, potato and sugar beet, respectively.

Fig. 7.4 Timing of the realisation of potential seed production (a) and the seed fall (b) of *Galium aparine* L. in 1989 in sugar beet.



emergence time *G. aparine* early: × late: ◊ (Table 7.1)
Standard error: I

Seed viability and seed weight

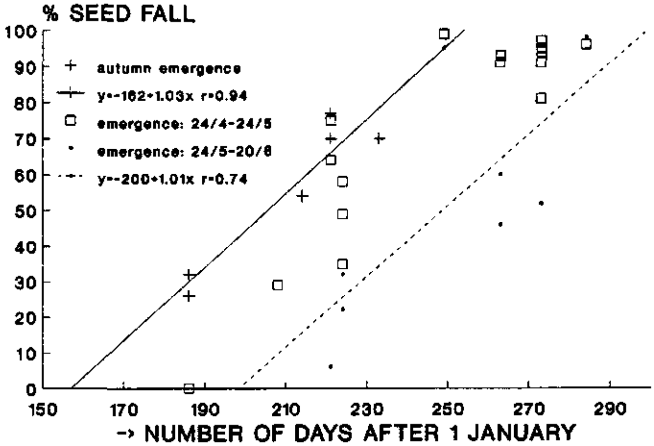
A large percentage of the seeds produced were viable (brown seeds 100%; red seeds 95%; green seeds 75%). Green seeds were only found on immature plants and in the early harvested crop spring barley.

The mature single seed weights were 6.1, 8.7, 8.7, 8.9 and 10.1 mg for *G. aparine* seeds produced in winter wheat, oilseed rape, potato, spring barley and sugar beet respectively.

Seed fall

To be able to assess the number of seeds left in the field after harvest, the date and method of harvest must be known. In case the crop is harvested with a combine (cereals and oilseed rape), the seeds of *G. aparine* which did not drop are often unintentionally taken from the field. Regression analysis on all the data collected showed that harvest time and emergence date both significantly affected the percentage of seed drop. Seed fall increased with time and decreased with late emergence (Fig. 7.5). From 7 June (autumn emerging *G. aparine*) until 18 July (late spring emerging *G. aparine*) around 1 % of the total seed production was dropped every day. Linear relationships between harvest date and percentage seed fall were fitted for autumn emerging or for spring emerging plants (Fig. 7.5).

Fig. 7.5 Seed fall of *Galium aparine* L. as influenced by its emergence and harvest time.



7.4 Discussion

Relationships between seed production and weed biomass

One specific relationship between the flower number and the vegetative biomass of *G. aparine* was presented here. This relationship did not differ with different companion crops, emergence dates and years. By contrast, Röttele (1980) fitted non-linear relationships between the flower number and the plant dry weight of *G. aparine* which differed with the companion crop. The divergence of the results in these two studies may be explained largely due to the non-inclusion and inclusion of seed dry weight in the calculations. Because the weight of the seeds is considerable compared with the vegetative shoot dry weight and seeds easily drop, it is very difficult to accurately measure shoot dry weight with seeds. Moreover, number of flowers and the weight of the shoot with seeds are interdependent. It is also easier to use one relationship between the flower number and dry weight without seeds for different situations.

A linear relationship between plant dry weight without seeds (V) and seed weight (R) was found for several weed species (Thompson *et al.*, 1991). The reproductive effort (R/V) of *G. aparine* is high (0.8 to 2) in comparison with these weed species (0.2 to 0.7). The reproductive effort also differed between populations of one weed species (Thompson *et al.*, 1991). Because the realised seed production (number of seeds per flower) differs with the surrounding crop, relationships such as those used by Thompson would also differ for *G. aparine* collected in different crops. Individual seed weight of *G.*

aparine differed between companion crops but also between years (mean seed weight of seeds collected in winter wheat was 14 mg in 1987, 12 mg in 1988 and 6 mg in 1989). Because of our emphasis on numbers of seeds and these differences in individual seed weight, a relationship between the flower number and dry weight without seeds as presented here, is more useful then data on the reproductive effort as a whole as measured by Thompson *et al.* (1991).

It is feasible to estimate the seed production of *G. aparine* based on its mature dry weight using the relationships between the number of flowers and mature dry weight without seeds and the number of seeds per flower produced in a particular crop. Late emerging plants did not reach maturity in relatively early harvested crops. Using the relationships for these immature plants will lead to an overestimation of seed production. Because of the enormous seed production of the early emerging plants compared with the late emerging plants on the same site, this overestimation is not substantial. But correction is necessary when we are interested in the seed production of a few late emerging plants that escaped chemical or mechanical control in early harvested crops.

Estimation of weed biomass

Mature dry weight without seeds of *G. aparine* can be measured or estimated. The present data demonstrate that for estimation of mature plant dry weight it is necessary to know at least the type of companion crop and the relative emergence time of the *G. aparine* plants. The observed dry weights of *G. aparine* with comparable relative emergence times in a specific crop vary somewhat between years (Fig. 7.1 sugar beet 1988 and 1989) and between localities (comparison with data from Röttele, 1980 and Peters, 1984). Wilson & Wright (1987 and 1990) measured substantial differences in the growth rate of *G. aparine* in winter wheat in June between years. They stated that this was possibly caused by differences in soil fertility. In addition to soil fertility and weather conditions, the absolute and the relative emergence time of *G. aparine* could possibly explain part of this variation as demonstrated in this paper. Simulation models that take into account how the growth and development of crop and weed are influenced by the environment (Spitters & Aerts, 1983; Kropff, 1988 and Spitters, 1989), can be used to evaluate the importance of weather conditions and cultivation practices like sowing time and sowing density. These eco-physiological models on crop-weed competition can also be used to adjust estimations of mature weed biomass. The other way around the relationships developed during this study can be used to extend such models to predict not only crop yield reduction but also weed seed production and weed population increases. Using these relationships this has been done for *G. aparine* competing with sugar beet (Chapter 8).

7.5 Conclusions

A linear relationship between the flower number and the shoot dry weight without seeds has been found for mature *G. aparine* plants. This relationship is not influenced by the companion crop type, the emergence time or the density of *G. aparine*.

The other components of seed production of an individual *G. aparine* plant are markedly influenced by the type of crop and the time of emergence of weed and crop. The resulting differences in shoot dry weight vary with a factor of 50; seed-filling varies with a factor of 2 and seed fall up to a factor of 3, depending on crop type. The differences in shoot dry weight due to emergence time vary up to a factor of 20. The differences in seed filling and seed fall due to emergence time vary less than a factor of 2 in most crops. Moreover, the importance of the difference in emergence times varies according to the type of crop. Dry weight reduction of *G. aparine* caused by late emergence is especially important in tall crops (oilseed rape) and in open crops (sugar beet). Density of *G. aparine* emerging after the crop (to 30 plants/m2) hardly influences the different components of seed production.

It is feasible to estimate the seed production of *G. aparine* based on its mature shoot dry weight per m^2 minus seeds, combined with information on crop type and harvest time.

Chapter 8

Effects of weather on competition between *Galium aparine* L. and sugar beet analysed with a simulation model.

Abstract To take rational decisions on the control of weeds, accurate estimates of crop-yield reduction and weed population dynamics are necessary.

Considerable variation in crop-weed competition under field conditions required the construction of an ecophysiological model on crop-weed competition. This general model is adjusted, parameterized and validated for growth and competition of *Galium aparine* L. in sugar beet. Simulation results show that mainly emergence times and densities of both crop and weed determine the outcome of competition. Lower nitrogen supply decreases the growth of and the yield reduction caused by *G. aparine*. Variation in yield reduction caused by variation in weather conditions over 10 years appears to be so small that it provides a basis for the use of thresholds involving weather caused uncertainty. The analyses presented may be applied to estimate various thresholds based on both short term crop-yield reduction and long term population dynamics of *G. aparine*.

8.1 Introduction

Weeds often have to be controlled to avoid their negative influence on crop growth, harvest operation and the quality of the harvested product and to minimise these effects in future crops. Ideally, weed control decisions should be based on economic cost-benefit analysis of control measures to reduce herbicide application and to maximize farmer's profit. To optimize decision making, it is essential to estimate crop-yield reduction and weed seed production of weeds tolerated accurately. Both factors are influenced by competition.

Crop-weed competition may vary considerably between years and locations (Spitters, 1984). This is especially true for the noxious weed *Galium aparine* L. (Wilson & Wright, 1987). Variation in competition can be explained to a large extend from differences in emergence times and densities of the crop and the weed and the weather conditions experienced (Kropff, 1988 and Lotz *et al.*, 1991). Furthermore, research of

Mahn (1984), Franz *et al.* (1990), Rooney *et al.* (1990), Baylis & Watkinson (1991) and Wright & Wilson (1992) demonstrated that an increase of nitrogen supply in winter wheat stimulates the performance and population growth of *G. aparine*.

Instead of analyzing competition under several conditions in many field experiments, the relative importance of the environment can be evaluated easier and cheaper using simulation models (Rabbinge *et al.*, 1989). The ecophysiological model for crop-weed competition used in this study, calculates the growth of the weed and the crop as a function of light intercepted and temperatures experienced. Parameters used to characterize species dependent reactions can be adjusted to suit the growth in environments with different nutrient regimes.

The objectives of this study are to parameterize and validate an ecophysiological model for growth and competition of *G. aparine* in sugar beet and to evaluate the importance of weather conditions, nitrogen supply and emergence times and densities of both crop and weed for competition. The results will be discussed with respect to the possibility to increase the robustness of estimates of crop-yield reductions and weed population dynamics.

8.2 Material and methods

The model

In an ecophysiological model for crop-weed competition, two (or more) mechanistic growth models for crop and one (of more) weeds are coupled. Growth of a species is mainly dependent on the amount of light intercepted and the temperature experienced. Competition is simulated through the relative amount of light each species is intercepting. This amount depends on the leaf areas, heights and extinction coefficients of the competing species. An extensive description of this model and the underlying growth models is given by Spitters & Aerts (1983), Kropff (1988), Spitters (1989) and Kropff *et al.* (in prep.).

For the growth simulation of *G. aparine* few adaptations were made:

- The developmental scale used was not based on temperature alone but included day length (Chapter 6).
- During periods were the specific stem length exceeded a maximum value determined in the field, height increase was assumed to be zero.
- During the period of seed fill, seeds are assumed to consume a minimum amount of assimilates. In case these assimilates are not available from the daily assimilation, rates of leaf and stem mortality and the corresponding redistribution are increased.
- Because of the occurrence of dead plant material mainly at the lower canopy layers, the light interception of dead leaf is neglected for species simulated before. Dead *G. aparine*

plant material is found above the crop canopy and therefore light interception of dead material can not be neglected. The area of dead material is set to 23 % percent of corresponding area of the living material, based on observations made in the field.

Possible effects of severe water stress were neglected in the simulations.

Parameter estimation

The estimation of the values of the parameter set for the weed species *G. aparine* was based on three experiments in greenhouses and climate chambers. The range of environmental conditions in these experiments correspond with the environmental conditions for a *G. aparine* plant in a sugar beet crop under field conditions in the Netherlands. The description of these experiments and the observed dry weight partitioning patterns and leaf area growth in relation to temperature and day length were presented in detail in chapter 6. In these experiments values of the specific leaf area (in ha leaf*kg^{-1} leaf) were 0.0035 at intermediate light conditions, 0.0045 at very low light levels and 0.0018 at relatively very high light levels at low temperatures. The actual maximum CO_2 assimilation rates at light saturation (AMAX) varied between 12.5 and 17.5 kg CO_2*ha^{-1} leaf area*hour^{-1} for relatively low and high nitrogen supply respectively. The lower bound was measured and the higher bound was set according to the measured growth of *G. aparine* in these experiments. This variation in AMAX with the nitrogen availability is justified by the observation that leaf nitrogen content and therewith assimilation capacity increases together with the nitrogen supply. All parameter values for *G. aparine* are set independently from field experiments and are listed in the Appendix.

The parameter set for sugar beet is listed in Spitters *et al.* (1989) and Kropff *et al.* (in prep.). Only the maximum height and the initial leaf area of a sugar beet plant were adjusted for the cultivar Univers used in the field experiments of 1988, 1989 and 1990 (see Appendix). This maximum height and initial leaf area were measured in the experiment of 1990.

Field data for evaluation of the model

Field data for validation of the model were obtained from competition experiments in 1988 and 1989 (chapter 7). In addition in 1990 a similar field experiment was carried out to analyze the growth and competition of *G. aparine* in sugar beet (sowing date 1-5-90) as influenced by nitrogen supply. Weeds were sown at 2.5 cm depth at 2-4-90 and 30-5-90. All field experiments were located on a clay soil in Randwijk in the Netherlands and treated according to normal Dutch farming practices, except that naturally occurring weeds were controlled by hand weeding and water was additionally supplied during periods of weed sowing. Crop and weed densities and relative emergence time in the experiments are presented in Table 8.1. Data were subjected to analysis of variance and the critical level of significance was set to $P<0.05$.

Table 8.1 Densities and relative emergence dates of *Galium aparine* L. and sugar beet density in the field experiments of 1988, 1989 and 1990.

Year	*G. aparine*		Sugar beet
	Relative emergence time (in number of days after crop emergence)	Densities (in plants/m^2)	Density (in plants/m^2)
1988	0	0; 1; 7; 33	15.6
1989	7	0; 1; 7; 20	10.0
1990	-12	0; 3; 30; 77	11.9
1990	32	18	11.9

The 1990 experiment was of split-plot design. Main treatments were blocks (4) and nitrogen supply (110, 140 and 170 kg N/ha or respectively reduced, normal and high supply according to Vereijken & Wijnands, 1990). Subtreatments were weed density and monthly harvest dates (starting on 15 May and finishing on 15 October). An additional subtreatment (not used for the analysis of variance) was a late *G. aparine* sowing date with a final harvest only. On each harvest date, height of sugar beet and *G. aparine* was measured. All *G. aparine* plants growing in the plot were counted and collected and their specific leaf area (cm^2/gram leaf in a sample) and their dry weight without seeds measured. Dry shoot weight without seeds of *G. aparine* was measured and simulated too., because this parameter is closely correlated with the seed production (chapter 7). With this estimated seed production and additional information on seed bank dynamics and mortality, estimates of crop-yield reduction can be extended with statements on weed population dynamics. Fresh weights of shoot and root of all sugar beets were measured. Four sugar beet plants from every plot were used to measure the specific leaf area and the dry matter content. Leaf nitrogen content of sugar beet and *G. aparine* were analyzed at the third harvest date. Sugar content of the sugar beets growing in plots without or with a high weed density were analyzed at the last harvest date. Plots sizes were 0.75*1.5 m^2.

