A quantitative analysis of inter-specific competition in crops with a row structure

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A quantitative analysis of inter-specific competition in crops with a row structure

Proefschrift

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STELLINGEN

1. Een vermindering van de rijafstand ten opzichte van de huidige, vergroot de productie van droge stof van een gewas, indien de onkruidplanten kleiner blijven dan de gewasplanten.
(Dit proefschrift)

2. De afstand tussen een onkruidplant en een witlofplant heeft een kleiner effect op de opbrengstreductie van een witlofplant ten gevolge van concurrentie, wanneer er een verschuiving plaatsvindt van concurrentie om licht naar concurrentie om stikstof.
(Dit proefschrift)

3. Onkruiden die opkomen tot een week na de opkomst van het witlofgewas moeten ten allen tijde worden bestreden om opbrengstverlies te voorkomen.
(Dit proefschrift)

4. Het economisch opbrengstverlies van witlof ten gevolge van concurrentie met onkruiden wordt in sterke mate bepaald door het effect van concurrentie op de wortelsortering.
(Dit proefschrift)

5. Het effect van de opkomstdatum van onkruiden op het opbrengstverlies van witlof is veel groter dan het effect van de positie van de onkruiden.
(Dit proefschrift)

6. De hoeveelheid neerslag die valt in grote delen van Ierland is niet in overeenstemming met het regenachtige imago van Ierland.
(Agro-Climatic Atlas of Ireland)

7. Het aantal wetenschappers dat werkzaam is in de onkruidkunde doet niet vermoeden dat de onkruidbeheersing een toenemend groot probleem zou kunnen zijn.

8. Over tien jaar zal de telefoon zoals we deze nu kennen, alleen nog maar te bewonderen zijn in een museum.

9. Iedere onderzoeker moet verplicht worden een deel van de tijd onderwijs te geven.

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10. Het feit dat circa 50 % van het EU budget wordt gebruikt voor het instandhouden van circa 5 % van de beroepsbevolking, is een bewijs van de "macht" van de landbouwsector, maar tegelijkertijd ook een bewijs van de "onmacht" van deze sector om hun eigen boontjes te doppen.

11. Het transport van data via electriciteitskabels zal leiden tot een explosieve groei van het aantal telecommunicatie-toepassingen binnenshuis.

12. Om de natuurdoelstellingen op het Nederlands grondgebied, zoals vermeld in het rapport "nieuwe kansen voor het natuurbeheer", voor de gestelde termijn te realiseren kan men het beste zo snel mogelijk alle dijken doorbreken.
    (Programma Beheer "nieuwe kansen voor het natuurbeheer", 1998, SDU, Den Haag)

Stellingen behorende bij het proefschrift van Bert Schnieders:
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ABSTRACT

Competition with weeds can cause high yield losses, especially in crops with incomplete canopy closure. This thesis reports on studies carried out to quantitatively explain the effects of spatial arrangements, emergence dates, plant densities, and physiological and morphological characteristics of competing species in a canopy with a row structure, on the growth of those species. A model for inter-specific competition (INTERROW), that explicitly takes into account the row structure of a crop, is described.

The main "model system" was a witloof chicory (*Cichorium intybus* L.) crop grown for its storage roots, in competition with the weeds *Senecio vulgaris* L., *Solanum nigrum* L., or *Chenopodium album* L. Weed competition caused high reduction in storage root dry weight, which was primarily caused by early weed emergence, and to a lesser extent by weed density and weed position. Weed competition increased the percentage of storage roots with a diameter smaller than 32.5 mm, which have very little economic value, because they do not contain sufficient redistributable carbohydrates to produce a chicon of good quality. The model INTERROW correctly simulated light interception inside a canopy consisting of witloof chicory and *S. vulgaris*. White cabbage (*Brassica oleracea* var. capitata), in which *Trifolium repens* L. or *Trifolium subterraneum* L. was grown as a cover crop, was selected as a second "model system", to evaluate the ability of the model INTERROW to simulate effects of competition in other multi-species associations.

This thesis shows that the model INTERROW was able to accurately explain competition between witloof chicory and weeds, and between white cabbage and clover species sown as cover crop. Model analyses helped to explain experimental results and were used to generate recommendations about growing crops in such a way that yield losses due to weeds or cover crop are minimised. This thesis elaborated robust linear relationships between vegetative plant weight and reproductive plant weight of weed species, and showed a strong allometric relationship between the average storage root diameter and the average storage root dry weight of witloof chicory. These relationships can be included in the model INTERROW and enable the analysis of the effects of crop-weed competition on the population dynamics of weeds and the marketable yield of witloof chicory crops. The recommendations based on feasibility studies may help to prevent yield reduction due to weeds, by using appropriate crop husbandry procedures.

Additional keywords: witloof chicory, *Cichorium intybus*, groundsel, *Senecio vulgaris*, black nightshade, *Solanum nigrum*, fat hen, *Chenopodium album*, cabbage, *Brassica oleracea*, clover, *Trifolium* spp., competition, simulation, model

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CONTENTS

CHAPTER 1

GENERAL INTRODUCTION

Weed control is a key issue and a major cost factor in producing most agricultural crops. Despite all weed control efforts, the average yield losses due to weeds are estimated at 7.5 % and 25 % in developed and developing countries, respectively (Parker & Fryer, 1975). Without weed control, even very low weed densities may cause yield losses of up to 100 % in some years in some crops. This was found, for example, in vegetable crops with incomplete canopy closure such as witloof chicory (Patel & Upadhyay, 1989), onions and carrots (Van Heemst, 1985; Bond, 1991), and lettuce and cabbage (Bond, 1991). Apart from having a negative effect on dry matter yield, weeds can also reduce the quality of the harvested products or hamper the harvest of the crop.

Weed control has been dominated by the use of herbicides for the last three decades. Increasing concerns about the effects of herbicides on the environment and the quality of food, the widespread development of herbicide resistance in weed species, and the necessity to reduce costs of inputs, has highlighted the need to reassess our present weed control methods (*e.g.* Kropff & Lotz, 1992a, 1992b; Liebman & Dyck, 1993; Lotz *et al.*, 1993; Morgan, 1992; Wyse, 1992). The Dutch government decided that the amounts of herbicides used, and the structural dependency on herbicides must be reduced (MJP-G, 1991). This policy document made clear that, amongst other things, integrated weed management systems must be developed in which the use of herbicides is minimised. The strategy to optimise weed management systems, such that the use of herbicides is minimised, includes both the adaptation of crop management practices and the development of advisory systems based on post-emergence observations of weed infestations (Kropff & Lotz, 1992a, 1992b). These changes in weed control practices require a thorough quantitative understanding of the processes underlying the outcome of crop-weed competition (Jordan, 1993; Kropff & Lotz, 1992a, 1992b; Radosevich, 1987; Wyse, 1992). An interim report on the effects of the government policies on herbicide use showed that in the period 1991 - 1995, the dependency on the use of herbicides was not at all reduced and the amounts of herbicides used were only slightly reduced (IKC, 1996).

Plant growth and inter-plant competition are complex phenomena, that are governed by various biological, environmental and proximity factors. The quantitative insight into all of the factors influencing crop-weed competition, can be provided by systems analysis using experimental studies and process-based models side by side (Kropff & Lotz, 1992a, 1992b).

Plant growth can be affected by various factors during the growing season, resulting in different yield levels. Rabbinge (1993) differentiated between potential, attainable and actual yields. The potential yield is determined by growth-defining factors, such as light, temperature, and species characteristics. The attainable yield is that what can be achieved under conditions of sub-optimal amounts of growth-limiting factors, such as water and nutrients. The actual yield is achieved when growth-reducing factors such as weeds, pests and diseases, further reduce the attainable yield. Crop growth-limiting and crop growth-reducing factors interact. For example, weeds compete with crops for environmental resources that are in limited supply. Quantification of the effects of the growth limiting and growth reducing factors on the underlying processes of light interception, assimilation, respiration and transpiration, and the effects on water and nutrient uptake, and the integration in crop-growth models, helps in understanding the various growth-reducing factors and provides a basis for the development of control measures (Rabbinge, 1993).

The competitive strength of a species in the absence of growth-limiting factors, is largely determined by plant characteristics that influence light interception and light use efficiency. Among the characteristics that influence the light interception of a species are plant height, specific leaf area, early leaf area development, light extinction coefficient of leaves, and assimilate partitioning patterns. Among the characteristics that influence the light use efficiency are the leaf photosynthesis at light saturation, and the initial light use efficiency (Kropff *et al.*, 1992, 1993b, 1993c). Proximity factors, such as plant density, species proportion, and spatial arrangement of the plants, also determine the outcome of competition (Radosevich, 1987; Kropff *et al.*, 1992, 1993b, 1993c; Schnieders & Lotz, 1993). Emphasis in modelling competition at this production situation should be placed on the processes that determine the light interception and the light use efficiency. When growth-limiting factors are present, the competitive strength of a species is partly influenced by plant characteristics that determine the rate of water and nutrient uptake, the transpiration rate, the water use efficiency, and the nutrient use efficiency. Competition models that take into account competition for water and nutrients should be extended with a water balance of the soil, and should put emphasis on the processes that determine the water and nutrient uptake, the water use efficiency, and the nutrient use efficiency.

France (1988) and Spitters (1990) found that eco-physiological models provide an important research tool:

- as a framework for the analysis of experimental results,
- to summarise and integrate knowledge in a quantitative way,
- to initiate further research
- to assess the impact of individual processes at a higher integration level
- to evaluate different scenarios.

Eco-physiological models of competition for light, water and nutrients were first introduced by Spitters & Aerts (1983), and were further developed in subsequent studies by Spitters, Kropff and co-workers (*e.g.* Kropff *et al.*, 1984; Spitters, 1989; Kropff & van Laar, 1993). Models based on similar approaches were developed by Graf *et al.* (1990) and Wilkerson *et al.* (1990). All these models are based on the principle that competition is a dynamic process, that can be understood from the distribution of the growth-determining (light) or growth-limiting (water and nutrients) resources over the competing species, and the efficiency with which each species uses these resources (Kropff & Lotz, 1992a). An assumption made by these models is that the horizontal distribution of leaves is homogeneous (Kropff & Lotz, 1992a, Kropff *et al.*, 1992), ignoring possible effects of plant arrangements on competition. However, plant arrangement and plant density usually are very important yield-determining factors in crops. Higher plant densities and narrower row spacings increase, to a certain maximum, total dry matter production of a crop, both in monoculture (Bleasdale, 1960) and in mixture with weeds (Fischer & Miles, 1973). This is due to a faster canopy closure, which results in a high light interception and a good competitive strength of the crop. The objective to obtain maximum marketable yields and the need to perform crop management practices (*e.g.* mechanical weed control, crop harvest) often result in the use of large row spacings. Obviously, these large row spacings are undesirable if one intends to use the competitive strength of the crop to suppress the weed population. Therefore, optimisation of factors such as row spacings and plant densities, to find an optimal solution for the various objectives is needed. That requires better insight in the trade-offs of each decision, which should be based on quantitative knowledge and understanding.

LIMITATION OF THE RESEARCH PROBLEM

This thesis deals with intra-specific and inter-specific competition in canopies with a row structure. To study this, two 'model systems' were chosen, *i.e.* witloof chicory + associated weeds, and white cabbage + clover.

Witloof chicory (*Cichorium intybus* L.) is a crop with an open canopy structure, due to the large row widths used (Schnieders, 1992; Schnieders & Lotz, 1993). The slow initial growth of witloof chicory (Stryckers, 1983; Groenwold & Van de Geijn, 1990; Meijer & Mathijssen, 1992) also contribute to its open canopy structure. Weed control is thus a critical issue in the management of a witloof chicory crop (Richards, 1944; Poll & Douglas, 1987). Witloof chicory is grown for its storage roots. After harvest the roots can be placed in the dark and forced to produce a blanched compact head (called chicons) of leaves which can be consumed as a salad or vegetable (Nicholson *et al.*, 1969). Alternatively, the storage roots can be processed for its fructose (Chubby & Dorrell, 1978; Coppens d'Eeckenbrugge *et al.*, 1989) or inulin contents (Meijer & Mathijssen, 1992, 1993), dried and roasted as a coffee substitute (Nicholson *et al.*, 1969). In the growing of the storage roots for chicon production, not only the total yield but also the diameter of the roots is important. The economic value of storage roots with diameters of 25 - 32.5 mm, 32.5 - 45 mm, and > 45 mm, was 0.015, 0.078, and 0.069 Dfl. per root, respectively (Van Kruistum, 1997). An irregular witloof chicory crop has negative effects, not only on root size distribution, but also on the ripening of the roots and the chicon quality (Anonymous, 1989, Van Kruistum *et al.*, 1993). A review of the sources of variability in plant weight in even-aged stands of monocultures, listed differences in photosynthetic growth and differences in available space per plant among the causes of this variability (Benjamin & Hardwick, 1986). Thus, it may well be that the presence of weeds competing for resources and space, not only reduces the total dry matter of storage roots, but also changes the fraction of storage roots with a favourable diameter.

Three weed species were selected to be grown in competition with witloof chicory, *i.e.* *Senecio vulgaris* L. (groundsel), *Chenopodium album* L. (fat hen) and *Solanum nigrum* L. (black nightshade). These species were chosen because they are (potentially) troublesome weeds in witloof chicory, and because the different species cover a wide range of physiological and especially morphological characteristics. The weed species increase in plant height and plant diameter, going from *S. vulgaris*, to *S. nigrum* and *C. album*. *S. vulgaris* cannot be controlled by any of the herbicides, permitted for use in witloof chicory (Anonymous, 1989). A complete data set was available for *C. album*, and some data was available for *S. vulgaris* and *S. nigrum*, at the start of this study.

To test the principles obtained from the witloof chicory system in other multi-species situations, a data set (Theunissen *et al.*, 1995; Lotz *et al.*, 1997) was available for the interaction between white cabbage and clover species, *i.e.* white clover (*Trifolium repens*) or subterranean clover (*Trifolium subterraneum*). White cabbage is grown in rows and does not achieve a complete soil cover, when grown for the fresh market production. Cabbage was intercropped with the clover species, because the presence of a clover canopy resulted in a lower pest infestation of cabbage. Although competition with clover reduced the fresh weights of the cabbage heads, the quality was higher and the resulting economic yield was higher (Theunissen *et al.*, 1995). This data set was used to parameterise and validate the simulation model, and to evaluate which measures can be taken to minimise the negative effects of clovers on the growth of cabbage while maintaining a full clover canopy.

OBJECTIVES AND APPROACH OF THE THESIS

The main objective of this thesis is to quantitatively explain the effects of spatial arrangements, emergence dates, plant densities, and physiological and morphological characteristics of competing species in a canopy with a row structure, on growth and dry matter production of those species. For the development of new weed management strategies, it is essential to have a good quantitative knowledge of the effects of all these factors on growth and development of weeds, and on the interaction between crops and weeds, at different growth situations. More quantitative insight in the whole life cycle of the weeds is also needed to predict at an early stage in the growing season: (1) the yield loss caused by weed competition, (2) the effects of weed management practices on this yield loss, and (3) the effects of weed management practices on the reproductive output of weeds and its consequences for subsequent crops.

Because, so many factors influence the outcome of crop/weed competition (Van Heemst, 1985; Radosevich, 1987; Kropff & van Laar, 1993), a system-analytical approach was adopted, in which experimental studies and simulation studies were performed side by side. The present eco-physiological models for crop-weed competition assume a horizontally homogeneous distribution of leaves (Kropff & Lotz, 1992a; Schnieders & Lotz, 1993). These models cannot correctly simulate competition in crops with a row structure. Models that are fine-tuned to such situations must therefore be developed.

The necessity to reduce the use of herbicides, has resulted in a growing interest in crop husbandry practices that enhance crop interference, such that fewer curative weed management practices are necessary. Simulation studies will be used to analyse the effects of crop husbandry practices (*e.g.* variety choice, row spacing) and weed management practices (*e.g.* timing and efficacy of control measurements) and it should be possible to indicate cropping measures that can be taken to optimise crop growth with respect to weed suppression in row crops. This study may provide tools, which can be used to develop advisory systems for integrated weed management.

OUTLINE OF THE THESIS

The importance of the spatial arrangements of plants and the type of resource competition on the growth of witloof plants and *S. vulgaris* plants were studied in two pot experiments in a greenhouse. The experimental results are described in Chapter 2.

A dynamic mechanistic model for intra-specific and inter-specific competition in a canopy with a row structure (INTERROW) is described in Chapter 3. Competition for the resources light, water and nitrogen, is described in terms of the underlying physiological and morphological processes. The simulation of experimentally determined light profiles in different canopy arrangements by the INTERROW model was evaluated. The model was used to simulate the theoretical effects of canopy dimensions on plant growth.

The results of field experiments, in which the effects of spatial arrangements, relative emergence dates, and plant densities of several weed species on growth and dry matter production of witloof were studied, are described in Chapter 4. Data from some of the experiments were used to parameterise the INTERROW model, and data from the other experiments were used to validate the model.

A data set from a series of field experiments in which white cabbage was intercropped with various clover species, was used to evaluate the ability of the INTERROW model to correctly simulate the effects of competition on growth and dry matter production (Chapter 5).

The effects of competition with weeds on the dry weight and the root diameter of individual storage roots of witloof chicory, are described in Chapter 6.

The effects of various levels of competition, both intra-specific competition and inter-specific competition with witloof chicory, on the reproductive output of *C. album*, *S. nigrum*, and *S. vulgaris*, are described in Chapter 7.

In Chapter 8 the results of the experimental and model studies, described in the previous Chapters, are integrated and discussed. Crop husbandry practices may lead to an increase in the competitive ability of a crop, such that crop yield and crop quality are not substantially reduced, and such that the reproductive output of the weeds can be minimised.

CHAPTER 2

EFFECTS OF SPATIAL ARRANGEMENTS ON COMPETITION BETWEEN THE PROSTRATE GROWING WITLOOF CHICORY AND THE ERECT GROWING *SENECIO VULGARIS*

B.J. Schnieders and L.A.P. Lotz

ABSTRACT

The effects of spatial plant arrangements and type of resource competition (asymmetric or symmetric) on growth of the prostrate growing witloof chicory (*Cichorium intybus* L.) and the erect growing *Senecio vulgaris* L., were studied in two pot experiments.

When resource competition was primarily asymmetric, *i.e.*, for light, the dry weight of a target witloof chicory plant was reduced more when a *S. vulgaris* plant grew at a shorter distance, whereas the dry weight of the *S. vulgaris* plant was not affected. The position of a *S. vulgaris* plant also affected the uniformity in dry weight of the witloof chicory plants in the pot.

When resource competition was shifted from being primarily asymmetric towards becoming more symmetric, *i.e.*, for nitrogen, the effects of the position of the *S. vulgaris* plant on the dry weight of the target witloof chicory plant and on the uniformity in dry weight of the witloof chicory plants became less pronounced or were absent.

Nine neighbourhood models were fitted to the data and compared for lack-of-fit. The best fits were obtained when only the density of neighbours was included in the measure of competition pressure. When the spatial arrangement or size (height and diameter) of neighbours was included in the measure of competition pressure, the model fits did not improve.

The analysis of variance showed clear effects of spatial arrangements on the outcome of competition, whereas the neighbourhood model fits did not improve when spatial arrangements were included in the measure of competition. A possible explanation for this discrepancy could be that the substantial effects of the presence of the *S. vulgaris* plant masked the effects of the spatial position of the *S. vulgaris* plant. Also, the way that the effects of spatial arrangements were incorporated in the models may have been inadequate.

Our experiments showed that the influence of spatial arrangements on the growth of individual plants may not be negligible when studying competition in plant communities, especially when resource competition is asymmetric.

INTRODUCTION

Individual plants interact primarily with nearby plants. The ability of an individual plant to capture resources necessary for growth, is affected by the spatial arrangement of plants in its locality, *i.e.*, neighbourhood (Mack & Harper, 1977; Weiner, 1982; Mithen *et al.*, 1984; Pacala & Silander, 1987; Radosevich, 1988, Bonan, 1991). Understanding of the relationship between spatial arrangement and intensity of competition has not been well developed (Firbank & Watkinson, 1990; Bonan, 1991, 1993).

Plants display strong plasticity in the response to environmental variation and to competitive influences of neighbouring individuals, which causes variation in plant growth and plant size (Harper, 1977). Several explanations for this variation in growth and size have been put forward. Firstly, variation in plant growth and plant size can be caused by intrinsic differences in plant growth, due to variation in seed mass, germination date, site quality, or genetic factors (Harper, 1977; Watkinson *et al.*, 1983; Firbank & Watkinson, 1987). Secondly, the type of resource competition can also cause variation in plant growth and plant size. If competition is asymmetric or one-sided (Weiner, 1985, 1988b, 1990), *i.e.*, if larger plants receive a disproportionate share of resources relative to their size, then differences in size will generate great variation in growth rates and consequently enhance variation in plant size. Size variability should also increase as the severity of competition increases (Bonan, 1991). On the other hand, if competition is symmetric, *i.e.*, if shared resources are distributed in proportion to plant size, then competition will not change the variation in growth rates or plant size among competing plants. Variation in plant size does not increase as the severity of competition increases. Thirdly, individual plants vary in the degree of crowding that they experience in their neighbourhood. Neighbourhood competition, in which resource availability depends on size, abundance and distance of neighbours, creates variability in growth rates and thus results in an increased variability in plant size, irrespective of whether resources are asymmetrically or symmetrically distributed among competing plants (Bonan, 1991). Neighbourhood analyses generally account for less than one-half of the total variation in individual plant performance (Bonan, 1991, 1993). It was suggested that this reflects both the relative importance of non-competitive factors (e.g. seed mass, germination date, site quality, or genetic factors) in affecting plant growth (Bonan, 1993), and the limitations in our understanding of the effects of spatially explicit competition on plant growth (Bonan, 1993; Stoll *et al.*, 1994).

Competition for light is thought to be primarily asymmetric (Watkinson *et al.*, 1983; Weiner, 1985, 1986, 1988b). Competition for nutrients and water is thought to be more symmetric (Weiner, 1985, 1986, 1988b; Weiner & Thomas, 1986; Tollenaar, 1992). Newman (1983) reported that the rate of nitrogen capture was proportional to the amount of roots, and argued that this would be expected when both root distribution and movement of nitrate or ammonium ions are random in the soil. However, there may be situations in which competition for nutrients is asymmetric, for example when nutrients can be pre-empted by individuals with larger roots (Weiner, 1986, 1988b).

In plant communities, competition for the available resources generally occurs between more than two plants, often of different species. If, for example, one plant of a tall, erect growing species competes with several plants of a short, prostrate growing species, a change in the distance between that tall plant and a specific short plant (henceforward referred to as the target plant) will, more than likely but not necessarily, alter the distances between that tall plant and the other short plants. When, in this situation, competition is mainly for light and the distance between the tall plant and the target plant is reduced, the amount of light absorbed by the target plant will become less. The light interception is reduced, because a larger part of the target plant gets into the zone of shading produced by the tall plant, within which the tall plant will exert a strong competitive effect. Consequently, if the resource use efficiency remains the same, the reduced capture of light by the target plant, will result in a reduced growth. A change in the distance between the tall plant and the target plant is also likely to affect the variability in plant weight of the shorter species. For example, when a reduction in distance between the tall plant and the target plant coincides with an increase in distance between the tall plant and the other plants of the shorter species, then the growth of the target plant will be reduced while the growth of the other plants of the shorter species will be increased. Due to these compensatory effects, the average plant weight of the shorter species may not be affected. Furthermore, the capture of light and growth of the tall plant may not be affected by the presence of a short plant, especially when most of the leaves of the tall plant are above the canopy of the short plant (Weiner & Thomas, 1986; Thomas & Weiner, 1989). When competition shifts from competition for light towards competition for nutrients, and the roots of all plants are evenly distributed through a restricted rooting volume, the spatial position of the tall plant should have less effect on the target plant weight, the variability in plant weight of the shorter species, and the average plant weight of the shorter species. The arguments given above are only valid if the size of the tall plant is relatively unaffected by its position, and the plants grow big enough to interact. It should be kept in mind that in most cases plants compete for both light and nutrients at the same time. One should also realise that asymmetric and symmetric competition are strongly related to competition for light and nutrients, respectively, but are not synonyms (Tollenaar, 1992).

Many descriptive models exist that relate plant weight to some measure of competition pressure. The simplest measure of competition pressure may be the plant density. The relationship between plant density and average plant weight (the reciprocal-yield law) is often used to describe the effects of intra-specific competition (*e.g.* Kira, Ogawa & Sakazaki, 1953; Bleasdale & Nelder, 1960; Holliday, 1960) and can be extended to a model for inter-specific competition (Spitters, 1983). Weiner (1982) and Soetono & Puckridge (1982) presented models that relate the individual plant weight to the density and the spatial arrangement of neighbouring plants. Weiner (1982) showed that in its simplest form, *i.e.*, when no influence of spatial arrangements is assumed, his model is identical with the reciprocal-yield law. Weiner (1984) extended his neighbourhood model with a variable that accounts for the size of the neighbouring plants. It was suggested by Weiner (1984) that neighbourhood models, in which the neighbour effects decrease when the distance gets larger, give a better fit when competition is asymmetric. In contrast, neighbourhood models in which the effect of a neighbour decreases with the square of its distance, give a better fit when competition is symmetric. One would also expect that including a measure of plant size in the neighbourhood models would give a better fit when competition is primarily asymmetric.

To study the effects of spatially explicit competition on plant growth, experiments are needed in which the non-competitive factors, the neighbourhood arrangements and the type of resource competition, can be controlled. The variability caused by seed mass, germination date and genetic factors can be reduced by using seeds of an agricultural species, because its seeds are often supplied in batches with a specified seed size or weight, and its plants are often genetically more homogeneous than plants of natural vegetations. By using pots filled with coarse sand as a growth medium, the site quality will be as equal as possible for all plants. If the roots of all plants and the nutrients are evenly distributed through this restricting rooting volume, then competition for nitrogen will be symmetric (Newman, 1983). By reducing the amount of nitrogen in the nutrient solution, resource competition will become less asymmetric (Thomas & Weiner, 1989; Hara & Yokozawa, 1994).

This study is an attempt to gain a better understanding of the effects of spatially explicit inter-specific competition for resources between a target plant and other plants in its 'restricted' neighbourhood, on plant growth. Such an understanding would be the first step towards a prediction of the effects of competition on dry matter production and population dynamics of each species involved. The effects of spatial arrangement of plants and the type of resource competition on growth, were studied using the prostrate growing witloof chicory (*Cichorium intybus* L.) and the erect growing *Senecio vulgaris* L. Two hypotheses were tested:

- If competition is mainly for light, and if competition for light is primarily asymmetric, then a decrease in distance between a *S. vulgaris* plant and a target witloof chicory plant will reduce the target plant weight. In this paper the term target plant refers to that witloof chicory plant, relative to which the distance of the *S. vulgaris* plant is measured and altered. The uniformity in plant weight of witloof chicory, expressed as the ratio between the target plant weight and the average weight of the other witloof chicory plants in the pot, will also be reduced. The weight of the *S. vulgaris* plant will not be influenced by its own position (experiment 1).
- If competition shifts from competition for light towards competition for nitrogen, and if competition for nitrogen is primarily symmetric, then the above mentioned effects of

distance between a *S. vulgaris* plant and a target witloof chicory plant will become less pronounced at lower nitrogen application rates, due to the decreasing influence of asymmetric competition for light (experiment 2).

MATERIALS AND METHODS

Experiment 1

The effects of the spatial arrangement of witloof chicory and *S. vulgaris* on competition for light were studied in a greenhouse experiment in Wageningen, The Netherlands, during the period April-June 1992. The experiment was done at alternating temperatures (25/15 °C from 06.00-18.00/18.00-06.00 h), under prevailing daylengths and a relative humidity of 75 %. During the experiment, the photosynthetic active radiation (PAR) outside the greenhouse increased from 30 to 42 $mol \cdot m^{-2} \cdot d^{-1}$, of which 50-60 % was transmitted into the greenhouse. An additional 3 $mol \cdot m^{-2} \cdot d^{-1}$ was given with Philips SON-T AGRO 400 W high pressure sodium lamps from 06.00-18.00 h. Water and nutrients were supplied to the pots three times a week with a Steiner solution (pH = 6.5, EC = 1.8 mS; Steiner, 1984), in sufficient quantities to prevent water and nutrient shortages. The nitrogen concentration of the target plant was not affected by any of the treatments, indicating that sufficient amounts of nitrogen were available and that competition for nitrogen was limited or absent. Seeds of witloof chicory and *S. vulgaris* were germinated in Petri-dishes (diameter 9 cm) with a blotting paper (diameter 8.5 cm), which was moistened with 10 ml demineralised water. The Petri-dishes were placed in an incubator (14 h light/10 h dark; 25/15 °C) for 48 hours. At that stage, the white root and shoot tops were just visible. The germinated seeds were planted in pots (7.6 litres, diameter 23 cm), filled with 10 kg coarse sand. Both witloof chicory and *S. vulgaris* emerged uniformly on the third day after planting.

The studied factors and their levels were:

- position of the *S. vulgaris* plant: 1.5, 3.0, 6.0 or 12.0 cm from a target witloof chicory plant (Figure 2.1a). Witloof chicory grown in monoculture was considered as a fifth level. The *S. vulgaris* plant is then at an imaginary infinite distance from the target plant.
- density of witloof chicory: 1, 2 or 3 plants per pot.
- harvest date: 25, 46, 67 and 88 days after planting.

The experiment had a Latin square design, with four replicates (rows) and four harvest dates (columns) in a 4x4 matrix. Within each matrix cell all 15 combinations of the position-of-*S.-vulgaris*-factor and the density-of-witloof-chicory-factor were randomly distributed, giving a total of 240 pots. The distance between the pots was sufficiently large to avoid interference between pots. The leaf area (LI-COR area meter, model 3100, Lincoln, NE, USA), plant height and plant diameter were measured. The dry weights of the plant organs were taken after drying at 75 °C for 48 hours.

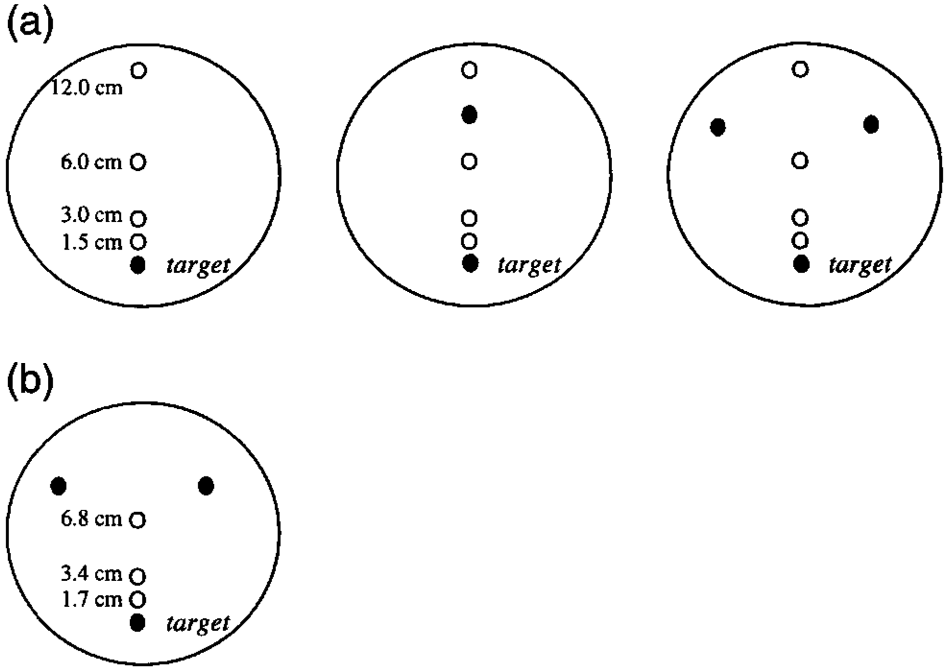

Figure 2.1 The plant arrangements in the pots of experiment 1 (a) and experiment 2 (b). A pot in experiment 1 contained one, two or three witloof chicory plants (•), and one *S. vulgaris* plant (o) at a distance of 1.5, 3.0, 6.0 or 12.0 cm from the target witloof chicory plant, except for the monoculture treatments where the *S. vulgaris* plant was absent. A pot in experiment 2 contained three witloof chicory plants, and one *S. vulgaris* plant at a distance of 1.7, 3.4 or 6.8 cm from the target plant, except for the monoculture treatments where the *S. vulgaris* plant was absent.