Sensitivity analyses

After evaluation the model was used to analyze the relative importance of weather conditions, crop- and weed emergence times and crop- and weed densities for yield reduction and the weed dry matter production. The total weed dry matter without seeds is presented because this parameter is closely correlated with the seed production (chapter 7). With estimated seed production based on the weed dry weight and additional information on seed bank dynamics and mortality, estimates of crop-yield reduction can be extended with statements on weed population dynamics.

The variation caused by the weather was analyzed by simulating competition based on the daily minimum and maximum temperatures and light quantities measured in Wageningen during 10 years (1981 to 1990).

8.3 Results

Growth of G. aparine under artificial conditions

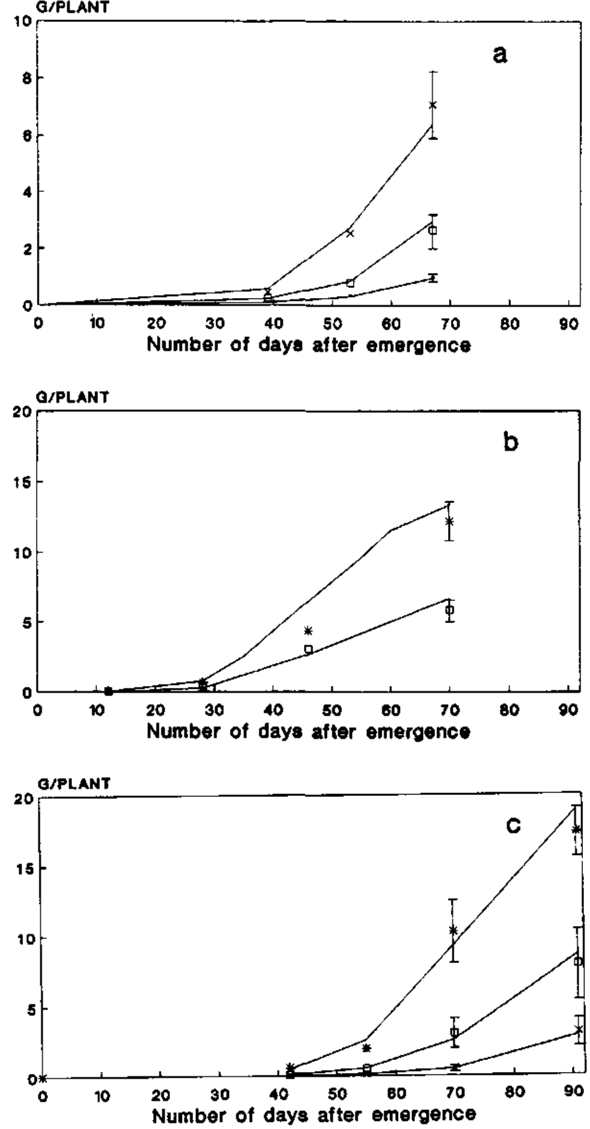
The measured growth of *G. aparine* was significantly influenced by temperature, nutrient supply and light level (Fig. 8.1). Growth at 20 °C (not presented) hardly differed from the growth at 16 °C. The simulation of the growth of *G. aparine* under these artificial conditions in climate chambers and greenhouses corresponded satisfactorily with the observations (Fig. 8.1).

Growth and competition at the field

Observed growth of both sugar beet and *G. aparine* plants in 1990 was significantly influenced by the density of the weed (Fig. 8.2). Individual *G. aparine* plant dry weight was lower at a reduced nitrogen supply level at lower densities of the weed (significant interaction, Table 8.2). At higher weed densities intraspecific competition prevented higher individual weed plant weights at higher nitrogen supply rates. Reduced nitrogen supply significantly decreased the sugar beet yield reduction caused by *G. aparine* (Table 8.3). Nitrogen content of weed leaves was lower after reduced nitrogen supply independently of the density of the weed, but not significantly influenced in the sugar beet leaves (data not presented). Sugar content of the sugar beets was 0.8 % higher at reduced nitrogen supply and not influenced by the presence of weeds.

Sugar beet growth without weeds or in competition with *G. aparine* at the field in 1990 could adequately be simulated (Fig. 8.2). The effects of nitrogen supply on the dry weight of *G. aparine* was simulated satisfactorily (Table 8.2) by varying the actual maximum CO_2 assimilation rate at light saturation for individual leaves. Observed sugar beet yield reduction at reduced nitrogen supply levels were lower than simulated (Table 8.3), although the sugar beet plant dry weight simulations were reasonable good (Fig. 8.2). At the normal nitrogen supply levels however simulation of both the maximum *G. aparine* plant dry weight (Table 8.2) and the sugar beet yield reduction (Table 8.3) were similar to the observations for three independent years and different emergence times and densities of sugar beet and *G. aparine*.

Fig. 8.1 Observed (markers) and simulated growth (fitted lines) of *Galium aparine* L. shoot weight (a,b) or plant weight (c) at different temperatures (a), nutrient levels (b) and light levels (c).



Bars indicate the standard deviation of the observations

a Temperatures in °C: ▪ 8 □ 12 × 16

(high nutrient supply, intermedate light level and relatively very high for 8 °C)

b Nutrient supply: ∗ high □ low

(day/night temperature 24/17 °C, high light level)

c Light level: ∗ high □ medium × low

(day/night temperature 21/15; 19/13 and 17/12 °C for the different light levels respectively, low nutrient supply)

More detailled information on the environmental conditions in chapter 6

Table 8.2 Observed (standard error between brackets) and simulated plant shoot dry weight without seeds (g*plant^{-1}) of *Galium aparine* L. growing in different densities in sugar beet with nitrogen supply according normal farming practices in 1988, 1989 and 1990 and 30 kg*ha^{-1} reduced nitrogen supply in 1990.

Year	Nitrogen supply	Density of *G. aparine*[*]:					
		Low		Medium		High	
		Observed	Simulated	Observed	Simulated	Observed	Simulated
1988	normal	2.4 (0.7)	2.9	2.0 (0.6)	2.7	1.4 (0.3)	2.1
1989	normal	2.1 (0.2)	2.0	1.7 (0.4)	1.9	1.7 (0.4)	1.7
1990	normal	45.8 (5.1)	43.5	10.4 (1.4)	11.3	9.3 (2.1)	5.9
1990[#]	normal			0.06 (0.01)	0.07		
1990	reduced	24.8 (6.5)	29.5	9.5 (1.4)	9.3	9.6 (4.2)	5.1

[*] see Table 8.1

[#] late emerging

Table 8.3 Observed (standard error between brackets) and simulated sugar beet root yield reduction percentage caused by different densities of *Galium aparine* L. in sugar beet with nitrogen supply according to normal farming practices in 1988, 1989 and 1990 and 30 kg*ha^{-1} reduced nitrogen supply in 1990.

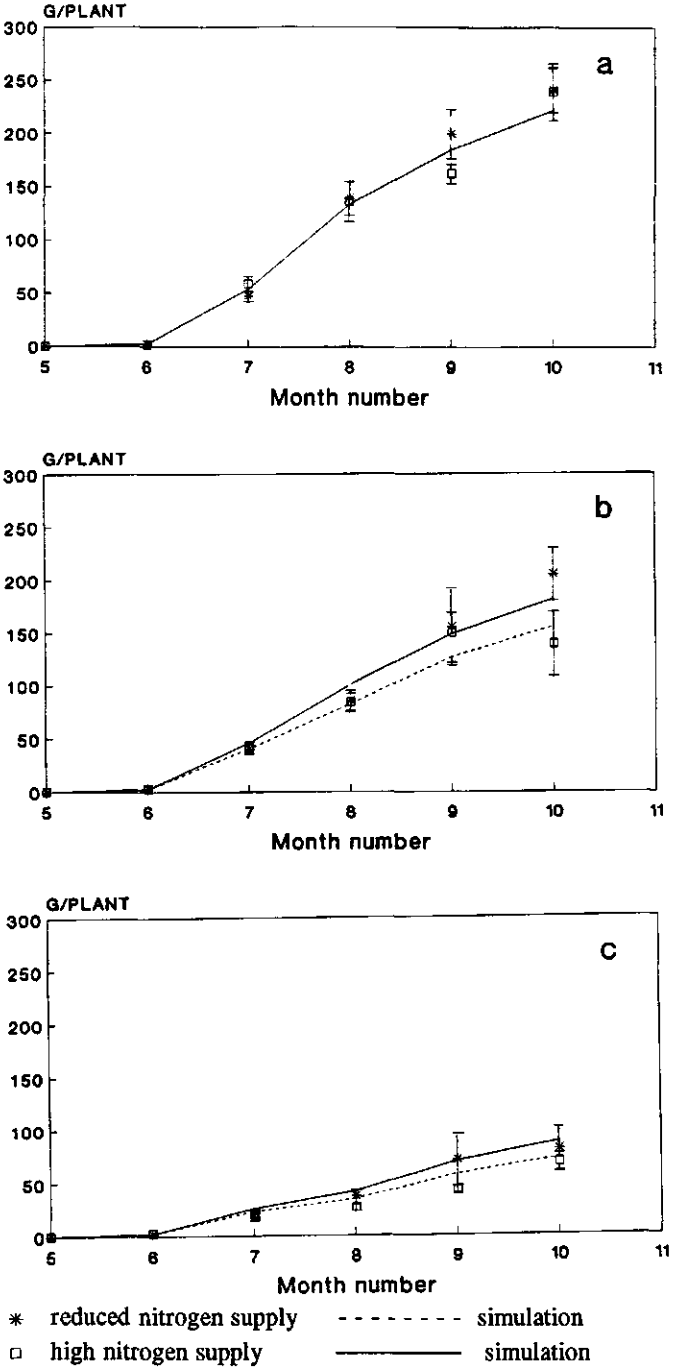
Year	Nitrogen supply	Density of *G. aparine*[*]:					
		Low		Medium		High	
		Observed	Simulated	Observed	Simulated	Observed	Simulated
1988	normal	n.s.	0	n.s.	3	13 (4)	11
1989	normal	n.s.	0	n.s.	2	n.s (8)	5
1990	normal	33 (20)	25	45 (14)	65	70 (8)	79
1990[#]	normal			n.s. (8)	0		
1990	reduced	n.s. (20)	18	27 (15)	59	60 (15)	73

[*] see Table 8.1

[#] late emerging

n.s. yield reduction not significant different from 0

Fig. 8.2 Observed and simulated growth of sugar beet plants competing with 0 (a), 3.3 (b) or 76.9 (c) *Galium aparine* L. plants*m^{-2} at different levels of nitrogen supply at the field.

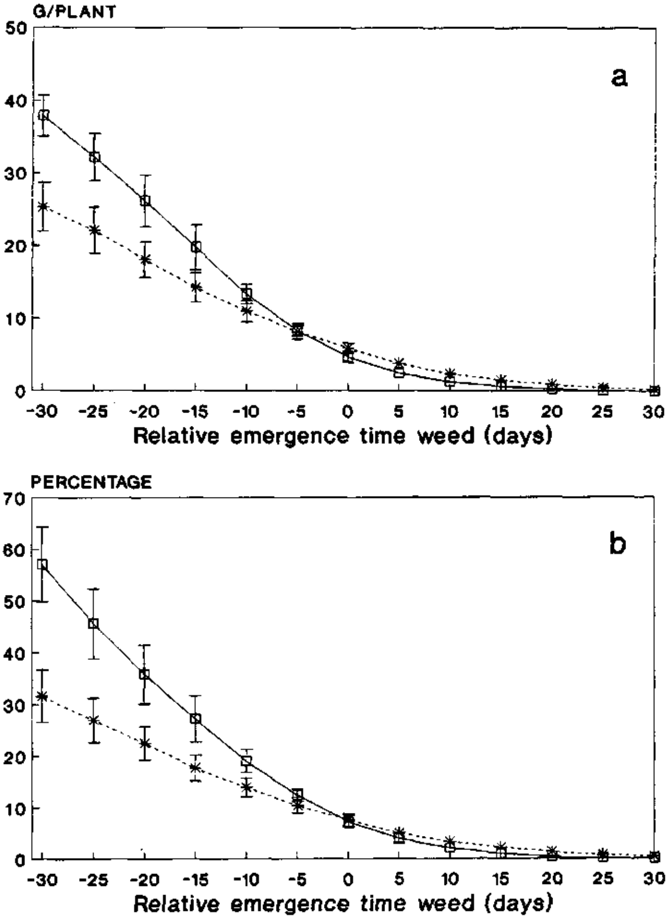


Bars indicate the standard deviation of the observations

Sensitivity analysis

Sensitivity analysis learned that the influence of the relative emergence time (difference in emergence date of the crop and the weed) of *G. aparine* affects dry matter production of both crop and weed plants more than crop- and weed density or weather conditions do (Fig. 8.3 and 8.4).

Fig. 8.3 The influence of emergence date of sugar beet and the relative emergence time of *Galium aparine* L. on weed shoot weight without seeds (a) and percentage sugar beet yield reduction (b) during 1981 to 1990.



Points reflect the mean simulation results for 10 separate years
Bars indicate the weather caused standard deviation
Emergence date sugar beet: ∗ 15 April □ 15 May

Relative emergence times were not chosen randomly. When there is a time interval between seed bed preparation and sowing of the crop, *G. aparine* can start to emerge (in extreme cases even months) before crop emergence. In case of seed bed preparation and sowing at the same date, most *G. aparine* emerge between 3 and 30 days after crop emergence (sugar beet: Smit, 1989; *G. aparine*: chapter 5). In Fig. 8.3 the effect of early *G. aparine* emergence is demonstrated for a density of 10 weed plants*m^{-2} for two crop emergence dates (sowing dates ± 31 March or 8 May; density sugar beets 10 plants*m^{-2}). In Fig. 8.4 early weed emergence was 3 days after crop emergence and late weed emergence was 30 days after the crop emergence on 30 april (sowing date ± 21 april).

The date of crop emergence affects the steepness of the relation between weed dry weight or crop yield reduction and relative emergence time (Fig. 8.3). Early emerging *G. aparine* is considerably more competitive in late sown crops than in early sown crops. Late emerging *G. aparine* is less competitive in late sown crops than in early sown crops.

Certainly the weed density also largely influences the sugar beet yield reduction (Fig. 8.4b). However if the relative emergence time of the weed is later, the effect of the density on the yield reduction is negligible. After late weed emergence, the weed density hardly influences the individual weed plant weight any more (Fig. 8.4a).

Given a lower crop density and relatively early weed emergence, intraspecific competition is affecting the individual *G. aparine* plant weight to a larger extend (Fig. 8.4a). Individual weed plant weights however, are even more affected by the crop density than by the weed density. The density of the crop clearly influences the weed caused yield reductions even at lower levels of yield reduction (Fig. 8.4b).