Experiment 2

The effects of the spatial arrangement of witloof chicory and *S. vulgaris* on competition for light and nitrogen were studied in a greenhouse experiment in Wageningen, The Netherlands, during the period February-April 1991. The experiment was done at alternating temperatures (23/13 °C from 06.30-18.30/18.30-06.30 h), under prevailing daylengths and a relative humidity of 80 %. During the experiment, the PAR outside the greenhouse increased from 11 to 30 $mol \cdot m^{-2} \cdot d^{-1}$, of which 50-60 % was transmitted into the greenhouse. An additional 3 $mol \cdot m^{-2} \cdot d^{-1}$ was given with Philips HLRG 400 W high pressure mercury lamps from 06.30-18.30 h. The nutrients were supplied to the pots with 300 ml of a modified Steiner solution (pH = 6.0, EC = 1.8 mS; Steiner, 1984), three times each week. The Steiner solution was modified, such that three levels of nitrogen concentration were established, while the other nutrients remained in ample supply. The pots were weighed and restored to original pot weight with water every week, with a correction for the estimated production of plant dry matter. The method to germinate the seeds was identical to the method described in experiment 1. The germinated seeds were planted in pots (7.6 litres, diameter 23 cm), filled with 10 kg coarse sand. Both witloof chicory and *S. vulgaris* emerged uniformly on the third day after planting.
The studied factors and their levels were:

- position of the *S. vulgaris* plant: 1.7, 3.4 or 6.8 cm from the target witloof chicory plant (Figure 2.1b). Witloof chicory grown in monoculture was considered as a fourth level. The *S. vulgaris* plant is then at an imaginary infinite distance from the target plant. At the 6.8 cm distance the *S. vulgaris* plant had equal distances towards all 3 witloof chicory plants.
- nitrogen application rate: 120, 240 or 480 mg·pot-1 for the 10 week growing period. The intermediate N-level is comparable with 60 kg·ha-1 N, which is equivalent to the amount of nitrogen available to the plants during a growth period of 70 days under field conditions.
- harvest date: 28, 49 and 70 days after sowing.

The experiment had a Latin square design, with four replicates (rows) and three harvest dates (columns) in a 4x3 matrix. Within each matrix cell all 12 combinations of the position-of-*S.-vulgaris*-factor and the nitrogen-application-rate-factor were randomly distributed, giving a total of 144 pots. The distance between the pots was sufficiently large to avoid interference between pots. The leaf area (LI-COR area meter, model 3100, Lincoln, NE, USA), plant height and plant diameter were measured. The dry weights were taken after drying at 75 °C for 48 hours. The total nitrogen contents of the plants was determined with the Dumas extraction procedure, using a Macro-N analyser (Elementar

Analysen-Systeme GmbH, Hanau, Germany).

Models

Weiner (1982) presented a neighbourhood model for competition between plants that takes into account both the numbers of neighbouring plants and their spatial arrangement:

$$[1] \quad Y_{1,t} = \frac{Y_{1,\max}}{1+C}$$

where $Y_{1,t}$ is the total plant weight (g) of a target plant of species 1, $Y_{1,\max}$ is the weight (g) of a plant of species 1 in the absence of competition, and C is a measure of competition pressure, which in its multi-species version is given by:

$$[2] \quad C = k_1 \sum_{i=1}^{i=N_1} \frac{1}{d_{i,1}{}^{a}} + \ldots + k_n \sum_{i=1}^{i=N_n} \frac{1}{d_{i,n}{}^{a}}$$

where k_n is a constant expressing the mean effect of an individual of species n on $Y_{1,t}$, N_n is the density (plants·m^{-2}) of species n, $d_{i,n}$ is the distance (cm) between the target plant and the i^{th} neighbouring plant of the n^{th} species, and a is a factor indicating that the influence of a neighbouring plant decreases linearly (a = 1) or quadratically (a = 2) with its distance. Weiner (1984) suggested that the neighbourhood effects are related to the distance when competition is for light, and to the square of the distance when competition is for nutrients or water. When a = 0, effects of distance are absent, *i.e.*, each neighbouring plant has the same competitive effect.

Weiner (1984) extended equation 2 with a measure for plant size:

$$[3] \quad C = k_1 \sum_{i=1}^{i=N_1} \frac{s_{i,1}}{d_{i,1}{}^{a}} + \ldots + k_n \sum_{i=1}^{i=N_n} \frac{s_{i,n}}{d_{i,n}{}^{a}}$$

where $s_{i,n}$ is the size of the i^{th} neighbouring plant of the n^{th} species. We extended equations (2) and (3) with a variable (F) to account for the effects of various nitrogen fertiliser treatments:

$$[4] \quad C = k_1 \sum_{i=1}^{i=N_1} \frac{F}{d_{i,1}{}^{a}} + \ldots + k_n \sum_{i=1}^{i=N_n} \frac{F}{d_{i,n}{}^{a}}$$

and:

$$[5] \quad C = k_1 \sum_{i=1}^{i=N_1} \frac{F \cdot s_{i,1}}{d_{i,1}{}^{a}} + \ldots + k_n \sum_{i=1}^{i=N_n} \frac{F \cdot s_{i,n}}{d_{i,n}{}^{a}}$$

The value of F is set to unity when competition for nitrogen is absent, *i.e.*, for experiment 1 and for the highest N-treatment in experiment 2. The theory of symmetric competition suggests that a reduction of nitrogen availability by 50 % will reduce the nitrogen availability for each plant by 50 %, which may lead to an increased competition. So, the value of F and consequently C, are doubled when the nitrogen availability is reduced by 50 %.

Statistical analysis

Analysis of variance (ANOVA) with the GENSTAT package (Genstat 5 Committee, 1993) was used to test the effects of the experimental factors on plant weight, uniformity in plant weight, plant height and specific leaf area. The ANOVA's on the data of plant weight and plant height were done on Log_{10}-transformed data.

The uniformity (U) in plant weight of witloof chicory, except when only one witloof chicory plant was present in a pot, was expressed by:

$$U = \frac{Y_t}{Y_r}$$

where Y_t is the target plant weight ($g{\cdot}plant^{-1}$) (Figures 2.1a, b) and Y_r is the average plant weight ($g{\cdot}plant^{-1}$) of the other witloof chicory plants in a pot. The uniformity measure is used, because it unambiguously shows the response of the target plant, relative to that of the other witloof chicory plants, to the position of the *S. vulgaris* plant. When the target plant and the other witloof chicory plants are equally affected, U equals 1. When the *S. vulgaris* plant affects the target plant more than the other witloof chicory plant $U < 1$. Our ratio is simple, matches our needs exactly, and is therefore preferred above indices such as the Gini coefficient or the coefficient of variation. The data of uniformity were Log_{10}-transformed, before ANOVA was done.

Orthogonal contrasts (Gilligan, 1986; Sokal & Rohlf, 1981) were used to test *a priori*, whether the presence of a *S. vulgaris* plant significantly affected growth of witloof chicory. Since Weiner (1984) suggested that the effect of a neighbouring plant decreases with its distance when competition is for light, and with the square of its distance when competition is for nutrients or water, orthogonal polynomial contrasts (Dawkins, 1983; Gilligan, 1986; Sokal & Rohlf, 1981) were used to test *a priori* the effects of the position of the *S. vulgaris* plant.

Non-linear regression analyses with the GENSTAT package (Genstat 5 Committee, 1993) were done to fit nine versions of Weiner's neighbourhood model to the data of the final harvest of the two experiments. Since the neighbourhood models can not be regarded as submodels, which have different numbers of predictor variables and thus different degrees of freedom of the rest variance, a straightforward comparison of the residual sums of squares was not possible. Instead, a method for model comparison presented by Linhart & Zucchini (1986) was used. The lack-of-fit or bias B_i of a model M_i was defined as the residual sum of squares of the model fit to the 'true state of nature'. This 'true state of nature' was assumed to be adequately described by the normal ANOVA model corresponding to the experimental design. This ANOVA model can accommodate arbitrary treatment effects. Thus, the bias B_i was estimated as the residual sum of squares obtained when the model M_i was adapted to the ANOVA-fit. For each pair of models M_i and M_j, this resulted in an estimated difference in bias (B_i - B_j). To test whether this estimated difference in bias was significantly different from zero, a two-sided equal-tailed 95% confidence interval for difference in bias was calculated for each model pair. The interval did not comprise the value zero. This procedure yields separate tests for each pair-wise comparison. The confidence intervals were calculated with a parametric bootstrap method, employing Studentisation (Hall, 1992). The bootstrap sample was 1000 and actual tests were performed by counting the fraction of negative differences in bias in the sample. Model M_i fitted significantly better than model M_j when this fraction was higher than 0.975, and fitted significantly worse when this fraction was smaller than 0.025. Note that the analysis performed, being based on the experimental design, enables the construction of confidence intervals and the execution of tests. Thus, the analysis leads to somewhat stronger statements than can be obtained by other relevant model selection criteria, like that of Akaike (*e.g.* Sakamoto *et al.*, 1986).

RESULTS

Experiment 1

The dry weight of the target witloof chicory plant at final harvest was reduced when a *S. vulgaris* plant was present, to approximately 33 % of that of the target plant grown in monoculture (Figure 2.2a). This effect of inter-specific competition was smaller at higher witloof chicory densities (interaction of mono_vs_mixture contrast of position x density; $F = 3.36$, $d.f._{res} = 168$, $P < 0.05$). A shorter distance between the target plant and the *S. vulgaris* plant resulted in a larger reduction of the weight of the target plant (linear

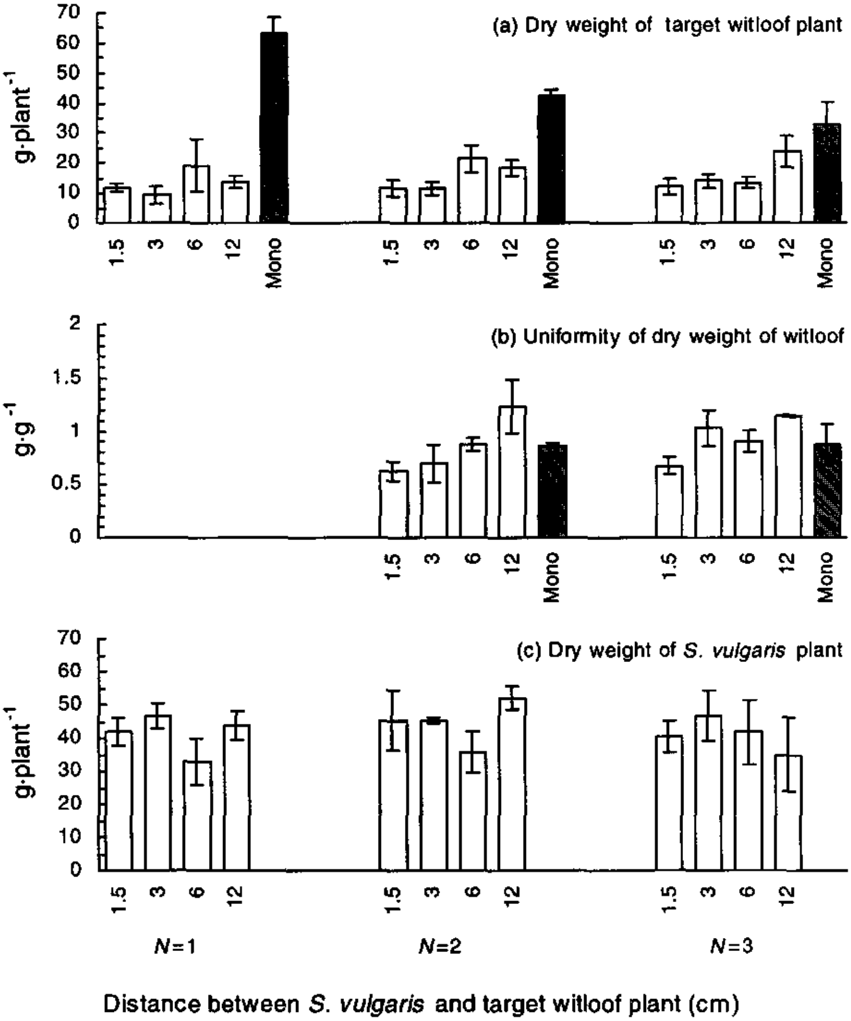

Figure 2.2 The effects of the position of the *S. vulgaris* plant (1.5, 3, 6 or 12 cm from the target witloof chicory plant) and plant density of witloof chicory (N = 1, 2 or 3 plants·pot^{-1}) on the dry weight of the target witloof chicory plant (a), the uniformity in dry weight of witloof chicory (b), and the dry weight of the *S. vulgaris* plant (c), at the final harvest of experiment 1.

contrast of position; $F = 44.33$, $d.f._{res} = 168$, $P < 0.001$), and in a reduction of the uniformity in plant weight of witloof chicory (Figure 2.2b). This effect on uniformity in plant weight was present in all but the first harvest (interaction of linear contrast of position x harvest; $F = 3.78$, $d.f._{res} = 108$, $P < 0.05$), and no interactions with the density of witloof chicory were found. The weight of the *S. vulgaris* plant was only slightly reduced when the density of witloof chicory was higher, and was not affected by its position (Figure 2.2c).

The height of the target plant at the final harvest was increased by circa 30 %, from 25 to 32 cm, at higher witloof chicory densities, when *S. vulgaris* was absent. The presence of a *S. vulgaris* plant reduced the height of the target plant by circa 20 %, irrespective of the position of the *S. vulgaris* plant. The specific leaf area of the target plant at the final harvest was increased by circa 4 % to 191 $cm^2 \cdot g^{-1}$ when the *S. vulgaris* plant grew at a shorter distance. Neither the height nor the specific leaf area of the *S. vulgaris* plant were affected by the position of the *S. vulgaris* plant, nor by the density of witloof chicory.

The nitrogen concentration of the target plant decreased from 0.050 $g \cdot g^{-1}$ at harvest 1 to 0.017 $g \cdot g^{-1}$ at harvest 4, and was not affected by any of the treatments, indicating that sufficient amounts of nitrogen were available and that competition for nitrogen was limited.

The parameter estimates and the biases of the fits of the different models are shown in Table 2.1a. The differences in lack-of-fit between model 1 (effect of distance not included in measure of competition pressure, d^{-0}) and model 2 (linear effect of distance included in measure of competition pressure, d^{-1}) were not significant (Table 2.1b). When plant height (models 4 and 5) or plant diameter (models 7 and 8) was included in the model, the lack-of-fit did not significantly change. The model fit became significantly worse when a quadratic effect of distance (d^{-2}) was included (models 3, 6 and 9). The model with the lowest bias, *i.e.*, model 1 from Table 2.1, to the data of the final harvest of experiment 1, accounted for 75.3 % ($r^2_{adj} = 0.753$) of the variance (Figure 2.3).

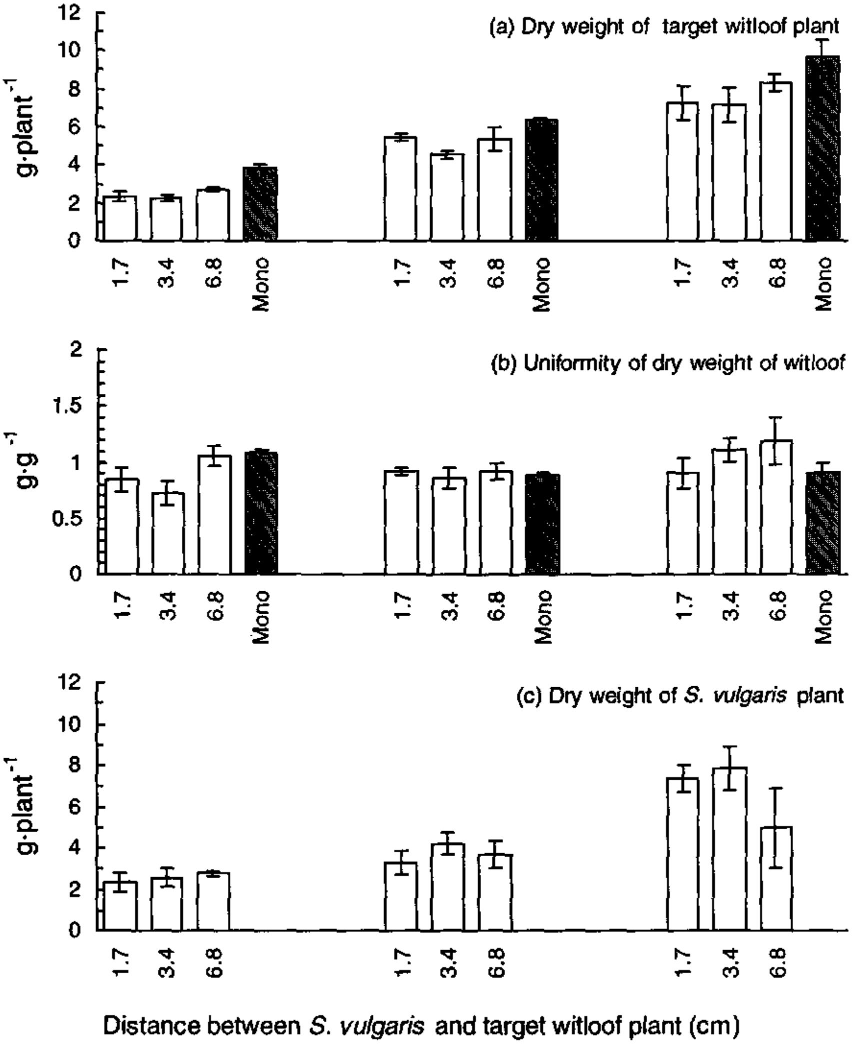

Figure 2.4 The effects of the position of the *S. vulgaris* plant (1.7, 3.4 or 6.8 cm from the target witloof chicory plant) and the nitrogen application rate (120, 240 or 480 mg·pot^{-1}) on the dry weight of the target witloof chicory plant (a), the uniformity in dry weight of witloof chicory (b) and the dry weight of the *S. vulgaris* plant (c), at the final harvest of experiment 2.

The height of the target plant at the final harvest was circa 7, 11 and 19 cm at 120, 240 and 480 mg·pot^{-1} N, respectively. The height of the target plant was increased by circa 15 % when the *S. vulgaris* plant grew at a shorter distance. The specific leaf area of the target plant at the final harvest at 120, 240 and 480 mg· pot^{-1} N was circa 280, 237 and 240 cm^2·g^{-1}, respectively. It was affected by the position of the *S. vulgaris* plant at the 240 mg·pot^{-1} N treatment only, where an increase of 16 % was found at the distance of 3.4 cm. The height of the *S. vulgaris* plant was circa 32, 39 and 40 cm at 120, 240 and 480 mg·pot^{-1} N, respectively. The height of the *S. vulgaris* plant was largest when the distance between the target plant and the *S. vulgaris* plant was 3.4 cm. The specific leaf area of the *S. vulgaris* plant was circa 307, 327 and 373 cm^2·g^{-1} at 120, 240 and 480 mg·pot^{-1} N, respectively, and was not affected by its position.

The nitrogen concentration of the target plant decreased in time, from 0.048 g·g^{-1} at harvest 1 at all levels, to 0.0083, 0.0086 and 0.0134 g·g^{-1} at 120, 240 and 480 mg·pot^{-1} N at the final harvest. This decrease tended to occur faster at lower N-levels and when a *S. vulgaris* plant was present. (interaction of mono_vs_mixture contrast of position x nitrogen x harvest; $F = 2.22$, $d.f._{res} = 99$, $P < 0.1$). The nitrogen concentration of the *S. vulgaris* plant also decreased in time, from 0.052 g·g^{-1} at harvest 1 at all N-levels, to 0.0134, 0.0143 and 0.0169 g·g^{-1} at 120, 240 and 480 mg·pot^{-1} N at final harvest. The position of the *S. vulgaris* plant did not affect the nitrogen contents of both the target plant and the *S. vulgaris* plant.

The parameter estimates and biases of the fits of the different models are shown in Table 2.2a. The differences in lack-of-fit between model 1 (effect of distance not included in measure of competition pressure, d^{-0}), model 2 (linear effect of distance included in measure of competition pressure, d^{-1}), and model 3 (quadratic effect of distance included in measure of competition pressure, d^{-2}) were not significant (Table 2.2b). With the exception of model 7, the model fit became significantly worse when the plant height or the plant diameter were included in the measure of competition pressure. The bias of the model fits increased (Table 2.2a), indicating a greater lack-of-fit, when going from d^0 to d^{-1} and d^{-2}. The model with the lowest bias, *i.e.*, model 1 from Table 2.2, to the data of experiment 2, accounted for 84.7 % ($r^2_{adj} = 0.847$) of the variance (Figure 2.5).

Table 2.2 (a) Parameter estimates (standard errors in parentheses) and biases, of the fits of nine versions of Weiner's neighbourhood model (1982, 1984) to the data of experiment 2. The parameters that could be included in the measure of competition pressure (*C*) were: *N* = number of neighbouring plants, *F* = level of fertiliser application, *d* = distance between the neighbouring plant and the target witloof chicory plant, *h* = height of neighbouring plants, Ø = diameter of neighbouring plants; (b) The comparison matrix, showing the differences in lack-of-fit of the neighbourhood models to the data of experiment 2. If the item in the i^{th} row and the j^{th} column > 0.975, model *i* fits better than model *j*; if the value is < 0.025 model *i* fits worse than model *j*. * marks significant differences. Note that in (b) the models are not in numerical order, but are sorted on ascending bias.

(a) Parameter estimates and biases

		parameters of the model			bias
model nr.	parameters included in C	$Y_{\max}$	$k_{\text{witloof chicory}}$	$k_{S.\ \text{vulgaris}}$	
	ANOVA				0.0
1	$N\cdot F\cdot d^{0}$	19.42 *(3.12)*	0.507 *(0.140)*	0.510 *(0.132)*	8.7
2	$N\cdot F\cdot d^{-1}$	19.56 *(3.39)*	5.890 *(1.700)*	1.149 *(0.354)*	14.1
3	$N\cdot F\cdot d^{-2}$	19.29 *(3.66)*	67.900 *(20.700)*	1.274 *(0.571)*	22.9
4	$N\cdot F\cdot h\cdot d^{0}$	26.70 *(16.90)*	0.066 *(0.060)*	0.026 *(0.017)*	92.6
5	$N\cdot F\cdot h\cdot d^{-1}$	30.90 *(26.00)*	0.900 *(1.000)*	0.084 *(0.073)*	113.9
6	$N\cdot F\cdot h\cdot d^{-2}$	48.10 *(78.00)*	18.900 *(34.900)*	0.179 *(0.302)*	150.3
7	$N\cdot F\cdot\varnothing\cdot d^{0}$	224.00*(563.00)*	0.341 *(0.813)*	0.353 *(0.971)*	16.4
8	$N\cdot F\cdot\varnothing\cdot d^{-1}$	73.70 *(79.00)*	1.180 *(1.400)*	0.260 *(0.296)*	36.6
9	$N\cdot F\cdot\varnothing\cdot d^{-2}$	43.70 *(31.30)*	7.670 *(6.540)*	0.185 *(0.153)*	58.2

(b) Comparison matrix

model nr.		1	2	7	3	8	9	4	5	6
1	$N\cdot F\cdot d^{0}$	—	0.789	0.922	0.920	0.988*	0.999*	1.000*	1.000*	1.000*
2	$N\cdot F\cdot d^{-1}$	0.211	—	0.569	0.970	0.999*	1.000*	1.000*	1.000*	1.000*
7	$N\cdot F\cdot\varnothing\cdot d^{0}$	0.078	0.431	----	0.785*	0.982*	0.999*	1.000*	1.000*	1.000*
3	$N\cdot F\cdot d^{-2}$	0.080	0.030	0.215	—	0.966	1.000*	1.000*	1.000*	1.000*
8	$N\cdot F\cdot\varnothing\cdot d^{-1}$	0.012*	0.001*	0.018*	0.034	----	1.000*	0.997*	1.000*	1.000*
9	$N\cdot F\cdot\varnothing\cdot d^{-2}$	0.001*	0.000*	0.001*	0.000*	0.000*	----	0.955	0.998*	1.000*
4	$N\cdot F\cdot h\cdot d^{0}$	0.000*	0.000*	0.000*	0.000*	0.003*	0.045	----	0.973	1.000*
5	$N\cdot F\cdot h\cdot d^{-1}$	0.000*	0.000*	0.000*	0.000*	0.000*	0.002*	0.027	----	1.000*
6	$N\cdot F\cdot h\cdot d^{-2}$	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	----

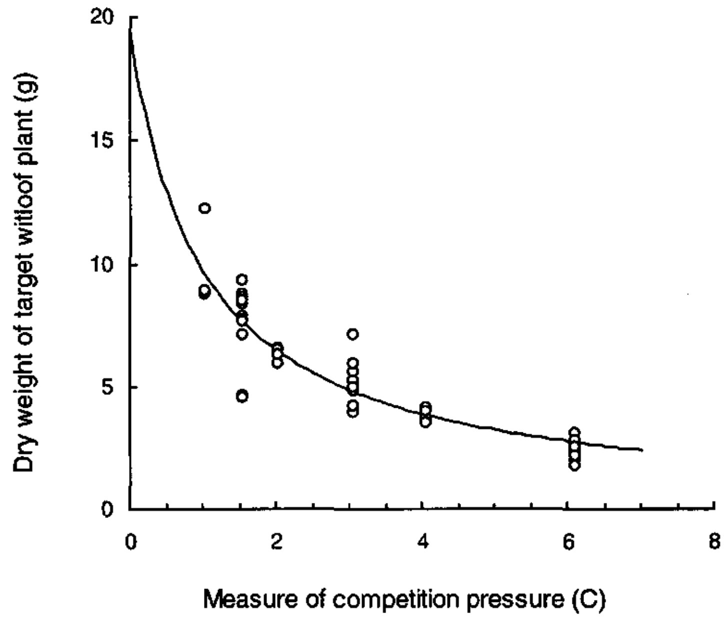

Figure 2.5 The fit of the neighbourhood model with the lowest bias (model 1 in Table 2.2), to the data of experiment 2. Only plant density and nitrogen application rate were included in the measure of competition pressure of model 1.

DISCUSSION

The results of the two experiments cannot be compared directly, since the experiments were performed at different times and had different experimental set-ups. As was presumed, the results of experiment 1 could be analysed in terms of the effects of spatially explicit competition on plant growth, in a situation where competition for resources was primarily asymmetric, *i.e.*, for light. Neither the nitrogen concentration, nor the shoot/root ratio (data not presented) of the target witloof chicory plant was decreased by any of the treatments, indicating that sufficient amounts of nitrogen were available and that competition for nitrogen was limited or absent in experiment 1. The taller *S. vulgaris* plant pre-empted the available light resource. This resulted in a reduced dry weight of the target witloof chicory plant. When the *S. vulgaris* plant was at a shorter distance to the target plant, even less light was available for the target plant and its dry weight was further reduced. When the distance between the target plant and the *S. vulgaris* plant was smaller, and the distance between the other witloof chicory plants and the *S. vulgaris* plant were larger, the uniformity in plant weight of witloof chicory was reduced. This implies that a reduction in target plant weight was compensated for by an increase in weight of the other witloof chicory plants. The presence of the taller *S. vulgaris* plant had such a dominant effect, that the effects of intra-specific competition between witloof chicory plants appeared to be absent. The *S. vulgaris* plant escaped competition for light, hence its dry weight was not affected by its position. These results support our first hypothesis on the effects of spatially explicit competition, in a situation where competition for resources was primarily asymmetric.

When competition was presumably both for light and nitrogen (experiment 2), the dry weight of the target witloof chicory plant was also reduced due to competition with the taller *S. vulgaris* plant. The effect of the position of the *S. vulgaris* plant on the target plant dry weight and on the uniformity in plant weight of witloof chicory appeared to be smaller when the nitrogen application rate was lower, *i.e.*, when resource competition was more symmetric. When the pots were harvested, it was indeed observed that the roots of all plants were uniformly distributed through the pot volume, making symmetric competition for nitrogen possible. The observation that the position of the *S. vulgaris* plant did not affect the nitrogen contents of both the target witloof chicory plant and the *S. vulgaris* plant, is further evidence that the nitrogen was shared in proportion to plant size as was suggested by the hypothesis of symmetric competition (Weiner, 1985, 1986, 1988b; Weiner & Thomas, 1986; Tollenaar, 1992). The dry weight of the taller *S. vulgaris* plant was not affected by its position. The results of experiment 2 support our second hypothesis on the effects of spatially explicit competition, in a situation where competition is shifted from competition for light towards competition for nitrogen, and where competition for nitrogen is primarily symmetric.

The erect growing *S. vulgaris* has an important advantage over the prostrate growing witloof chicory, when competition is for light. The *S. vulgaris* plant can escape from competition for light through an increased stem elongation. Since witloof chicory has a rosette growth form, its potential to escape from competition for light is limited to an increase in leaf angle, leaf size or specific leaf area. As expected, the height advantage of *S. vulgaris* had substantial effects when competition was primarily for light (experiment 1), and was less important when competition for nitrogen became more apparent (experiment 2). Witloof chicory responded to competition for light with an increase in specific leaf area (experiment 1 and 2) and also an increase in height (experiment 2). Other studies have shown that *Plantago major*, another prostrate growing species with a rosette growth form, also responded with an increased specific leaf area to increased competition with taller growing grasses and shrubs, and with an increased leaf length to competition with shorter grasses (Lotz, 1990; Lotz *et al.*, 1990b).

The neighbourhood of a plant can be described by the density, spatial arrangement and size (height and diameter) of its neighbours. It was shown that the spatial arrangement of competing species can have effects on the outcome of competition, both in terms of the individual plant weight and the uniformity in plant weight. When models, both descriptive yield prediction models and mechanistic dynamic simulation models, are used to study competition, it may be necessary to allow for these effects of spatial arrangement. However, fitting the nine versions of Weiner's (1982) model to the data, gave results that appeared to be inconsistent with the results from the ANOVA's, and also with the hypotheses of asymmetric and symmetric competition. The model fits did not support the hypothesis (Weiner, 1984) that neighbourhood effects were related to the distance (d^{-1}) when competition was asymmetric, and to the square of the distance (d^{-2}) when competition was symmetric. In both experiments, the model which only included plant density (d^0) in the measure of competition pressure, showed the lowest lack-of-fit. The model fits did not improve when distance was included in the explanatory variables of the model, although the analyses of variance showed significant effects of spatial position of *S. vulgaris*. A possible explanation for this discrepancy could be that in these two experiments the substantial effects of the presence of the *S. vulgaris* plant masked the effects of the spatial position of the *S. vulgaris* plant. Also, the way that effects of distance (d^{-1} and d^{-2}) were incorporated in the model may have been inadequate.

Several studies showed that the intensity of inter-specific competition was related to the spatial arrangement of the competing species (Mortensen & Coble, 1989; Cousens & O'Neill, 1993). However, the effect of spatial arrangement of the competing species on uniformity in plant weight had not been the subject of detailed research. Our experiments showed that the influence of spatial arrangements on the growth of individual plants may not be negligible when studying competition in plant communities, especially when resource competition is asymmetric.

CHAPTER 3

A MODEL FOR INTER-SPECIFIC COMPETITION IN ROW CROPS

B. J. Schnieders, M. van der Linden, L.A.P. Lotz and R. Rabbinge

ABSTRACT

A model (interrow) for intra-specific and inter-specific competition in a canopy with a row structure, is described. In the model, special attention has been given to the simulation of light interception by each species, taking into account the distribution of leaf area over the soil area, the row dimensions, the orientation of the rows, and the relative position of rows of different species.

The simulation of light interception inside a canopy with a row structure was consistent with measured light interception data. The model interrow simulated peaks of light interception that corresponded with the position of rows. The model also correctly simulated low light interception levels in between the rows early in the growing season. A complete closure of the canopy at small row spacings and consequently a 100 % light interception was also correctly simulated, as well as a less complete canopy closure and a less than 100 % light interception at larger row spacings.

A sensitivity analysis showed that attempts to increase the competitiveness of crops by obtaining a more uniform spatial arrangement by means of a decrease in the row spacing, is not a valuable weed management strategy when weeds succeed in growing to at least the same height as the crop. However, reducing the row spacing such that a more uniform plant arrangement is obtained will result in the highest dry matter production, if the height growth of weeds can be controlled or the emergence date of weeds can be delayed. When it is necessary to use wide row spacings, the row orientation that gives maximum dry matter production under Dutch conditions (52 °N) is approximately north west - south east.

The model interrow simulated the light interception inside a canopy with a row structure in correspondence with measured light interceptions. A first test of the model, showed that the simulated effects of intra-specific and inter-specific competition on dry matter production of witloof chicory and Senecio vulgaris matched the experimental data. After further testing of the model behaviour with data from field experiments, the model will be a powerful tool to gain understanding of the mechanisms underlying competition and in the development of weed management systems. The model can also be used to study competition in intercropping systems.

INTRODUCTION

Various crops are grown in rows, and these row crops do retain bare soil between the rows for either a substantial part, or for all of the growing season. As a result, light penetration into the canopy can be very heterogeneous, depending on the row dimensions. Wherever the crop canopy is thin or absent, weeds can grow vigorously. Yield losses of up to almost one-hundred percent, due to weed competition, have been reported for crops with incomplete canopy closure, *e.g.* witloof chicory (Patel & Upadhyay, 1989), and carrots and onions (Van Heemst, 1985). Witloof chicory is a row crop, due to sub-optimal plant arrangements (Schnieders & Lotz, 1993), and a slow initial growth (Dhellemmes, 1987; Groenwold & Van de Geijn, 1990; Meijer & Mathijssen, 1992).

Weed control is a critical issue in the management of a witloof chicory crop (Richards, 1944; Poll & Douglas, 1987). Weed control is carried out mainly with pre-emergence herbicides (Dhellemmes, 1987; Sellin *et al.*, 1992), or is carried out mechanically. Weeds from the *Compositae* family, *e.g. Senecio vulgaris* L., are especially difficult to control chemically (Dhellemmes, 1987; Sellin *et al.*, 1992). Many governments stimulate the reduction of the amounts of herbicides used, and the reduction of the dependence on the use of herbicides (MJP-G, 1991). Thus, the need to develop new strategies of weed management in this crop is clear. The quantitative insight in the mechanisms underlying competition that is needed to develop these new strategies, can be obtained using mechanistic dynamic simulation models for inter-specific competition (Kropff & van Laar, 1993).

Spitters & Aerts (1983) developed a mechanistic dynamic simulation model for inter-specific competition in crops that obtain complete soil cover. This model, INTERCOM, was further elaborated (Kropff & Spitters, 1992, Kropff & Van Laar, 1993) and successfully used to simulate crop-weed competition in sugar beet (Kropff *et al.*, 1992), winter wheat (Lotz *et al.*, 1990a), maize, rice and tomatoes (Kropff *et al.*, 1993c). However, the INTERCOM model did not correctly simulate inter-specific competition for light in witloof chicory (Schnieders & Lotz, 1993). The assumption in the INTERCOM model that the leaf area is distributed homogeneously over the soil area, was invalid for witloof chicory. Wiles & Wilkerson (1991) presented a model for inter-specific competition for light, in which competition between weeds and widely spaced rows of soybeans occurs only within the area of influence of the weeds. However, the light interception within this area of influence was calculated in a way, similar to that described by Spitters & Aerts (1983), and no attention was given to the row geometry and its consequences for light absorption.

In this paper a model for intra-specific and inter-specific competition in row crops, INTERROW, is described. Special attention has been given to the simulation of light interception by each species, taking into account the distribution of leaf area over the soil area, the row dimensions, the orientation of the rows, and the relative position of rows of different species.

MODEL DESCRIPTION

General structure

In a potential production situation, where light, temperature, and species specific characteristics determine the growth of a plant community, plants compete primarily for light (*e.g.* Kropff, 1993a). The model INTERROW calculates the vertical and horizontal light profile within the multi-species row canopy, from the leaf area indices and the spatial distributions of the leaf area. Subsequently, the photosynthesis profile in both the vertical and horizontal direction inside a canopy row is calculated for each species, using the light profiles, the leaf area distributions, and the photosynthetic characteristics of single leaves. The instantaneous canopy photosynthesis of each species is obtained, by integrating the photosynthesis profile over the height and the width of the row, and applying a correction for incomplete soil cover. Subsequent integration over the day gives the daily gross CO_2 assimilation rate of each species. The amount of assimilated CO_2 is then converted into carbohydrates, and decreased with the carbohydrate requirements for maintenance respiration. The remaining carbohydrates are converted into dry matter, using the assimilate requirement for dry matter production, resulting in the net daily growth rate. The amounts of dry matter partitioned to the various plant organs depend on the phenological development stage. The rate of leaf area growth is a function of the daily average temperature in the early stage of the growth, reflecting a sink limited growth. When the plants start shading each other, the rate of leaf area growth is a function of the daily increase in leaf dry matter, reflecting a source limited growth. Finally, the daily dry matter growth rates and leaf area growth rate are added to the existing amounts, resulting in the time courses of dry matter and leaf area index during the growing season.

The concept behind the calculation of the horizontal and vertical light profile in the canopy should become clearer, by visualising the canopy as a series of rectangular-shaped boxes. Each box contains the leaf area of one row of a certain species. The height and width of these boxes, and the leaf area inside the boxes are changing in time, simulating the canopy dynamics of a species. When a light beam enters a row, it will be, either partially or totally, intercepted by leaves inside that row. However, when a beam of light does not enter a row but falls directly on the bare soil between the rows, it will be completely lost for photosynthesis. Thus, the percentage of light that will be intercepted depends on the size of the rows, the size of the gaps between the rows, the leaf area density inside the rows, the row orientation, and the position of the sun. The light intensity at any point inside a row can be calculated from the interception of a series of light beams originating from carefully chosen positions on the hemisphere. The light intensity at that point inside the row canopy is subsequently used to calculate the local instantaneous photosynthetic rate at that specific point.

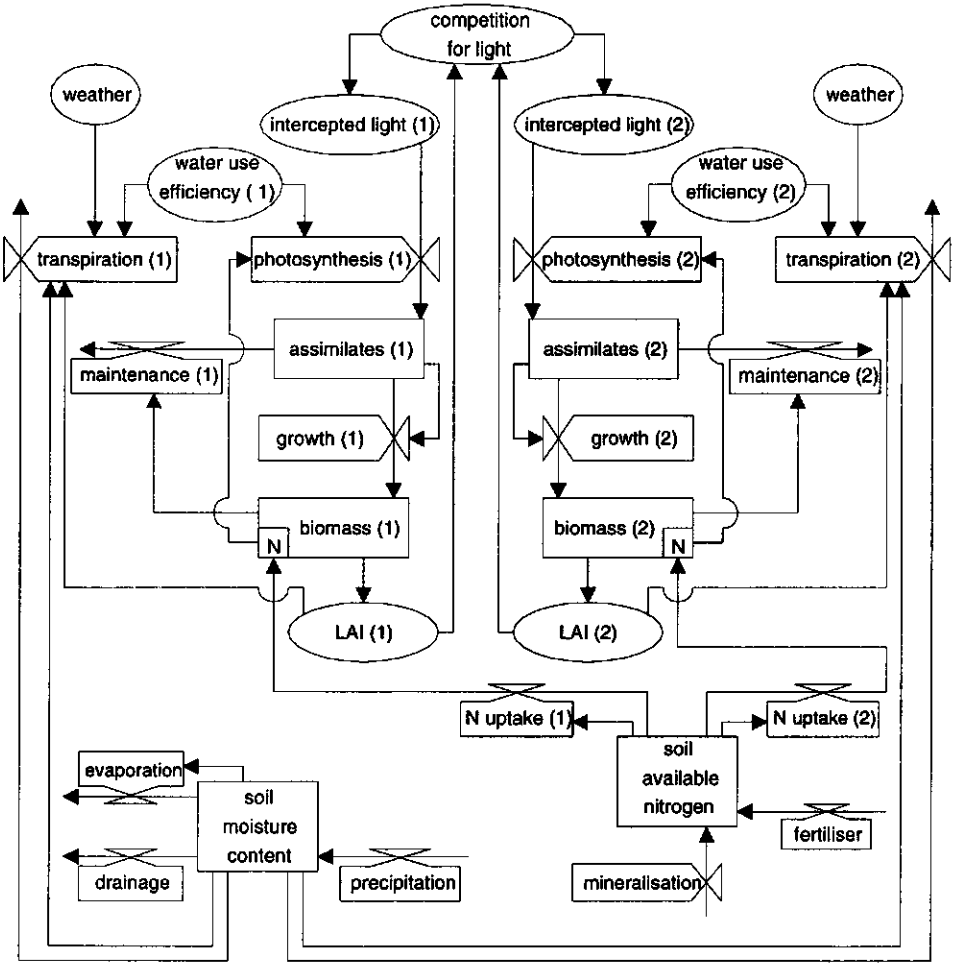

Figure 3.1 A relational diagram showing the general structure of the model INTERROW, for competition between 2 species. Boxes represent state variables, valves represent rate variables, circles represent intermediate variables, solid lines are flows of material, and broken lines are flows of information.

A relational diagram of the INTERROW model (Figure 3.1) shows that the model consists of two growth models (one for each species), which are linked through the interception of light, water and nitrogen. The INTERROW model has been derived from the INTERCOM model of Kropff & van Laar (1993), by replacing the modules for light interception and photosynthesis with new modules, that take into account the 3-dimensional geometry of the canopy and the solar geometry. These new modules were derived from the model for light distribution and photosynthesis in single-species row crops, developed by Gijzen & Goudriaan (1989).

Row geometry of the multi-species canopy

The canopy can be visualised as a series of rectangular-shaped boxes (Figure 3.2). Each box represents a row, with a rectangular cross-section (the *xz*-plane) and an indefinite length (*y*-direction). In the model INTERROW, rows of different species can entirely overlap, partially overlap, or not overlap at all. The canopy dimensions are defined by the row dimensions of each species, by the intra-specific row distance of each species, and by the relative spatial position of rows of different species:

- The row dimensions of species *i* are defined by the row height (h_i, cm) and the row width (w_i, cm), both of which are described with logistic functions in time (see section 'Row height and row width dynamics' for detailed description).
- The intra-specific row distance is the distance between 2 rows of the same species, *i.e.* it is the row spacing of species *i*. It is the sum of the row width (w_i, cm) and the path width (p_i, cm).
- The relative spatial position of rows of different species is described by two parameters. The first parameter is the distance between the row centres of the two species (δ_c, cm), and the second parameter is the distance between the left-side borders of the rows of the two species (δ_l, cm). The first parameter can also be expressed as a relative value, *i.e.* as the position of the row centre of species *i*, relative to the position of the row centre of the other species. This relative displacement of species 2 is 0.0 when the row centres are at identical positions, 0.5 when the row centre of species 2 is exactly in between two row centres of species 1, and -0.25 or 0.25 when the row centre of species 2 is 25% of the row spacing to the right (-0.25) or to the left (0.25) of a row centre of species 1.

Light interception

The percentage of the incoming radiation that is intercepted by a species, depends on the size of its leaf area, the spatial distribution of its leaf area in the multi-species canopy, and the light extinction characteristics of the leaves. In a canopy with incomplete soil cover, the light interception is also affected by the azimuth of the sun. For example, the extinction path of a light beam travelling parallel to the row direction, can be very different from that of a light beam travelling perpendicular to the row direction.

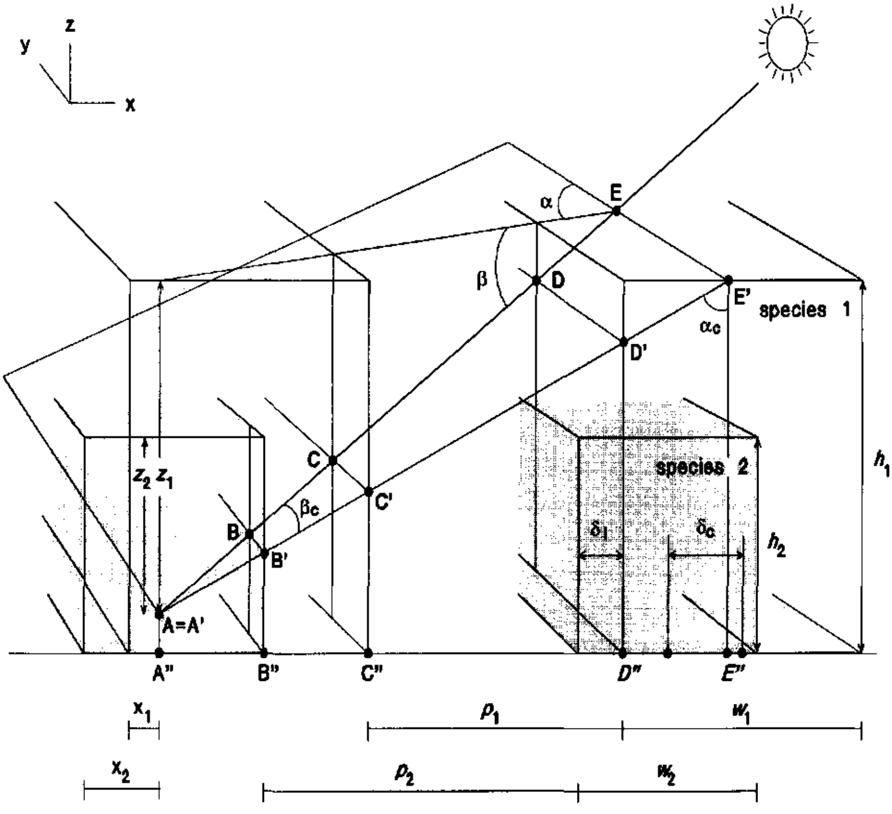

Figure 3.2 A schematic representation of a row canopy, consisting of rows of two species. The canopy dimensions of species i are defined by the row width (w_i), the row height (h_i) and the path width between the rows (p_i). The position of a row of species 2 relative to a row of species 1, is defined by the distance between the left sides of the rows (δ_l) and by the distance between the centres of the rows (δ_c). See text for further explanation.

The model distinguishes between direct and diffuse radiation. Direct radiation is regarded as a single beam originating from the direction of the sun. Diffuse radiation is by definition coming from all directions, and can therefore be regarded as being composed of an infinite number of beams originating from an infinite number of directions in the hemisphere. Gijzen & Goudriaan (1989) developed a calculation procedure for the interception of diffuse radiation in a row crop, in which the interception of only a limited number of light beams needs to be calculated. In this procedure, the hemisphere is divided into ten segments. In each segment, the interception of three single light beams is calculated, and a 3-point Gaussian integration method is applied to calculate the total interception of diffuse radiation in that segment.

The co-ordinate system of Goudriaan (1977) is used, to describe the canopy geometry and the extinction path of a light beam with a known elevation and azimuth (Figure 3.2). In this co-ordinate system, β is the angle of a light beam with the horizontal (*i.e.*, the inclination), β_c is the angle of the light beam with the xz-plane (*i.e.*, the converted inclination), α is the difference between the azimuth of the row and the azimuth of the light beam, and α_c is the angle of the projection of the light beam in the xz-plane with the z-axis (*i.e.*, the converted azimuth).

The gridpoint A is defined by its co-ordinates (x_i, y_i, z_i). The amount of radiation that is absorbed by leaf area at point A, from each of the light beams (*i.e.*, one direct light beam and a limited number of diffuse light beams) is calculated. The total amounts of absorbed direct and diffuse radiation at point A are subsequently used to calculate the local instantaneous photosynthetic rate at point A.

The calculation of the absorption of a single light beam will now be explained in detail for species 1, using the situation schematised in Figure 3.2. The light beam travelling from the top of the canopy (E) to gridpoint A inside the row canopy of species 1, will be gradually extinguished by the leaf area of species 1 in the sections DE and AC, and by the leaf area of species 2 in the section AB. In section CD, there is no leaf area of either species to intercept the light beam. The light absorption by leaf area of species 1 at point A can be calculated, when the leaf area index that is traversed by the light beam before it reaches point A (LA_i, ha·ha^{-1}) is known for each species. For species 1, LA_1 is calculated as the length of the extinction path of the light beam inside the canopy of species 1 (l_1, cm), multiplied by the leaf area density of species 1 (LD_1, cm^2·cm^{-3}). The length of the extinction path l_1, is calculated using the projection of that light beam on the xz-plane (projection of AE yields A'E' in Figure 3.2), and a further projection on the horizontal axis, *i.e.*, on the x-axis (projection of A'E' yields A"E" in Figure 3.2). The total length of the projection of the light beam on the horizontal axis (A"E") is given by:

$$\mathrm{A''E''} = z_1 * \tan\alpha_c$$

where z_1 is the distance from point A to the top of the row of species 1. The projection A"E" is partly inside the rows (A"C" + D"E") and partly outside the rows (C"D") of species 1. The length of the projection A"E" inside the first row of species 1 that is penetrated by the light beam (D"E"), is given by:

$$\mathrm{D''E''} = \left(\left|\mathrm{A''E''} + x_1\right|\right) \mathrm{mod}\left(w_1 + p_1\right)$$

in which the 'mod' operator (Fortran programming language) calculates the remainder after division of (A"E" + x_1) by (w_1+p_1), *i.e.*, 11 mod 3 stands for the remainder after division of 11 by 3, giving the value 2. The length of the projection A"E" inside the other rows of species 1, including the row that contains point A (A"C"), is given by:

$$\mathrm{A''C''} = N_1 * w_1 - x_1$$

where N_1 is the number of rows of species 1 that are traversed by the light beam, other than the first row that was penetrated by the light beam:

$$N_1 = \left(\mathrm{A''E''} + x_1 - \mathrm{D''E''}\right) / \left(w_1 + p_1\right)$$

In the example of Figure 3.2, the value of N_1 equals 1. The total length of the extinction path of the light beam inside the canopy of species 1 (l_1, cm) can now be calculated as:

$$l_1 = \mathrm{AC} + \mathrm{DE} = \left(\mathrm{A''C''} + \mathrm{D''E''}\right) / \left(\sin\alpha_c * \cos\beta_c\right)$$

Sinα_c corrects for the projection of the light beam on the horizontal axis ($\sin\alpha_c$ = (A"C"+D"E")/(A'C'+D'E')), and cosβ_c corrects for the projection of the light beam on the *xz*-plane ($\cos\beta_c$ = (A'C'+D'E')/(AC+DE)). The leaf area index of species 1 that is traversed by the light beam on its way to point A (LA_1, ha·ha^{-1}) is given by:

$$LA_1 = l_1 * LD_1$$

where LD_1 is the leaf area density (cm^2·cm^{-3}) of species 1. The leaf area density is calculated from the leaf area index (LAI_1, ha·ha^{-1}), and the row height (h_1, cm) of species 1:

$$LD_1 = LAI_1 * \left(\frac{w_1 + p_1}{w_1} \right) \Big/ h_1$$

The simulated leaf area index is multiplied with the ratio of the row spacing (w_1+p_1) and the row width (w_1). This correction accounts for the fact that leaf area is increasingly clustered inside the rows, when the row width is decreased relative to the row spacing. The calculations for species 2 can be performed in the same way, giving AB as the length of the extinction path, in the example of Figure 3.2. Finally, the amount of light absorbed from this particular beam by leaves of species 1 at point A ($I_{\mathrm{abs,A,1}}$, J·m^{-2}·s^{-1}), is obtained from the light intensity above the canopy (I_0, J·m^{-2}·s^{-1}), the scattering coefficient of leaves (σ, -), the light extinction coefficients of leaves (k_i, -), and the leaf area index that is traversed inside the canopy of each species (LA_i, ha·ha^{-1}):

$$I_{\mathrm{abs,A,1}} = I_0 * (1-\sigma) * k_1 * \exp\left(\sum_{i=1}^{i=n} \left(-k_i * LA_i \right) \right)$$

For direct radiation, the extinction path of only one light beam coming from the direction of the sun, needs to be calculated to obtain the absorbed direct radiation at point A. For diffuse radiation, the extinction paths of several beams coming from a limited number of directions in the hemisphere are calculated (Gijzen & Goudriaan, 1989), and the absorbed radiation from all those directions is used to calculate the total absorbed diffuse radiation at point A.

Photosynthesis and dry matter production

The amounts of absorbed direct and diffuse radiation at point A are used to calculate the leaf CO_2 assimilation at gridpoint A. The CO_2 assimilation-light response curve of individual leaves is described by a negative exponential function (*e.g.* Goudriaan, 1982; Gijzen & Goudriaan, 1989; Kropff, 1993b):

$$A_{\mathrm{s,i}} = A_{\mathrm{m,i}} * \left(1 - \exp\left(-\varepsilon_i * I_{\mathrm{abs,A,i}} / A_{\mathrm{m,i}} \right) \right)$$

Here, $A_{\mathrm{s,i}}$ is the instantaneous gross assimilation rate of single leaves (kg CO_2·ha^{-1} leaf·h^{-1}), $A_{\mathrm{m,i}}$ is the gross assimilation rate at light saturation (kg CO_2·ha^{-1} leaf·h^{-1}), ε_i is the initial light use efficiency (kg CO_2·ha^{-1} leaf·h^{-1} / (J·m^{-2} leaf·s^{-1})), and $I_{\mathrm{abs,A,i}}$ is the amount of absorbed radiation (J·m^{-2} leaf·s^{-1}) by species *i* at point A. The instantaneous gross leaf assimilation rate of species *i* at the selected gridpoint, is calculated separately for sunlit leaves ($A_{\mathrm{sl,i}}$) and shaded leaves ($A_{\mathrm{sh,i}}$). Multiplication of the rates by the fractions of sunlit

(f_{sl}) and shaded leaf area at point A, gives the local instantaneous gross assimilation rate ($A_{L,i}$):

$$A_{L,i} = A_{sl,i} * f_{sl} + A_{sh,i} * (1 - f_{sl})$$

The CO_2 assimilation rate for the total canopy of a species, is calculated from the local assimilation rates at various gridpoints, using a 5-point Gaussian integration procedure (Goudriaan, 1986; Goudriaan & Van Laar, 1994). The Gaussian integration procedure, first selects the various gridpoints at certain heights and widths inside a row for calculation of the local assimilation rates, which are subsequently integrated to an instantaneous rate of canopy photosynthesis (A_i, kg $CO_2 \cdot ha^{-1}$ soil$\cdot h^{-1}$) (Gijzen & Goudriaan, 1989). For each species, the daily gross assimilation rate ($A_{d,i}$, kg $CO_2 \cdot ha^{-1}$ soil$\cdot d^{-1}$) is calculated from the instantaneous photosynthetic rates at three moments during the day, using a 3-point Gaussian integration procedure (Goudriaan, 1986; Goudriaan & Van Laar, 1994). The daily dry matter growth rate (G_i, kg DM$\cdot ha^{-1}$ soil$\cdot d^{-1}$) is calculated according to De Wit *et al.* (1978):

$$G_i = \left(\left(A_{d,i} * (30/44) - R_{m,i}\right)/Q_i\right) * F_{W,i} * F_{N,i}$$

The factor 30/44 accounts for the conversion of CO_2 (molecular weight 44) into CH_2O (molecular weight 30), $R_{m,i}$ is the maintenance respiration (kg $CH_2O \cdot ha^{-1} \cdot d^{-1}$), Q_i is the assimilate requirement for dry matter production (kg $CH_2O \cdot kg^{-1}$ dry matter), and $F_{W,i}$ (-) and $F_{N,i}$ (-) are growth reduction factors, to account for growth at limited soil moisture and nitrogen. The daily total dry matter production is partitioned to the different plant organs using partitioning coefficients, which are functions of the phenological development stage of the species. The daily dry matter growth rates and leaf area growth rate are added to the existing amounts, resulting in the time course of dry matter and *LAI* during the growing season.

Limitation of the growth rate by water shortages

To account for the effects of water shortages on the growth rate of each species, the approach described by Kropff & Spitters (1992) and Kropff (1993b) is used. A simple moisture balance keeps track of the soil moisture availability. $F_{W,i}$ expresses the ratio of the actual (T_a, mm$\cdot d^{-1}$) and potential (T_p, mm$\cdot d^{-1}$) transpiration rate, and is calculated from the actual soil moisture content (w_{act}, mm), a critical soil moisture content below which water shortage occurs ($w_{\text{crit,i}}$, mm), and a minimum soil moisture content ($w_{\text{min,i}}$, mm) (Doorenbos & Kassam, 1979):

$$F_{\text{W,i}} = \frac{T_{\text{a}}}{T_{\text{p}}} = \frac{w_{\text{act}} - w_{\text{min,i}}}{w_{\text{crit,i}} - w_{\text{min,i}}} \qquad 0 \leq F_{\text{W,i}} \leq 1$$

Below the minimum soil moisture content ($w_{\text{min,i}}$, mm), no water is available for uptake and the transpiration is totally inhibited. The reduction in growth rate due to water shortage, is proportional to the ratio between the actual and potential transpiration rate (*e.g.* de Wit, 1958; Kropff & Spitters, 1992).

Limitation of the growth rate by nitrogen shortages

To account for the effects of nitrogen shortages on the growth rate of each species, the approach described by Spitters (1989) and Kropff (1993c) is used. A simple nitrogen balance keeps track of the amount of available nitrogen in the soil. The actual nitrogen concentration in the plant ($N_{\text{act,i}}$, kg N·kg^{-1} dry matter) is reduced when the nitrogen supply by the soil is lower than the nitrogen demand by the plant. A growth reduction factor accounting for nitrogen shortage ($F_{\text{N,i}}$, -) is calculated, in a way similar to that for water shortage:

$$F_{\text{N,i}} = \frac{N_{\text{act,i}} - N_{\text{min,i}}}{N_{\text{crit,i}} - N_{\text{min,i}}} \qquad 0 \leq F_{\text{N,i}} \leq 1$$

Here, $N_{\text{crit,i}}$ (kg N·kg^{-1} dry matter) is the critical plant nitrogen content, and $N_{\text{min,i}}$ (kg N·kg^{-1} dry matter) is the minimum plant nitrogen content. If $N_{\text{act,i}}$ remains higher than $N_{\text{crit,i}}$, no reduction in the growth rate occurs. If $N_{\text{act,i}}$ falls below $N_{\text{crit,i}}$, the growth rate is reduced. The size of the growth limitation is determined by the value of $F_{\text{N,i}}$, which equals 1 when the actual plant nitrogen concentration is higher than $N_{\text{crit,i}}$ and which linearly decreases to 0 until the actual plant nitrogen concentration has fallen to $N_{\text{min,i}}$. If $N_{\text{act,i}}$ drops below $N_{\text{min,i}}$, growth is completely inhibited.

Leaf area dynamics

The leaf area growth ($G_{\text{lai,i}}$, ha soil·ha^{-1} soil·d^{-1}) in the early stages of plant growth is limited by the leaf expansion rate, which is a temperature driven process. There is no mutual shading of leaves at these early stages, and the assimilation rate is sufficient to fulfill the assimilate needs for leaf expansion. In this situation, the leaf area growth is sink limited, and an exponential leaf area growth is simulated (Kropff, 1993a). In later stages of plant growth, the growth of leaf area becomes increasingly limited by the assimilate supply, *i.e.*, source limited, because an increasing amount of other plant organs require assimilates and leaves are increasingly shading each other. Leaf area growth is then expressed as a function of dry matter growth of green leaves ($G_{\mathrm{leaf,i}}$, kg·ha^{-1}·d^{-1}) and specific leaf area of newly formed leaves (SLA_{i}, ha·kg^{-1}). Kropff & Spitters (1992) used a total leaf area index of 0.75 to mark the end of the exponential leaf area growth period, and this value reflects the fact that mutual shading of leaves usually starts before soil cover is complete. When the leaf area is increasingly concentrated in rows, *i.e.* when the ratio of the row spacing ($w_{\mathrm{i}}+p_{\mathrm{i}}$) and the row width ($w_{\mathrm{i}}$) is increased, mutual shading of leaves will start at a lower total leaf area index:

$$G_{\mathrm{lai,i}} = \begin{cases} LAI_{\mathrm{i}} * \left(\exp\left(rgrl_{\mathrm{i}} * hu_{\mathrm{i}}\right) - 1\right) & \left(\text{if} \sum_{i=1}^{n}\left(LAI_{\mathrm{i}} * \left(\frac{w_{\mathrm{i}}+p_{\mathrm{i}}}{w_{\mathrm{i}}}\right)\right) \le 0.75\right) \\ G_{\mathrm{leaf,i}} * sla_{\mathrm{i}} & \left(\text{if} \sum_{i=1}^{n}\left(LAI_{\mathrm{i}} * \left(\frac{w_{\mathrm{i}}+p_{\mathrm{i}}}{w_{\mathrm{i}}}\right)\right) > 0.75\right) \end{cases}$$

where $rgrl_{\mathrm{i}}$ (°Cd^{-1}) is the relative growth rate of leaves, and hu_{i} (°C) the daily accumulated temperature sum.

Row height and row width dynamics

The plant height (h_{i}, in cm) development can be described by a logistic function of temperature sum (ts_{i}, in °Cd; Kropff, 1993a; Spitters, 1989) and is identical to the row height:

$$h_{\mathrm{i}} = h_{\mathrm{max,i}} \Big/ \left(1 + b_{\mathrm{h,i}} * \exp\left(-s_{\mathrm{h,i}} * ts_{\mathrm{i}}\right)\right)$$

where $h_{\mathrm{max,i}}$ (cm) is the maximum obtainable height and $b_{\mathrm{h,i}}$ (-) and $s_{\mathrm{h,i}}$ (°C^{-1}·d^{-1}) are parameters of the logistic growth function.

The plant diameter (d_{i}, in cm) is modelled with a logistic function of temperature sum (ts_{i}):

$$d_{\mathrm{i}} = a_{\mathrm{d,i}} + d_{\mathrm{max,i}} \Big/ \left(1 + b_{\mathrm{d,i}} * \exp\left(-s_{\mathrm{d,i}} * ts_{\mathrm{i}}\right)\right)$$

where $d_{\mathrm{max,i}}$ (cm) is the maximum obtainable plant diameter, and $a_{\mathrm{d,i}}$ (cm), $b_{\mathrm{d,i}}$ (-) and $s_{\mathrm{d,i}}$ ($°C^{-1} \cdot d^{-1}$) are parameters of the logistic diameter growth function. The row width of each species is calculated from its plant diameter.

DATA SETS

Data sets from two experiments and data from literature were used to parameterise the model for competition between witloof chicory (*Cichorium intybus* L. var foliosum cv. Flash) and groundsel (*Senecio vulgaris* L.). The experiments were carried out in Lelystad (Lelystad_91) and Wageningen (Wageningen_91), the Netherlands, in 1991. The row spacing was 75 cm, the crop density was 20 plants·m^{-2}, and the weeds were placed in the centre of the crop row, in both experiments. The weed densities were 10 and 20 plants·m^{-2} in experiments Lelystad_91 and Wageningen_91, respectively. In experiment Lelystad_91, the emergence of the crop was on 4 June, and the emergence of the weed was on 18 June. In experiment Wageningen_91, the emergence of the crop was on 17 June, and the emergence of the weed was on 20 June. The row orientation was east-west (E-W) in experiment Lelystad_91, and WSW-ENE in experiment Wageningen_91.

Data from a third experiment carried out in Wageningen in 1993 (Wageningen_93) was available to test if the model could correctly simulate the light interception in a row crop. Witloof chicory was grown in rows (orientation NNW-SSE) with a row spacing of 25, 50 or 75 cm and the weeds planted inside the crop row or between crop rows. Both crop- and weed densities were 20 plants·m^{-2}, and the emergence of both species was on 2 June.