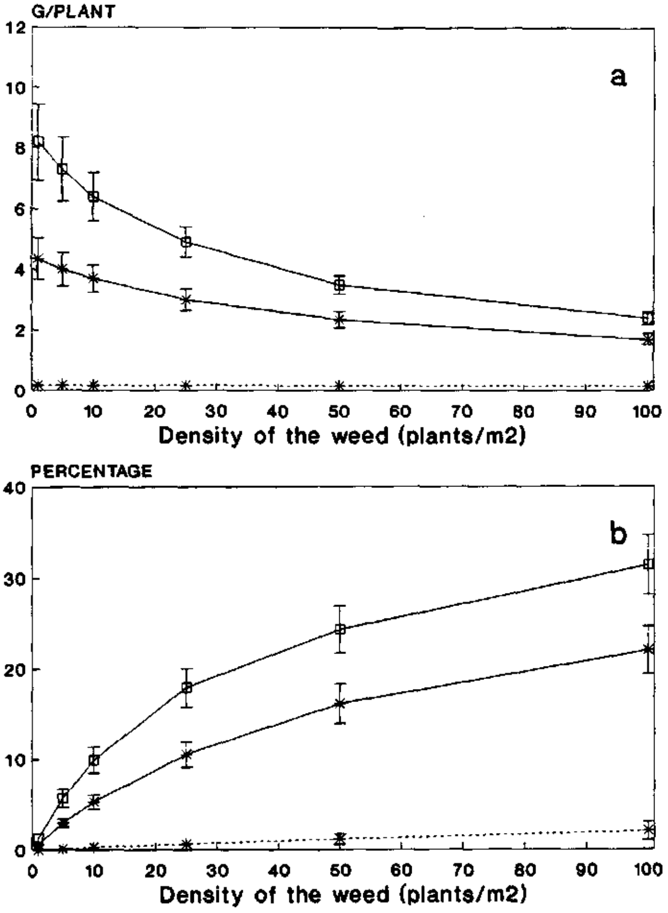
When the growing conditions for an individual *G. aparine* plant are improving (relatively early weed emergence especially in a late sown crop; low *G. aparine* density or low crop density), the influence of weather conditions is more distinct. This can be concluded from the ratio of the weather caused standard deviations relative to the values of means in Fig. 8.3 and 8.4. In general it is noteworthy that weather conditions are surprisingly unimportant for the outcome of competition compared to the effect of relative emergence dates of the weed and the densities of the crop and the weed (Fig. 8.3 and 8.4). At the 5 % yield reduction level, the weather caused standard deviation is around 2 % yield reduction.

8.4 Discussion

Prediction of sugar beet yield reduction

The model performed well in predicting sugar beet yield reduction for quite different situations in three years without severe water limitations and with a normal nitrogen supply. Therefore it made sense to increase our insight of the variability in competition by analysing the outcome of sensitivity analyses. Differences in relative emergence dates and densities proved to be of uttermost importance for the outcome of competition.

Fig. 8.4 The influence of sugar beet and *Galium aparine* L. density for two relative emergence times of the weed (3 and 30 days) on weed shoot weight without seeds (a) and percentage sugar beet yield reduction (b) during 1981 to 1990.



Points reflect the mean simulation results for 10 separate years

Bars indicate the weather caused standard deviation

Density sugar beet in plants*m^{-2}: □ 6 ✱ 10

Relative emergence date of *G. aparine* (in days after crop emergence): —— 3 ---- 30

Simulations of the growth of *G. aparine* at reduced nitrogen supply match also the observed values. But a few additional experiments and some adjustments of the competition model (especially the distribution of dry matter to the sugar beet root) are needed for a reliable quantitative evaluation of the consequences of reduced nitrogen supply on sugar beet yield reduction caused by *G. aparine*. Without severe water stress, the model showed accurate predictions. *G. aparine* is mainly a problem at clay and other soils where important moisture shortage rarely is a problem (Hanf, 1983). An exception are the peaty soils in North of the Netherlands. Because of its sensitivity for severe water stress, it can be expected that the outcome of competition will be influenced negatively for *G. aparine* in case of more severe water stress (Baylis & Watkinson, 1991). The simulations, the presented field experiment and the experiences of others (see introduction) in winter wheat showed a similar effect for the reduction of nitrogen supply. Using the sensitivity analyses for situations with severe moisture shortage and/or reduced nitrogen supply, probably overestimates the yield reduction caused by *G. aparine*. For practical decisions overestimation is less problematic then underestimation.

Nowadays the system of frequently applied low dosages of herbicides on small weeds is promoted for weed control in sugar beet (Wevers, 1991). At the moment the decision for a renewed application has to be taken, one can observe the density of the crop and the weed and estimate the difference in crop emergence date and the emergence date of the just emerged weeds which will be controlled by the application. Hereby the most important factors determining the outcome of competition can be observed before taking a control decision. The sensitivity analyses showed that *G. aparine* emerging after crop emergence are not very competitive and the variation caused by weather conditions is not very big. This confirms the potential for using threshold levels to decide whether or not to control *G. aparine* without the risk of significant sugar beet yield losses.

Prediction of weed population dynamics

Ecophysiological models on crop-weed competition can also predict the dry weight of individual weed shoots without seeds and the variation in this weight caused by variation in weather conditions (PLWGHT in Fig. 8.3a and 8.4a). For *G. aparine* dry shoot weight without seeds can be used to estimate the population increase related to the plants to control. General assumptions on biological features of this species and the already achieved level of control are used for this. The increase factor is calculated with the next formula:

SURSE+(EMSE*SURPL*PLWGHT*SEPFAC)

in which

SURSE:	yearly fraction of seeds surviving,
EMSE:	fraction of seeds responsible for the emergence of these plants,
SURPL:	survival of plants (1-fraction of control achieved of plants since last years seed production and the moment of decision),
PLWGHT:	expected maximum shoot dry weight without seeds of an individual weed plant,
SEPFAC:	factor with which PLWGHT has to be multiplied to estimate the individual plant seed production.

SURSE and EMSE can be estimated using the knowledge on germination and emergence in chapter 5 and the fraction natural mortality of ungerminated *G. aparine* seeds of 0.33 observed by Röttele (1980) and confirmed by own unpublished results. For a normally cultivated arable clay soil in the Netherlands with a weed seed bank homogenously distributed till ploughing depth at 30 cm, SURSE is 0.52 and EMSE is 0.11. SEPFAC can be calculated with the knowledge on the relation between seed production and PLWGHT in chapter 7. For *G. aparine* growing in sugar beet the conversion factor SEPFAC is 198. SURPL should be estimated by the farmer.

Not controlling 10 *G. aparine* plants*m^{-2} emerging 3 days after sugar beet emergence results in ± 5% sugar beet yield reduction but also an *G. aparine* population increase with a factor 81. After already achieved control of 90 % before crop emergence, not controlling 10 plants*m^{-2} emerging 3 days after crop emergence, still results in a population increase with a factor around 8.6. After 90 % control of plants emerging after crop emergence, yield reduction caused by 10 *G. aparine* plants*m^{-2} emerging 30 days after crop emergence and escaping control can be neglected, and the population increase factor is 0.91. So this results in 9% reduction of the population with a weather dependent variation of 13% increase (yearly increase factor 1.13) to 33% reduction (yearly increase factor 0.67) (onesided tailprobability of 0.05).

The decision to tolerate a certain level of *G. aparine* with a certain increase factor resulting from it, depends on the crop rotation and the possibilities to control *G. aparine* in the other crops. It appears that incorperation of knowledge on the population dynamics of *G. aparine* results in a requirement for more control then the level of control purely necessary to avoid significant yield losses in the short term. However, there is a ground for saving the last treatment(s) in a low dosage system without yield losses and *G. aparine* population increases. The presented sensitivity analyses on yield reduction and weed dry weight provide, together with other biological information on *G. aparine*, a basis to take rational decisions on control of this weed in sugar beets.

8.5 Conclusions

The growth and competition between *G. aparine* and sugar beet at arable fields is simulated satisfactorily.

Biomass production of both sugar beet and *G. aparine* are mainly determined by emergence times and the densities of crop and weed. The weather caused variation is small compared to these factors. After reduced nitrogen supply *G. aparine* is less competitive.

The simulations provide a sound basis including uncertainty caused by variation in weather conditions for control decisions taking into account both sugar beet yield reduction and population dynamics of *G. aparine*.

Appendix

The next parameter estimations were used for *G. aparine* (parameters not mentioned had the same value as for sugar beet in Spitters *et al.* (1989) and Kropff *et al.* (in prep.):

AMAXM=15.0; AMAXS=0.; AMAXF=30.

Actual maximum CO_2-assimilation rates at light saturation for individual leaves, stems and seeds in kg CO_2*ha^{-1} area leaf (a.o.)*$hour^{-1}$.

At reduced nitrogen supply rates these values are 16.8 % lower and at high nitrogen supply levels these values are 16.8 % higher.

TMD = 5.3; TMDLV = 0.9

Base temperature for plant development and for leaf area development in °C.

RGRL = 0.01208

Relative growth rate of leaf area in $(°C*day)^{-1}$.

FAGTB = 0.,0.8, 3500.,0.8, 5000.,1., 30000.,0.6, 50000.,0.6

FRTTB = 0.,0.2, 3500.,0.2, 5000.,0., 30000.,0.4, 50000.,0.4

Table of the fraction of total dry matter increase allocated to the shoot or the root versus the developmentsum.

FLVTB = 0.,0.9, 17300.,0.45, 20000.,0., 50000.,0.

FSTTB = 0.,0.1, 17300.,0.55, 20000.,0., 50000.,0.

FSOATB = 0.,0., 17300.,0., 20000.,1., 50000.,1.

Table of the fraction of dry matter increase of the shoot allocated to the leaves or the stems or the seeds versus the developmentsum.

MSCF = 0.0002475

Minimal seed call for assimilates factor in $(°C*hour\ daylight)^{-1}$.

Calculated by multipliying 110 (number of ends the gram vegetative above ground plant weight) * 1 (min. number of seeds per end) * 0.009 (indiv. seed weight in gram) / 4000 (heatunits in °C*hour daylight necessary for seed fill).

TSSF = 18500.

Sum heatunits before start seedfill in °C*hour daylight.

MXERED = 0.10

Maximum amount of extra redistribution for seed fill the day.

DRL=-0.0001

Death rate of leaves and stems in $(°C*hour\ daylight)^{-1}$.

TSLAM= 24500.

Developmentsum at which death of leaves and stems starts independently of seed fill in °C*hour daylight.

REDLM = 0.18; REDST = 0.18

Redistribution coefficient for yellowing leaves and stems.

RDRSOT = 0.,0., 18500., 0., 18501., 0.00025, 50000., 0.00025

Table of the relative rate of loss of seeds in day^{-1} versus the developmentsum.

SLATB = 0.,0.002, 1550., 0.0035, 500000.,0.0035

Table of the specific leaf area in ha leaf*kg^{-1} leaf versus the developmentsum.

In greenhouses or climate chamber it was measured that for very low light levels the specific leaf area can become 0.0045 and for relatively very high light levels at low temperatures the specific leaf area didnot not exceed 0.0018. Adjustments were not necessary for *G. aparine* growing in a sugar beet crop at the field.

SSA=0.0011; SFA=0.0002

Specific stem or seed area in ha stem or seed*kg^{-1} stem or leaf.

HMAX = 140.; HS = 0.0002; HB = 45.

Potential plant height in cm; Logistic height growth parameters in (°C*hour daylight)$^{-1}$ and without dimension.

These parameters should be adjusted for *G. aparine* growing in less open crops as sugar beet, because *G. aparine* can become longer and heigth growth is faster in for example oilseed rape and winter wheat (unpublished).

TSSTHI = 17300.

Developmentsum at which height growth stops in °C hour*daylight.

SSLMAX = 655.

Maximum length per weight stem cm*gram^{-1}.

LA0 = 1.65; HGHTI=1.0

Initial leaf area in cm^2 and heigth in cm.

WLVGI=0.0825; WSTGI=0.0092; WRTI=0.0229

Initial dry weight of leaves or stems or roots in kg dry matter*ha^{-1} for a density of 1 plant*m^{-2}.

Changed parameters for sugarbeet (other parameters in Spitters *et al.* (1989) and Kropff *et al.* (in prep.):

HMAX=54; HB=12; LAO=5.0

Chapter 9

General discussion

9.1 Modelling population dynamics

Weed science based on an understanding of population biology helps to improve weed management (Mortimer, 1983; Radosevich & Holt, 1984; Norris, 1992). Modelling the population dynamics of weed species is an adequate way of integrating existing knowledge and of revealing gaps in knowledge. Models can be used to predict the infestations that will result from the decision to follow a particular control strategy and also to evaluate different management strategies. In chapter 2 several methods for modelling the population dynamics of plant species were reviewed. It was demonstrated that the model required depends on the objectives. An extended demographic model which is explanatory at population level and descriptive at plant level is sufficient for comparing the effects of different cropping practices or control strategies on the population dynamics of a weed. Such a model presented in this thesis (chapter 2) describes flows of individuals between several plant stages (ungerminated and germinated seeds at different depths in the soil or on the soil surface, seedlings, plants with one, 2 to 4 and more than 4 whorls of leaves) from day to day, based on data on *Galium aparine* L. reported in literature. This first model ignored intraspecific competition in *G. aparine*, because high densities of *G. aparine* rarely occur in practice. Several attempts to measure reliable seed densities in soils with a severe *G. aparine* infestation failed, because less than 1 seed per kg of sampled soil was found. Furthermore, studies done for this thesis (chapter 7 and 8) demonstrate that the effects of intraspecific competition on the growth and seed production of this species are small compared with the effects of emergence time and type of surrounding crop. The first model developed accounts for the effects of these latter factors.

The results of feasibility studies with this model on different management strategies corresponded with various field observations derived from non-related experiments done by other researchers. The simulated differences in population increase after shallow cultivation or after ploughing reported in chapter 2 were comparable with those observed by Wilson and Froud-Williams (1988). With the knowledge available it was not possible to correctly predict the absolute population increases resulting from a management strategy in experiments reported by other researchers. The main causes were:

- The observations on population dynamics of *G. aparine* published by Catizone & Viggiani (1990) and Zwerger *et al.* (1990) lacked exact data on, for example, the timing of soil tillage operations. The observations of Catizone & Viggiani (1990) were made in southern Italy, where the climate is not comparable with the Dutch climate. The sampling of soil seed densities was not precise enough in the experiment of Kaiser (1989). Observations by Zwerger *et al.* (1990), Wilson & Froud-Williams (1988), Mortimer *et al.* (1990) and some of the observations of Wilson & Wright (1991) were done at unrealistically high weed densities.
- The estimated parameter values used in the model constructed were based on the information found in the literature. However, the literature data showed a great variation in parameter values. The uncertainty about the parameter values endangered the reliability of predictions of the population dynamics. Germination and emergence based on the data presented by Röttele (1980) resulted in a simulated yearly population increase rate of 6 for *G. aparine* in winter wheat. When the germination and emergence was based on the observations of Aarts (1986), this population increase rate was 38. Observed differences in emergence patterns between years also resulted in important differences in population growth rates (chapter 2). The growth rates and seed production of *G. aparine* plants with different emergence dates relative to the crop emergence date in different crops used in the model, had usually been measured in one year only, in one location. But it is common knowledge that growth rates and the outcome of the competition between crop and weed in terms of weed seed production are also influenced by weather conditions, soil type, nitrogen supply, crop density and emergence time and weed density (Spitters, 1984; Wilson & Wright, 1987 and 1992; Kropff, 1988; Franz *et al.*, 1990 and Lotz *et al.*, 1991). The priority was to obtain more details on parameter values and to validate the individual parameters, because until this was done the absolute population growth rate could not predicted reliably, nor could these predictions be validated.