RESULTS

Simulation of parameterisation experiments

A first test of the model INTERROW was to study whether the model was able to correctly describe the dry matter production patterns of the two experiments used for parameterisation. The simulated total dry matter production matched the experimental data of Lelystad_91 reasonably well, both for witloof chicory grown in monoculture (Figure 3.3a) and for witloof chicory grown competition with *Senecio vulgaris* (Figure 3.3b). The almost complete suppression of the growth of *Senecio vulgaris* due to competition with witloof chicory in experiment Lelystad_91, was correctly simulated by the model (Figure 3.3b). The simulated dry matter production of *Senecio vulgaris* grown

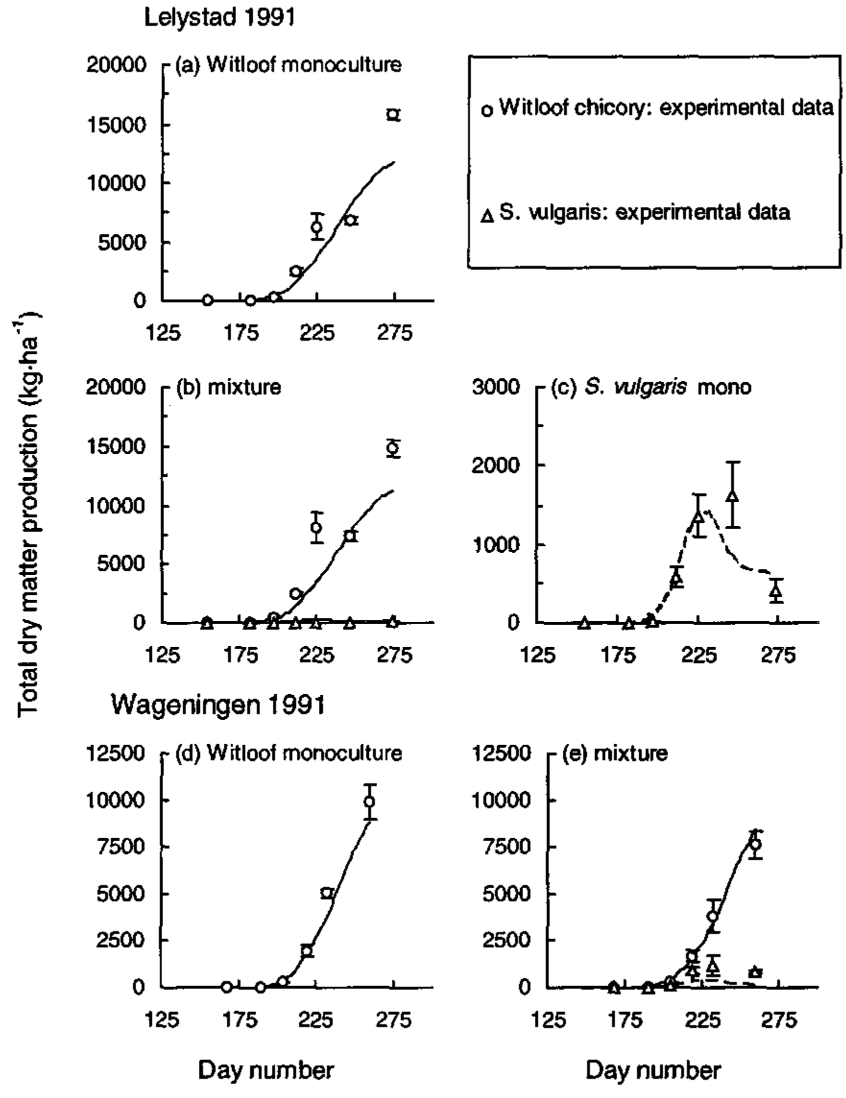

Figure 3.3 The simulated and measured total plant dry weights (DM in kg.ha^{-1}) of witloof chicory and *Senecio vulgaris*, for the two parameterisation experiments. Simulation results are presented with lines, experimental data with O symbols for witloof chicory and Δ symbols for *Senecio vulgaris*.

in monoculture in experiment Lelystad_91, matched the observed data well, except near the end of the growing season when the decline in dry matter due to seed fall, leaf fall and decomposition of stem material was not adequately simulated (Figure 3.3c). The simulated dry matter production closely matched the experimental data of Wageningen_91, both for witloof chicory grown in monoculture (Figure 3.3d) and for witloof chicory grown in competition with *Senecio vulgaris* (Figure 3.3e). The simulated dry matter production of *Senecio vulgaris* grown in competition with witloof chicory (Figure 3.3e) was also consistent with the experimental data.

Simulation of light interception

To test whether the mechanisms of light interception in a row crop were correctly incorporated in the model INTERROW, the simulated light interceptions that were obtained with the parameterised model were compared with light measurements taken in a third experiment (Wageningen_93). The measurements were taken on 6 July and 10 October.

On 6 July, the witloof chicory crop growing in monoculture was still very open, *i.e.* large gaps existed between rows of witloof chicory (Figures 3.4a, d, g), especially at larger row spacings. Light interception occurred only inside the crop rows, and the simulated light interception profile perfectly described the experimentally determined light interception profile. On 10 October, the percentage light interception was much higher, which was accurately reproduced in the simulation results. The model INTERROW also correctly simulated the complete closure of the canopy in the 25 cm row spacing (Figure 3.4a), and a less complete closure at larger row spacings (Figures 3.4d, g).

On 6 July, the measured and simulated light interception inside the witloof chicory row were higher when *Senecio vulgaris* plants were present inside the witloof chicory rows (Figures 3.4b, e, h), compared to the monoculture situations (Figures 3.4a, d, g). The combined leaf area of witloof chicory and *Senecio vulgaris* inside the witloof chicory rows was higher than that of witloof chicory growing in monoculture, which resulted in a higher light interception. On 6 July, a second series of light interception peaks appeared when *Senecio vulgaris* plants were growing in between the rows of witloof chicory (Figures 3.4c, f, i). This reflected the presence of leaf area of *Senecio vulgaris* in separate rows in between the witloof chicory rows. At a row spacing of 25 cm, the plants in different rows were already closing in on each other, resulting in more or less equal values of measured light interception at all positions in the transect through the canopy (Figure 3.4c). The simulated light interceptions were also more or less equal at all positions in the transect through the canopy (Figure 3.4c). On 6 July, the simulated light

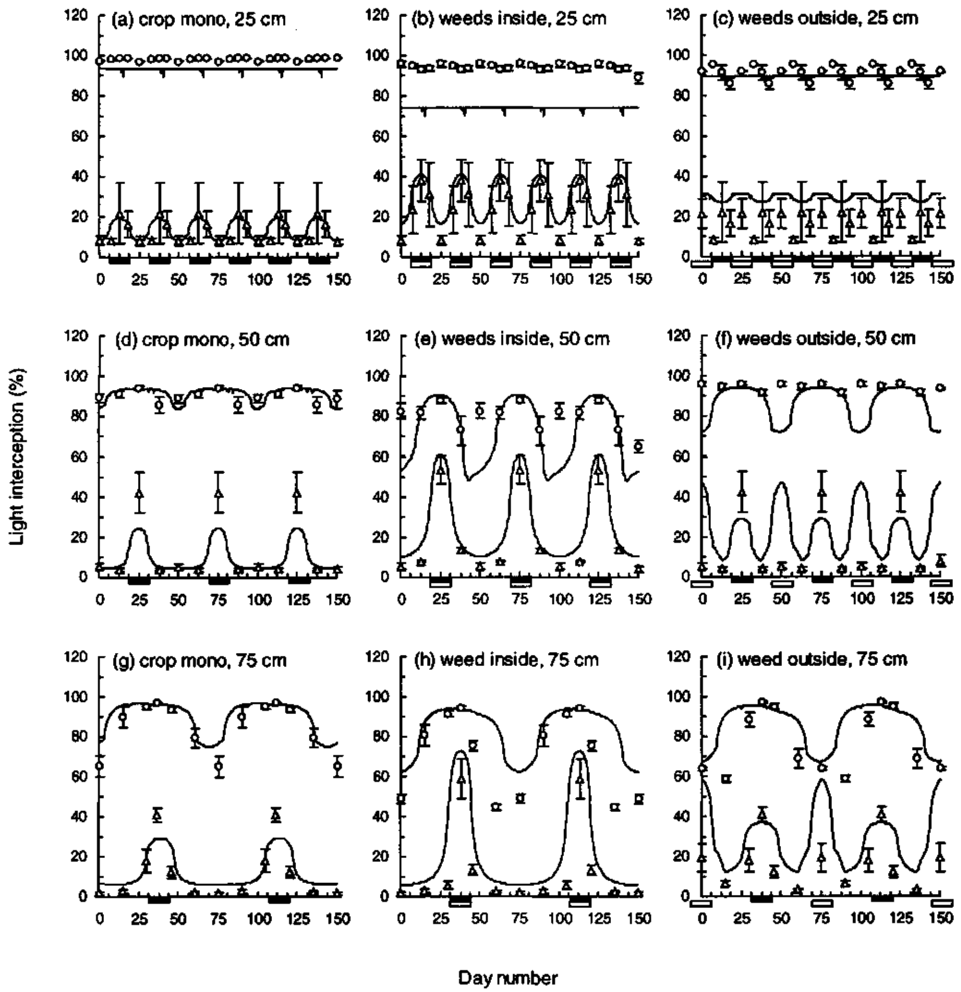

Figure 3.4 Simulated (lines) and measured (symbols) interception of photosynthetic active radiation (PAR, in % of the incoming PAR) in a transect of 150 cm through the canopy of a row crop, with a row width of 25 cm (a, b, c), 50 cm (d, e, f) or 75 cm(g, h, i); at 6 July (Δ) and 10 October (O). Witloof chicory monocultures are presented in a, d, g; mixtures with *Senecio vulgaris* plants grown inside the rows of witloof chicory are in b, e, h and mixtures with *Senecio vulgaris* grown in between rows of witloof chicory are in c, f, i. The position of the centres of the crop rows and weed rows are indicated by the filled boxes and open boxes, respectively.

interception inside the *Senecio vulgaris* rows was too high at the larger row spacings (Figures 3.4f, i). The measured light interception underneath the *Senecio vulgaris* plants was very low, despite the fact that the measured leaf area of the *Senecio vulgaris* plants was higher than that of the witloof chicory plants (data not shown). On 10 October, all the *Senecio vulgaris* plants had senesced. However, inter-specific competition occurring earlier in the growing season had reduced the leaf area of witloof chicory (data not shown). This resulted in a slightly lower measured and simulated light interception in the mixtures compared to the witloof chicory in monoculture, especially at the largest row spacing (compare Figures 3.4h, i with Figure 3.4g).

Test of model behaviour

A sensitivity analysis was performed to study the effects of row orientation, row spacing and row width, on the simulated total dry matter production of a fictitious species 1. This species 1 was grown in monoculture or in mixture with another fictitious species 2. The two species had identical physiological and morphological characteristics (parameter set of witloof chicory used for both species), with the exception of the maximum row height of species 2, which was fixed at 50%, 100% or 200% of that of species 1. The emergence dates, plant densities, row spacings, maximum row width, and row orientations were identical for both species in this sensitivity analysis. The simulations were performed for a potential production situation, *i.e.*, growth is determined only by light interception, temperature and species characteristics and not by capture of water or nutrients.

Simulations were carried out for all combinations of 4 row spacings (25, 50, 75, and 100 cm), 4 maximum attainable row widths (expressed as fraction of the row spacing, *i.e.* 0.25, 0.5, 0.75, and 1.0), 4 row orientations (N - S, SW - NE, W - E, and NW - SE), 3 maximum attainable row heights of species 2 (50%, 100%, and 200% of that of species 1), and 4 relative positions of the row centre of species 2 (displacement = 0, 0.5, -0.25 or 0.25).

There was a clear effect of row spacing and maximum attainable row width on the simulated dry matter production of species 1 in monoculture (Figure 3.5). The simulated dry matter production was higher at the row spacing was decreased, especially at small maximum attainable row widths. This was due to the shorter time it took for a species to complete soil cover and maximise light interception when the row spacing was smaller. Furthermore, the gaps between the rows remained wider when the maximum row width was smaller, resulting in a reduced light interception and dry matter production. No further substantial increases in dry matter production were simulated, when the row

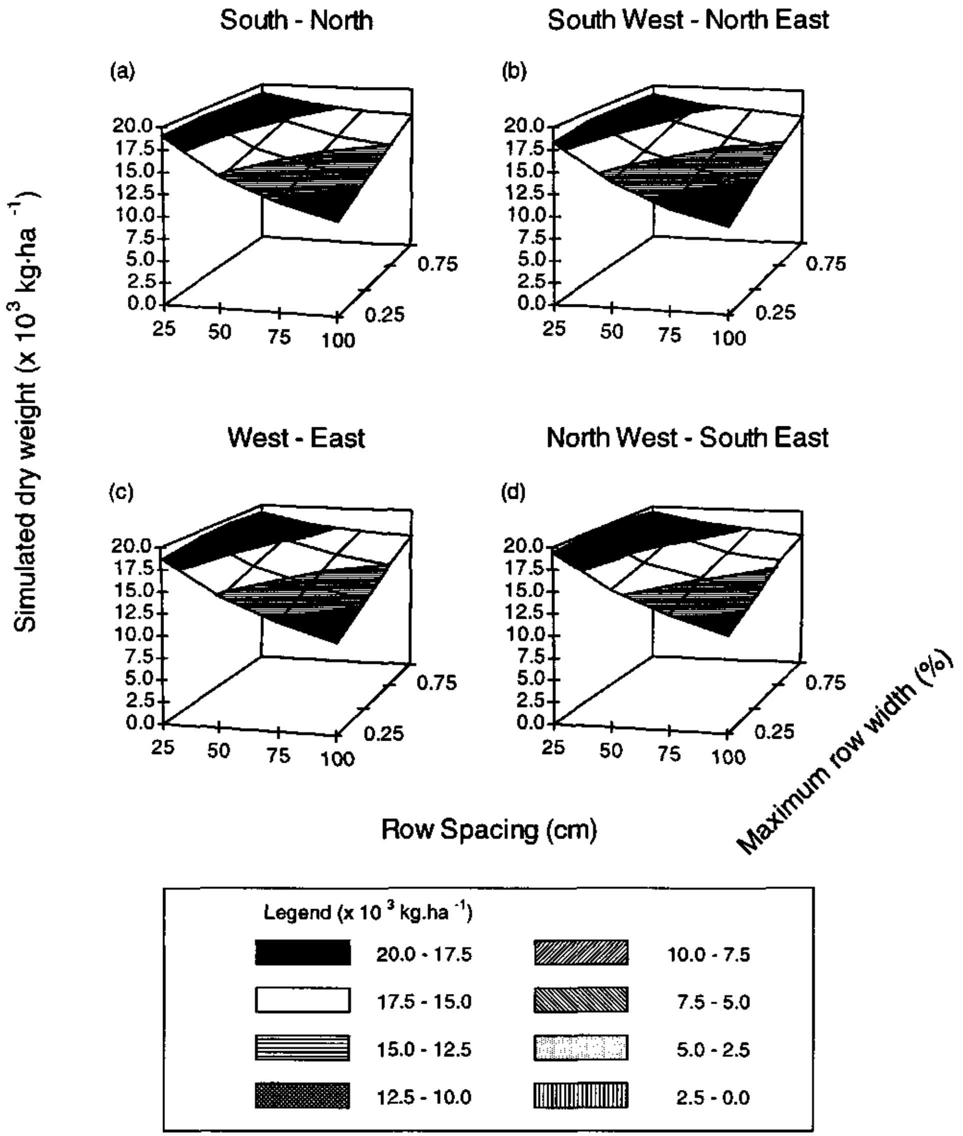

Figure 3.5 The simulated total dry matter production (kg·ha^{-1}) of a fictitious row-crop-species 1 grown in monoculture, in rows of various combinations of row spacings (25, 50, 75 or 100 cm), maximum attainable row widths (expressed as fraction of the row spacing, 0.25, 0.50, 0.75 or 1.00), and row orientation (S-N, SW-NE, W-E, or NW-SE).

spacing was made smaller than 25 cm, (results not shown). The row orientation had a small effect, such that the simulated dry matter production was highest when the row orientation was NW-SE. In this situation, the rows are more or less perpendicular to the direction of the sun during the period of the day with the highest light intensities, resulting in the highest light interception. The differences between row orientation NW-SE (Figure 3.5d) and row orientation SW-NE (Figure 3.5b) were very small (< 2%) when the canopy reached full soil cover, but increased to more than 10% at large row spacings and small maximum attainable row widths.

These sensitivity analysis results indicate that a species growing in monoculture obtains maximum dry matter production, when the row orientation is such that light interception is maximised during the period of the day with the highest light intensities. The results also indicate that for maximum dry matter production in monoculture, obtaining a complete soil cover is more important at large row spacings than at small row spacings.

The row orientation, and the displacement of rows of species 2, had little influence on the effects of inter-specific competition on the simulated dry matter production of species 1. Only the simulation results of row orientations NW - SE, and the two most extreme displacements (displacement = 0.0, species 2 inside row of species 1; and displacement = 0.5, species 2 in between rows of species 1) are therefore shown in Figure 3.6. When the maximum attainable height of species 2 was 50% of that of species 1 (Figures 3.6a, b), the maximum simulated yield loss of species 1 due to inter-specific competition was 3.5%. The differences with the surface plots of species 1 in monoculture were small, irrespective whether species 2 grew inside the rows of species 1 or in between the rows of species 1 (compare Figures 3.6a, b with Figure 3.5d).

The simulated dry matter production of species 1 was severely reduced due to inter-specific competition, when the maximum attainable row height of species 2 was equal to (Figure 3.6c, d), or double (Figure 3.6e, f) that of species 1. The effects of inter-specific competition were on average strongest when the plants of species 2 were positioned inside the rows of species 1 (displacement = 0, Figures 3.6c, e). When the maximum attainable height of species 2 was equal or double that of species 1, yield reductions of 48-50 % (Figure 3.6c) and 87-97 % (Figure 3.6e) were simulated, respectively. When plants of species 2 were positioned between the rows of species 1 (displacement = 0.5, Figures 3.6d, f), yield reductions of 21-49 % (Figure 3.6d) and 59-92 % (Figure 3.6f) were simulated, respectively. Plants of species 1 have a prolonged period without inter-specific competition when plants of species 2 are positioned in between the rows of species 1, especially when the row spacings are large and the maximum attainable row widths are

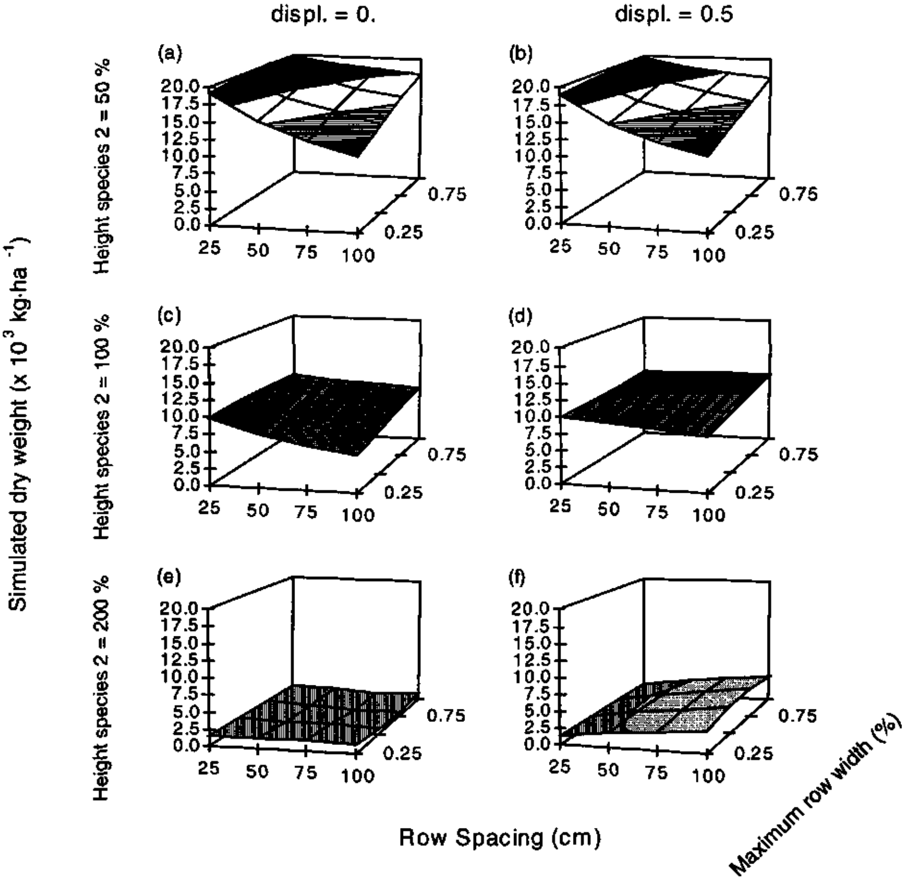

Figure 3.6 The simulated total dry matter production (kg·ha^{-1}) of a fictitious row-crop-species 1, grown in competition with a fictitious row-crop species 2. The species were grown in rows with a certain row spacing (25, 50, 75 or 100 cm) and maximum attainable row width (expressed as fraction of the row spacing, 0.25, 0.50, 0.75 or 1.00). Species 2 differed from species 1 in its maximum attainable row height, and in the relative position of its row centres (*i.e.* relative displacement). The row centre of species 2 was inside the row of species 1 (displ. = 0; a, c, e), or in between the rows of species 1 (displ. = 0.5; b, d, f). The maximum attainable row height of species 2 was 50 % (a, b), 100 % (c, d) and 200 % (e, f) of that of species 1, respectively. The relative position of the row centre of species 2 was 0 (a, c, e) and 0.5 (b, d, f), respectively. Only results for row orientation NW-SE are shown. See text for further explanation.

small. The slopes of the surface plots that were observed for species 1 growing in monoculture (Figure 3.5) or in competition with species 2 of lower maximum attainable height (Figures 3.6a, b), disappeared (Figures 3.6c, d) or were reversed (Figures 3.6e, f) when the maximum attainable height of species 2 was larger.

The results from this simulation analysis indicate that the outcome of inter-specific competition in row crops is mainly determined by the relative heights of the species. When species 2 has a small maximum attainable height, it will be a weak competitor and yield losses of species 1 due to inter-specific competition will be small. Furthermore, if species 2 has a small maximum attainable height, the strong effects of spatial arrangement (row spacing, maximum row width) on the dry matter production are identical to those found for species 1 growing in monoculture. When species 2 has a large height compared to species 1, it will be a strong competitor and yield loss of species 1 will be high. The percentage yield reduction was lowest when species 1 was grown at large row spacing and small maximum row width, with species 2 growing in between the rows of species 1.

DISCUSSION

The model for intra-specific and inter-specific competition in row crops, INTERROW, was parameterised for competition between witloof chicory and *Senecio vulgaris*. A first test of the model showed that the simulated effects of intra-specific and inter-specific competition on dry matter production of witloof chicory and *Senecio vulgaris*, matched the data of the experiments used for the parameterisation of the model. Data from an experiment not used in the parameterisation of the model, was used to test whether the mechanisms of light interception in a row crop were correctly incorporated in the model INTERROW. The simulated light interception profile satisfactorily described the experimentally determined light interception profile, when witloof chicory grew in monoculture or when *Senecio vulgaris* plants grew inside the crop row. The low light interceptions that occurred in between the rows early in the growing season, due to the large gaps that existed between the rows, especially at larger row spacings or when *Senecio vulgaris* was growing inside the crop rows, were adequately simulated. When *Senecio vulgaris* plants grew between the witloof chicory rows, the simulated light interception by the *Senecio vulgaris* rows was too high. The measured light interception underneath the *Senecio vulgaris* plants was very low, despite the fact that the measured leaf area of the *Senecio vulgaris* plants was higher than that of the witloof chicory plants (data not shown). This inconsistency between the higher leaf area and the lower measured light interception may be explained by the way the light interception measurements were taken. The light meter was placed at different positions around the *Senecio vulgaris* plants, but it proved very difficult to insert the light meter near the stem of the plants. Hence, the measured light interceptions underneath the *Senecio vulgaris* may have been too low.

A sensitivity analysis showed that a species growing in monoculture obtains maximum dry matter production, when the row orientation is such that light interception is maximised during the period of the day with the highest light intensities. This effect of row orientation was more important at larger row spacing than at smaller row spacings. The simulated dry matter production was always largest at small row spacings and large maximum row widths, where near-complete soil cover was quickly obtained. For Dutch conditions this means that the row spacing should be small, and that the row orientation should be approximately NW-SE when wider row spacings are needed. These simulation results are supported by experimental research which showed that reducing the row spacing, increased the dry matter production of onions (Bleasdale, 1966; Frappell, 1973), carrots (Bleasdale, 1961), cereals (Holliday, 1963), and maize (Hodges & Evans, 1990). It was shown that this increased dry matter production of soya bean at reduced row spacings was caused by an increased light interception (Board & Harville, 1992). The preferential NW-SE orientation of the rows is in agreement with Mutsaers (1980), who found that for northern latitudes the row orientation giving the maximum light interception in row crops was approximately NW-SE, with some seasonal fluctuations.

The sensitivity analysis showed that the size of the yield reduction due to inter-specific competition for light, largely depended on the relative heights of the species. The simulated dry matter production of species 1 was hardly reduced by inter-specific competition, when the maximum height of species 2 was only 50 % of that of species 1. However, high yield losses of species 1 were simulated when species 2 was a strong competitor, *i.e.*, when the maximum height of species 2 was 100 % or 200 % of the height of species 1. The simulated yield loss of species 1 was highest when the plants of species 2 grew inside the rows of species 1, because in such a situation inter-specific competition will commence almost immediately. The relative yield loss of species 1 was lowest when species 2 grew in between the rows of species 1, the row spacing was large and the maximum row width was small. Unfortunately, the lowest dry matter production of species 1 in monoculture was also simulated for situations with a large row spacing and a small maximum row width. Thus, the simulation results showed that attempts to increase the competitive ability of a crop by obtaining a more uniform spatial arrangement, *i.e.*, by decreasing the row spacing, is not a valuable weed management strategy if the weeds succeed to grow to at least the same height as the crop. In the sensitivity analysis, the fictitious species emerged at the same day, and, except for plant height, were similar in physiological and morphological characteristics. Several experimental studies have shown that narrower row spacing can be an effective weed management tool, especially when weeds emerge later than the crop and the crop quickly developed a closed canopy. A narrower row spacing in soya beans reduced the weed resurgence after an initial control treatment, due to a better and quicker canopy formation (Yelverton & Coble, 1991). Narrower row spacing in snap bean, maize and onions, also resulted in lower yield losses due to weed competition (Williams *et al.*, 1973). Légère & Schreiber (1989) found that soya bean's competitiveness, due to its rapid early growth, is most obvious at narrow row spacings, but that pigweed still managed to cause yield loss at narrow row spacings because of its greater height. Weed suppression by narrow rows of snap beans is explained by a higher rate of crop canopy closure. However, weeds that are allowed to emerge with the snap bean crop are less suppressed by narrower row spacing, than weeds that emerge later in the season (Teasdale & Frank, 1983). A theoretical analysis by Fischer & Miles (1973) also suggests that, for maximum weed suppression, the crop plants should be sited in a square lattice. Nygren & Jiménez (1993) found that light availability for maize or bean crops, which were grown between rows of trees, were highest when the tree rows were far apart and the rows were orientated such that shading between the tree rows was lowest. Interpreting the results of Nygren & Jiménez for crop-weed competition in row crops, this suggests that the row spacing of a crop should be small, and the row orientation such that a maximum shading of weeds growing between the crop rows is obtained. In conclusion, reducing the row spacing such that a more uniform plant arrangement is obtained remains a good idea, because it results in the highest dry matter production, if the height growth of weeds can be controlled or the emergence date of weeds can be delayed.

The model INTERROW simulates the light interception inside a canopy with a row structure in a correct way. A first test of the model, showed that the simulated effects of intra-specific and inter-specific competition on dry matter production of witloof chicory and *Senecio vulgaris* matched the experimental data. After further testing of the model behaviour with data from field experiments, the model will be a powerful tool to gain a better understanding of the mechanisms underlying competition and in the development of weed management systems.

APPENDIX

List of symbols, definitions and units. The subscript i found throughout the main text refers to the species number for which the values are calculated.

symbol	definition	unit
a_d	parameter of logistic plant diameter growth	cm
A	instantaneous rate of canopy photosynthesis	kg CO_2·ha^{-1} soil·h^{-1}
A_d	daily rate of canopy photosynthesis	kg CO_2·ha^{-1} soil·d^{-1}
A_L	local instantaneous rate of photosynthesis	kg CO_2·ha^{-1} leaf·d^{-1}
A_m	maximum photosynthetic rate at light saturation	kg CO_2·ha^{-1} leaf·h^{-1}
A_s	instantaneous photosynthetic rate of leaf	kg CO_2·ha^{-1} leaf·h^{-1}
A_{sh}	instantaneous photosynthetic rate of shaded leaves	kg CO_2·ha^{-1} leaf·h^{-1}
A_{sl}	instantaneous photosynthetic rate of sunlit leaves	kg CO_2·ha^{-1} leaf·h^{-1}
α	difference between row azimuth and beam azimuth	radians
α_c	angle of projection of light beam in *xz*-plane with *z*-axis (converted azimuth)	radians
b_d	parameter of logistic plant diameter growth	-
b_h	parameter of logistic height growth	-
β	angle of light beam with horizontal (inclination)	radians
β_c	angle of light beam with *xz*-plane (converted inclination)	radians
d	plant diameter	cm
d_{max}	maximum obtainable plant diameter	cm
δ_c	distance between row centres	cm
δ_l	distance between left-hand borders of the rows	cm
ε	initial light use efficiency	kg CO_2·ha^{-1}·h^{-1}·J^{-1}·m^2·s
f_{sl}	fraction sunlit leaf area at gridpoint	-
F_N	factor accounting for effect of competition for nitrogen on growth rate	-
F_W	factor accounting for effect of competition for water on growth rate	-
G	dry matter growth rate	kg DM·ha^{-1} soil·d^{-1}
G_{lai}	leaf area growth rate	ha leaf·ha^{-1} soil·d^{-1}
G_{leaf}	leaf dry matter growth rate	kg leaf DM·ha^{-1}·d^{-1}
h	plant height	cm
hu	daily accumulated temperature sum	°C
h_{max}	maximum obtainable plant height	cm
I_{abs}	amount of light absorbed at gridpoint	J·m^{-2} leaf·s^{-1}

I_0	light intensity above the canopy	$J \cdot m^{-2}$ soil$\cdot s^{-1}$
k	light extinction coefficient of leaves	-
l	length of extinction path of light beam	cm
LA	leaf area index that is traversed by light beam	ha leaf$\cdot$ha^{-1} soil
LAI	leaf area index	ha leaf$\cdot$ha^{-1} soil
LD	leaf area density	$cm^2 \cdot cm^{-3}$
N	number of rows traversed by light beam, other than the first row that was penetrated by light beam	-
N_{act}	actual nitrogen content of the plant	kg N$\cdot$kg^{-1} DM
N_{crit}	critical nitrogen content of the plant	kg N$\cdot$kg^{-1} DM
N_{min}	minimum nitrogen content of the plant	kg N$\cdot$kg^{-1} DM
p	path width	cm
Q	assimilate requirement for DM production	kg $CH_2O \cdot$kg^{-1} DM
$rgrl$	relative growth rate of leaves	$°C^{-1} \cdot d^{-1}$
R_m	maintenance respiration rate	kg $CH_2O \cdot$ha^{-1} soil$\cdot d^{-1}$
sla	specific leaf area	ha leaf$\cdot$kg^{-1} leaf
s_d	parameter of logistic height growth	$°C^{-1} \cdot d^{-1}$
s_h	parameter of logistic height growth	$°C^{-1} \cdot d^{-1}$
σ	scattering coefficient of leaves	-
ts	temperature sum	$°C \cdot d$
$t_{d,max}$	maximum temperature for development	°C
T_a	actual transpiration rate	$mm \cdot d^{-1}$
T_p	potential transpiration rate	$mm \cdot d^{-1}$
w	row width	cm
w_{act}	actual soil moisture content	mm
w_{crit}	critical soil moisture content	mm
w_{min}	minimum soil moisture content	mm
x	distance from gridpoint to left border of row	cm
z	distance from gridpoint to top of row	cm

CHAPTER 4

THE EFFECTS OF SPATIAL ARRANGEMENT, PLANT DENSITY AND EMERGENCE DATE ON COMPETITION BETWEEN WITLOOF CHICORY AND THREE WEED SPECIES, ANALYSED WITH A SIMULATION MODEL

B. J. Schnieders, P. C. de Man, L. A. P. Lotz and R. Rabbinge

ABSTRACT

The effects of spatial plant arrangements, plant densities, and emergence dates, on competition between witloof chicory (*Cichorium intybus* L.) and the weed species *Senecio vulgaris* L., *Solanum nigrum* L., and *Chenopodium album* L. were studied. The model INTERROW was tested on its ability to accurately simulate the outcome of competition under a wide variety of conditions.

Strong reductions of the storage root dry weight of witloof chicory due to competition with *S. vulgaris*, *S. nigrum* or *C. album*, were found to be primarily caused by an early emergence of the weeds, and to a lesser extent by weed density and weed position. The simulation analysis and experimental data showed, that weeds emerging up to at least one week after the witloof chicory crop must be removed to limit the yield loss to acceptable levels. High initial growing temperatures and a uniform plant distribution, *i.e.* a small row spacing, may be essential for witloof chicory to establish a strong competitive position, especially when weeds emerge later than the crop.

The model INTERROW accurately simulated the growth of all species, both in monocultures and in mixtures, under a wide range of conditions. The model simulated small effects of spatial position of weeds on the storage root dry weight, consistent with the experimental results. There were no systematic underestimations or overestimations of the dry weights of witloof chicory, *S. vulgaris*, *S. nigrum* or *C. album*. The model INTERROW explicitly takes into account the row structure of a crop, and all important processes involved in competition have been incorporated into the model. Model analyses carried out in this paper have helped to explain experimental results and were used to generate recommendations about growing witloof chicory in such a way that yield loss is eliminated, or minimised if elimination is impossible.

Witloof chicory has a high base temperature for growth and development, compared to many weed species. With respect to the development of new weed management methods which take into account crop husbandry measures to increase the crop competitiveness, this implies that witloof chicory should be sown when soil and air temperatures are sufficiently high to ensure a quick establishment of the crop. Model analysis showed that an increase in air temperatures increases the dry matter production of witloof chicory when grown in monoculture. Model analysis also showed that early emerging weeds caused a great reduction in dry matter production of witloof chicory, especially at higher air temperatures. It was suggested that a soil cover by "bio-degradable" non-transparent plastic with holes through which the crop plants can grow, will allow the crop plant to profit from the higher temperatures while inhibiting the growth of weeds underneath the plastic.

INTRODUCTION

Witloof chicory (*Cichorium intybus* L.) is a row crop with incomplete canopy closure between the rows (Schnieders & Lotz, 1993). Witloof chicory has a high base temperature for growth (Groenwold & Van de Geijn, 1990; Meijer & Mathijssen, 1992), which causes a slow initial growth in spring time and contributes to the open canopy structure. The ability of a witloof chicory crop to suppress weeds is therefore low, and large yield losses due to competition may occur. Consequently, weed control is a critical issue in the management of a witloof chicory crop (Richards, 1944; Poll & Douglas, 1987). New weed management methods must be developed, because the choice of chemical weed control solutions in witloof chicory is limited (Anonymous, 1989) and chemical weed control in general should be reduced (Anonymous, 1989; MJP-G, 1991).

The reduction in crop dry matter due to competition with weeds depends on many factors, such as plant densities, relative dates of emergence, species specific growth rates (*e.g.* Kropff & Van Laar, 1993; Lotz *et al.*, 1993), and also spatial plant arrangements (*e.g.* Mack & Harper, 1977; Radosevich, 1988). Experimental research and the use of a systems approach has increased our quantitative knowledge of the processes that determine the outcome of competition, and resulted in the development of new weed management methods (*e.g.* Kropff & Van Laar, 1993).

Spitters & Aerts (1983) developed a mechanistic dynamic simulation model for inter-specific competition in crops that attain complete canopy closures. This model, INTERCOM, was further elaborated (Kropff & Spitters, 1992, Kropff & Van Laar, 1993) and successfully used to simulate the effects of crop-weed competition on the dry matter production of many crops. However, the simulation results obtained with INTERCOM differed structurally from the results of competition experiments in witloof chicory row crops (Schnieders & Lotz, 1993). The assumption in the INTERCOM model that the leaf area is distributed in a horizontally homogeneous way, was invalid for witloof chicory (Schnieders & Lotz, 1993). We developed a mechanistic dynamic simulation model for inter-specific competition in row crops, INTERROW, which explicitly takes into account the row structure of the crop (Schnieders & Lotz, 1993; Chapter 3).

The aim of this study was to quantify the effects of spatial arrangement, plant density, and emergence date, on the outcome of competition between witloof chicory and the weed species *Senecio vulgaris* L., *Solanum nigrum* L., and *Chenopodium album* L. The model INTERROW was consequently used to analyse the processes determining the outcome of competition, and to generate recommendations about growing witloof chicory in such a way that yield loss is eliminated.

MATERIALS AND METHODS

Experiments

Six experiments were carried out in 1992 and 1993, at three locations (Lelystad, Westmaas and Wageningen) in the Netherlands. Witloof chicory was sown at a high seed rate and thinned back to the desired plant densities. Seeds of the weeds were germinated on blotting paper in 1992 and on a water agar medium in 1993 (Kempenaar & Schnieders, 1995). Clusters of germinated seeds were subsequently planted into the soil. After establishment of the seedling clusters, each cluster was thinned back to a single plant. This enabled manipulation of dates of emergence, plant densities and plant positions. A number of harvests were taken in each experiment. At each harvest, the dry weights of the plant organs after drying for 48 hours at 75 °C, and the leaf area (LI-COR area meter, model 3100, Lincoln, NE, USA) were measured.

Lelystad, 1992. Plants of the species *S. vulgaris* or *S. nigrum* were positioned in the centre of the witloof chicory row. The witloof chicory plants emerged on 19 May, and established at a plant density of 20 $\text{pl}\cdot\text{m}^{-2}$. The weed plants emerged on 7 June (s1) or 16 June (s2), and established at plant densities of 10 (d1), 20 (d2) or 40 (d3) $\text{pl}\cdot\text{m}^{-2}$. Witloof chicory was grown at a row spacing of 0.75 m. The row orientation was East-West.

Westmaas, 1992. Plants of the species *S. vulgaris* or *S. nigrum* were positioned in the centre of the witloof chicory row. The witloof chicory plants emerged on 22 May, and established at a plant density of 20 $\text{pl}\cdot\text{m}^{-2}$. The weed plants emerged on 31 May (s1) or 14 June (s2), and established at plant densities of 10 (d1), 20 (d2) or 40 (d3) $\text{pl}\cdot\text{m}^{-2}$. Witloof chicory was grown at a row spacing of 0.75 m. The row orientation was North-South.

Wageningen, 1992. Plants of the species *S. vulgaris*, *S. nigrum* or *C. album* were positioned in the centre of the witloof chicory row (p1) or in between the witloof chicory rows (p2). The witloof chicory plants emerged on 22 May, and established at a plant density of 20 $\text{pl}\cdot\text{m}^{-2}$. The weed plants emerged on 1 June (s1) or 9 June (s2), and established at plant densities of 10 $\text{pl}\cdot\text{m}^{-2}$. Witloof chicory was grown at a row spacing of 0.75 m. The row orientation was SSE-NNW.

Lelystad, 1993. Plants of the species *S. vulgaris*, *S. nigrum* or *C. album* were positioned in the centre of the witloof chicory row (p1) or in between the witloof chicory rows (p2). The witloof chicory plants emerged on 19 May and established at a plant density of 20 pl·m^{-2}. The weed plants emerged on 17 May, and established at a plant density of 20 pl·m^{-2}. Witloof chicory was grown at a row spacing of 0.75 m. The row orientation was West-East.

Westmaas, 1993. Plants of the species *S. vulgaris* or *S. nigrum* were positioned in the centre of the witloof chicory row. The witloof chicory plants emerged on 21 May and established at a plant density of 20 pl·m^{-2}. The weed plants emerged on 22 May, and established at plant densities of 20 (d1), 40 (d2) or 80 (d3) pl·m^{-2}. Witloof chicory was grown at a row spacing of 0.75 m. The row orientation was North-South.

Wageningen, 1993. Plants of the species *S. vulgaris* were positioned in the centre of the witloof chicory row (p1) or in between the witloof chicory rows (p2). The witloof chicory and *Senecio vulgaris* plants emerged on 2 June, and established at plant densities of 20 pl·m^{-2}. Witloof chicory was grown at row spacings of 0.25 (r1), 0.50 (r2) or 0.75 (r3) m. The row orientation was NNW-SSE.

All experiments had a completely randomised block design with 4 replicates, with the exception of the experiment in Wageningen in 1993 which had a split plot design with 4 replicates. The results were analysed by analysis of variance using GENSTAT (Genstat 5 Committee, 1993). The experiments had factorial arrangements of several types of treatment, *i.e.*, weed density, weed emergence date, weed position, weed species, or crop row width. In addition there were one or more control treatments, *i.e.*, crop in monoculture or weed species in monoculture (Genstat 5 Committee, 1993, page 490-493). This structure of factorial plus added control allows the analysis of interactions between treatments, but also allows the analysis of treatment versus control treatment.

Short description of the INTERROW model

The INTERROW model is described in detail in Chapter 3. The INTERROW model is derived from the INTERCOM model of Kropff & Van Laar (1993).
The modules for light interception and photosynthesis in INTERCOM have been replaced with new modules, that take into account the 3-dimensional geometry of the canopy and also the solar geometry. These new modules were derived from a model for light distribution and photosynthesis in single-species row crops, developed by Gijzen & Goudriaan (1989). The model INTERROW explicitly takes into account the distribution of leaf area over the soil area, the row dimensions, the orientation of the rows, and the

relative position of rows of different species. The light interception by each species is simulated, based on these geometrical characteristics.

In a potential production situation, where light, temperature, and species specific characteristics determine the growth of a plant community, plants compete primarily for light (*e.g.* Kropff, 1993a). The model INTERROW calculates the vertical and horizontal light profile within the multi-species row canopy, from the leaf area indices and the spatial distributions of the leaf area over the soil area.

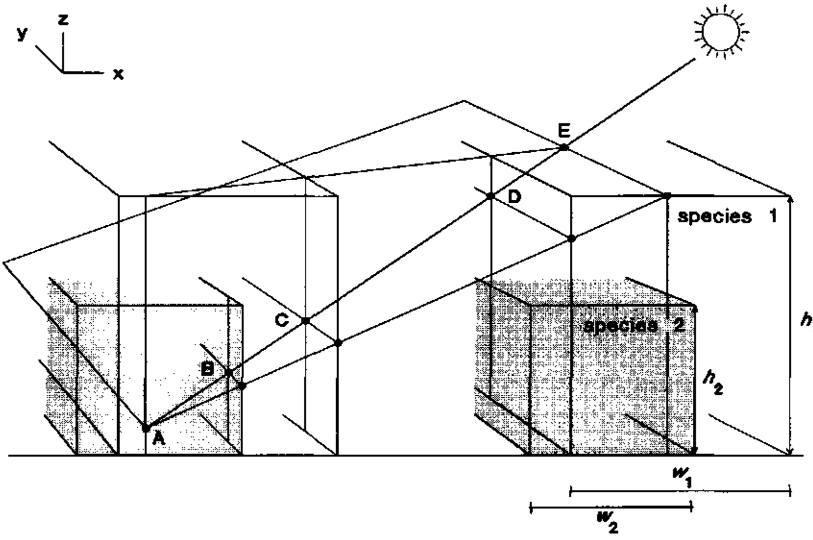

Figure 4.1 A schematic representation of the interception of a light beam within a row canopy, consisting of two species. The canopy dimensions of species *i* are defined by the row width (wi), and the row height (hi)

The canopy can be visualised as a series of rectangular-shaped boxes (Figure 4.1), where each box represents a canopy row of certain height (h_i), width (w_i) and infinite length. Each box contains the leaf area of one row of a certain species. The height and width of these boxes, and the leaf area inside the boxes are changing in time, simulating the canopy dynamics of a species. The light intensity at any point A inside a row of species 1, can be calculated from the interception of a series of light beams originating from carefully chosen positions on the hemisphere, according to a method described by Gijzen & Goudriaan (1989). For example, a light beam of photosynthetically active radiation (PAR) entering a row of species 1 in point E, will be partially intercepted by leaves of species 1 in the trajectories ED and CA, and by leaves of species 2 in trajectory BA. When the length of these trajectories are quantified and the leaf area density inside the rows is known, the remaining PAR intensity at point A can be calculated. This remaining PAR can be absorbed by a leaf of a certain species at point A. Using the photosynthetic characteristics of single leaves, the local photosynthetic rate at point A can then be calculated.

Subsequently, the photosynthesis profile in both the vertical and horizontal direction inside a canopy row is calculated for each species, using the light profiles, the leaf area distributions, and the photosynthetic characteristics of single leaves. The instantaneous canopy photosynthesis of each species is obtained, by integrating the photosynthesis profile over the height and the width of the row using Gaussian integration (Goudriaan, 1986), and applying a correction for incomplete soil cover. Subsequent integration over the day gives the daily gross CO_2 assimilation rate of each species. The amount of assimilated CO_2 is then converted into carbohydrates, and decreased with the carbohydrate requirements for maintenance respiration. The remaining carbohydrates are converted into dry matter, using the assimilate requirement for dry matter production, resulting in the net daily growth rate.

Plants also may have to share a limited supply of water and nitrogen. To account for the effects of water shortages on the growth rate of each species, the approach described by Kropff & Spitters (1992) and Kropff (1993b) is used. This approach is based on a simple water balance. To account for the effects of nitrogen shortages on the growth rate of each species, the approach described by Spitters (1989) and Kropff (1993c), was applied. A simple nitrogen balance keeps track of the amount of available nitrogen in the soil.

Model parameterisation

The model parameters for witloof chicory, *S. vulgaris*, and *S. nigrum*, were derived from data in literature and from experimental data of two competition experiments carried out in 1991 (Chapter 3). The model parameters for *C. album* were taken from Kropff & Spitters (1992) and Kropff *et al.* (1992).

RESULTS

Experiments

Lelystad, 1992. The storage root dry weight of witloof chicory in monoculture was marginally greater ($P<0.05$) than the average storage root dry weight of witloof chicory in the weed treatments (Figure 4.2a). Between the weed treatments (species, emergence date or plant density), no different effects ($P>0.05$) on the storage root dry weights were found, mainly because the emergence of the weed species (19 and 28 days after emergence of the crop for sowing date 1 and 2, respectively) was too late to cause severe competition of the weeds with witloof chicory.

Westmaas, 1992. The storage root dry weight of witloof chicory in monoculture was not different ($P>0.05$) from the average storage root dry weight of witloof chicory in the weed treatments (Figure 4.2b). Competition with *S. vulgaris* reduced the storage root dry weight by 13 %, which was more ($P<0.05$) than the 4 % reduction caused by competition with *S. nigrum*. The emergence date or plant density of the weed species had no effect ($P>0.05$) on the storage root dry weight of witloof chicory. Even when the weed plants emerged only 9 days after the witloof chicory plants, no effects of competition on storage root dry weight were recorded.

Wageningen, 1992. The storage root dry weight of witloof chicory in monoculture was not different ($P>0.05$) from the average storage root dry weight of witloof chicory in the weed treatments (Figure 4.2c). The weed treatments (species, emergence date or spatial plant position) had no effects ($P>0.05$) on the storage root dry weights, although competition with *C. album* and to a lesser extend also *S. vulgaris* tended to cause some reduction in storage root dry weight (Figure 4.2c).

Lelystad, 1993. The storage root dry weight of witloof chicory in monoculture was 29 % greater ($P<0.001$) than the average storage root dry weight of witloof chicory in the weed treatments (Figure 4.2d). There was a strong species effect ($P<0.001$), which was such that competition with *C. album* caused the greatest reduction (60 %) in storage root dry weight and competition with *S. vulgaris* caused the smallest reduction (23 %). The position of the weed plants, inside or in between witloof chicory rows, did not affect ($P>0.05$) the storage root dry weight of witloof chicory.

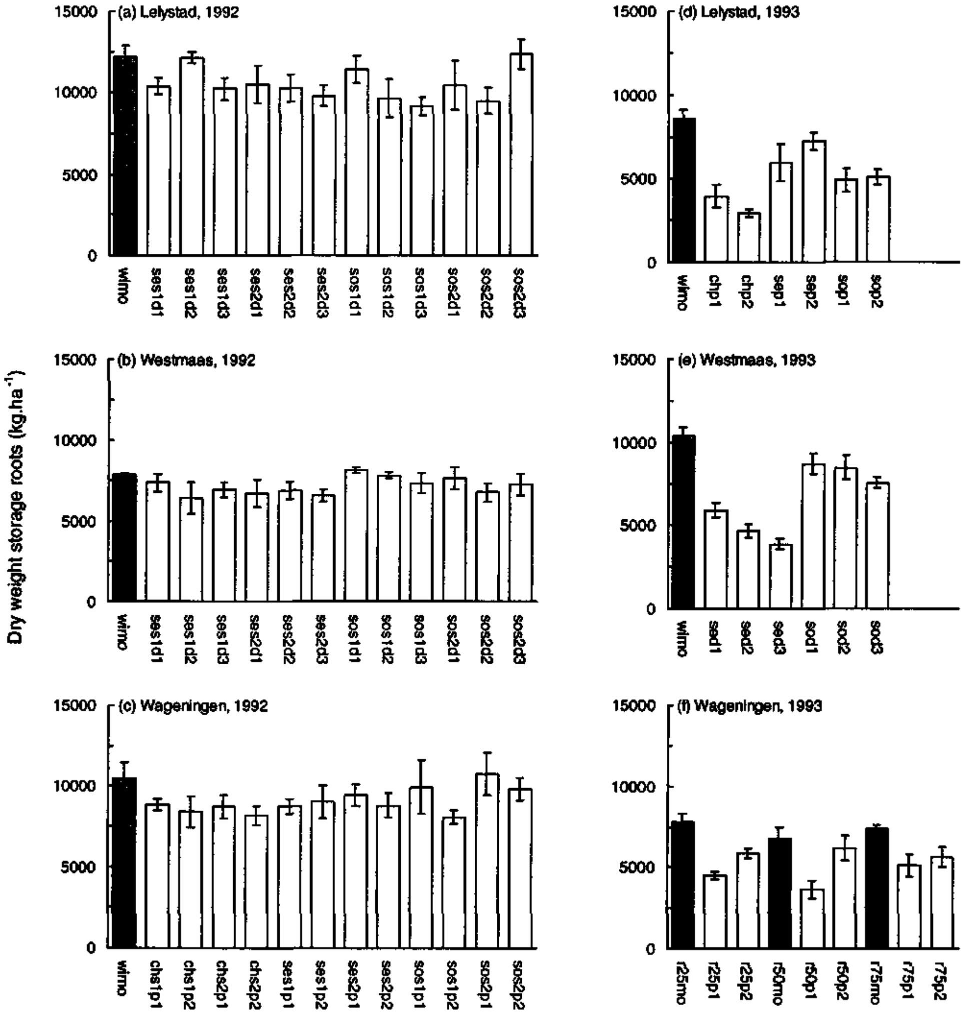

Figure 4.2 Dry weights of storage roots of witloof chicory at final harvest, for six experiments. Values are averages of 4 replicates, vertical bars represent standard errors of the means. The treatments (see also the Material & Methods) consisted of a combination of weed species (Ch, Se or So for *C. album*, *S. vulgaris* or *S. nigrum*, respectively), weed emergence date (s1 or s2), weed density (d1, d2 or d3), weed position (p1 or p2) and row spacing (r25, r50 or r75). Witloof chicory grown in mono is represented by the code mo, and the filled bars.

Westmaas, 1993. The storage root dry weight of witloof chicory in monoculture was 41 % greater ($P<0.001$) than the average storage root dry weight of witloof chicory in the weed treatments (Figure 4.2e). There was a strong species effect ($P<0.001$), which was such that competition with *S. vulgaris* reduced the storage root dry weight by 54 %, which was greater than the 20 % reduction caused by competition with *S. nigrum*. There was also a plant density effect ($P<0.001$), which was such that competition with 80 weed $\text{pl}\cdot\text{m}^{-2}$ reduced the storage root dry weight by 45 %, which was greater than the reductions of 37 and 29 %, caused by competition with 40 or 20 weed $\text{pl}\cdot\text{m}^{-2}$, respectively.

Wageningen, 1993. The storage root dry weight of witloof chicory in monoculture was 35 % greater ($P<0.001$) than the average storage root dry weight of witloof chicory in the weed treatments (Figure 4.2f). There was an effect of spatial position of the weed plants ($P<0.01$). Competition with *S. vulgaris* plants growing inside the witloof chicory rows reduced the storage root dry weight by 39 %, which was greater than the 19 % reduction caused by competition with *S. vulgaris* plants growing in between the crop rows. Decreasing the row spacing did not affect ($P>0.05$) the storage root dry weight of witloof chicory, neither when growing in monoculture nor when growing in competition with *S. vulgaris*.

Model parameterisation

Figure 4.3 shows the parameterisation results of the INTERROW model. The storage root dry weights of witloof chicory grown in monoculture were accurately simulated throughout the growing period (Figures 4.3a, f). The dry matter production of *S. vulgaris* and *S. nigrum* grown in monoculture (Figures 4.3b, d), was simulated accurately during most of the growing period. The strong reduction in the dry weight of *S. vulgaris* at the end of the growing period due to seed fall and leaf fall was not properly simulated (Figure 4.3b). The simulated reduction in green leaf area at the end of the growing period corresponded with the measured effects. The model INTERROW also accurately simulated the dry matter production of all species in the mixtures of witloof chicory and *S. vulgaris* (Figure 4.3c, 3g), or witloof chicory and *S. nigrum* (Figure 4.3e).

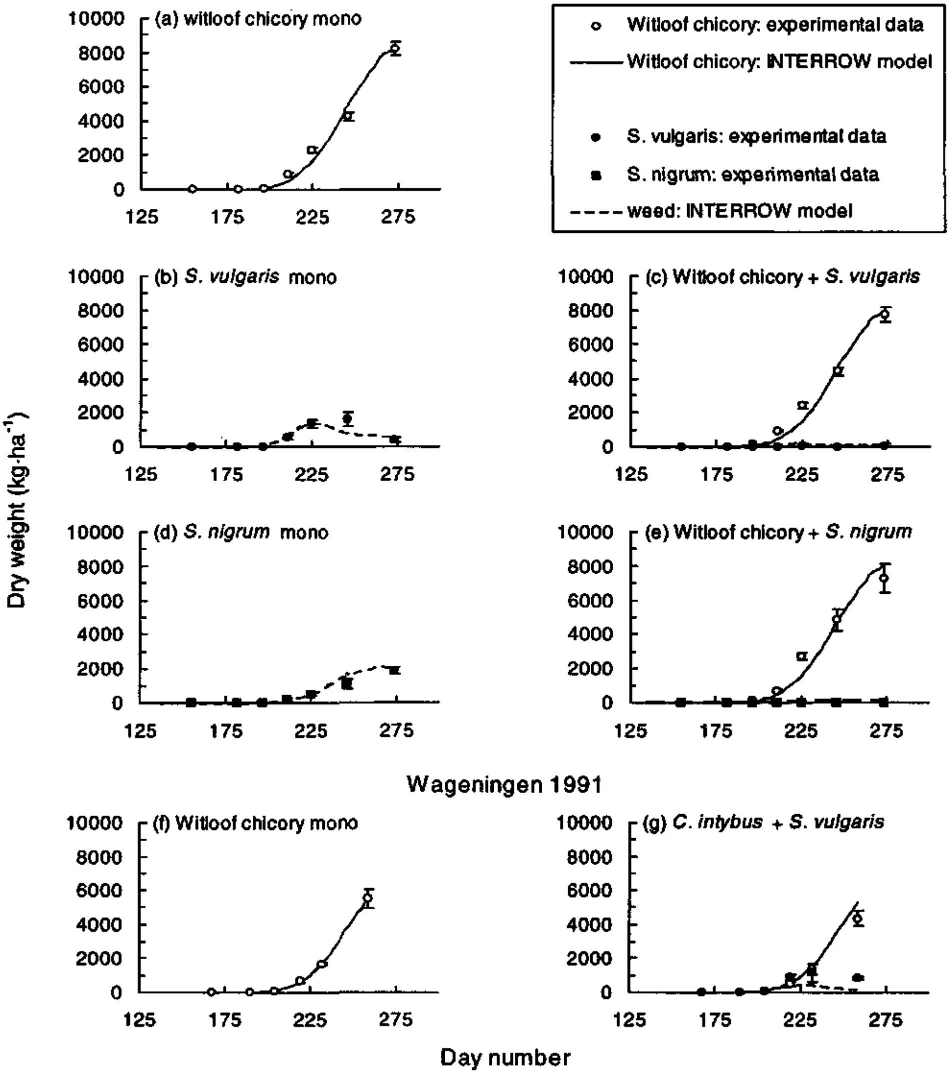

Figure 4.3 Parameterisation results of the model INTERROW, showing the simulation of the storage root dry weight of witloof chicory and total shoot dry weight of *S. vulgaris* and *S. nigrum*, grown in monoculture and mixture at Lelystad in 1991 (a, b, c, d, e) and at Wageningen in 1991 (f, g). Results are presented for monoculture growings of witloof chicory (a, f), *S. vulgaris* (b), and *S. nigrum* (d), and for competition between witloof chicory and *S. vulgaris* (c, g) or S..nigrum (e).

Feasibility study with the model INTERROW

The experiments carried out in 1992 and 1993 were not used for the parameterisation of the models, and were thus suitable to test whether the model INTERROW was simulating the effects of competition in a correct way.

Effects of spatial arrangements. The INTERROW model adequately simulated the production of storage root dry weight of witloof chicory, grown in monoculture (Figs 4a, d) and mixture (Figures 4.4b, c, e, f, g, h), and the production of total shoot dry weight of *S. vulgaris* (Figures 4.4b, c, e, f) and *C. album* (Figures 4.4g, h).

Both the simulated and experimental reductions in storage root dry weight of witloof chicory, tended to be greater when *S. vulgaris* was positioned inside the crop row (Figures 4.4b, e) than when it was positioned in between two crop rows (Figures 4.4c, f). The experimental and simulated total shoot dry weights of *S. vulgaris* were slightly higher when it was growing in between two crop rows. The greater yield reduction caused by *S. vulgaris* growing inside the crop row, can be explained by assuming that *S. vulgaris* growing inside the crop row started to exert its competitive effect earlier in the growing season. In contrast to *S. vulgaris*, the yield reduction caused by *C. album* growing inside the crop row (Figure 4.4g) tended to be smaller than the yield reduction caused by *C. album* growing in between the crop rows (Figure 4.4h).

The most obvious differences between *S. vulgaris* and *C. album* are the maximum obtainable plant height and the leaf area duration. Both are much larger for *C. album*. To study whether one of these morphological parameters was responsible for the difference in effects caused by the two weed species, a model analysis was performed using weather data of Lelystad, 1993, and assuming potential growth conditions. Both the experimental and simulation results did not show effects of inter-specific competition on either plant nitrogen levels or soil water levels, which justifies the assumption of potential growth conditions in the model analysis. All species emerged at the same day, which was set to 20 May. The plant height (relative to the maximum obtainable plant height of the witloof chicory crop, which was 0.6 m) of both weed species was varied. The model was also used to study the effect of doubling the leaf area duration of *S. vulgaris*, to a value identical to that of *C. album*. The results of the model analysis showed that when the plant height of weeds is smaller than that of witloof chicory, the yield reduction will be greater when weeds are growing in between the rows, irrespective of the weed species or the leaf area duration (Figure 4.5).

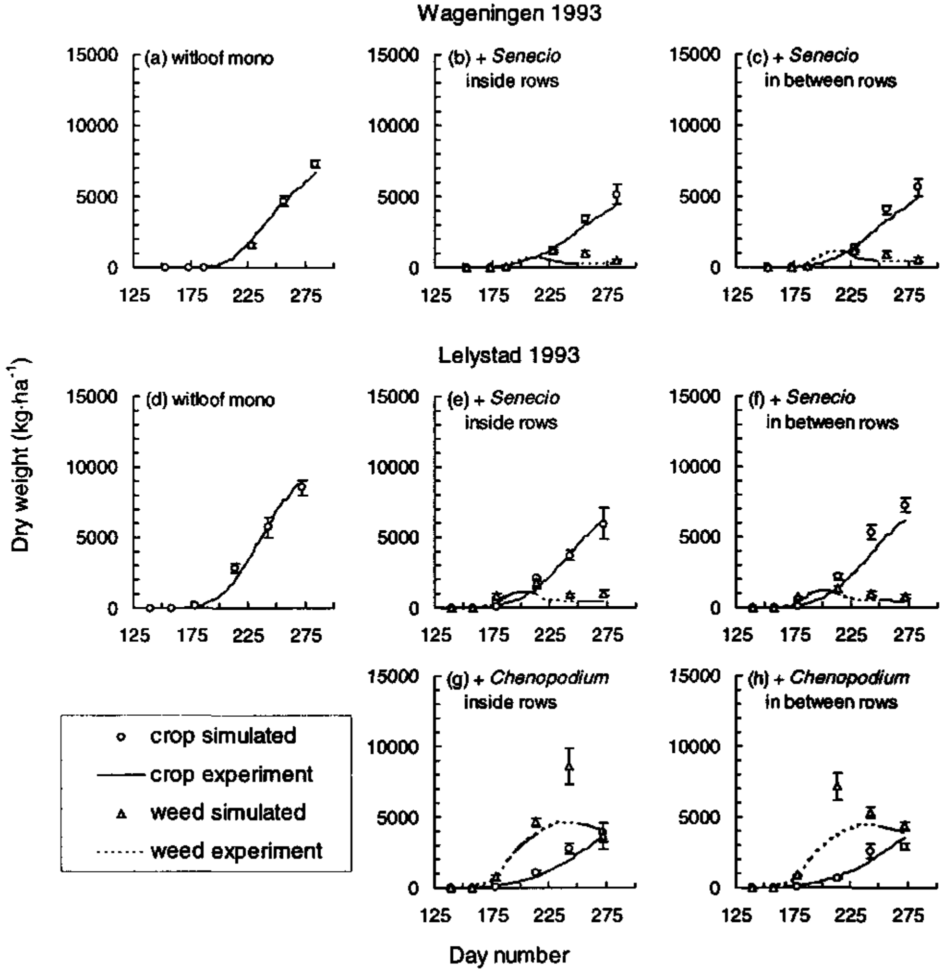

Figure 4.4 Measured and simulated effects of spatial plant arrangements on the production of storage root dry weight of witloof chicory and total shoot dry weight of weeds. Results are presented for witloof chicory grown at a row spacing of 75 cm at Wageningen in 1993 (a, b, c) and at Lelystad in 1993 (d, e, f, g, h). Witloof chicory was grown in monoculture (a, d), in competition with *S. vulgaris* positioned inside the crop rows (b, e) or in between the crop rows (c, f), and in competition with *C. album* positioned inside the crop rows (g) or in between the crop rows (h).

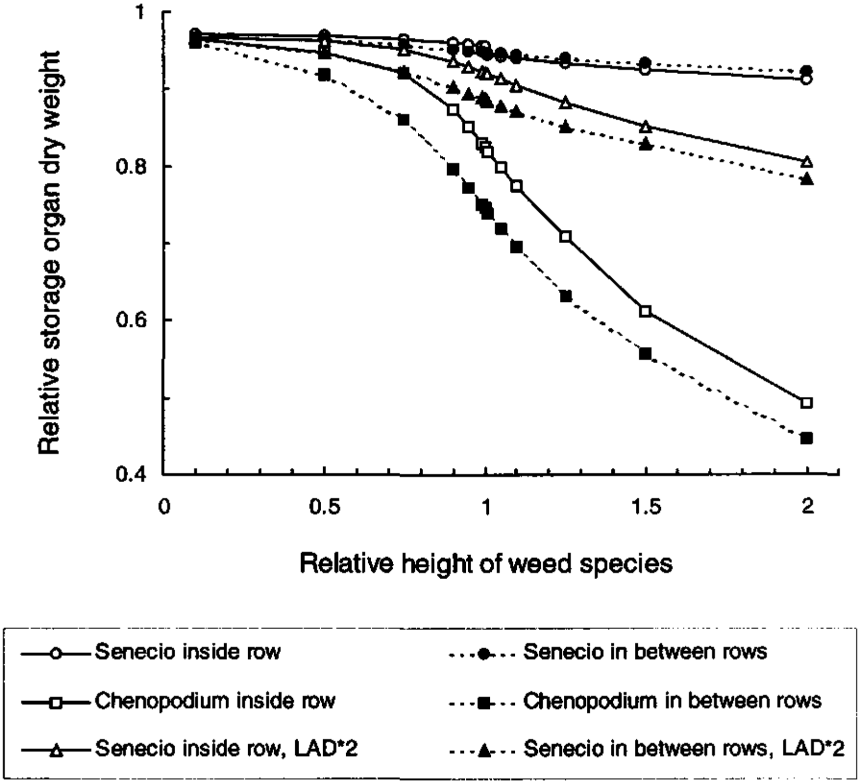

Figure 4.5 Model analysis of the effects of the plant height (expressed as a fraction of the maximum obtainable plant height of the witloof chicory crop, which was 0.6 m) of the weed species *S. vulgaris* and *C. album*, and of the leaf area duration (LAD) of *S. vulgaris* which was doubled in value to a value identical to that of *C. album*, on the yield reduction of witloof chicory. For the model analysis, weather data of Lelystad, 1993, were used, and potential growth conditions were assumed. Witloof chicory emergence and weed emergence was 20th May, and final harvest was set at 2nd October. Plant densities were 20 plants·m^{-2} for each species.