9.2 Obtaining more details on parameters

Germination and emergence

The number of *G. aparine* seeds germinating depended on dormancy patterns, microclimate and soil compaction (chapter 3). Primary dormancy was not observed in fresh seeds that had developed late in the season in stands of sugar beet or potato. However, seeds that matured early in the season in stands of winter wheat or oilseed rape could not germinate immediately. After primary dormancy had been released during the first autumn, secondary dormancy patterns enabled seeds to germinate both in autumn and in spring. No distinct arable ecotypes which could only germinate in spring or in autumn (as known for some weed species), were found. Whether the seeds actually germinate depends on the soil compaction and the absence of light for several hours a day, not on fluctuations in temperature. In this aspect *G. aparine* differs from many weed species that are stimulated to germinate in the topsoil because they react positively to temperature fluctuations and/or the presence of light with adequate quality. The timing of soil tillage regulates whether most *G. aparine* seeds germinate in autumn or in spring.

It was demonstrated (chapter 4) that soil compaction and depth of the seeds in the soil determined the mortality of the germinated seeds during emergence. Differences in soil compaction may explain why there is such a discrepancy between Röttele (1980) and Aarts (1986) regarding mortality during emergence. The high percentage mortality of germinated seeds at different depths used for most simulations in chapter 2 were based on Röttele's research. For the simulations in chapter 8 and this chapter germination and emergence parameters were adjusted to the soil resistances found in the Netherlands at various depths after tillage.

The mean rate of germination and the variation around the mean were both influenced by temperature (chapter 3). The rate of emergence of germinated seeds at different depths in the soil was influenced by temperature and soil structure (chapter 4). A noticeable wave in emergence results from the different depths at which seeds germinate, even if seeds germinate at one date.

A simulation model for germination and field emergence of *G. aparine* in relation to weather and soil conditions was constructed and validated with three independent sets of field observations (chapter 5). The varying temperature requirements for germination during the year (dormancy patterns) are incorporated in the model as well as the influence of the temperature and the soil structure on the actual induction of germination and on the rate of germination and emergence. The effect of differences in dormancy patterns between seed collections and years was neglected in this model. Sensitivity analyses showed that these simplifications are justified for *G. aparine*. A great deal of research is devoted to increasing insight in dormancy patterns of weeds (Karssen, 1982; Baskin & Baskin, 1987; Bouwmeester, 1990). The effect of environmental factors on germination and emergence rates is treated superficially in their papers. However for understanding patterns of weed emergence in the field this aspect proved to be of great importance.

Development, growth and seed production

Additional research enabled the construction of an empirical description of the development of *G. aparine* in relation to day length and temperature (chapter 6). Flowering date under field conditions could be correctly predicted for cohorts of plants emerging at different dates in the Netherlands and in England.

Observations in field experiments were used to investigate the feasibility of predicting the seed production of *G. aparine* from its mature biomass (chapter 7).

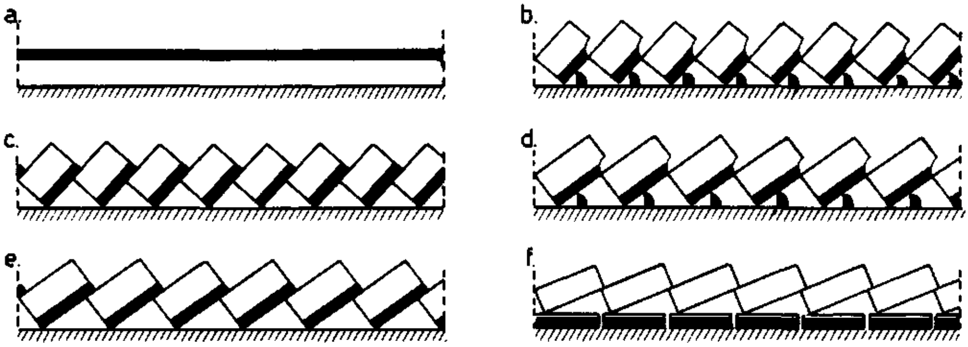
Compared to some other weed species (Thompson *et al.*, 1991) the reproductive effort of *G. aparine* is great, but because the seed weight is variable, the reproductive effort is not a useful parameter for predicting the number of seeds. The large proportion of dry weight invested in seeds, coupled with the easy drop of seeds mean that the relationships presented by Röttele (1980) between number of seeds and shoot weight with seeds for *G. aparine* are also unpractical. In our field experiments, a linear relationship was found between the number of flowers or seed-producing tips and the mature shoot dry weight without seeds. This relationship was not affected by the companion crop species, the year, the emergence time or the density of *G. aparine*.

Dry mature shoot weight of *G. aparine* without seeds was markedly influenced by crop species and the time of emergence of weed and crop (chapter 7). To analyze variability in competition between crop and weed caused, for example, by weather conditions, sensitivity analyses were done with an ecophysiological model of crop-weed competition (chapter 8). This mechanistic model explanatory operating at plant level instead of at population level as in the original model, was introduced, adapted and validated for competition between *G. aparine* and sugar beet in chapter 8. The model calculates the growth of the weed and the crop as a function of the amount of light intercepted and the ambient temperature. It enables crop yield reduction and weed growth to be predicted. The relationship between seed production and vegetative weed biomass and the information on germination and emergence and mortality was used to predict the weed population increase or decrease also with this model. Sensitivity analyses revealed that both yield reduction of sugar beet and biomass production of *G. aparine* are mainly determined by time of emergence and the density of both the crop and weed. Furthermore, the growth and competitiveness of *G. aparine* decrease after less nitrogen is supplied. The variation caused by the weather in a sugar beet crop proved to be small compared with the factors mentioned earlier. The results of the sensitivity analyses are used to adjust the descriptive relation between relative emergence time of the weed and its seed production in the original population dynamics model for differences in sugar beet sowing time and density. The results in chapter 8 proved that adjustments that can be made for variability in weather conditions and intraspecific competition are less essential for predicting population increases of *G. aparine* in sugar beet in practical situations.

9.3 Further research needs

Parameter values for germination, emergence, seed mortality, development, growth and seed production and their environmentally determined variance were determined in this research. Parameter estimation was validated using independent sets of data. Environmental dependent variability in mortality of *G. aparine* in several plant stages was not determined. The degree of mortality is influenced by control method, herbicide choice and dosage, weed plant stage, soil type, weather conditions and the surrounding crop (cultivar) and its development (Hammerton, 1967; Koch, 1970; Kudsk, 1989). Few exact data are available on many control methods and collecting information on this aspect is very time-consuming. In the 1980s a group of Danish researchers started to investigate the level of control of different weed species in several plant stages and for various weather conditions. They proved that this information could be used to adjust the herbicide dose to take account of different situations, and that herbicide use in spring wheat could thereby be reduced without a drop in the level of weed control (Baandrup & Ballegaard, 1989). Literature data on the effects of different control methods on mortality of *G. aparine* (Fisher, 1965; Arndt & Kötter, 1968; Koch, 1970; Schmidt, 1972; Berendt & Menck, 1974; Sieberhein *et al.*, 1977; Urban, 1980; Aarts & Dekkers, 1985; Aarts, 1986; Snel *et al.*, 1990) were used to set control levels for several plant stages and even to estimate dry weight reduction caused by harrowing (Gerowitt, 1992). Additional research was not carried out because the most important question for this thesis was the degree of control that is required anyhow for different cropping situations.

Fig. 9.1 The effect of type of plough on the vertical redistribution of soil by ploughing: a) before plouging b) plough with skimcoulter and working width 30 cm c) plough without skimcoulter and working width 30 cm d) plough with skimcoulter and working width 40-45 cm e) plough without skim-coulter and working width 40-45 cm f) two layers plough (Håkansson, 1984).



The parameter values in the model as introduced in chapter 2, were adapted in the light of the information obtained during subsequent research and maximum seed production of *G. aparine* growing in winter wheat was adapted in accordance with the observations of Kaiser (1989). Further validation of the model with the adjusted parameter values is time consuming. To overcome the problems with sampling soil seed densities, the densities of plants and seeds produced in the field need to be counted frequently. The provisional results of such a validation are promising (Wallinga *et al.*, in prep.), except that more plants than expected emerged in the year after no control of *G. aparine*. This is probably attributable to the calculation in the population dynamical model of changes in the vertical distribution of the seeds brought about by ploughing. Observations on the changes in vertical distributions of weed seeds caused by ploughing are done by Röttele (1980) and Cousens & Moss (1990). The data of Röttele (1980) collected with a plough with skimcoulter and a working width of probably 40-45 cm (not mentioned in this publication) were used for the calculations with the population dynamical model. Cousens & Moss (1990) did not state the type of plough and working width they used in their experiment, but their seeds are less buried. It is known that different type of ploughs turn the soil in different ways (Fig. 9.1; Håkansson, 1984). If the model is refined to take account of this and the type of plough is known, the reliability of the predictions of numbers of emerging weeds will improve and it will be possible to compare the effect of different types of ploughs. Observations of Wilson & Wright (1991) on population decrease or increase after control or after one year of no control of *G. aparine* L. in winter wheat after ploughing were also very similar to the predictions with the population dynamical model. In their experiment Wilson & Wright (1991) observed a yearly increase factor of 34 after no control, compared with the 38 predicted. The observed decreases in two consecutive years with 100 % control were 71 and 46 %. Decreases of 75 % and 32 % were predicted.

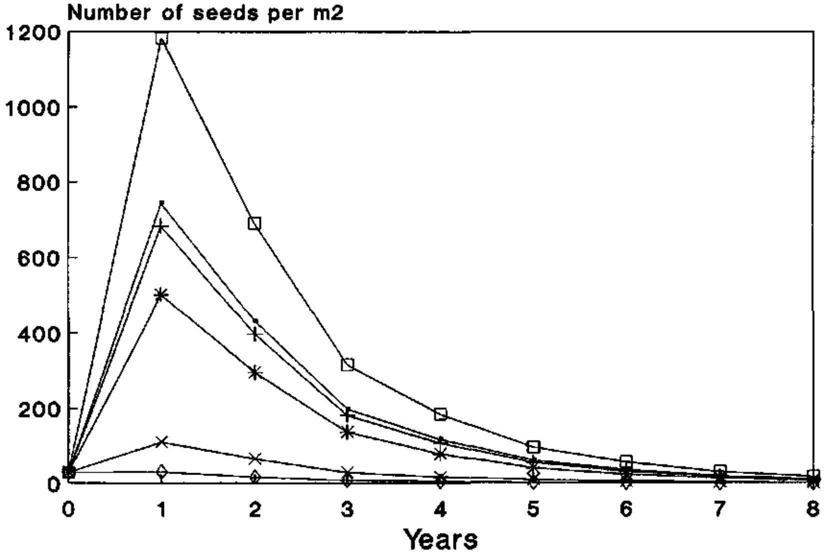
The ecophysiological model for growth and competitiveness of *G. aparine* needs to be adjusted and validated for crops other than sugar beet. The growth of *G. aparine* in other crops has to be adjusted in terms of the description of the height growth. The height growth of *G. aparine* is influenced because the surrounding crop species determines the light quality and hence the internode elongation (Bain & Attridge, 1988) and *G. aparine* leans on the crop. No other parameters of *G. aparine* in the ecophysiological model are expected to be influenced by the surrounding crop. These ecophysiological models not only provide a sound basis for the prediction of *G. aparine* seed production but also for predicting crop yield reduction. Not only interspecific competition is included but also intraspecific competition in both the crop (sowing densities) and the weed (density dependence in the case of high weed densities) (chapter 8). Research is proceeding on the validation of the ecophysiological model for competition between *G. aparine* and winter wheat (Wallinga, pers. comm.). The information in this thesis on germination, emergence, growth and seed production provides a sound basis for extending the ecophysiological models to models of the population dynamics of *G. aparine*, including variation caused by climate, soil conditions and differences in cultural measures such as sowing date and sowing density.

9.4 Practical application

Biology and weed management

The model of germination and field emergence of *G. aparine* (chapter 5) and the information obtained on the development of *G. aparine* (chapter 6) can be used to time control measures optimally.

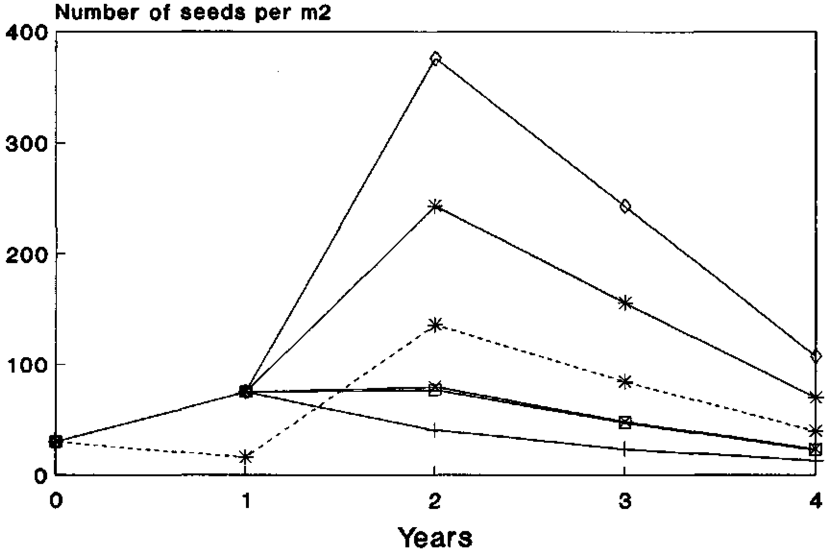
Fig. 9.2 The influence of cropping practice and control strategy during the first year and complete control in further years on the population dynamics of *Galium aparine* in a monoculture of winter wheat.