Effects of plant densities. The simulation results of model INTERROW correspond with the measured production of the storage root dry weight of witloof chicory, grown in monoculture (Figure 4.6a) and in mixture (Figures 4.6b, c, d, e), and the production of total shoot dry weight of *S. vulgaris* (Figures 4.6b, c) and *S. nigrum* (Figures 4.6d, e), for the experiment at Westmaas in 1993. Both the simulated and experimental reductions in storage root dry weight of witloof chicory were greater at higher weed densities, and the reductions were greatest when competition occurred with *S. vulgaris*. The measured and simulated shoot dry weights of *S. vulgaris* showed a very strong juvenile growth, which made *S. vulgaris* a strong competitor, despite its short leaf area duration. This indicates that witloof chicory is very susceptible to competition early in the growing season. The growth rate of *S. nigrum* was much slower, and it required a high plant density to cause substantial yield loss of witloof chicory during the later part of the growing season.

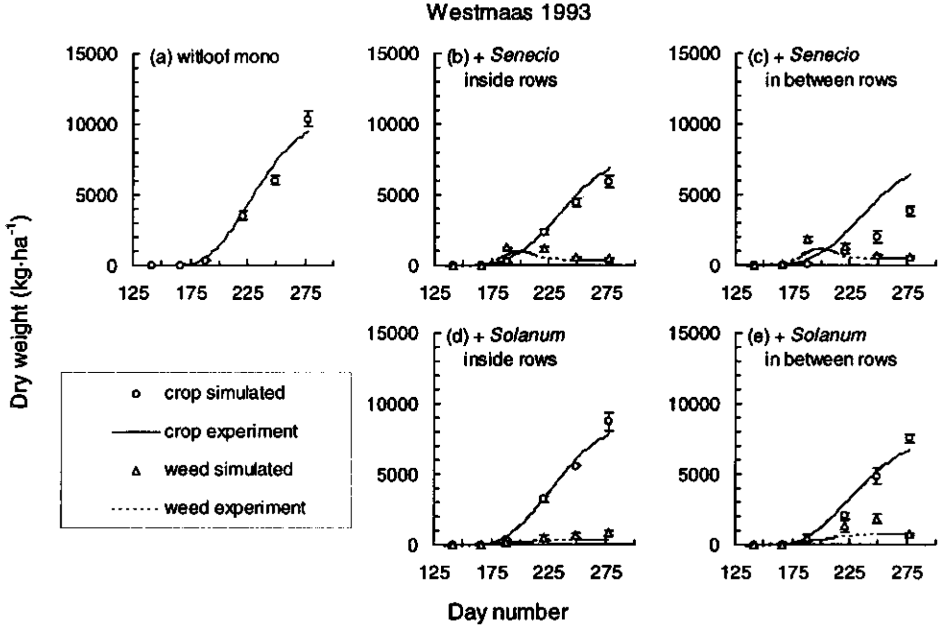

Figure 4.6 Measured and simulated effects of weed densities on the production of storage root dry weight of witloof chicory and total shoot dry weight of weeds. Results are presented for witloof chicory grown at Westmaas in 1993, grown in monoculture (a), and in competition with 20 *S. vulgaris* plants·m^{-2} (b), 80 *S. vulgaris* plants·m^{-2} (c), 20 *S. nigrum* plants·m^{-2} (d), or 80 *S. nigrum* plants·m^{-2} (e).

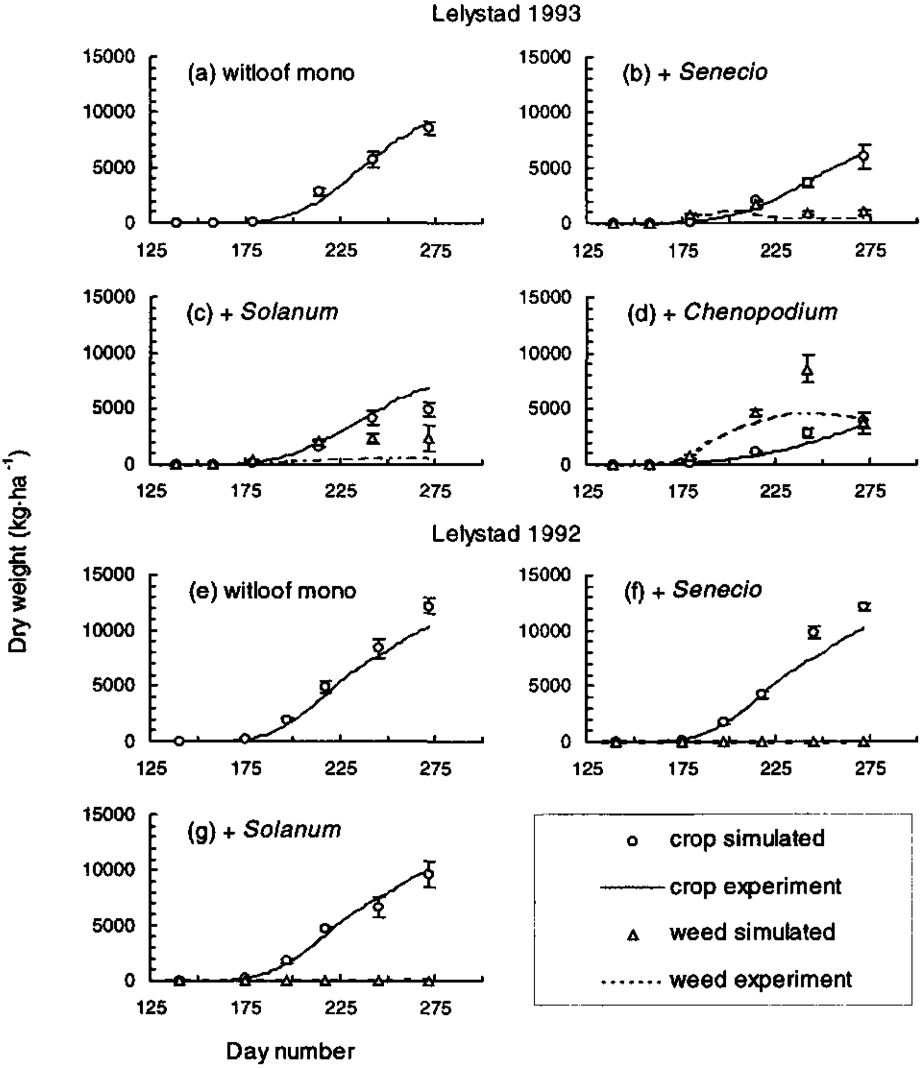

Figure 4.7 Measured and simulated effects of weed emergence dates on the production of storage root dry weight of witloof chicory and total shoot dry weight of weeds. Results are presented for witloof chicory grown at Lelystad in 1993 (a, b, c, d) and 1992 (e, f, g), grown in monoculture (a, e) and in competition with *S. vulgaris* (b, f), *S. nigrum* (c, g), or *C. album* (d), where the weed emergence occurred 2 days before (b,c,d) or 19 days after (f, g) crop emergence.

Effects of emergence dates. The model INTERROW adequately simulated the production of the storage root dry weight of witloof chicory, grown in monoculture (Figures 4.7a, e) and in mixture (Figures 4.7b, c, d, f, g), and the production of total shoot dry weight of *S. vulgaris* (Figures 4.7b, f), *S. nigrum* (Figures 4.7c, g) and *C. album* (Figure 4.7d), for the experiments at Lelystad in 1992 and 1993. An early emergence of the weeds relative to the crop (-2 days) in the experiment at Lelystad in 1993, gave the weeds a competitive advantage over witloof chicory. *C. album*, positioning its leaf area above the witloof chicory plants, captured much of the available light resources and caused a 61 % reduction of the simulated storage root dry weight of witloof chicory (Figure 4.7d). *S. nigrum* also grew vigorously and caused a 31 % reduction of the simulated storage root dry weight of witloof chicory (Figure 4.7c). *S. vulgaris* has a very strong juvenile growth, comparable to that of *C. album*, and thus has potential to be a strong competitor. Competition with *S. vulgaris* caused a 25 % reduction of the simulated storage root dry weight of witloof chicory (Figure 4.7b). However, the leaf area duration of *S. vulgaris* is very short compared to the other two weed species. After senescence of *S. vulgaris* plants, the growth of witloof chicory during the second half of the growing season was not further reduced, and the yield reduction at the end of the growing season was less than that caused by *C. album* or *S. nigrum*. In the experiment at Lelystad in 1992, the weeds emerged 19 days after the crop, and neither the experimental results nor the simulation results showed any reduction in storage root dry weight, due to competition with *S. vulgaris* (Figure 4.7f) or *S. nigrum* (Figure 4.7g).

The two main differences between the experiments at Lelystad in 1992 and 1993, were the relative emergence dates of the weeds and the average air temperature. Weeds emerged 19 days after the crop and 2 days before the crop, in 1992 and 1993 respectively. The temperatures in the early growth stages of 1992 and 1993, were 5-10 °C and 0-5 °C higher than the 30-year average for Wageningen, respectively (data not shown). There is a large difference in the minimum temperature required for growth between the species. Witloof chicory (6 °C) and *S. nigrum* (6 °C) require high temperatures, whereas *S. vulgaris* (3 °C) and *C. album* (0 °C) grow at much lower temperatures. A model analysis was carried out to study the effect of various dates of weed emergence (relative to that of witloof chicory) and average daily air temperatures on the storage root dry weight of witloof chicory. The results of the model analysis showed that an earlier date of weed emergence generally increased the yield loss of witloof chicory (Figure 4.8). However, the extent of the yield loss, depended primarily on the weed species and the average air temperature during the growing season. Competition with *C. album* reduced the storage root dry weight of witloof chicory, irrespective of the air temperature, and even when *C. album* emerged 10 days after witloof chicory (Figure 4.8a).

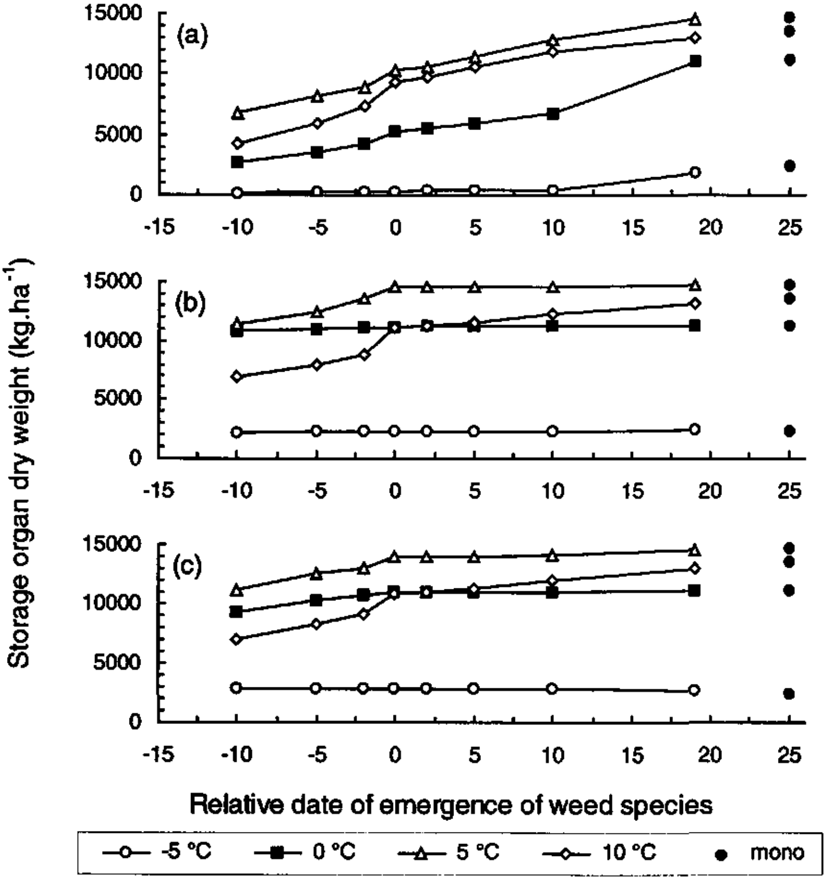

Figure 4.8 Model analysis of the effects of date of weed emergence (relative to that of witloof chicory) and average air temperature, on the storage root dry weight of witloof chicory, for competition with *C. album* (a), *S. vulgaris* (b) and *S. nigrum* (3). For the model analysis, 30-year average weather data (1960-1990) of Wageningen were used as the basis (0 °C), and potential growth conditions were assumed. The range of air temperatures (-5, 5, and 10 °C) was obtained by increasing the average daily air temperatures with -5, 5, and 10 °C, respectively. The storage root dry weight of witloof chicory grown in monoculture at each of the temperatures is represented by the "mono" symbol. Witloof chicory and weed emergence was 20th May, and final harvest was set at 2nd October. Plant densities were 20 plants·m^{-2} for each species, and weeds were positioned inside the crop rows.

Competition with *S. vulgaris* (Figure 4.8b) or *S. nigrum* (Figure 4.8c) only causes severe reductions in storage root dry weight, when air temperatures are higher than the 30-year average (0 °C line) and the weed emergence date was earlier than that of witloof chicory. A higher temperature increases the leaf area development of both *S. vulgaris* and *S. nigrum* more than that of witloof chicory, resulting in a more severe competition in the early growth stages and thus a higher yield loss. The analysis also showed that the storage root dry weight of witloof chicory reached the highest values when temperature was raised by about 5 °C.

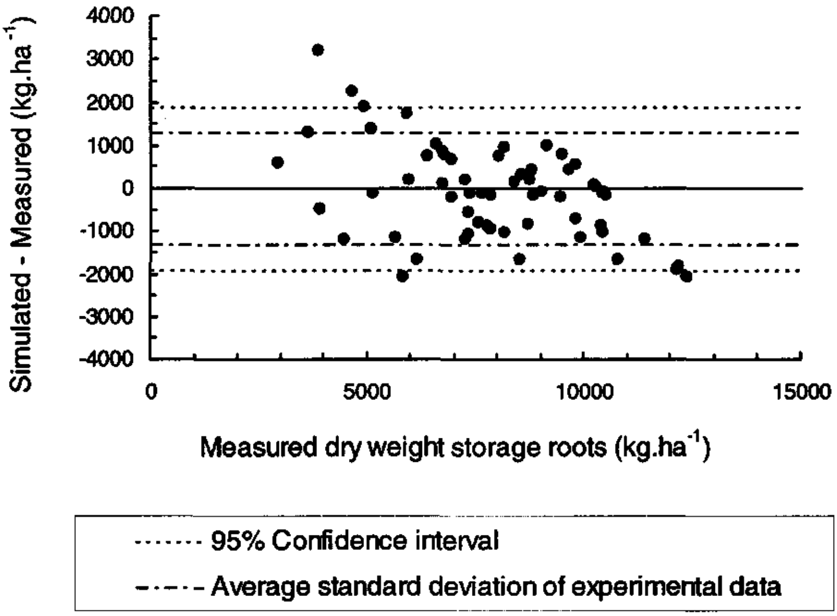

Figure 4.9 The deviation between simulated storage root dry weights and measured storage root dry weight, versus the measured storage root dry weight of witloof chicory, for all treatments from Figure 4.2.

A simple, objective and quantitative method (Michell & Sheehy, 1997) to empirically validate the adequacy of the INTERROW model is to plot the deviation of the simulated dry weight from the experimental dry weight against the experimental dry weight (Figure 4.9). There are two criteria of adequacy, firstly the envelope of acceptable precision which is the region on the graph in which deviations are considered to be acceptably small, and secondly the proportion of points that must lie within the envelope of acceptable precision (Mitchell & Sheehy, 1997). The proportion of points within the envelope was chosen to be 95 %, which is widely used as the first threshold at which experimental differences are taken to be statistically significant (Sokal & Rohlf, 1981), and can be used in this context as well (Mitchell & Sheehy, 1997). When 95 % of the points must lie within the envelope, a critical value of ± 1900 $kg \cdot ha^{-1}$ was found (Figure 4.9). This value is only slightly higher than the average experimental standard deviation of all experiments, which was ± 1300 $kg \cdot ha^{-1}$.

DISCUSSION

The storage root weight of witloof chicory was not reduced, when the weeds emerged more than approximately 1 week after the witloof chicory crop (Westmaas and Wageningen in 1992) or only slightly reduced (Lelystad in 1992). A period of approximately 1 week between emergence of witloof chicory and the weeds, ensured that witloof chicory obtained a strong competitive position, such that it could easily outcompete the weeds. Model analysis demonstrated that weeds emerging more than 10 days after witloof chicory, cause little yield reduction of witloof chicory, especially when temperatures are high during the early growth period, as was the case in the 1992 growing season.

The storage root dry weight of witloof chicory was strongly reduced due to competition with weeds, when the emergence dates of witloof chicory and the weeds were approximately the same (Lelystad, Westmaas, and Wageningen in 1993). *C. album*, positioning its leaf area above the witloof chicory plants, captured much of the available light resources and caused a 61 % reduction of the simulated storage root dry weight of witloof chicory. *S. nigrum* also grew vigorously and caused a 31 % reduction of the simulated storage root dry weight of witloof chicory. *S. nigrum* appeared to be a strong competitor only when its date of emergence was earlier than that of witloof chicory. Allowing *S. nigrum* time and space to grow undisturbed, it will grow more laterally than in height, and it can cause large yield reductions. *S. vulgaris* has a very strong juvenile growth, comparable to that of *C. album*, and thus has potential to be a strong competitor. Competition with *S. vulgaris* caused a 25 % reduction of the simulated storage root dry weight of witloof chicory. However, the leaf area duration of *S. vulgaris* is very short compared to the other two weed species. After senescence of *S. vulgaris* plants, the growth of witloof chicory during the second half of the growing season was not further reduced, and the yield reduction at the end of the growing season was less than that caused by *C. album* or *S. nigrum*. These results agree with Kropff & van Laar (1993), who showed that a high relative growth rate of leaves was the most important factor in determining the competitive ability of a species. Model analysis showed that higher than average temperatures, which occurred in the early growth period of 1993, combined with an early weed emergence, resulted in high yield reductions due to competition with *S. vulgaris* or *S. nigrum*.

Witloof chicory has a high base temperature (6 °C used in the model) for growth and development, compared to many weed species. With respect to the development of new weed management methods which take into account crop husbandry measures to increase the crop competitiveness, this implies that witloof chicory should be sown when soil and air temperatures are sufficiently high to ensure a quick establishment of the crop. Model analysis showed that an increase in air temperatures increases the dry matter production of witloof chicory when grown in monoculture. Model analysis also showed that early emerging weeds caused a great reduction in dry matter production of witloof chicory, especially at higher air temperatures. One practical way of increasing the temperature is to cover the soil with a "bio-degradable" plastic. If an increase in temperature is the only effect of covering the soil with "bio-degradable" plastic, then it may increase the growth and competitiveness of witloof chicory if early emerging weeds can be controlled. A total soil cover by "bio-degradable" transparent plastic will enhance growth of both crop and weeds, and may therefore increase the yield loss caused by weeds. A soil cover by "bio-degradable" non-transparent plastic with holes through which the crop plants can grow, will allow the crop plant to profit from the higher temperatures while inhibiting the growth of weeds underneath the plastic.

Reductions in storage root dry weight of more than 50 % were recorded at relatively low weed densities (20 pl·m^{-2}), but only when weeds emerged early. An increase in weed density to 40 or 80 pl·m^{-2} increased the reduction in storage root dry weight, although the added effect of a higher weed density was not as large as the effect of the first 20 pl·m^{-2}. The effects of increasing weed density on dry matter production of witloof chicory and the weed species were correctly simulated by the INTERROW model. Other research also reported large yield reductions at low weed densities and a small added effect of increased weed density, especially when weed emergence was early (*e.g.* Spitters *et al.*, 1989 ; Kropff & van Laar, 1993).

The experimental results alone, could not explain the effect of the spatial position of weed plants on the reduction of storage root dry weight. In one of the experiments, the reductions in storage root dry weight of witloof chicory tended to be greater when *S. vulgaris* was positioned inside the crop row than when it was positioned in between two crop rows. When growing inside the crop row, *i.e.* at small distances to the crop plants, *S.*

vulgaris started to exert its competitive effect earlier in the growing season and was able to cause a greater yield reduction of the storage root dry weight. However, in all the other experiments the effect of spatial position of S. *vulgaris* was absent. Model analysis showed that when the weed plant height is greater than that of witloof chicory and the leaf area duration is large, the yield reduction will be greatest when weeds are growing in between the crop rows. However, when the weed plant height is greater than that of witloof chicory, but the leaf area duration is very short, the yield reduction will be greatest when weeds are growing inside the crop rows. Model analysis showed that *S. vulgaris*, with an actual maximum height that is about 10% higher than that of witloof chicory, caused marginally more yield loss when positioned inside the crop rows. *S. vulgaris* only caused yield loss when it is growing in the proximity of crop plants, because competition will have to start early, due to its short leaf area duration. The reduction in storage root dry weight of witloof chicory tended to be higher when *C. album* was positioned in between the crop rows. Model analysis showed that *C. album*, with an actual maximum height that is more than twice that of witloof chicory, caused more yield loss when positioned outside the crop rows. A possible explanation is that *C. album* with its great maximum plant height will shade witloof chicory plants, wherever *C. album* is positioned. When *C. album* is growing outside the crop row, it will develop faster and will subsequently compete with the crop for a longer part of the growth period because of its long leaf area duration. Results from Chapter 2 showed that the effects of spatial weed position on dry matter production of witloof chicory were more pronounced for *S. vulgaris* plants which are approximately of the same height as witloof chicory, than for *S. vulgaris* plants which grows much higher.

Experimental results showed that growing witloof chicory at a smaller row spacing, while total plant density per m^2 remained unchanged, did not reduce the yield loss caused by weed competition, in a situation where weeds were able to grow vigorously due to an early emergence date. An earlier model analysis carried out with the INTERROW model, also showed that a more uniform spatial crop arrangement, *i.e.* a smaller row spacing, may only be advantageous when the height growth of the crop was higher than that of the weeds (Chapter 3).

Strong reductions of the storage root dry weight of witloof chicory due to competition with *S. vulgaris*, *S. nigrum* or *C. album*, were found to be primarily caused by an early emergence of the weeds, and to a lesser extent by weed density and weed position. The simulations and experimental data showed, that weeds emerging up to at least one week after the witloof chicory crop must be removed to limit the yield loss to acceptable levels. High initial growing temperatures and a uniform plant distribution, *i.e.* a small row spacing, may be essential for witloof chicory to establish a strong competitive position, especially when weeds emerge later than the crop. The model INTERROW accurately simulated the growth of all species, both in monocultures and in mixtures, under a wide range of conditions. The model simulated small effects of spatial position of weeds on the storage root dry weight, consistent with the experimental results. There were no systematic underestimations or overestimations of the dry weights of witloof chicory, *S. vulgaris, S. nigrum* or *C. album*. The model INTERROW explicitly takes into account the row structure of a crop, and all important processes involved in competition have been incorporated into the model. It was concluded that the INTERROW model was generally able to correctly and accurately simulate the storage root dry weight of witloof chicory over a wide range of yield losses due to crop-weed competition. This was done without an extensive calibration procedure which may easily lead to curve fitting, and would have degenerated an explanatory model into a descriptive model.

CHAPTER 5

A SIMULATION ANALYSIS OF COMPETITION BETWEEN WHITE CABBAGE (*BRASSICA OLERACEA* VAR. CAPITATA) AND TWO CLOVER SPECIES (*TRIFOLIUM REPENS* AND *TRIFOLIUM SUBTERRANEUM*)

B. J. Schnieders, L. A. P. Lotz and R. Rabbinge

ABSTRACT

A model for inter-specific competition in row crops, INTERROW, was successfully employed to study competition between white cabbage (*Brassica oleracea* L. var. *capitata*) and two clover species (*Trifolium repens*, and *Trifolium subterraneum*), that were used as cover crops. The model INTERROW simulated smaller reductions in cabbage dry weight when competition occurred with *T. subterraneum* than when competition occurred with *T. repens*, which was also found in experiments. The lower yield loss caused by *T. subterraneum* could be explained by the smaller height of *T. subterraneum*, which resulted in a reduced competitive ability of *T. subterraneum*, relative to *T. repens*.

The model INTERROW correctly simulated a higher yield loss of cabbage due to competition, when the emergence date of *T. subterraneum* was closer to the transplanting date of "autumn" cabbage. The leaf area index of early sown *T. subterraneum* was already in decline when the "autumn" cabbage was transplanted, which resulted in less severe competition for light and thus a smaller reduction in dry matter production.

The model INTERROW could not correctly simulate the effect of a rotary cultivation strip of 0.3 m wide, on the growth of cabbage. Rotary cultivation especially stimulated the growth of cabbage grown in monoculture. It was suggested that rotary cultivation improved the soil aeration, and processes associated with effects of aeration on plant growth are not included in this competition model.

A model analysis showed that when *T. subterraneum* was mown at a temperature sum between 400 and 600 °C·d after emergence, the reduction in dry weight of cabbage due to competition would be minimised. Mowing at this stage reduced the plant height, leaf area and biomass of *T. subterraneum* to such extent, that the ability of *T. subterraneum* to capture light resources was greatly reduced. The model analysis further showed that reduction in cabbage head dry weight due to competition with *T. subterraneum* will be very small, when a *T. subterraneum* variety with very low plant height will be used as cover crop.

This study showed that the model INTERROW is a valuable research tool, that was successfully used to study the effects of crop management approaches, such as a mowing of the clover cover crop or the choice of clover cultivars, in order to minimise yield loss due to competition with clover.

INTRODUCTION

The economic yield of white cabbage, grown to be sold on the fresh market or after a storage period, is determined by both the weight and the quality of the cabbage heads. Competition with neighbouring cabbage plants (Shanmuganathan & Benjamin, 1993), intercropped clover (Lotz *et al.*, 1997) or weeds (Weaver, 1984; Freyman *et al.*, 1992), can reduce the weight of the individual cabbage heads. Cropping practices such as a later planting date can also reduce the weight of the cabbage heads (Bradshaw, 1984; de Moel & Everaarts, 1990). Infestation or herbivory of the cabbage head by pests and diseases can result in allocation of the cabbage head to a lower quality class, which further reduces the economic value per unit weight (Theunissen *et al.*, 1995).

Intercropping, in which a main crop and other vegetation are covering the soil to a certain degree such that they interact (Vandermeer, 1989), is drawing continuous attention as a means to control pests and diseases without the need to use pesticides. The other vegetation is called a cover crop if it is covering the soil to replace another agricultural input (Lotz *et al.*, 1997). Because of its economic importance, interest in the use of cover crops in vegetable crops has focused on brassica crops (*e.g.* Dempster & Coaker, 1974; Theunissen & den Ouden, 1980; Andow *et al.*, 1986; Kloen & Altieri, 1990). Intercropping white cabbage with clover species (*Trifolium repens* or *Trifolium subterraneum*) reduced the damage done by various pest organisms, such that the percentage marketable cabbage heads was increased (Theunissen *et al.*, 1995). The explanations for this reduced pest damage are outside the scope of this paper, and are reviewed by *e.g.* Vandermeer (1989). Ilnicki & Enache (1992) reported that intercropping cabbage with *T. subterraneum* resulted in good weed suppression. However, besides the positive effects on crop quality and weed suppression, intercropping white cabbage with clover also resulted in a lower weight of the cabbage heads due to inter-specific competition (Theunissen *et al.*, 1995; Lotz *et al.*, 1997).

The practice of using cover crops invokes management decisions, additional to those involved in growing a monoculture crop, such as which cover crop species or variety to grow, when and where to sow the cover crop, and at what plant density. The criteria for choosing the cover crop include its suitability to suppress pest populations, its competitive ability relative to the main crop, and its potential to contribute to a weed problem in the following season. Thus, the decision whether or not to use a cover crop involves an optimisation problem: which intercropping situation of decreased crop quantity and increased crop quality gives the highest economical yield? To solve this problem, it is essential to be able to predict how much the crop weight will be reduced due to competition with the cover crop. Simulation models for inter-specific competition can be used to obtain insight into how the available resources can be used most efficiently by changing relative times of emergence, densities and cultivars in intercropping systems (Kropff & Van Laar, 1993), and also in predicting the reduction in the crop weight at various intercropping situations.

In this paper, a model for inter-specific competition was parameterised for white cabbage and clover species, and tested for its ability to adequately simulate the effects of using clover as a cover crop in white cabbage. This model, INTERROW, explicitly simulates the row structures of the canopy (Chapter 3), and was used because white cabbage grown to be directly sold on the fresh market often does not complete soil cover between the rows, while the white cabbage grown to be sold after storage completes soil cover only late in the growing season. The validated model was subsequently used to identify the characteristics that the species should possess and the management decisions that can be taken, in order to minimise the yield loss of the cabbage crop due to competition while enabling the development of sufficient clover foliage to deter the development of pest organisms.

MATERIALS AND METHODS

Experiments

Data on growth and dry matter production of white cabbage (*Brassica oleracea* L. var. *capitata*), *Trifolium repens* (white clover), and *Trifolium subterraneum* (subterraneum clover) were available from 4 experiments (Table 5.1, see for full details Theunissen *et al.*, 1995; and Lotz *et al.*, 1997).

The experiments were carried out at the experimental station 'De Schuilenburg' near Lienden, the Netherlands in 1990 and 1991, and at the Regional Experimental Station in Zwaagdijk, the Netherlands in 1992 and 1993 (Table 5.1). In 1990 and 1991 an early "summer" variety (cv Minicole) of white cabbage destined for the fresh market was grown, while in 1992 and 1993 a late "autumn" variety (cv Slawdena) of white cabbage destined for winter storage was grown. To ensure N-fixation, the clover seeds were inoculated with the appropriate strain of *Rhizobium* bacteria prior to sowing.

In 1990 and 1991, white cabbage was grown in monoculture and in mixture with *T. repens* or *T. subterraneum* (*i.e.* 3 treatments). In 1992, white cabbage was grown at row distances of 50 and 75 cm, in monoculture and in mixture with *T. subterraneum* (*i.e.* 4 treatments). In 1993, white cabbage was grown in monoculture and in mixture with

Table 5.1 Details of the four experiments of competition between white cabbage and the clover species, *Trifolium repens* and *Trifolium subterraneum* (see for full details Theunissen *et al.*, 1995; and Lotz *et al.*, 1997).

Experiment	**1**	**2**	**3**	**4**
year	1990	1991	1992	1993
location	Lienden	Lienden	Zwaagdijk	Zwaagdijk
white cabbage				
cultivar	Minicole	Minicole	Slawdena	Slawdena
purpose	fresh market	fresh market	storage	storage
transplanting date	1 May (day 121)	7 May (day 127)	21 May (day 142)	19 May (day 139)
plant density	2.67 plants·m^{-2}	2.67 plants·m^{-2}	2.67 pl.m^{-2} (0.75 m) 4.00 pl.m^{-2} (0.50 m)	2.67 pl.m^{-2}
row spacing	0.75 m	0.75 m	0.50 m 0.75 m	0.75 m
row orientation	90° (West-East)	135°	0° (south-north)	135°
T. subterraneum				
cultivar	Geraldton	Geraldton	Trifoli	Geraldton
sowing date	21 Mar. (day 80)	26 Mar. (day 85)	9 Apr. (day 100)	5 Apr. (day 95) 27 Apr. (day 117)
sowing rate	20 kg·ha^{-1}	20 kg·ha^{-1}	15 kg·ha^{-1}	15 kg·ha^{-1}
emergence date	4 Apr. (day 94)	9 Apr. (day 99)	23 Apr. (day 114)	19 Apr. (day 109) 11 May (day 131)
plant density	341 plants·m^{-2}	341 plants·m^{-2}	256 plants·m^{-2}	256 plants·m^{-2}
T. repens				
cultivar	Pertina	Pertina	---	---
sowing date	21 Mar. (day 80)	26 Mar. (day 85)	---	---
sowing rate	10 kg·ha^{-1}	10 kg·ha^{-1}	---	---
emergence date	4 Apr. (day 94)	9 Apr. (day 99)	---	---
plant density	416 plants·m^{-2}	416 plants·m^{-2}	---	---
Soil characteristics				
soil type	sandy loam	sandy loam	silty clay (6% OM)	silty clay (6% OM)
max. soil moisture	320 l·m^{-3}	320 l·m^{-3}	320 l·m^{-3}	320 l·m^{-3}
fertiliser N	120 kg·ha^{-1}	120 kg·ha^{-1}	250 kg·ha^{-1}	300 kg·ha^{-1}
Nmin (spring)	50 kg·ha^{-1}	50 kg·ha^{-1}	50 kg·ha^{-1}	50 kg·ha^{-1}
mineralisation	50 kg·ha^{-1}	50 kg·ha^{-1}	50 kg·ha^{-1}	50 kg·ha^{-1}
harvest dates	11 June 04 July 24 July 23 August	07 May 05 June 26 June 17 July 07 August 29 August	22 May 17 June 07 July 29 July 19 August 08 September 29 September 03 November	19 May 15 June 13 July 10 August 07 September 05 October

T. subterraneum, with the clover sown 3 or 6 weeks before the cabbage, and with the cabbage transplanted directly into the clover or into rotary cultivation strips of 18 or 32 cm wide (*i.e.* 9 treatments; 3 crop-weed combinations x 3 transplantation methods).

At each harvests the dry weights of the plant organs were taken. Other plant parameters, *e.g.* plant height and leaf area (LI-COR area meter, model 3100, Lincoln, NE, USA) were also measured.

Short description of the INTERROW model

The INTERROW model is described in detail in Chapter 3. The INTERROW model is derived from the INTERCOM model of Kropff & Van Laar (1993).

The modules for light interception and photosynthesis in INTERCOM have been replaced with new modules, that take into account the 3-dimensional geometry of the canopy and also the solar geometry. These new modules were derived from a model for light distribution and photosynthesis in single-species row crops, developed by Gijzen & Goudriaan (1989). The model INTERROW explicitly takes into account the distribution of leaf area over the soil area, the row dimensions, the orientation of the rows, and the relative position of rows of different species, in the simulation of light interception by each species.

In a potential production situation, where light, temperature, and species specific characteristics determine the growth of a plant community, plants compete primarily for light (*e.g.* Kropff & Van Laar, 1993). The model INTERROW calculates the vertical and horizontal light profile within the multi-species row canopy, from the leaf area indices and the spatial distributions of the leaf area over the soil area.

In the calculations of the horizontal and vertical light profile, the canopy is considered as a series of rectangular-shaped boxes, with a certain height and with and an infinite length (Chapter 3). Each box contains the leaf area of one row of a certain species. The height and width of these boxes, and the leaf area inside the boxes are changing in time, simulating the canopy dynamics of a species. When a light beam enters a row, it will be partially or totally intercepted by leaves inside that row. When a light beam is only partially intercepted, the remainder of the radiation may be intercepted by an adjacent row. However, when a beam of light does not enter a row but falls directly on the bare soil between the rows, it will be completely lost for photosynthesis. Thus, the percentage of light that will be intercepted depends on the size of the rows, the size of the gaps between the rows, the leaf area density inside the rows, the row orientation, and the position of the sun (elevation and azimuth). The light intensity at any point inside a row can be calculated from the interception of a series of light beams originating from carefully chosen positions on the hemisphere, according to a method described by Gijzen & Goudriaan (1989). The light intensity at that point inside the row canopy is then used to calculate the local photosynthetic rate at that specific point. Subsequently, the photosynthesis profile in both the vertical and horizontal direction inside a canopy row is calculated for each species, using the light profiles, the leaf area distributions, and the photosynthetic characteristics of single leaves. The instantaneous canopy photosynthesis of each species is obtained, by integrating the photosynthesis profile over the height and the width of the row using Gaussian integration (Goudriaan, 1986), and applying a correction for incomplete soil cover. Subsequent integration over the day gives the daily gross CO_2 assimilation rate of each species. The amount of assimilated CO_2 is then converted into carbohydrates, and decreased with the carbohydrate requirements for maintenance respiration. The remaining carbohydrates are converted into dry matter, using the assimilate requirement for dry matter production, resulting in the net daily growth rate.

Plants also may have to share a limited supply of water and nitrogen. To account for the effects of water shortages on the growth rate of each species, the approach described by Kropff & Spitters (1992) and Kropff & Van Laar (1993) is used. A simple moisture balance keeps track of the soil moisture availability. To account for the effects of nitrogen shortages on the growth rate of each species, the approach described by Spitters (1989) and Kropff & Van Laar (1993) is used. A simple nitrogen balance keeps track of the amount of available nitrogen in the soil.

Parameterisation of the INTERROW model

The INTERROW model was parameterised for white cabbage, *Trifolium repens* and *Trifolium subterraneum* using the data from the experiments of 1990 ("summer" variety of white cabbage) and 1992 ("autumn" variety of white cabbage) and data from literature.

The simulation of shoot dry weight, cabbage head dry weight, leaf area index and plant height of the "summer" variety of white cabbage, in monoculture and in competition with *T. repens* and *T. subterraneum*, closely matched the experimental data of 1990 (data not shown). The dry weights, leaf area index and plant height of *T. repens* and *T. subterraneum* were also adequately simulated by the model. The only exception was the simulation of the leaf area index of *T. repens*, where the INTERROW model was not able to correctly simulate the re-growth of *T. repens* near the end of the growing season. However, the effects of this re-growth of *T. repens* on the growth of the "summer" variety of white cabbage was negligible.

The simulation of shoot dry weight, cabbage head dry weight, leaf area index and plant height of the "autumn" variety of white cabbage grown at row spacings of 0.50 m. or 0.75

m., in monoculture and in competition with *T. subterraneum*, adequately described the experimental data of 1992 (data not shown). The simulation of dry weights, leaf area index and plant height *T. subterraneum* also closely matched the experimental data.

RESULTS

Validation of the INTERROW *model*

Data of competition between white cabbage and clover, from the experiments in 1991 ("summer" variety, Figure 5.1) and 1993 ("autumn" variety, Figures 5.2 and 5.3), were used to validate the INTERROW model.

The shoot dry weight (Figures 5.1a, b) of "summer" cabbage in monoculture tended to be higher than that of "summer" cabbage in competition with clovers, and the reduction in shoot dry weight of cabbage in competition with *T. subterraneum* (15 %) tended to be smaller than that of cabbage in competition with *T. repens* (21 %; Lotz *et al.*, 1997). The simulated reduction in shoot dry weight of cabbage in competition with *T. subterraneum* (2 %) was also smaller than that of cabbage in competition with *T. repens* (31 %). The simulated reduction in the dry weight of the cabbage heads due to competition with *T. subterraneum* was 3 % (Figure 5.1c; 8 % in the experiment), compared to 41 % due to competition with *T. repens* (Figure 5.1d; 20 % in the experiment). The simulated shoot dry weights of *T. subterraneum* (Figure 5.1a) and *T. repens* (Figure 5.1b) were somewhat lower than the experimental data, especially in the second half of the growing period. The simulated leaf area indices (Figures 5.1e, f) and plant heights (Figures 5.1g, h) of all species, differed little from the experimental data. There was very little effect of inter-specific competition on the simulated and experimentally determined leaf area indices and plant heights of cabbage. The senescence and regrowth of the leaf area of *T. repens* (Figure 5.1f) was correctly simulated, although the simulated regrowth was not as high as the experimentally determined regrowth.

The shoot dry weight of "autumn" cabbage in monoculture was higher than that of "autumn" cabbage in competition in clovers, especially when cabbage was transplanted into a rotary cultivation strip of 0.3 m wide (Lotz *et al.*, 1997).

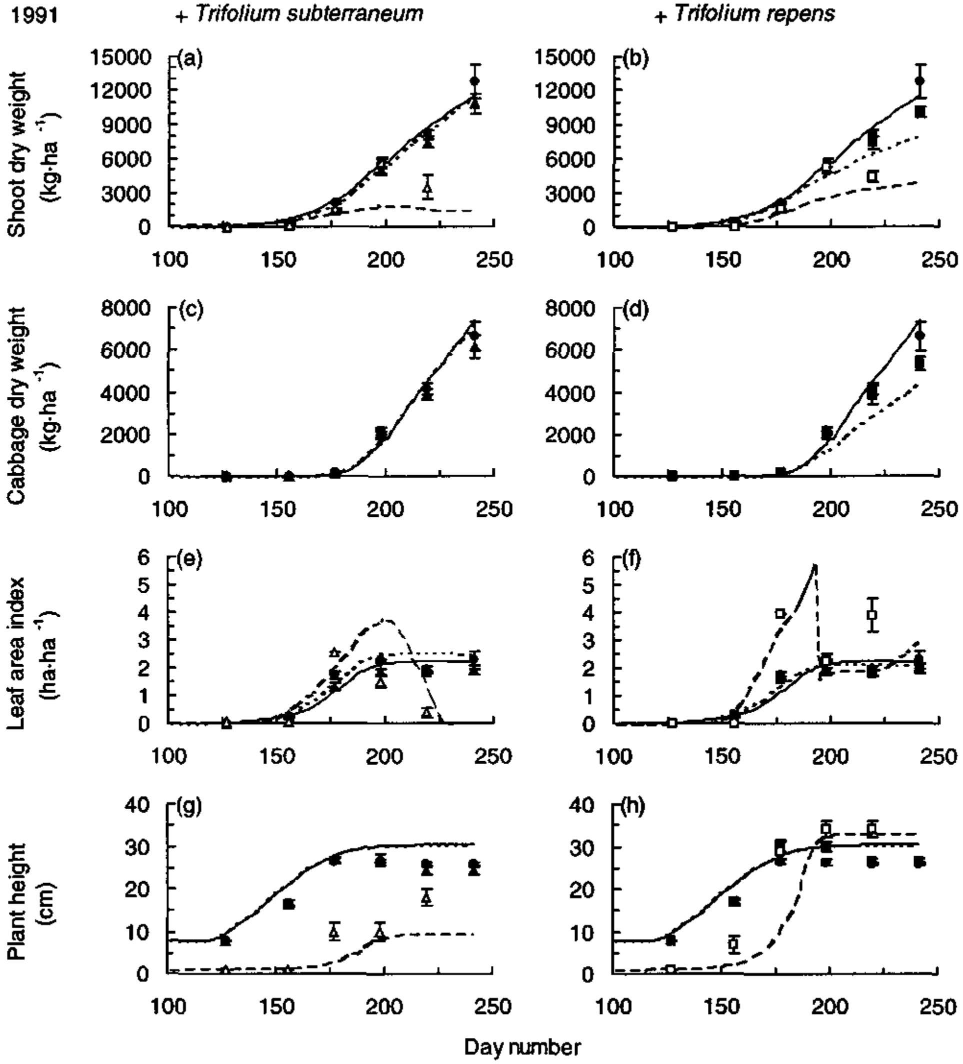

Figure 5.1 Measured and simulated effects of inter-specific competition between white cabbage and *T. subterraneum* (a, c, e, g) or *T. repens* (b, d, f, h) at Lienden in 1991. (closed circles and solid line: cabbage in monoculture; closed triangles and dotted line: cabbage in competition with clover; open triangles and broken line: clover in competition with cabbage).

Figure 5.2 shows the "autumn" cabbage treatments without a rotary cultivation strip. In the absence of a rotary cultivation strip, the simulated reduction in shoot dry weight of cabbage in competition with *T. subterraneum* sown 3 weeks before transplantation was 12 % (Figure 5.2a; 19 % in the experiment), and that of cabbage in competition with *T. subterraneum* sown 6 weeks before transplantation was 4 % (Figure 5.2b; 15 % in the experiment). Both the experimental and simulated shoot dry weight were more reduced when *T. subterraneum* was sown 3 weeks before transplantation (compare Figure 5.2a with Figure 5.2b). The simulated reduction in the dry weight of the cabbage heads due to competition with *T. subterraneum* sown 3 weeks before transplantation was 9 % (Figure 5.2c; 17 % in the experiment), and was also 9 % when competition occurred with *T. subterraneum* sown 6 weeks before transplantation (Figure 5.2d; 8 % in the experiment). The simulated shoot dry weight of *T. subterraneum* (Figures 5.2a, b) was somewhat higher than the experimental data, especially when sown 6 weeks before transplantation. The simulated leaf area indices (Figures 5.2e, f) and plant heights (Figures 5.2g, h) of all species, differed little from the experimental data. There was very little effect of inter-specific competition on the simulated and experimentally determined leaf area indices and plant heights of cabbage. The senescence of the leaf area of *T. subterraneum* (Figures 5.2e, f) was correctly simulated.

Figure 5.3 shows the "autumn" cabbage treatments with a rotary cultivation strip of 0.3 m. When the rotary cultivation strip was 0.3 m, the simulated reduction in shoot dry weight of cabbage in competition with *T. subterraneum* that was sown 3 weeks before transplantation was 5 % (Figure 5.3a; 44 % in the experiment), and that of cabbage in competition with *T. subterraneum* that was sown 6 weeks before transplantation was -4 % (Figure 5.3b; 27 % in the experiment). The simulated reduction in the dry weight of the cabbage heads due to competition with *T. subterraneum* that was sown 3 weeks before transplantation was 5 % (Figure 5.3c; 50 % in the experiment), and was 6 % when competition occurred with *T. subterraneum* that was sown 6 weeks before transplantation (Figure 5.3d; 25 % in the experiment). The model was unable to accurately simulate the apparent positive effects of rotary cultivation on dry matter production of "autumn" cabbage in monoculture at the end of the growing period. As a result, the simulated reductions in dry weight of cabbage at the end of the growing period were much too low. The simulated shoot dry weight of *T. subterraneum* (Figures 5.3a, b) was accurately simulated. The simulated leaf area indices (Figures 5.3e, f) and plant heights (Figures 5.3g, h) of all species, differed little from the experimental data. There was very little effect of inter-specific competition on the simulated and experimentally determined leaf area indices and plant heights of cabbage. The senescence and regrowth of the leaf area of *T. subterraneum* (Figures 5.3e, f) was correctly simulated.

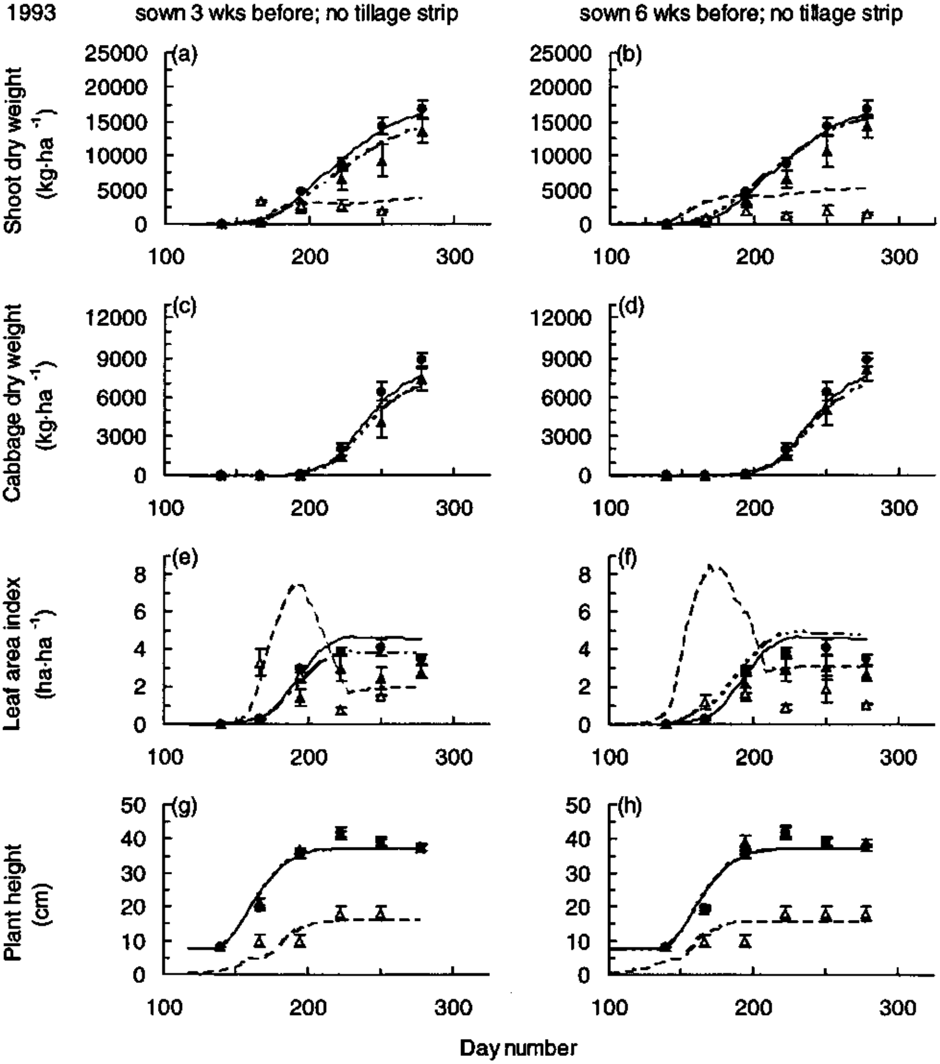

Figure 5.2 Measured and simulated effects of inter-specific competition between white cabbage and *T. subterraneum* at Zwaagdijk in 1993, without a rotary cultivation strip. (closed circles and solid line: cabbage in monoculture; closed triangles and dotted line: cabbage in competition with clover; open triangles and broken line: clover in competition with cabbage).

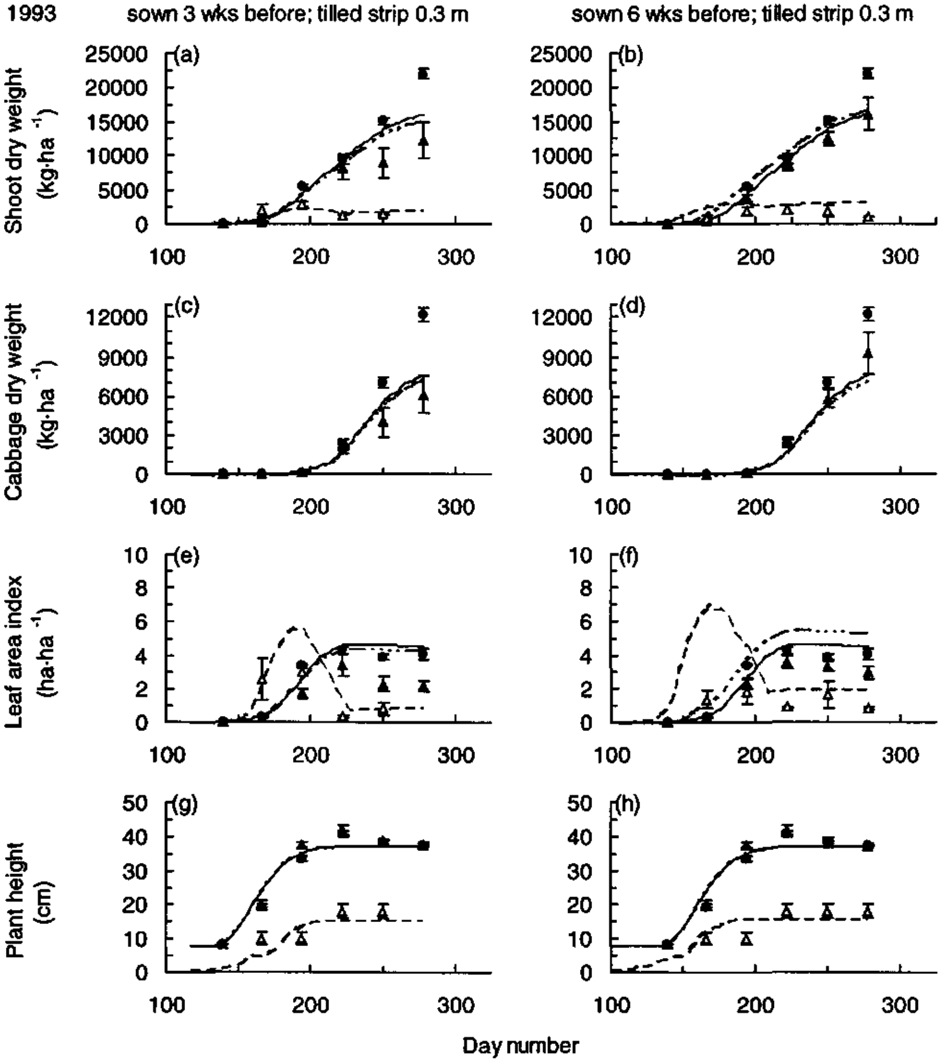

Figure 5.3 Measured and simulated effects of inter-specific competition between white cabbage and *T. subterraneum* at Zwaagdijk in 1993, with a rotary cultivation strip of 0.3 m wide. (closed circles and solid line: cabbage in monoculture; closed triangles and dotted line: cabbage in competition with clover; open triangles and broken line: clover in competition with cabbage).

Model analysis

The results above showed that the yield loss of "autumn" cabbage in competition with *T. subterraneum* sown 3 weeks after transplanting was greater than that of "autumn" cabbage in competition with *T. subterraneum* sown 6 weeks after transplanting. Furthermore, Lotz *et al.* (1997) stated that quantitative information about different cropping strategies in growing cabbage is needed, such that yield loss due to competition with the cover-crop can be minimised, while at the same time the cover-crop is needed to reduce yield loss due to pest damage. The model INTERROW has been shown to accurately simulate competition, and can thus be used to gain this quantitative information.

A model analysis was therefore carried out, to study the effects of the emergence date of *T. subterraneum*, the maximum obtainable plant height of *T. subterraneum*, and a mowing strategy, on the dry matter production of cabbage heads. In the model analysis, the emergence date of *T. subterraneum* was set to 0, 7 or 28 days before "autumn" cabbage, while the maximum plant height of *T. subterraneum* was set 10 or 20 cm (0.3 and 0.6 times the plant height of "autumn" cabbage, respectively). Furthermore, a mowing date of *T. subterraneum* was set to 150, 300, 450 or 600 °C·d after emergence of *T. subterraneum*. In the model analysis, it was assumed that plant height, leaf area and dry weight of *T. subterraneum*, was reduced to 25 % of that of the maximum attainable plant height. The model analysis was done only for the situation where "autumn" cabbage was sown directly into the *T. subterraneum*, because the effects of rotary cultivation could not be explained by the model (see model validation section). Furthermore, both the experimental and simulation results did not show any effects of competition on either plant nitrogen levels or soil water levels (data not shown). Therefore it was decided to perform the model analysis for potential growth conditions. Also, 30-year average weather data from Wageningen were used for the analysis.

The model analysis showed that the reduction of cabbage head dry weight of "autumn" cabbage was smallest when *T. subterraneum* emerged 28 days before the transplantation date of "autumn" cabbage, and highest when the emergence of *T. subterraneum* was close to transplantation date of "autumn" cabbage (Figure 5.4a, b). This was consistent with the experimental and simulation results of Figure 2. When *T. subterraneum* emerges several weeks before the cabbage crop, its leaf area index is already decreasing at the time of transplantation of the cabbage. Thus, competition for light will be less with early emerging *T. subterraneum* plants, than with *T. subterraneum* plants that just started growing during the transplantation of the cabbage. The model analysis also showed that the reduction in cabbage head dry weight of "autumn" cabbage due to competition with *T. subterraneum* would be minimised, when *T. subterraneum* was mown at a temperature sum between 400 and 600 °C·d after emergence. Mowing at this temperature sum would remove the 2^{nd} growth (re-growth) of *T. subterraneum*, and thus delay or prevent that inter-specific competition for light can become severe again. Model analysis further showed that reduction of cabbage head dry weight due to competition with *T. subterraneum* will be very small, when a *T. subterraneum* variety with very low plant height (compare Figure 5.4b with Figure 5.4a) would be available. Reducing the maximum plant height of *T. subterraneum* from 0.2 m to 0.1 m, reduced the maximum yield loss from 11 % to 3 %, respectively. To illustrate the importance of relative plant height, a separate simulation run with *T. subterraneum* and "autumn" cabbage having equal plant heights (0.35 m) and *T. subterraneum* emerging 7 days before transplantation date of cabbage, showed that the cabbage head dry weight of "autumn" cabbage would have been reduced to 5892 kg.ha^{-1}, a yield reduction of 35 %.

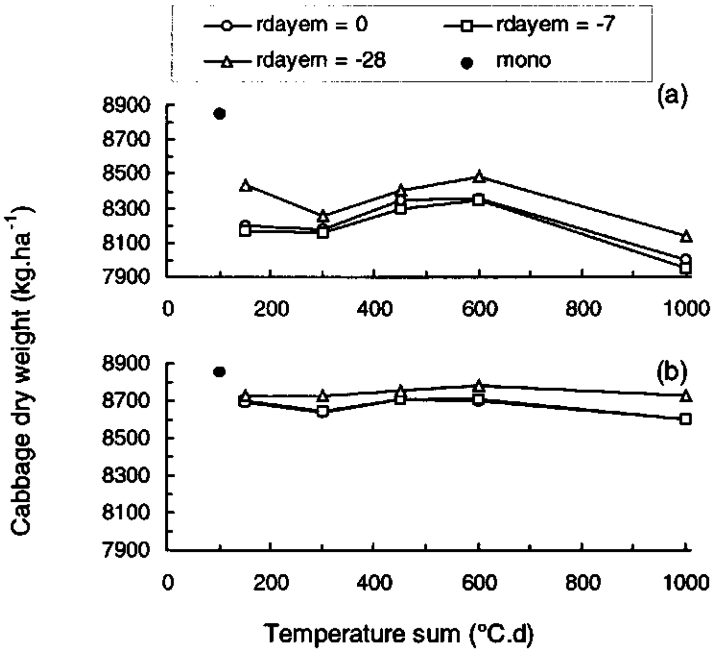

Figure 5.4 The effects of mowing regime and emergence date of *T. subterraneum* on the cabbage head dry weight of "autumn" cabbage, with the maximum attainable height of *T. subterraneum* being 20 cm (a) or 10 cm (b)

DISCUSSION

Lotz *et al.* (1997) concluded that research was needed to study the competition between cabbage and clover in more detail, to determine what resources (light, water, nutrients) are competed for during the growing season. From this, approaches to reduce the yield loss may be designed. Therefore, a model for inter-specific competition in row crops, INTERROW, was successfully employed to study competition between white cabbage and two clover species, that were used as cover crops.

The model INTERROW simulated smaller reductions in dry matter production of a "summer" variety of white cabbage in competition with *T. subterraneum* than for a "summer" variety of white cabbage in competition with *T. repens*. The simulated growth curves accurately matched the experimental data. Both simulation data and experimental data showed very little effects of inter-specific competition on morphological parameters, such as leaf area index and plant height, of cabbage. The simulated and experimental plant height of *T. repens* was greater than that of *T. subterraneum*. The simulated and experimental plant height of *T. repens* was also higher than that of "summer" cabbage, causing increased competition for light and resulting in reduction of dry mater production of cabbage during the second half of the growing period. Plant height appeared to be a very important factor in determining the extent of the yield loss, which was also reported for other crops such as witloof chicory (Chapter 3), and sugarbeet (Kropff & van Laar, 1993).

The simulated effects of competition with *T. subterraneum*, on dry weight cabbage heads of "summer" cabbage were very small. Lotz *et al.*, (1997) also reported that the effects of competition on dry weight or fresh weight of the cabbage heads were not statistically significant. However, Lotz et *al.* (1997) also showed that competition with *T. subterraneum* did significantly reduce the fresh weight of the cabbage heads in the quality class 'no pest damage'. Thus, one should be careful to translate conclusions based on dry weights to the actual value of the marketable product.

The model INTERROW simulated reductions in dry matter production of an "autumn" variety of white cabbage in competition with *T. subterraneum*. The model correctly simulated a higher yield loss of "autumn" cabbage due to competition, when the sowing date and thus emergence date of *T. subterraneum* was closer to the transplanting date of "autumn" cabbage. The leaf area index of early sown *T. subterraneum* was already in decline when the "autumn" cabbage was transplanted, which resulted in less severe competition for light and thus a smaller reduction in dry matter production. The simulated growth curves accurately matched the experimental data.

The simulation of the dry matter production of "autumn" cabbage transplanted into a rotary cultivation strip of 0.3 m wide, particularly the growth in monoculture, was incorrect. The experimentally determined dry matter production of "autumn" cabbage growing in monoculture was much higher, when the cabbage was transplanted into a rotary cultivation strip of 0.3 m wide than when there was no rotary cultivation strip. Lotz *et al.* (1997) suggested that this effect of rotary cultivation may be caused by an improved soil aeration. The processes associated with effects of aeration on plant growth are not included in the model, so one cannot expect the model to handle this rotary cultivation effect in a correct way. However, the increase in cabbage yield due to rotation tillage suggest that more research on the effect of rotation tillage is appropriate.

A subsequent model analysis of the effects of sowing date on dry weights, also showed that the reduction of cabbage head dry weight of "autumn" cabbage was smallest when *T. subterraneum* emerged 28 days before the transplantation date of "autumn" cabbage, and highest when the emergence of *T. subterraneum* was close to transplantation date of "autumn" cabbage. This was consistent with the experimental and simulation results of Figure 5.2. When *T. subterraneum* emerges several weeks before the cabbage crop, its leaf area index is already decreasing at the time of transplantation of the cabbage. Thus, competition for light will be less with early emerging *T. subterraneum* plants than with *T. subterraneum* plants that just started growing during the transplantation of the cabbage. The model analysis also showed that when *T. subterraneum* was mown at a temperature sum between 400 and 600 °C·d after emergence, the reduction in cabbage head dry weight of "autumn" cabbage would be smallest. When mowing was done around this temperature sum, the regrowth of the *T. subterraneum* would be removed, before competition for light could become severe again. The model analysis further showed that reduction in cabbage head dry weight due to competition with *T. subterraneum* will be very small, when a *T. subterraneum* variety with very low plant height will be used as cover crop. Reducing the maximum plant height of *T. subterraneum* from 0.2 m to 0.1 m, reduced the maximum yield loss. From the model analysis it was concluded that if a *T. subterraneum* cover crop is needed for pest reduction, a cultivar with small height should be selected and sown early, in order to minimise the reduction in cabbage head dry weight of cabbage due to inter-specific competition. Also, *T. subterraneum* should be mown at a temperature sum between 400 and 600 °C·d after emergence, in order to reduce the height, leaf area and dry matter of *T. subterraneum.*

The model INTERROW was able to explain the effects of competition on dry weight of white cabbage, by assuming competition for light only. Model analysis showed that a low plant height of clover species used as cover crop, is essential to minimise yield loss of cabbage. Model analysis also showed that *T. subterraneum* sown 28 days before transplanting of cabbage cause less yield loss than *T. subterraneum* sown 0 or 7 days before transplanting, because the biomass and leaf area of the early sown clover was already in decline when cabbage was transplanted. This study showed that the model INTERROW is a valuable research tool, that was successfully used to study the effects of crop management approaches such as the mowing of the clover cover crop, in order to minimise yield loss due to competition with clover.

CHAPTER 6

THE EFFECTS OF COMPETITION WITH WEEDS ON DRY WEIGHT AND DIAMETER OF INDIVIDUAL STORAGE ROOTS OF WITLOOF CHICORY

B. J. Schnieders, P. C. De Man, L. A. P. Lotz and R. Rabbinge

ABSTRACT

The effects of competition with *Senecio vulgaris* , *Solanum nigrum* or *Chenopodium album* on the growth and dry matter production of witloof chicory (*Cichorium intybus*), and in particular on the dry weight and diameter of individual storage roots, were studied under field conditions.

Competition with weeds reduced the storage root dry weight between 10 and 75 % and the storage root diameter between 9 and 44 %. The magnitude of the reductions in total plant dry weight, storage root dry weight and storage root diameter due to competition with weeds, depended on the size of the weed biomass (expressed by its leaf area index), and on the timing and duration of the weed competition within the growing season.

The percentage of storage roots with a diameter smaller than 32.5 mm was greatly increased by weed competition, and was found to be as high as 95 %. These roots have little economic value because they do not contain sufficient redistributable carbohydrates to produce a chicon of good quality, indicating the actual yield loss caused by weed competition can be much greater than expected from the reduction in storage root dry weight.

INTRODUCTION

Witloof chicory (*Cichorium intybus* L.) is grown for its storage roots. The storage roots are harvested and placed in the dark, and forced to produce a blanched compact head of leaves (chicons). These chicons can be consumed as a salad or vegetable (Nicholson *et al.*, 1969). The storage root diameter is a very important yield aspect of witloof chicory. Storage roots with a diameter smaller than 32.5 mm (measured at the top of the root) have little economic value, because they do not contain sufficient redistributable carbohydrates to produce a chicon of good quality (Anonymous, 1989; Van Kruistum *et al.*, 1997).