□ No control at after sowing short strawed winter wheat on 15 October
• As □ but sowing on 15 November
+ As □ but using a long straw cultivar
✱ As □ but early crop harvest (early August)
× As □ but control of *G. aparine* by harrowing
◊ Combination of above measures

Constructing an adequate model of the population dynamics enabled us to compare different integrated control strategies in terms of population dynamics, such as differences in population growth rate (Fig. 9.2 and 9.3). Fig. 9.2 presents simulations of different control strategies in a monoculture of winter wheat. When *G. aparine* is not controlled at all in one year in winter wheat grown according to normal Dutch farming practice, six years of 100 % control are needed to nullify the increase. *G. aparine* can be totally controlled by applying fluroxypyr (Snel *et al.*, 1990). By harrowing in winter wheat (effect as observed during 3 years by Gerowitt, 1992) the period required to equal the increase is 2 years. By also adapting the cropping practice, population increase in winter wheat can be prevented without the use of herbicides. The simulations depicted in Fig. 9.3 demonstrate the feasibility of decreasing control in a crop rotation of winter wheat, sugar beet, spring barley and potato. Harrowing late-sown, short-strawed and late harvested winter wheat is not enough to prevent a population increase that can be nullified by one year of complete control in sugar beet. Further adaptation of cropping practice (long straw cultivar) or alternate years of winter wheat harrowing and years of 100 % control in winter wheat are needed to prevent population increase in a rotation of winter wheat, sugar beet, winter wheat and potato with 100 % control in sugar beet and potato.

Fig. 9.3 The influence of cropping practice and control strategy on the population dynamics of *Galium aparine* in a rotation of winter wheat, sugar beet, spring barley and potato.



----- 100 % control in winter wheat, spring barley and potato

—— late sowing and harrowing in winter wheat, harrowing in spring barley and 100 % control in potato

In sugar beet:

+ 100 % control

∗ 10 % escape control

□ 100 % control until 2 weeks after sugar beet emergence, followed by no control

◇ 100 % control until 1 week after sugar beet emergence, followed by no control

× As ◇ but false seedbed preparation, sowing on 30 april instead of on 15 april and optimized nitrogen application

If spring barley is cultivated during the third year, as in Fig. 9.3, harrowing the cereals and 100 % control in sugar beet and potato even result in a population decrease during the rotation. Problems arise if 10 % of the *G. aparine* (including plants that have emerged early) in sugar beet escapes control. In this case 100 % control in the other three crops is not enough to prevent population increase. Failure to control early emerging *G. aparine* in sugar beet can occur in practice if the timing of herbicide applications of the low dosage system (Wevers, 1991) is not optimal. Complete control of all *G. aparine* plants up to 2 weeks after sugar beet emergence is at least necessary to prevent a population increase in the integrated rotation in Fig. 9.3. This period can be reduced to 1 week in the case of false seedbed preparation (stimulating the seeds to germinate before crop sowing by early tillage and controlling emerged weeds by preparing a seedbed for the crop), sowing on 30 April rather than on 15 April and optimized nitrogen usage. These simulation results also help explain why *G. aparine* became a problem weed species and the insights can be used to formulate more precise hypotheses on which future research can be based.

Rationalization of control decisions

Post-emergence control has the advantage that it enables the actual situation in the field to be analyzed before a decision on control has to be taken. Simple field observations, such as relative leaf area have been proposed as essential for estimating crop yield reduction (Kropff, 1988). However, an observed relative leaf area is not suitable as an input for predicting population dynamics. Relative leaf area can probably roughly be correlated with seed production for *G. aparine*, provided that the observation is done after all plants have emerged and the date of observation is also taken into account (relations between relative leaf area and crop yield reduction in sugar beet in 1990 varied: a yield reduction of 45 % was correlated with an observed relative leaf area of 55 % in May but also with an observed relative leaf area of 20 % in October). In addition, late-emerging *G. aparine* plants will not increase the relative leaf area of this species, but these late-emerging plants still produce seeds. Another important drawback is that without additional data a simple observation such as relative leaf area gives no information on the initial density of the population. Observations of the density and the emergence date of the crop and the density and the emergence date of *G. aparine* are needed, in order to be able to predict both crop yield reduction and weed population increase or decrease caused by *G. aparine* plants that have not been controlled. The simulation studies reported in chapter 8 provide information on the small variation in crop yield reduction and weed population increases caused by differences in weather conditions, which the farmer can use if he opts for control based on actual observations in sugar beet. However, a farmer should make up his own mind on whether weed increase in a crop is acceptable, because he chooses the rotation, adapts his cropping practice, and knows the constraints of his situation. The information in this thesis provides insight on population dynamics which farmers can use to improve their control decisions. The often used adage "One years's seeding means seven years' weeding" is not adequate as a general premise on which to base farmer control decisions. Accepting that some of the *G. aparine* plants produce seeds does not result in increases in the *G. aparine* population. Only partly preventing *G. aparine* seed production by harrowing in a monoculture of winter wheat with modified cropping practice results in an almost stable *G. aparine* density (Fig. 9.2). Totally eradicating *G.*

aparine from sugar beet is not necessary either. Eradicating 90 % early emerging *G. aparine* plants in a sugar beet crop with a high nitrogen supply is enough to prevent population increases. In a rotation of winter wheat, sugar beet, spring barley and potato, with control in the cereals by harrowing and 100 % control in potato, complete control of all *G. aparine* plants that emerge up to 2 weeks after crop emergence is sufficient (Fig. 9.3). The feasibility of obviating late herbicide applications increases if as many *G. aparine* plants as possible are destroyed before crop sowing (false seedbed preparation), if the crop stand is dense and nitrogen supply is optimized (chapter 8 and Fig. 9.3). In more competitive crops in which *G. aparine* plants produce fewer seeds, as for example spring barley (chapters 2 and 7), it becomes more feasible to reduce control without risks of population increases.

This thesis has confirmed that scientific studies aiming to quantify the minimum degree of weed control should not only consider crop yield reduction caused by weeds but should also take account of weed population dynamics. This study also showed that to reduce herbicide use to control a species such as *G. aparine*, it is probably more effective to increase mechanical control and to optimize choices, application times and herbicide doses, rather than to reduce the levels of control.

Summary

Population dynamics and population control of *Galium aparine* L.

Introduction and objective (Chapter 1)

Increasing public concern about environmental pollution has resulted in government policy to reduce herbicide use in the Netherlands by 30% by 1995, 40% by 2000 and 55% by 2010 (relative to mean annual use during 1984 - 1988). To achieve this reduction a sound knowledge of the biology of weeds is needed to improve weed control with minimum use of herbicides. *Galium aparine* L. (cleavers) is one of the four most important weeds in the Netherlands, because in many situations this species determines which control methods are needed and, furthermore, can cause problems in many different crops. For these reasons this species was chosen as an example in a study which integrated information on its population biology in order to evaluate the effects of different control strategies in a single crop and in relation to crop rotation.

Model of the population dynamics (Chapter 2)

Data from the literature were used to develop a model which calculates, per day, the number of individuals at certain stages of the species' life cycle. This model could estimate the effect of several methods of control on the trends in numbers of *G. aparine* within a single year or over a period of years. Although the model enabled some strategies to be compared, more information on the parameter values which formed the basis of the model was needed to predict the absolute increase or decrease of the population. Supplementary research had to be done to obtain a more reliable estimate of the parameters for different situations, because too little was known about environmentally-induced variation in parameter values and yet it is this variation that largely determines the simulated trends in numbers.

Germination (Chapter 3)

The occurrence of primary dormancy and the dormancy rhythms of *G. aparine* were researched on seeds that had been collected at different locations and at different times.

Various laboratory experiments were done to ascertain the influence of temperature, light, nitrate, moisture and soil compaction on the actual germination process.

Primary dormancy was especially common in unripe seeds, or seeds that had ripened early in the season. Because primary dormancy disappeared after 1 to 3 months, it can be said to be of secondary importance to emergence patterns on ploughed soils where the fresh seeds are buried first.

Dormancy rhythms emerged in the graphs of temperature conducive to germination. In the Netherlands, the weather in spring and autumn is favourable for germination. No exclusively spring- or autumn-germinating ecotypes were found.

Light was found to inhibit the germination of *G. aparine* on the soil surface. Temperature and soil compaction determined the degree of germination in the soil in the field. The duration of the germination was closely related to the temperature. (75 degree-days above 2.5 °C).

Emergence (Chapter 4)

The mortality of germinated seeds at different depths in the soil and the speed of emergence in relation to temperature, moisture and soil compaction were researched. Seed mortality (between 0 and 100 %) could be calculated from data on the depth of the seeds in the soil and the compaction of the soil. The duration of emergence was especially influenced by the depth of the seeds and temperature (60 to 300 degree-days above 2.5 °C)

Model of germination and emergence (Chapter 5)

The quantitative data on germination and emergence were integrated in a dynamic model which simulates the germination and emergence of *G. aparine* in relation to weather and soil conditions. Simulations were compared with observations obtained from three field experiments. This model could largely predict emergence patterns and their environment-related fluctuations. The factors influencing emergence were found to be, in order of importance, the time of tillage, the compaction of soil after this tillage, the distribution of seeds in the soil and the actual temperatures.

Development (Chapter 6)

Various experiments were done in greenhouses or climate cells to study the development of *G. aparine* plants in relation to soil and weather conditions. The moisture regime and the amount of light did not prove to be important for the period needed by *G. aparine* plants to flower. Though fertilization had a minor influence, day length and temperature proved to be most important in determining time of flowering. An empirical scale was developed, relating the cumulative temperature and day length to the development of the plants and the changes in the distribution patterns of newly produced dry matter. It enabled the flowering date of *G. aparine* plants with different emergence dates in the Netherlands and England to be correctly predicted.

Seed production (Chapter 7)

The seed production of *G. aparine* under field conditions in 1988 and 1989 was determined for plants with different emergence dates and densities in stands of potato, oilseed rape, winter wheat, spring barley and sugar beet. The shoot weight of *G. aparine* was primarily influenced by the crop in which it grew and the date of emergence in relation to the date of crop emergence. The effects of intraspecific density (< 30 plants/m^2 after the emergence of the crop) and the influence of weather and the crop stand were less important.

In the fully-grown plant a linear relationship was found between the number of seed-producing tips and the shoot weight without seeds. This relationship was not influenced by the crop in which the plants grew, the date of emergence, the density, or the year. A maximum of two seeds can develop on every seed-producing tip. The extent to which this occurred varied between 1.0 in plants growing in spring barley to 1.8 in plants growing in sugar beet. The seeds produced were very viable. Their seed weight was variable. Seed drop of *G. aparine* during the harvest of the crop increases with early emergence and late harvest. Seeds that have not been shed are harvested together with the crop in case a combine is used and are removed from the field.

Model of growth, competition and population increase (Chapter 8)

The influence of fertilization, amount of light and temperature on the growth of *G. aparine* were determined in three experiments in greenhouses or climate cells. These data and the data collected for the development scale (Chapter 6) were used to set the parameters for a model of the competition between *G. aparine* and sugar beet, based on ecophysiological principles. The model was tested by comparing the results of simulations with observations obtained from competition experiments involving *G. aparine* and sugar beet in the field done in 1988, 1989 and 1990. Both the competition-induced losses in sugar beet yield and the shoot weight of *G. aparine* without seeds could be predicted correctly by this model. The reduction in the shoot weight of *G. aparine* resulting from a lower nitrogen dose in sugar beet also corresponded with the observations in the field.

The model can be used to predict the variation caused by weather conditions in the growth of *G. aparine* under field conditions. However, the emergence date in relation to the crop, the sowing date and the crop density proved to be more decisive for the mature shoot weight than the weather. If *G. aparine* emerges three days after a good emergence of the sugar beet, it suffers little intraspecific competition.

The relationships found between shoot weight and seed production (Chapter 7) and the information obtained on germination and emergence (Chapters 3, 4 and 5) were used to complement predictions on the reduction in crop yield due to competition with statements on the expected increase or decrease of the *G. aparine* population. To make these predictions it is necessary to record the density and the time of emergence of *G. aparine* and sugar beet. Furthermore, an estimate is needed of the percentage of control of *G. aparine* during the season achieved by earlier measures. The predictions on the expected yield of sugar beet and the population increase of non-controlled *G. aparine* are only slightly influenced by variations in weather conditions.

Discussion (Chapter 9)

Two models were developed in order to determine the trend in numbers of *G. aparine* in relation to different management strategies. The first model with the parameters adapted on the basis of the research, is explanatory at the level of the population, and descriptive at the level of the plant (Chapter 2). The second model is explanatory at the level of the plant and descriptive with regard to the underlying physiological processes (Chapter 8). Each approach has its pros and cons and repercussions for future research. Given our present state of knowledge, the first model is the most suitable for comparing total control strategies in relation to crop rotations. The second is more suitable for rationalizing weed control strategies by making use of the actual field situation and of the crop yield depressions and increase in the weed population to expect if no control were practised. Illustrations of both applications are given.

Simulation results demonstrated that it is unnecessary to remove all *G. aparine* from crops to prevent its population from increasing. Population increase of *G. aparine* in an monoculture of winter wheat can be prevented by harrowing (only partly control) and an adapted cropping practice. In a rotation of winter wheat, sugar beet, spring barley and potato partly controlling *G. aparine* in the first three crops, combined with 100 % control in potato seems acceptable. In this situation herbicide usage is reduced by harrowing in the cereals and not controlling late emerging *G. aparine* in sugar beet. Controlling an appreciable proportion of the weed seedlings before crop emergence (by preparing a false seedbed to stimulate weed germination and control by crop sowing), ensuring that the crop stand is sufficiently dense and optimal application of nitrogen, increases the possibilities to skip late sprayings in sugar beet.

Samenvatting

Aantalsverloop en aantalsbeheersing van *Galium aparine* L.

Inleiding en doelstelling (Hoofdstuk 1)

De toenemende zorg voor ons milieu heeft geresulteerd in een beleidsvoornemen om het verbruik van onkruidbestrijdingsmiddelen te verminderen met 30 % voor 1995, 45 % voor 2000 en 55 % voor 2010. Teneinde deze reduktie te bereiken lijkt een gedegen kennis van de biologie van onkruiden nodig om de beheersing van de onkruiden te verbeteren met een zo gering mogelijk gebruik van herbiciden. *Galium aparine* L. (kleefkruid) is in Nederland één van de vier belangrijkste onkruiden omdat deze soort in veel situaties bepalend is voor de bestrijdingsmaatregelen die genomen worden en bovendien in vele gewassen problemen kan veroorzaken. Daarom werd deze soort gekozen als voorbeeld om verworven kennis van zijn populatiebiologie zodanig te integreren dat de effekten van verschillende beheersingsstrategieën zowel in een gewas als in bouwplanverband geëvalueerd kunnen worden.

Model van de populatiedynamica (Hoofdstuk 2)

Op basis van literatuurgegevens werd een model ontwikkeld dat per dag berekent hoeveel individuën in verschillende fasen van hun levenscyclus aanwezig zijn. De effekten van een aantal beheersmaatregelen op het aantalsverloop van *G. aparine* zowel binnen een jaar als over een reeks van jaren konden met dit model geschat worden. Hoewel sommige strategieën m.b.v. dit model wel ten opzichte van elkaar vergeleken konden worden, was voor voorspelling van de absolute groei of afname van de populatie meer kennis nodig van de parameterwaarden die aan het model ten grondslag lagen. De mate waarin parameters variëren en de consequenties daarvan voor de populatiedynamica werden nagegaan.

Kieming (Hoofdstuk 3)

Het voorkomen van primaire kiemrust en de kiemrustritmes van *G. aparine* werd onderzocht aan zaad dat op verschillende lokaties en op verschillende tijdstippen verzameld werd. De invloed van temperatuur, licht, nitraat, vocht en bodemverdichting op het actuele kiemingsproces werd in diverse experimenten in het laboratorium onderzocht.

Primaire kiemrust kwam vooral voor bij onrijpe of vroeg in het seizoen afgerijpte zaden. Daar de primaire kiemrust binnen 1 tot 3 maanden verdwenen was, is deze primaire kiemrust op geploegde gronden waar de verse zaden eerst begraven worden van secundair belang voor de patronen in opkomst.

Kiemrustritmes kwamen tot uiting in het traject van temperaturen waarbij kieming op kon treden. Geschikte temperaturen voor de kieming treden onder de Nederlandse weerscondities in het najaar en in het voorjaar op. Verschillende oecotypen die of alleen in het najaar dan wel alleen in het voorjaar kunnen kiemen werden niet gevonden.

Licht bleek de kieming van *G. aparine* óp de grond te remmen. Temperatuur en bodemverdichting bleken bepalend voor de mate van kieming ín de grond onder veldomstandigheden. De kiemingsduur hing nauw samen met de temperatuur (75 graaddagen boven 2.5 °C).

Opkomst (Hoofdstuk 4)

De mortaliteit van gekiemde zaden op verschillende diepten in de grond en de opkomstsnelheid in relatie tot temperatuur, vocht en bodemverdichting werd onderzocht. Mortaliteit van de zaden (tussen 0 en 100 %) kon berekend worden met gegevens over de diepte van de zaden in de grond en de verdichting van de grond. De opkomstduur werd vooral bepaald door de diepte van de zaden en de temperatuur (60 tot 300 graaddagen boven 2.5 °C).

Model van de kieming en opkomst (Hoofdstuk 5)

De kwantitatieve gegevens over de kieming en opkomst werden geïntegreerd in een dynamisch model dat de kieming en veldopkomst van *G. aparine* in relatie tot weer en bodemcondities simuleert. Simulaties werden vergeleken met waarnemingen in drie veldexperimenten. Veldopkomst patronen en hun omgevingsafhankelijke variaties konden met dit model in belangrijke mate voorspeld worden. Het tijdstip van grondbewerking, de verdichting van de grond na deze bewerking, de verdeling van de zaden in de bodem en de actuele temperaturen bleken in deze volgorde van belangrijkheid bepalend voor de veldopkomst.

Ontwikkeling (Hoofdstuk 6)

De ontwikkeling van *G. aparine*-planten in relatie tot klimaat en bodem condities werd onderzocht in een aantal experimenten in kas of klimaatcellen. Vochtregime en lichthoeveelheid bleken niet belangrijk voor de periode die *G. aparine*-planten nodig hebben om in bloei te geraken. Hoewel bemesting een geringe invloed had, waren vooral de daglengte en de temperatuur bepalend voor het tijdstip van bloei. Een empirische schaal werd ontwikkeld die de geaccumuleerde temperaturen en daglengten koppelde aan ontwikkeling van de plant en de veranderingen in distributiepatronen van nieuw geproduceerde droge stof. Met behulp van deze ontwikkelingsschaal konden waargenomen bloeidata van *G. aparine* met verschillende opkomsttijdstippen in Nederland en Engeland, correkt voorspeld worden.

Zaadproduktie (Hoofdstuk 7)

De zaadproduktie van *G. aparine* onder veldomstandigheden werd bepaald voor planten met verschillende opkomstdata en dichtheden in aardappel, koolzaad, wintertarwe, zomergerst en suikerbiet in 1988 en 1989. Het spruitgewicht van *G. aparine* werd vooral beïnvloed door het gewas waarin het groeide en de opkomstdatum relatief ten opzichte van het gewas. De effekten van intraspecifieke dichtheid (< 30 planten/m^2 na het gewas opgekomen) en invloed van weer en gewasstand in verschillende jaren waren geringer.

Een lineaire relatie werd gevonden tussen het aantal zaadproducerende uiteinden en spruitgewicht zonder zaden van de volgroeide plant. Deze relatie werd niet beïnvloed door het gewas waarin de planten groeiden, de opkomstdatum, de dichtheid of het jaar. Aan elk zaadproducerend uiteinde kunnen zich maximaal twee zaden ontwikkelen. De mate waarin dat gebeurde varieerde tussen 1.0 voor planten die groeiden in zomergerst tot 1.8 voor planten die groeiden in suikerbiet. Vitaliteit van de geproduceerde zaden was zeer hoog, hun zaadgewicht variabel. Zaadval van *G. aparine* ten tijde van de gewasoogst neemt toe met een vroege opkomst en een late gewasoogst. Niet afgevallen zaden worden bij een oogst met een combine met het gewas meegeoogst en van het veld verwijderd.

Model van de groei, concurrentie en populatietoename (Hoofdstuk 8)

De invloed van bemesting, lichthoeveelheid en temperatuur op de groei van *G. aparine* werd vastgelegd in drie experimenten in de kas en in klimaatcellen. Deze gegevens en de gegevens verzameld ten behoeve van de ontwikkelingsschaal (Hoofdstuk 6) werden gebruikt om een model van de concurrentie tussen *G. aparine* en suikerbiet dat gebasseerd is op de fysiologische basisprincipes, te parametriseren. Het model werd getest door simulatieresultaten te vergelijken met waarnemingen in concurrentie experimenten tussen *G. aparine* en suikerbiet onder veldomstandigheden in 1988, 1989 en 1990. Met behulp van het model konden zowel de door concurrentie veroorzaakte opbrengstredukties van suikerbiet als het spruitgewicht van *G. aparine* zonder zaad correkt voorspeld worden. De reduktie van het spruitgewicht van *G. aparine* tengevolge van een geringere stikstofgift in suikerbiet stemde ook overeen met de veldwaarnemingen.

Het model is bruikbaar om de variatie in de groei van *G. aparine* onder veldomstandigheden veroorzaakt door het weer te voorspellen. De opkomstdatum van *G. aparine* ten opzichte van het gewas, de zaaidatum en de dichtheid van het gewas waren echter meer doorslaggevend voor het volwassen spruitgewicht van *G. aparine* dan het weer. Bij opkomst van *G. aparine* 3 dagen na een goede opkomst van de suikerbiet heeft *G. aparine* maar in beperkte mate last van intraspecifieke concurrentie.

De gevonden relaties tussen spruitgewicht en zaadproduktie (Hoofdstuk 7) en de kennis van de kieming en opkomst (Hoofdstuk 3,4 en 5), werden gebruikt om voorspellingen van door concurrentie veroorzaakte redukties van de gewasopbrengst aan te vullen met uitspraken over de te verwachten *G. aparine* populatie toename of afname. Voor deze voorspellingen is het nodig om de dichtheid en de opkomstdata van *G. aparine* en van suikerbiet waar te nemen. Bovendien is een schatting nodig van het percentage bestrijding van *G. aparine* gedurende het seizoen tengevolge van eerdere maatregelen. De voorspellingen van de te verwachten opbrengstreduktie van suikerbiet en de populatietoename van niet bestreden *G. aparine* worden slechts in beperkte mate door eventuele verschillen in weerscondities beinvloed.

Discussie (Hoofdstuk 9)

Twee verschillende modellen werden ontwikkeld om uitspraken te doen over het aantalsverloop van *G. aparine* in relatie tot verschillende beheersstrategieën. Het eerste model met de op grond van het onderzoek aangepaste parameterwaarden, is verklarend op het populatieniveau en beschrijvend op het individu niveau (Hoofdstuk 2). Het tweede model is verklarend op het individu niveau en beschrijvend ten aanzien van de onderliggende fysiologische processen (Hoofdstuk 8). Beide benaderingen hebben hun voor- en nadelen en consequenties voor toekomstig onderzoek. Het eerste model is bij de huidige stand van de kennis het meest geschikt om hele bestrijdingsstrategieën in bouwplanverband te vergelijken. Het tweede model leent zich beter voor de rationalisering van bestrijdingsbeslissingen gebruikmakend van de actuele situatie op het veld en de te verwachten opbrengst-reduktie van het gewas en de populatietoename van het onkruid indien dit niet bestreden wordt. Illustraties van beide toepassingen werden gegeven.

Simulaties demonstreerden dat om populatietoename van *G. aparine* te voorkomen, het niet nodig is om zaadproduktie van deze soort in gewassen helemaal te verhinderen. In een monocultuur wintertarwe lijkt populatietoename van *G. aparine* voorkomen te kunnen worden door eggen (slechts een gedeeltelijke bestrijding) en een aangepaste teeltwijze. In een rotatie van wintertarwe, suikerbiet, zomergerst en aardappelen lijkt een gedeeltelijke bestrijding van *G. aparine* in de eerste drie gewassen, gecombineerd met 100 % bestrijding in aardappelen acceptabel. Reduktie van herbicidengebruik wordt dan mogelijk door te eggen in de granen en het tolereren van laat opkomende *G. aparine* planten in suikerbiet. De mogelijkheden latere bespuitingen in suikerbiet achterwege te laten worden bevorderd door vooropkomst van het gewas een aanzienlijk deel van de planten te bestrijden (vals zaaibed), te zorgen voor een voldoende dicht gewas en een optimaal stikstof gebruik.

References

AARTS, H.F.M. (1985) Let op de schadedrempels bij onkruidbestrijding in wintertarwe. *Boerderij/Akkerbouw*, **70**, 25-27.

AARTS, H.F.M. (1986) A computerized model for predicting changes in a population of *Galium aparine*. *Proceeding E.W.R.S. Symposium Economic Weed Control*, 277-284.

AARTS, H.F.M. & DEKKERS, W.A. (1985) De bestrijding van onkruiden in suikerbieten. *PAGV teelthandleiding*, **15**, 56 pp.

AMMON, H.U. (1978) Unkrautbekämpfung in Getreide unter Berücksichtigung der wirtschaftichen Schadschwelle. *Mitteilungen für die Schweizerische Landwirtschaft*, **26**, 8-14.

ARNDT, F. & KÖTTER, C. (1968) Zur Selektivität von phenmedifam als nachauflauf herbicid in Betarüben. *Weed Research*, **8**, 259-271.

AUGE, H. & MAHN, E.G. (1988) Zur Plastizität von *Galium aparine* L. Populationen - Wachstum und Biomasseverteilung bei sommerannuellem Lebenszyklus. *Flora*, **180**, 429-443.

AULD, B.A., MENZ, K.M. & TISDELL, C.A. (1987) *Weed control economics*. Academic Press 'Applied biology and crop science series', London, 177 pp.

BAANDRUP, M. & BALLEGAARD, T. (1989) Three years field experience with an advisory computer system applying factor adjusted doses. *Brighton Crop Protection Conference-Weeds*, 555-560.

BAIN, A.B. & ATTRIDGE, T.H. (1988) Shade-light mediated responses in field and hedgerow populations of *Galium aparine* L. *Journal of Experimental Botany*, **39**, 1759-1764.

BALLARÉ, C.L., SCOPEL, A.L., GHERSA, C.M. & SANCHEZ, R.A. (1987) The population ecology of *Datura ferox* in soybean crops. A simulation approach incorporating seed dispersal. *Agriculture, Ecosystems and Environment*, **19**, 177-188.

BANNISTER, P. (1980) *Introduction to physiological plant ecology*. Blackwell Scientific Publications, Oxford, 273 pp.

BASKIN, J.M. & BASKIN, C.M. (1987) Environmentally induced changes in the dormancy states of buried weed seeds. *British crop protection conference-weeds*, 695-706.

BASKIN, J.M. & BASKIN, J.M. (1989) Role of temperature in regulating timing of germination in soil seed reserves of *Thalspi arvense* L. *Weed Research*, **29**, 317-326.

BAYLIS, J.M. & WATKINSON, A.R. (1991) The effect of reduced nitrogen fertilizer inputs on the competitive effect of cleavers (*Galium aparine*) on wheat (*Triticum aestivum*). *Brighton Crop Protection Conference - Weeds*, 129-134.

BEHRENDT, S. & MENCK, B.M. (1974) Wirkungspectrum von Bentazon und Dichloprop unter besonderer Berücksichtigung der Unkrautstadien, de Temperatur zum Zeitpunkt der Niederschläge vor und nach der Behandlung. *Zeitschrift Pflanzenkrankheiten und Pflanzenschutz*, Sonderheft **4**, 233-250.

BENECH ARNOLD, R.L., GHERSA, C.M., SANCHEZ, R.A. & INSAUSTI, P. (1990 a) Temperature effects on dormancy release and germination rate in *Sorghum halpense* L. Pers. seeds: a quantitative analysis. *Weed Research*, **30**, 81-90.

BENECH ARNOLD, R.L., GHERSA, C.M., SANCHEZ, R.A. & INSAUSTI, P. (1990 b) A mathematical method to predict *Sorghum halpense* L. Pers. seedling emergence in relation to soil temperature. *Weed Research*, **30**, 91-100.

BERKEFELD, K. (1988) Untersuchungen zur Ökotypenbildung bei *Galium aparine* L. (*Rubiaceae*) und *Lapsana communis* L. (*Compositae*). *Flora*, **181**, 111-130.

BERRY, G.J., CAWOOD, R.J. & FLOOD, R.G. (1988) Curve fitting of germination data using the Richards function. *Plant , Cell and Environment*, **11**, 183-188.

BLOM, C.W.P.M. (1988) The realism of models in plant demography. *Acta Botanica Neerlandica*, **37**, 421-438.

BOUWMEESTER, H.J. (1990) *The effect of environmental conditions on the seasonal dormancy pattern and germination of weed seeds.* PHD thesis Agricultural University Wageningen the Netherlands, 157 pp.

BOUWMEESTER, H.J. & KARSSEN, C.M. (1992) The dual role of temperature in the regulation of the seasonal changes in dormancy and germination of seeds of *Polygonum persicaria* L. *Oecologia*, **90**, 88-94.

BOUWMEESTER, H.J. & KARSSEN, C.M. (in press) The effect of environmental conditions on the annual dormancy patterns of seeds of *Spergula arvensis* L. *Canadian Journal of Botany.*

BOYDSTON, R.A. (1989) Germination and emergence of longspine sandbur (*Cenchrus longispinus*). *Weed Science*, **37**, 63-67.

BROWN, R.F. & MAYER, D.G. (1988) Representing cumulative germination. 2. The use of the Weibull function and other empirically derived curves. *Annals of Botany*, **61**, 127-138.

BRIDGES, D.C., WU, H., SHARPE, P.J.H. & CHANDLER, J.M. (1989) Modelling distributions of crop and weed seed germination time. *Weed Science* **37**, 724-729.

CARBERRY, P.S. & CAMPBELL, L.C. (1989) Temperature parameters useful for modeling the germination and emergence of pearl millet. *Crop Science*, **29**, 220-223.

CASWELL, H. (1989) *Matrix population models. Construction, analysis and interpretation.* Sinauer Associates, Inc. Publishers Sunderland, Massachusetts, 328 pp.

CATIZONE, P. & VIGGIANI, P. (1990) Aspects of the biology and control of *Galium apar-*

ine L. *Proceedings EWRS Symposium on Integrated Weed Management in Cereals*, p. 421-428.

CHAEM, A.H. (1986) Seed production and seed dormancy in wild radish (*Raphanus raphanistrum* L.) and some possibilities for improving control. *Weed Research*, **26,** 405-413.

CHARLES-EDWARDS, D.A., DOLEY, D. & RIMMINGTON, G.M. (1986) *Modelling plant growth and development*. Academic Press, Australia, 235 pp.

COUSENS, R., DOYLE, C.J., WILSON, B.J. & CUSSANS, G.W. (1986) Modelling the economics of controlling *Avena fatua* in winter wheat. *Pesticide Science*, **17**, 1-12.

COUSENS, R. & MOSS, S.R. (1990) A model of the effects of cultivation on the vertical distribution of weed seeds within the soil. *Weed Research*, **30,** 61-70.

CORRÉ, W.J. (1983) Growth and morphogenesis of sun and shade plants II. The influence of light quality. *Acta Botanica Neerlandica,* **32,** 185-202.

CRESWELL, E.G. & GRIME, J.P. (1981) Induction of a light requirement during seed development and its ecological consequences. *Nature,* **291,** 583-585.

CUDNEY, D.W., JORDAN, L.S., CORBETT, C.J. & BENDIXEN, W.E. (1989) Developmental rates of wild oats (*Avena fatua*) and wheat (*Triticum aestivum*). *Weed Science,* **37,** 521-524.

CUSSANS, G.W., COUSENS, R.D. & WILSON, B.J. (1986) Thresholds for weed control - the concepts and their interpretation. *Proceedings EWRS Symposium Economic Weed Control*, 253-260.

DENNIS, F.G. (1984) Flowering. In: *Physiological basis of crop growth and development* (ed. M.B. Tesar) The American Society of Agronomy Inc. and the Crop Science Society of America, Wisconsin, pp. 237-264.

DE WIT, C.T. & GOUDRIAAN, J. (1974) *Simulation of ecological processes* Pudoc, Wageningen, 159 pp.

DE WIT, C.T., GOUDRIAAN, J., VAN KEULEN, H., VAN LAAR, H.H., LOUWERSE, W., PENNING DE VRIES, F.W.T., RABBINGE, R. & SIBMA, L. (1978) *Simulation of assimilation, respiration and transpiration of crops.* Simulation Monographs, Pudoc, Wageningen, 140 pp.

DOYLE, C.J., COUSENS, R. & MOSS, S.R. (1986) A model of the economics of control ling *Alopecurus myosuroides* Huds. in winter wheat. *Crop Protection,* **5,** 143-150.

EGLEY, G.H. (1986) Stimulation of weed seed germination in soil. *Reviews of Weed Science,* **2,** 67-89.

FERNANDEZ-QUINTANILLA, C. (1988) Studying the population dynamics of weeds. *Weed Research,* **28**, 443-447.

FERRIS, R. (1988) Inter-population variation in *Galium aparine L.* (cleavers). *PHD thesis Department of Agricultural Botany University of Reading*, 190 pp.

FINCH-SAVAGE, W.E. (1987) A comparison of seedling emergence and early seedling growth from dry-sown natural and fluid-drilled pregerminated onion (*Allium cepa* L.) seeds in the field. *Journal of Horticultural Science*, **62**, 39-47.

FISHER, A. (1975) Versuche zur Verbesserung von Pyramin (H119) im Nachauflaufverfahren met Hilfe von Netzmittel zusätzen und mit den neuen Versuchsprodukt 1-Phenyl-4-Co-hydroxy-B'B'B'- trichloräthyl)-amino-5 chlorpyridazon- 6 CH176-1). *Zeitschrift Pflanzenkrankheiten und Pflanzenschutz*, Sonderheft **3**, 207-217.

FITTER, A.H. & HAY, R.K.M. (1981) *Environmental Physiology of Plants*, Academic Press, London, 355 pp.

FRANZ, K., KAISER, F. & GEROWITT, B. (1990) Wirkung unterschiedlich hoher Stickstoffdüngung auf Entwicklung und Samenproduction ausgewählter Unkrautarten im Winterweizen. *Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz Sonderheft*, **13**, 127-135.

FROUD-WILLIAMS, R.J. (1985) The biology of cleavers (*Galium aparine* L.). *Aspects of Applied Biology*, **9**, 189-195.

FROUD-WILLIAMS, R.J., CHANCELLOR, R.J. & DRENNAN, D.S.H. (1984) The effects of seed burial and soil disturbance on emergence and survival of arable weeds in relation to minimal cultivation. *Journal of Applied Ecology*, **21**, 629-641.

FROUD-WILLIAMS, R.J. & FERRIS-KAAN, R. (1991) Intraspecific variation among populations of cleavers (*Galium aparine* L.). *Brighton Crop Protection Conference - Weeds*, 1007-1014.

GENSTAT 5 COMMITTEE (1988) *GENSTAT 5 Reference manual.* Clarendon press, Oxford, 749 pp.

GEPTS, P. (1987) Characterizing plant phenology: growth and development scales. In: *Plant growth modelling for resource management vol. II Quantifying plant processes* (ed. K. Wisiol & J.D. Hesketh), CRC Press, pp. 3-23.

GEROWITT, B. (1992) Klettenlabkraut im Getreide mechanisch bekämpfen ? *Pflanzenschutz Praxis*, **1**, 16-19.

GHERSA, C.M., SATORRE, E.H., VAN ESSO, M.L., PATARO, A. & ELIZAGARAY, R. (1990) The use of thermal calender models to improve the efficiency of herbicide applications in *Sorghum halpense* (L.) Pers. *Weed Research*, **30**, 153-160.

GOUDRIAAN, J. (1986) Boxcartrain methods for modelling of ageing, development, delay and dispersion. *The dynamics of phyiologically structured populations* (ed. J.A.J. Metz and O. Diekman), Springer Lecture Notes in Biomathics, **68**, 453-473.

GRIME, J.P., MASON, G., CURTIS, A.V., RODMAN, J., BAND, S.R. , MOWFORTH, M.A. G., NEAL, A.M. & SHAW, S. (1981) A comparative study of germination characteristics in a local flora. *Journal of Ecology*, **69**, 1017- 1059.

GRIME, J.P. & THOMPSON, K. (1976) An apparatus for measurement of the effect of amplitude of temperature fluctuation upon the germination of seeds. *Annals of Botany*, **40**, 795-799.

GROLL, U. & MAHN, E.G. (1986) Zur Entwicklung ausgewahlter Populationen des Klettenlabkrautes (*Galium aparine* L.)'. *Flora,* **178,** 93-110.

GUTTERMAN, Y. (1973) Differences in the progeny due to daylength and hormone treatment of the motherplant. In: *Seed Ecology, proceedings of the Nineteenth Easter School in Agricultural Science, University of Nottingham* (ed. W. Heydecker), London Butterworths, 59-80.

HAIG, D. & WESTOBY, M. (1988) On limits to seed production. *The American Naturalist,* **131,** 757-759.

HÅKANSSON, S. (1983) Seasonal variation in the emergence of annual weeds - an introductory investigation in Sweden. *Weed Research,* **23,** 313-327.

HÅKANSSON, S. (1984) Jordbearbetningen och ogräset. *Ogräs-nyckeln- Aktuellt från lantbrukuniversitetet Mark Växter Uppsala,* **328,** 11-19.

HÅKANSSON, S. (1986) Competition between crops and weeds- influencing factors, experimental methods and research needs. *Proceedings EWRS Symposium Economic Weed Control,* 49-60.

HAMMERTON, J.L. (1967) Environmental factors and susceptibility to herbicides (a literature survey). *Weeds,* **15,** 330-335.

HANF, M. (1941) Keimung und Entwicklung des Klettenlabkrautes (*Galium aparine*) in verschiedene Aussaattiefen. *Angewandte Botanik* **23,** 152-163.

HANF, M. (1983) *The arable weeds of Europe.* Ludwigshafen: BASF Aktiengesellschaft, 347 pp.

HARPER, J.L. (1977) *Population Biology of Plants,* Academic Press, London, 892 pp.

HARTMANN, K.M. & NEZEDAL, W. (1990) Photocontrol of weeds without herbicides. *Naturwissenschaften,* **77,** 158-163.

HIELKEMA, J.U. (1974) Literatuurstudie en onderzoek naar de indringingsweerstanden van klei- en zavelgronden. *Stiboka rapport,* **1200,** Wageningen the Netherlands, 34 pp.

HILTON, J.R. & OWEN, P.D. (1985) Light and dry storage influence on the respiration of germinating seeds of 5 species. *New Phytologist,* **99,** 523-532.

HILTON, J.R. & THOMAS, J.A. (1987) Changes in Respiratory Potential of Dormant and Non-dormant *Galium aparine* L. (cleavers) seeds during Dry Storage. *Journal of Experimental Botany,* **38,** 1484-1490.

HIRDINA, F. (1959) Beitrage zur Biologie und Bekampfung des Klettenlabkrauts (*Galium aparine* L.). *Zeitschrift für Acker-und Pflanzenbau,* **109,** 173-197.

HOLM, L.G., PLUCKNETT, D.V., PANCHO, J.V. & HERBERGER, J.P. (1977) *The world's worst weeds distribution and biology.* The university press of Hawaii, Honolulu, 609 pp.

HOLZMANN, A. & NIEMANN, P. (1988) Prognose der Verunkrautung mit *Viola arvensis* auf der Basis populationdynamischer Parameter. *Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz,* Sonderheft, **11,** 91-96.

HOOGERKAMP, M. (1989) Weed control In: *Development of Farming Systems: Evaluation of the five-year period 1980-1984* (ed. J.C. Zadoks), PUDOC, Wageningen the Netherlands, 40-46.

JANSSEN, J.G.M. (1973) A method of recording germination curves. *Annals of Botany* **37**, 705-708.

JANSSEN, J.G.M. (1974) Simulation of germination of winter annuals in relation to microclimate and microdistribution, *Oecologia (Berl)* **14**, 197-228.

JOENJE, W. & KROPFF, M.J. (1987) Relative time of emergence, leaf area development and plant height as major factors in crop-weed competition. *British crop protection conference - Weeds*, 971-978.

KAISER, F. (1989) Langfristige beurteilung und Vorausschätzung der Unkrautdichte in der Fruchtfolge Rüben-Winterweizen-Wintergerste bei unterschiedlicher Bekämpfungshaüfigkeit im Getreide unter berücksichtigung von Schadensschwellen. *Dissertation Universität Göttingen*, 191 pp.

KARSSEN, C.M. (1982) Seasonal patterns of dormancy in weed seeds. In: *The physiology and biochemistry of seed development, dormancy and germination* (ed. A.A. Khan), Elsevier Biomedical Press, 243- 270.

KOCH, W. (1969) Einfluss von Umweltfactoren auf die Samenfase annueler Unkrauter. *Arbeiten der Universitat Hohenheim*, **50**, 204 pp.

KOCH, W. (1970) *Unkrautbekämpfung*, Verlag Ulmer, Stuttgart, 342 pp.

KROPFF, M.J. (1988) Modelling the effects of weeds on crop production. *Weed Research*, **28**, 465-472.

KROPFF, M.J. & VAN LAAR, H.H. (in prep.) *Simulation of interplant competition.*

KUDSK, P. (1989) Experiences with reduced herbicide doses in Denmark and the development of the concept of factor-adjusted doses. *Brighton Crop Protection Conference - Weeds*, 545-554.

LARCHER, W. (1975) *Physiological Plant Ecology*. Springer-Verlag, Berlin Heidelberg New York, 252 pp.

LÉGÈRE, A. & DESCHÊNES, J. (1989) Effects of time of emergence, population density and interspecific competition on hemp-nettle (*Galeopsis tetrahit*) seed production. *Canadian Journal of Plant Science*, **69**, 185-194.

LOCHER, W.P. & BAKKER, H. (1990) *Bodemkunde van Nederland. Deel 1, Algemene bodemkunde*, Malmberg, Den Bosch, the Netherlands, 439 pp.

LOTZ, L.A.P., GROENEVELD, R.M.W. & DE GROOT, N.A.M.A. (1991) Perspectives of reducing herbicide inputs in sugar beet by selecting early closing varieties. *Proceedings British Crop Protection Conference - Weeds*, **3**, 1241-1247.

LOTZ, L.A.P., KROPFF, M.J. & GROENEVELD, R.M.W. (1990) Modelling weed competition and yield losses to study the effect of omission of herbicides in winter wheat. *Netherlands Journal of Agricultural Science* **38**, 711-718.

MAHN, E.G. (1984) The influence of different nitrogen levels on the productivity and structural changes of weed communities in agro-ecosystems. *International Symposium Weed Biology, Ecology and Systematics. COLUMA-EWRS*, **7**, 421-429.

MALIK, N. & VAN DEN BORN, W.H., (1987) Germination response of *Galium spurium* L. to light. *Weed Research,* **27**, 251-258.

MALIK, N. & VANDEN BORN, W.H. (1988) The biology of Canadian weeds. 86. *Galium aparine* L. and *Galium spurium* L. *Canadian Journal of Plant Science*, **68**, 481-499.

MAXWELL, B.D., WILSON, M.V. & RADOSEVICH, S.R. (1988) Population modelling approach for evaluating leafy spurge (*Euphorbia esula*) development and control. *Weed Technology*, **2**, 132-138.

MCCANNY, S.J. & CAVERS, P.B. (1988) Spread of proso millet (*Panicum miliaceum* L.) in Ontario, Canada. II. Dispersal by combines. *Weed Research,* **28**, 67-72.

MINISTRY OF AGRICULTURE, NATURE MANAGEMENT AND FISHERIES (1990) Rapportage Werkgroep Akkerbouw. *Achtergronddocument Meerjarenplan Gewasbescherming*, Ministerie van Landbouw, Natuurbeheer en Visserij te 's Gravenhage, the Netherlands, 103 pp.

MOORE, R.J. (1970) Tetrazolium seed aids. *Proceedings Association of Seed Analysts North America,* **60**, 100-103.

MOORE, R.J. (1975) The *Galium aparine* complex in Canada. *Canadian Journal of Botany*, **53**, 877-893.

MORROW, L.A., YOUNG, F.L. & FLOM, D.G. (1982) Seed germination and seedling emergence of jointed goatgrass (*Aegilops cylindrica*). *Weed Science,* **30**, 395-398.

MORTIMER, A.M. (1983) On weed demography. In: *Recent Advances in Weed Research* (ed. W.W. Fletcher), Commonwealth Agricultural Bureau, Slough, 3- 40.

MORTIMER, A.M. (1987) The population ecology of weeds - implications for integrated weed management, forecasting and conservation. *Proceedings British Crop Protection Conference-Weeds*, 935-944.

MORTIMER, A.M., PUTWAIN, P.D. & MCMAHON, D.J. (1978) A theoretical approach to the prediction of weed population sizes. *Proceedings British Crop Protection Conference-Weeds*, 467-474.

MORTIMER, A.M., SUTTON, J.J. & GOULD, P. (1989) On robust weed population models. - *Weed Research*, **29**, 229-238.

MORTIMER, A.M., SUTTON, J.J., PUTWAIN, P.D. & GOULD, P. (1990) The dynamics of mixtures of arable weed species. *Proceedings EWRS Symposium Integrated Weed Management in Cereals*, 19-26.

MULLVERSTEDT, R. (1963) Untersuchungen über die Kiemung von Unkrautsamen in Abhängigkeit vom Sauerstoffpartialdruck. *Weed Research,* **3**, 154-163.

NEURURER, H. (1975) Weitere Erfahrungen in der Beurteilung der tolerierbaren Verunkrautungsstärke. *Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz, Sonderheft*, **7**, 63-69.

NIEMANN, P. (1981) Schadschwellen bei der Unkrautbekämpfung. *Angewandte Wissenschaft*, **257**, 67 pp.

NIEMANN, P. (1988) Zur Variabilität des Klettenlabkrauts (*Galium aparine*). *Gesunde Pflanzen*, **40**, 368-373.

NIETO, J.H., BRONDO, M.A. & GONZALEZ, J.T. (1968) Critical periods of the crop growth cycle for competition from weeds. *PANS(C)* , **14**, 159-166.

NORRIS, R.F. (1992) Have ecological and biological studies improved weed control strategies? *Proceedings of the First International Weed Control Congress*, Melbourne, 7-33.

ORWICK, P.L., SCHREIBER, M.M. & HOLT, D.A. (1978) Simulation of Foxtail (*Setaria viridis* var. *robusta-alba, Setaria viridis* var. *robusta-purpurea*) Growth: the development of SETSIM. *Weed Science*, **26**, 691-699.

PACALA, S.W. (1986) Neighbourhood models of plant population dynamics. 4. Single-species and multispecies models of annuals with dormant seeds. *The American Naturalist*, **128**, 859-878.

PETERS, N.C.B. (1984) Competition between *Galium aparine* (cleavers) and cereals. *Abstract of AAB meeting Understanding Cleavers (Galium aparine) and their control*, 3-4.

POLLARD, F. (1982) A computer model for predicting changes in a population of *Bromus sterilis* in continuous winter cereals. *Proceedings British Crop Protection Conference - Weeds*, 973-979.

PORTER, J.R. & DELECOLLE, R. (1988) Interaction of temperature with other environmental factors in controlling the development of plants. *Plants and temperature. Symposia of the Society for Experimental Biology* (ed. S.P. Long & F.I. Woodward), **42**, Cambridge, pp. 133-156.

RABBINGE, R., WARD, S.A. & VAN LAAR, H.H. (1989) Simulation and Systems Management in Crop Protection , *Simulation Monographs*, Pudoc, Wageningen, 420 pp.

RADOSEVICH, S.R. & HOLT, J.S. (1984) *Weed Ecology: Implications for Vegetation Management.* John Wiley and Sons, New York, 265 pp.

RIMMINGTON, G.M. & CHARLES-EDWARDS, D.A. (1987) Mathematical description of plant growth and development. In: *Plant growth modelling for resource management. Vol. I. Current models and methods* (ed. K. Wisiol & J.D. Hesketh), CRC Press, Florida, pp. 3-17.

ROBERTS, H.A. & LOCKETT, P.M. (1978) Seed dormancy and field emergence in *Solanum nigrum* L. *Weed Research*, **18**, 231-241.

ROONEY, J.M., CLARKSON, D.T.,HIGHETT, M., HOAR, J.J. & PURVES, J.V. (1990)

Growth of *Galium aparine* L. (cleavers) and competition with *Triticum aestivum* L. (wheat) for N. *Proceedings EWRS Symposium on Integrated Weed Management in Cereals*, 271-280.

RÖTTELE, M.A. (1980) Populationdynamik des Klettenlabkrautes (*Galium aparine*), *Dissertation Universität Hohenheim*, 133 pp.

SCHMIDT, R.R. (1972) Bekämpfung von *Galium aparine* L. mit mecoprop in Abhängigkeit von verschiedener Bodenarten. *Weed Research*, **12**, 174-181.

SIEBERHEIN, K., KROOSS, G., & SEEVER, H. (1977) Zum Applikationstermin von SYS-Herbiziden bei de Bekämpfung von Klebkraut (*Galium aparine* L.) in Winterweizen. *Nachrichtenblatt für den Pflanzenschutz in der DDR*, **28/12**, 237-242.

SIEBERHEIN, K. & SEEVER, H. (1974) Bedeutung und Bekämpfung des Klettenlabkrautes (*Galium aparine* L.) in Getreidekulturen. *Nachrichtenblatt für den Pflanzenschutz in der DDR*, **28/12**, 237-242.

SJÖSTEDT, S. (1959) The germination biology of cleavers. *Växtodling*, **10**.

SMIT, A.H.L. (1989) Overzaaien van suikerbieten. *PAGV verslag* **91,** 78 pp.

SMITH, D.L.O. (1987) Measurement, interpretation and modelling of soil compaction. *Soil use and Management*, 3, 87-93.

SNEL, M., SCHLOTTER, P. & DELAOUTRE, J.F. (1990) Correlation between time of application of fluroxypyr or tank mixes based on fluroxypyr, degree of control of *Galium aparine*, and crop yield. *Proceedings EWRS Symposium Integrated Weed Management in Cereals*, 382-390.

SPITTERS, C.J.T. (1980) Simulating the vegetation dynamics in sahelian pastures. *Paper presented at the Workshop of European Population Biologists 9 May 1980 in Bangor (U.K.)* 16 pp.

SPITTERS, C.J.T. (1984) A simple simulation model for crop-weed competition. *International Symposium Weed Biology, Ecology and Systematics. COLUMA-EWRS*, **7**, 355-366.

SPITTERS, C.J.T. (1989) Weeds: population dynamics, germination and competition. in: *Simulation and Systems Management in Crop Protection* (ed. Rabbinge R., Ward S.A. & van Laar H.H.), *Simulation Monographs*, Pudoc, Wageningen, 182-216.

SPITTERS, C.J.T. & AERTS, R. (1983) Simulation of competition for light and water in crop-weed associations. *Aspects of Applied Biology*, **4**, 467-483.

SPITTERS, C.J.T., VAN KEULEN, H. & VAN KRAAILINGEN, D.W.T. (1989) A simple and universal crop growth simulator: SUCROS87. in: *Simulation and Systems Management in Crop Protection* (ed. Rabbinge R., Ward S.A. & van Laar H.H.), *Simulation Monographs*, Pudoc, Wageningen, 182-216.

STANDIFER, L.C. & WILSON, P.W. (1988) A high temperature requirement for after ripening of imbibed dormant *Poa annua* L. seeds. *Weed Research*, **28,** 365-371.

STEINER, A.A. (1968) Recipe for a universal nutrient solution. *Centre for Plant Physio-*

logical Research, Wageningen, Report **35**, 4 pp.

TERPSTRA, R. (1986) Behaviour of weed seeds in soil clods. *Weed Science*, **34**, 889-895.

TESTER, M. & MORRIS, C. (1987) The penetration of light through soil (mini-review). *Plant, Cell and Environment*, **10**, 281-286.

THOMPSON, B.K., WEINER, J. & WARWICK, S.I. (1991) Size-dependent reproductive output in agricultural weeds. *Canadian Journal of Botany*, **69**, 442-446.

URBAN, J. (1980) Applikation von Herbiziden in Zuckerrüben. *Tagungsbericht Akademie Landwirtschaften DDR*, **182**, 99-104.

VAN DEN BRAND, W.G.M. (1984) Biologie en ecologie van kleefkruid (*Galium aparine*), *PAGV Verslag*, Lelystad the Netherlands, 31 pp.

VAN GROENENDAEL, J.M. (1988) Patchy distribution of weeds and some implications for modelling population dynamics: a short literature review. *Weed Research*, **28**, 437-441.

VAN GROENENDAEL, J.M., DE KROON, H. & CASWELL, H. (1988) Projection matrices in population biology. *Trends in Ecology and Evolution*, **3**, 264-269.

VAN KEULEN, H., GOUDRIAAN, J. & SELIGMAN, N.G. (1988) Modelling the effects of nitrogen on canopy development and crop growth. In: *Plant canopies: Their growth, form and function* (ed. G. Russell, B. Marshall and P.G. Jarvis) SEB Seminar Series **31**, Cambridge, pp. 83-104.

VAN DER WEIDE, R.Y. (1987) De populatiedynamica van kleefkruid in landbouwgewassen. *Verslag afstudeervak onkruidkunde Landbouwuniversiteit Wageningen*, 116 pp.

VEREIJKEN, P. (1989) From integrated control to integrated farming, an experimental approach. *Agriculture, Ecosystems and Environment*, **26**, 37-43.

VEREIJKEN, P. & WIJNANDS, F.G. (1990) Geïntegreerde akkerbouw naar de praktijk - Strategie voor bedrijf en milieu. *PAGV Publikatie*, **50**, 86 pp.

VLEESHOUWERS, L.M. & STREIBIG, J.C (1986) How often must we theoretically control weeds ? *Proceedings Meeting EC Experts - Weed control in vegetable production*, 85-98.

WAHMHOFF, W. (1986) Erfahrungen mit der praktische Anwendung von Schadensschwellen bei der Unkrautbekämpfung im Getreide. *Proceedings EWRS Symposium on Economic Weed Control*, 379-384.

WALL, D.A. & MORRISON, I.N. (1990) Phenological development and biomass allocation in *Silene vulgaris* (Moench) Garcke. *Weed Research*, **30**, 279-288.

WALLINGA, J., VAN DER WEIDE, R.Y., LOTZ, L.A.P. & GROENEVELD, R.M.W. (1993) Weed population dynamics in a rotation of potato, winter wheat, sugar beet and winter wheat as influenced by control in winter wheat. *Proceedings EWRS symposium Braunsweig: Quantitative approaches in weed and herbicide research and their practical application* (in prep.)

WASHITANI, I. (1987) A convenient screening testsystem and a model for thermal germination responses of wild plant seeds: behavior of model and real seeds in the system. *Plant, Cell and Environment* **10,** 587-598.

WEBSTER, R.H. (1979) Growing weeds from seeds and other propagules for experimental purposes. *Technical report Agric. Res. Council Weed Research Organisation,* **56.**

WEVERS, J.D.A. (1991) Low dosage systems for controlling broadleaf and annual grass weeds in sugarbeet. *Mededelingen Faculteit Landbouwuniversiteit Gent,* **56/3a,** 611-615.

WILSON, J.B. (1988) A review of evidence on the control of shoot:root ratio, in relation to models. *Annals of Botany,* **61,** 433-449.

WILSON, B.J. & FROUD-WILLIAMS, R.J. (1988) The effect of tillage on the population dynamics of *Galium aparine* (L.) (cleavers). *Colloque international sur la biologie, l'écologie et la systematique des mauvaises herbes,* Dijon, **8,** 81-90.

WILSON, B.J. & WRIGHT, K.J. (1987) Variability in the growth of cleavers (*Galium aparine*) and their effect on wheat yield. *British Crop Protection Conference - Weeds,* 1051-1058.

WILSON, B.J. & WRIGHT, K.J. (1990) Predicting the growth and competitive effects of annual weeds in wheat. *Weed Research,* **30,** 201- 211.

WILSON, B.J. & WRIGHT, K.J. (1991) Effects of cultivation and seed shedding on the population dynamics of *Galium aparine* in winter wheat crops. *Brighton Crop Protection Conference - Weeds,* 813-820.

WRIGHT, K.J. & WILSON, B.J. (1992) Effects of nitrogen fertiliser on competition and seed production of *Avena fatua* and *Galium aparine* in winter wheat. *Aspects of Applied Biology,* **30,** 381-386.

ZADOKS, J.C. & RABBINGE, R. (1985) Modelling to a purpose. *Advances in Plant Pathology,* **3,** 231-244.

ZADOKS, J.C. & SCHEIN, R.D. (1979) *Epidemiology and plant disease management* Oxford University Press, 427 pp.

ZANIN, G. & SATTIN, M. (1988) Threshold level and seed production of velvetleaf (*Abutilon theophrasti*) in maize. *Weed Research,* **28,** 347-352.

ZOON, F.C., HAGE, F.J. & DE ZWART, A. (1990) A device for automatic soil moisture control and registration of water use in pot experiments. *Plant and Soil,* **125,** 281-284.

ZWERGER, P. & HURLE K. (1988) Simulationsstudien zum Einfluss von Fruchtfolge und Bekampfungsmassnahmen auf die Verunkrautung. *Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz,* Sonderheft, **9,** 71-82.

ZWERGER, P., HURLE, K. & KEMMER, A. (1990) Untersuchungen zum Einfluss von Fruchtfolge und Anbauintensität auf die Entwicklung des Unkrautsamangehaltes im Boden. *Proceedings EWRS Symposium Integrated Weed Management in Cereals,* 127-134.

Curriculum vitae

Rommie van der Weide werd geboren op 4 januari 1964 te Den Haag. Na het behalen van het V.W.O. diploma aan de Rijswijkse Openbare Scholengemeenschap studeerde zij Plantenziektekunde (vrije oriëntatie, oude stijl) aan de Landbouwuniversiteit, waarvan zij in 1987 het diploma (met lof) behaalde. Het vakkenpakket bestond uit een hoofdvak Fytopathologie en de bijvakken Onkruidkunde, Nematologie, Informatica en Didactiek. Aansluitend werd zij aangesteld als Assistent in Opleiding bij de vakgroep Vegetatiekunde, Plantenoecologie en Onkruidkunde, waar zij het onderzoek voor dit proefschrift verrichtte. In 1991 werd zij aangesteld bij het Nederlands Graan Centrum en gedetacheerd bij de afdeling Onkruidfysiologie en -oecologie van het CABO_DLO met de taak onderzoek te verrichten naar de mogelijkheden het herbicidenverbuik in granen te reduceren. Sinds 1992 is zij werkzaam bij de afdeling Technische Ondersteuning Bedrijfssystemen van het Proefstation voor Akkerbouw en Groenteteelt in de Vollegrond te Lelystad als wetenschappelijk onderzoeker Onkruidkunde.