Weed control is a major problem in the growing of witloof chicory, mainly due to the lack of suitable herbicides (Poll and Douglas, 1987; Anonymous, 1989). Competition with weeds can severely reduce the storage root weight of witloof chicory (Schnieders and Lotz, 1993). The presence of weed plants also affects the available space of individual witloof plants. These differences in available space per plant can cause variability in plant weight (Benjamin and Hardwick, 1986), and thus cause variability in storage root weight and storage root diameter. It has been shown that an irregularly growing witloof chicory crop has negative effects on the size distribution of the storage roots and on the quality of the chicons produced from those roots (Anonymous, 1989, Van Kruistum *et al.*, 1993).

The objective of the present study was to determine how competition with weed species, that have different morphological characteristics and that were growing at various densities and spatial positions, affects the growth and dry matter production of witloof chicory. The effects of weed competition on the weight and diameter of the individual storage roots were quantified, and evaluated with respect to the development of weed management systems and the use of 'dry weight based' competition models in the study of crop-weed competition.

MATERIALS AND METHODS

Field experiments were carried out in 1993 at three different locations in the Netherlands, to study the effects of weed competition on the growth of storage roots of witloof chicory. In all experiments, witloof chicory was sown in high densities and thinned back to the desired density of 20 plants per m^2. Seeds of the weeds were germinated on a water agar medium (Kempenaar & Schnieders, 1995) and then planted into the soil, which enabled the manipulation of the emergence dates, densities and spatial positions of the weed plants.

The experiment at Lelystad (5°27" E, 52°31" N) was done on a sandy loam soil (1.7 % humus; 22 % lutum; pH-KCL=7.3). Weed plants of the species *Senecio vulgaris* L., *Solanum nigrum* L. or *Chenopodium album* L., were positioned in the centre of the witloof chicory row (p1) or in between the witloof chicory rows (p2). The witloof chicory plants emerged on 19 May. The weed plants emerged on 17 May and established at a plant density of 20 $pl \cdot m^{-2}$. Witloof chicory was grown at a row spacing of 0.75 m. The experiment had a completely randomised block design with four replicates and two factors (weed position and weed species), plus a control treatment (witloof chicory in monoculture).

The experiment at Westmaas (4°25" E, 51°50" N) was done on a sandy clay loam soil (2.2 % humus; 29 % lutum; pH-KCL=7.4). Weed plants of *S. vulgaris* or *S. nigrum*, were positioned in the centre of the witloof chicory row. The witloof chicory plants emerged on 21 May. The weed plants emerged on 22 May and established at plant densities of 20 (d1), 40 (d2) or 80 (d3) $pl \cdot m^{-2}$. Witloof chicory was grown at a row spacing of 0.75 m. The experiment had a completely randomised block design with four replicates and two factors (weed density and weed species), plus a control treatment (witloof chicory in monoculture).

The experiment at Wageningen (5°40" E, 51°58" N) was done on a course sand soil (3.1 % humus; 0 % lutum; pH-KCL=5.2). Weed plants of *S. vulgaris* were positioned in the centre of the witloof chicory row (p1) or in between the witloof chicory rows (p2).

The witloof chicory plant emerged on 2 June. The *Senecio vulgaris* plants also emerged on 2 June and established at a plant density of 20 pl·m^{-2}. Witloof chicory was grown at row spacings of 0.25 (r25), 0.50 (r50) or 0.75 (r75) m. The experiment had a split-plot design with four replicates and two factors (crop row spacing in the main level and weed position in the split level). Witloof chicory in monoculture was considered as a special level of the 'weed position' factor, with the weed plants at an imaginary indefinite distance.

Harvests were taken at regular intervals, to quantify the development of leaf area, plant height and plant weights of all species over the length of the growing season. At the end of the growing season, weights and diameters of individual storage roots were also measured.

The results were analysed by analysis of variance using GENSTAT (Genstat 5 Committee, 1993). The experiments had factorial arrangements of several types of treatment (weed density, weed emergence date, weed position, weed species, or crop row width), plus an additional control treatment (witloof chicory in monoculture) in two of the experiments. This structure of factorial plus added control allows the analysis of interactions between treatments (Genstat 5 Committee, 1993, page 490-493). It also allows the analysis of treatment versus a control treatment, *i.e.*, effect of growth in competition versus growth in monoculture. Statistical analyses on the percentage of storage roots with a diameter smaller than 32.5 mm, were carried out on arcsine transformed data (Sokal and Rohlf, 1981; pp. 427).

RESULTS

In the experiment at Lelystad, competition with weeds reduced the leaf area index (Figure 6.1a; $P< 0.001$) and the total plant dry weight (Figure 6.1b; $P<0.001$) of witloof chicory from the second harvest onwards. These reductions were greatest ($P<0.001$) when competition occurred with *C. album*, and smallest when competition occurred with *S. vulgaris*. The increase in leaf area index of the weeds was faster and greater for *C. album* than for the other weed species (Figure 6.1c; $P<0.001$). The weed species also obtained a greater maximum plant height (0.55, 0.75 and 1.15 m, for *S. vulgaris*, *S. nigrum* and *C. album*, respectively) than witloof chicory (0.45 m). Consequently, competition with

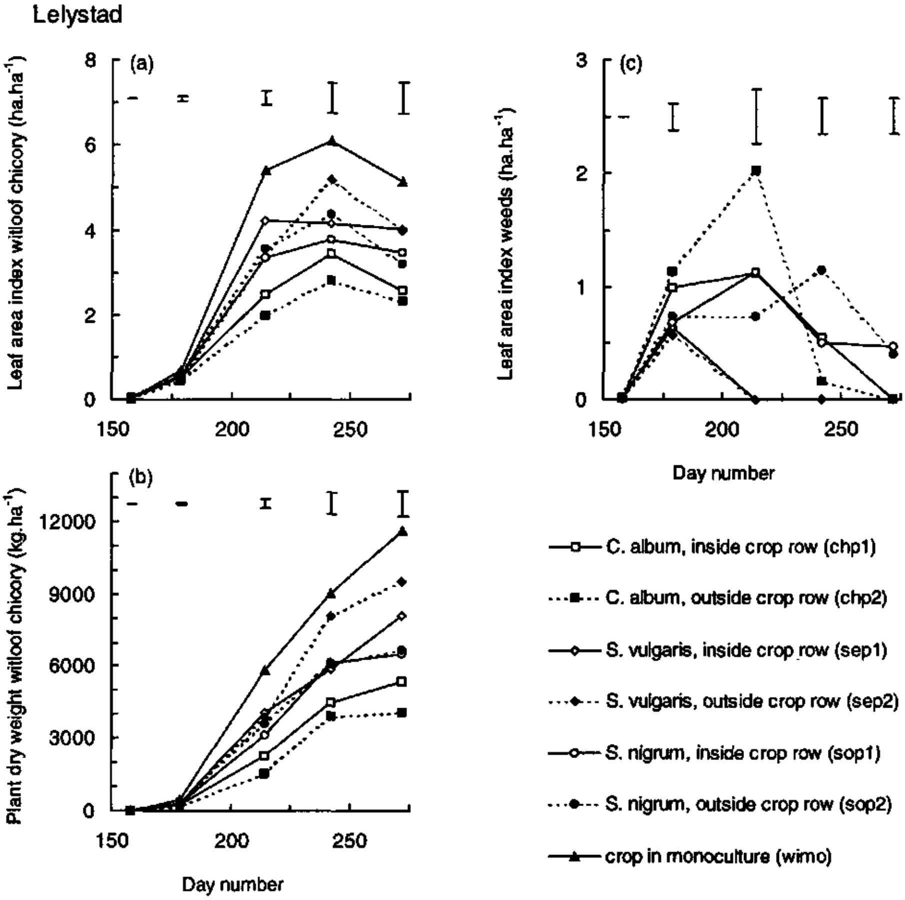

Figure 6.1 The seasonal development of leaf area index (a) and total plant dry weight (b) of witloof chicory, and of leaf area index (c) of the weed species *C. album*, *S. vulgaris* and *S. nigrum* in the experiment at Lelystad. Vertical bars represent 1 SED.

weeds reduced the storage root dry weights of witloof chicory between 30 and 75 % (Figure 6.2a; $P<0.001$), and the storage root diameters between 19 and 44 % (Figure 6.2b; $P<0.001$). The reductions in storage root dry weight and storage root diameter were greatest ($P<0.001$) when competition occurred with *C. album*, and smallest when competition occurred with *S. vulgaris*. The position of the weed plants did not affect the reduction in storage root weight or storage root diameter. Competition with weeds greatly increased the percentage of storage roots with a diameter smaller than 32.5 mm (Figure 6.2c; $P<0.001$). The percentage of storage roots with a diameter smaller than 32.5 mm could be as high as 95 %.

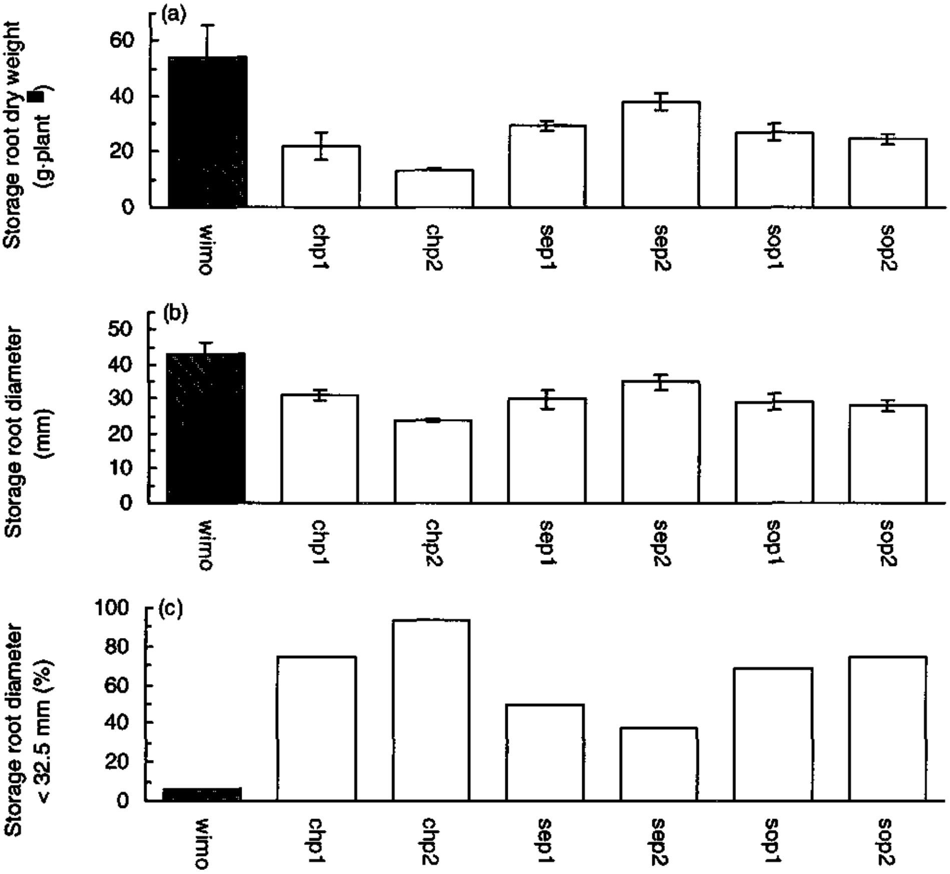

Figure 6.2 The average storage root dry weight (a), the average storage root diameter (b), and the percentage of storage roots with a diameter smaller than 32.5 mm (c) of witloof chicory in the experiment at Lelystad. See Figure 6.1 and Materials & Methods for explanation of the treatment codes. Vertical bars represent standard errors of means.

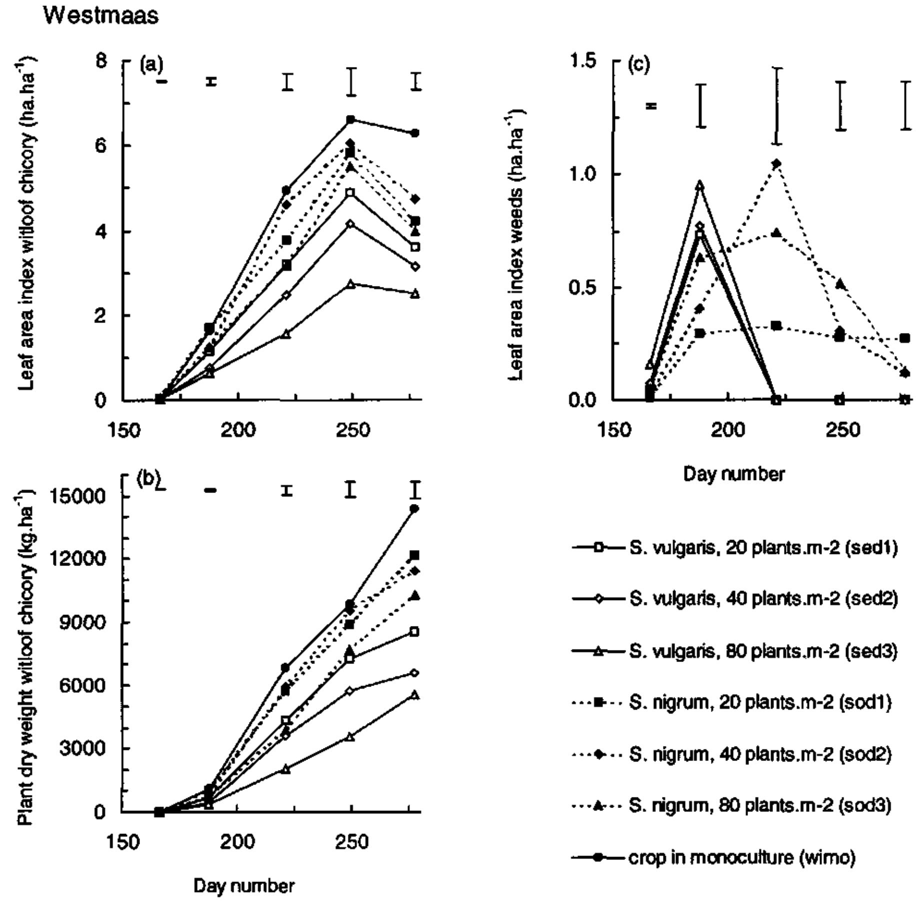

Figure 6.3 The seasonal development of leaf area index (a) and total plant dry weight (b) of witloof chicory, and of leaf area index (c) of the weed species *S. vulgaris* and *S. nigrum* in the experiment at Westmaas. Vertical bars represent 1 SED.

In the experiment at Westmaas, competition with weeds reduced the leaf area index (Figure 6.3a; $P < 0.001$) and the total plant dry weight (Figure 6.3b; $P < 0.001$) of witloof chicory from the second harvest onwards. These reductions were greater at higher weed densities and when competition occurred with *S. vulgaris*. The increase in leaf area index of the weeds (Figure 6.3c) occurred earlier in the growing season for *S. vulgaris*

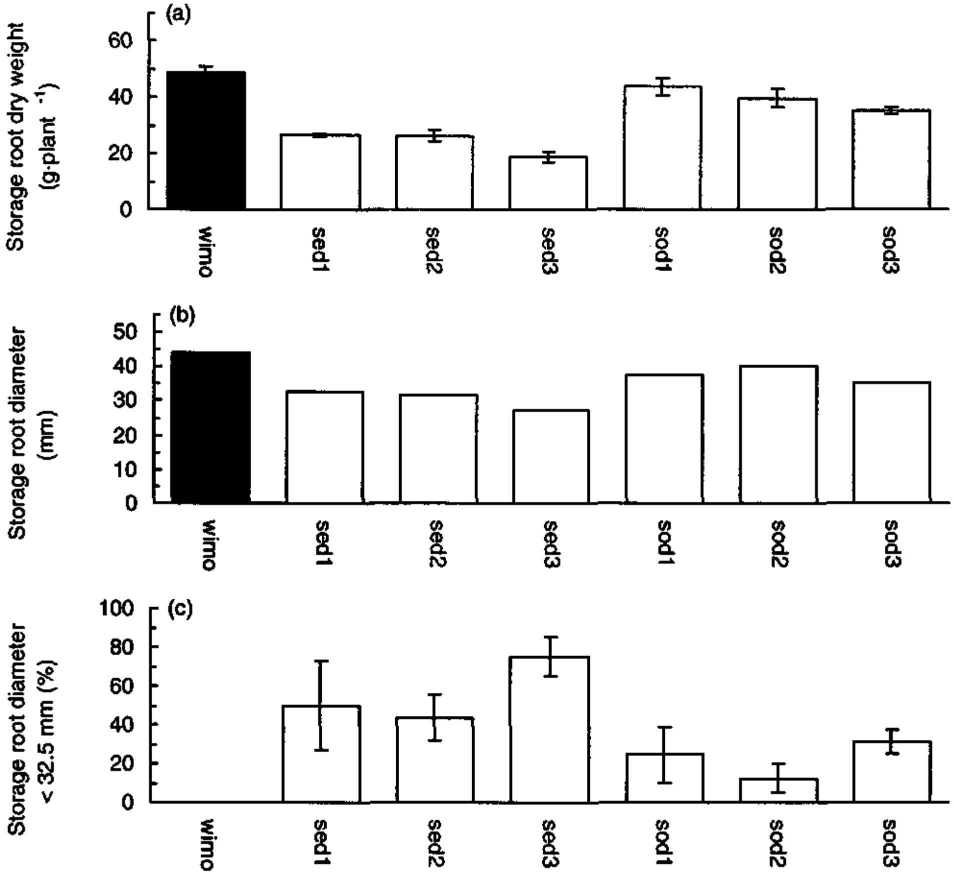

Figure 6.4 The average storage root dry weight (a), the average storage root diameter (b), and the percentage of storage roots with a diameter smaller than 32.5 mm (c) of witloof chicory in the experiment at Westmaas. See Figure 6.3 and Materials & Methods for explanation of the treatment codes. Vertical bars represent standard errors of means.

($P<0.001$), and was generally greater at higher weed densities ($P<0.001$). The weed species also obtained a greater maximum plant height (0.5 m for both *S. vulgaris* and *S. nigrum*) than witloof chicory (0.45 m). Consequently, competition with weeds reduced the storage root dry weights of witloof chicory between 10 and 61 % (Figure 6.4a; $P<0.001$), and the storage root diameters between 9 and 39 % (Figure 6.4b; $P<0.001$). The reductions in storage root dry weight and storage root diameter were greatest ($P<0.001$) when competition occurred with *S. vulgaris*, and smallest when competition occurred with *S. nigrum*. A higher plant density of the weeds increased ($P<0.001$) the reductions in storage root weight and storage root diameter. Competition with weeds greatly increased the percentage of storage roots with a diameter smaller than 32.5 mm (Figure 6.4c; $P<0.001$). Competition with *S. vulgaris* plants resulted in a higher ($P<0.001$) percentage of storage roots with a diameter smaller than 32.5 mm, than

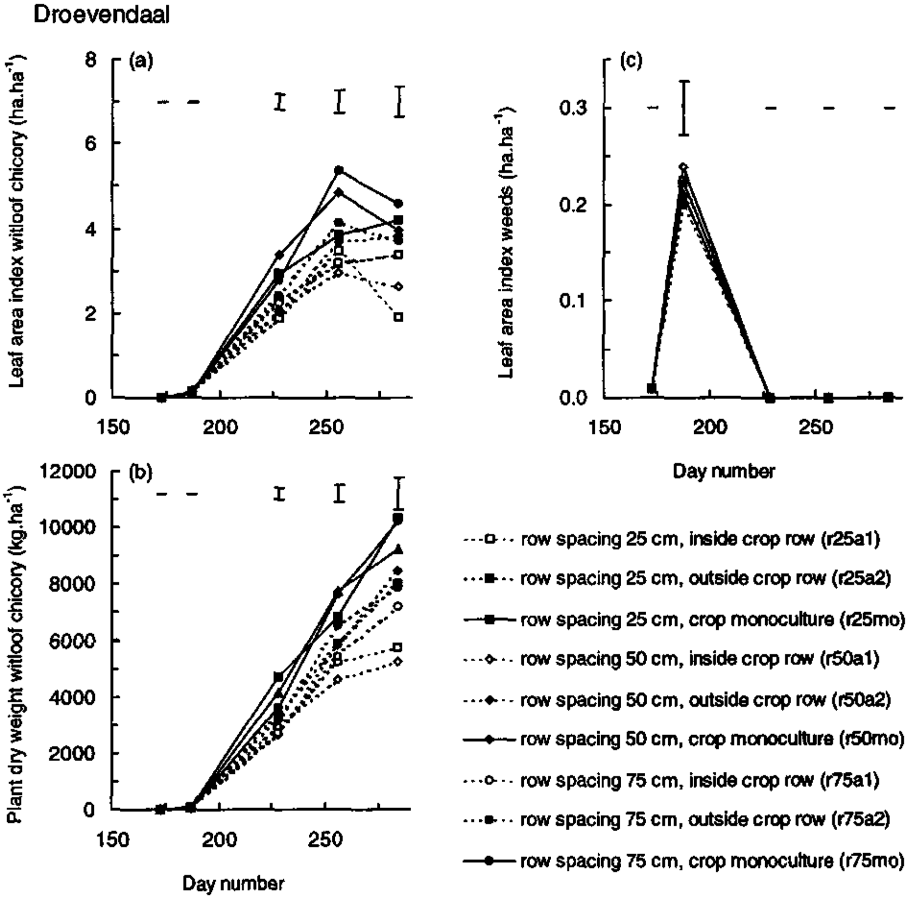

Figure 6.5 The seasonal development of leaf area index (a) and total plant dry weight (b) of witloof chicory, and of leaf area index of the weed species (c) *S. vulgaris* in the experiment at Wageningen. Vertical bars represent 1 SED.

competition with *S. nigrum*. The percentage of storage roots with a diameter smaller than 32.5 mm could be as high as 75 %.

In the experiment at Wageningen, competition with weeds reduced the leaf area index (Figure 6.5a; $P< 0.001$) and the total plant dry weight (Figure 6.5b; $P<0.001$) of witloof chicory from the second harvest onwards. These reductions were greatest ($P<0.001$) when

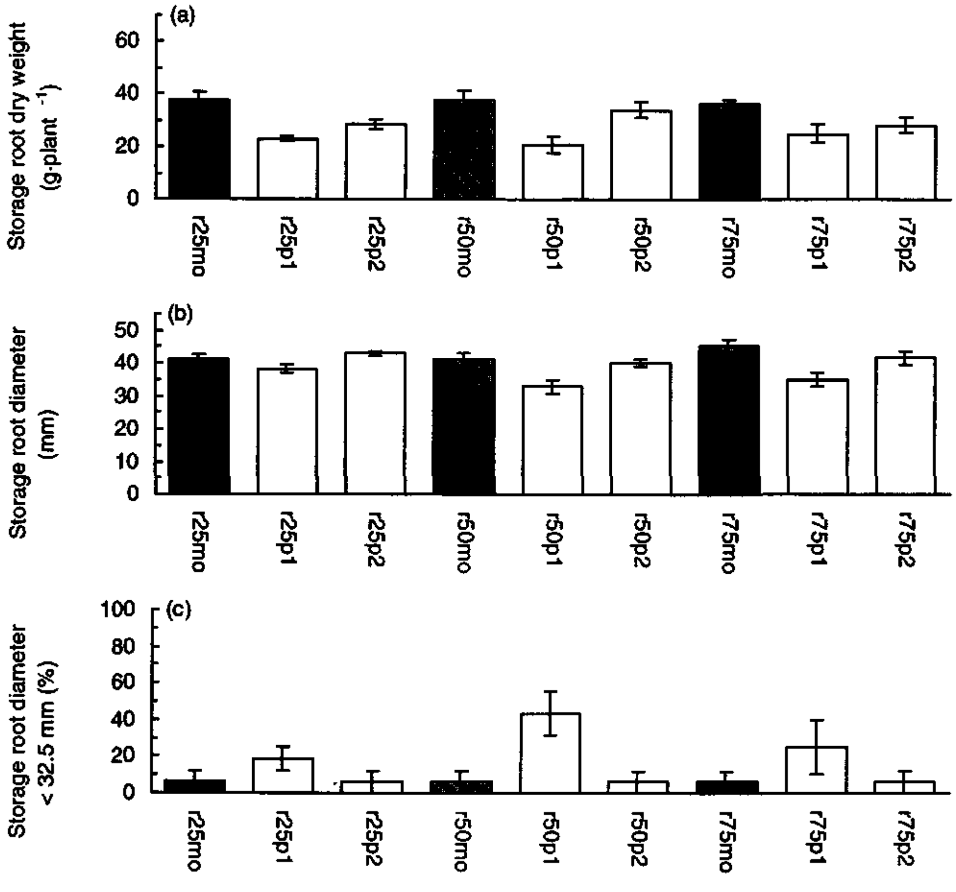

Figure 6.6 The average storage root dry weight (a), the average storage root diameter (b), and the percentage of storage roots with a diameter smaller than 32.5 mm (c) of witloof chicory in the experiment at Wageningen. See Figure 6.5 and Materials & Methods for explanation of the treatment codes. Vertical bars represent standard errors of means.

S. vulgaris was positioned inside the crop rows. The seasonal course of leaf area index of *S. vulgaris* was not affected by the row spacing of the crop or by its spatial position (Figure 6.5c; P>0.05). The maximum plant height obtained by *S. vulgaris* was identical (0.4 m) to that of witloof chicory, but the increase in height of *S. vulgaris* occurred earlier in the growing season.. Consequently, competition with weeds reduced the storage root dry weights of witloof chicory between 10 and 45 % (Figure 6.6a; P<0.001), and the storage root diameters between -5 and 23 % (Figure 6.6b; P<0.01). The reductions in

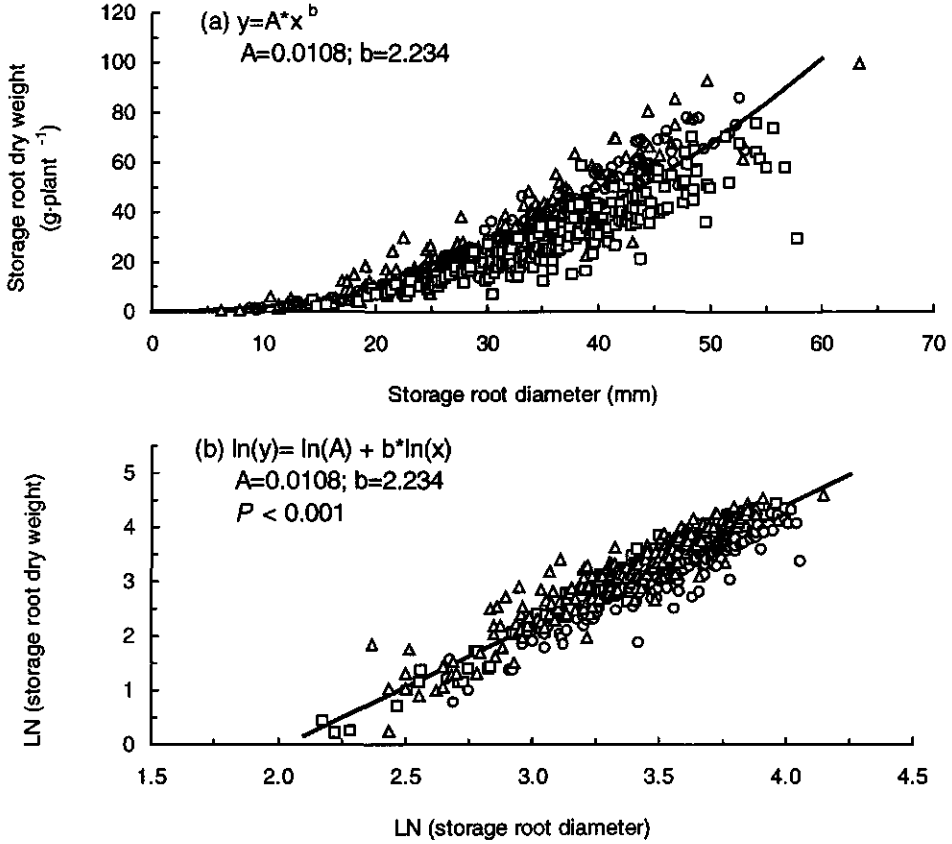

Figure 6.7 The relationship between the diameter and the dry weight of individual storage roots of witloof chicory (a). The relationship between the ln-transformed storage root diameter and the ln-transformed storage root weight (b). The Δ, O and ☐ represent data of the experiments at Lelystad, Westmaas and Wageningen, respectively.

storage root dry weight and storage root diameter were greatest ($P<0.01$) when *S. vulgaris* plants were positioned inside the crop rows. Competition with *S. vulgaris* increased the percentage of storage roots with a diameter smaller than 32.5 mm, but only when *S. vulgaris* plants were positioned inside the crop rows (Figure 6.6c; $P<0.001$). The percentage of storage roots with a diameter smaller than 32.5 mm could be as high as 45 %.

There was a strong allometric relationship between the diameter and the dry weight of individual storage roots from all three experiments (Figure 6.7a). A linear regression of the ln-transformed storage root dry weights on the ln-transformed storage root diameters explained 88 % of the variation in the ln-transformed storage root fresh weights (Figure 6.7b). The average storage root with a diameter of 32.5 mm had a dry weight of 25.8 grams.

DISCUSSION

The reductions in total plant dry weight of witloof chicory due to competition with weeds were already highly significant about one month after crop emergence, indicating that the plants started competing for the same resources very soon after crop emergence. In all three experiments, the emergence of the weed plants occurred very shortly before or after the emergence of the witloof chicory plants. At the end of the growing season, weed competition had reduced the storage root dry weight between 10 and 75 % and the storage root diameter between 9 and 44 %. Other studies also showed that weeds cause severe yield reductions, when there is a relatively short period between crop and weed emergence (Kropff *et al.*, 1992, 1993b). More importantly, the number of storage root with a diameter smaller than 32.5 mm could be as high as 95 %. Storage roots below a diameter of 32.5 mm have little economic value, because they do not contain sufficient redistributable carbohydrates to produce a chicon of good quality (Anonymous, 1989; Van Kruistum *et al.*, 1997). For any weed management system geared to avoid or minimise yield reduction of witloof chicory due to competition with weeds, the results of this study imply that early emerging weeds should be controlled as soon as possible.

The magnitude of the reductions in total plant dry weight, storage root dry weight and storage root diameter due to competition with weeds, depended on the size of the weed biomass (expressed as leaf area index), and on the timing and duration of the weed competition within the growing season. Plants of *C. album* grew faster and higher, and produced more leaf area than plants of *S. vulgaris* or *S. nigrum*. Thus, plants of all weed species but especially *C. album* plants, could intercept a disproportionally large part of the incoming radiation. As a result, *C. album* caused a greater reduction in storage root dry weight and storage root diameter than *S. vulgaris* or *S. nigrum*. The maximum leaf area index of *S. vulgaris* and *S. nigrum* was quite similar in the experiment at Westmaas, however, *S. vulgaris* caused a greater reduction in growth and dry matter production of witloof chicory than *S. nigrum*. This was due to the much faster leaf area index development of *S. vulgaris*, which resulted in an earlier start of competition and yield reduction. A contrasting effect was found in the experiment at Lelystad, where *S. nigrum* caused a greater reduction in the growth and dry matter production of witloof chicory than *S. vulgaris*. In this experiment, the initial growth of leaf area index of *S. nigrum* was equally fast than that of *S. vulgaris* and its leaf area index was sustained over a much longer period than that of *S. vulgaris*. This importance of early leaf area development in determining the yield loss was also shown by Kropff *et al.* (1993b). The position of the weed plants affected the reduction of storage root dry weights and storage root diameter, but only when the maximum plant height of the weeds was similar to that of the witloof chicory crop. Weed plants that grow higher than the crop plants can still exert their competitive influence when growing outside the crop row, whereas this would less possible for small plants growing outside the crop row. Other studies also showed that the intensity of inter-specific competition was related to the spatial arrangement of the competing species (Mortensen & Coble, 1989; Cousens & O'Neill, 1993).

Models for crop-weed competition are usually based on dry matter calculations for the "average plant" (Kropff & van Laar, 1993). However, this study showed that the actual yield loss due to weed competition can be much greater than suggested by the reduction in dry weight. The usefulness of these models in the study of the effects of crop-weed competition and in the development of weed management strategies in witloof chicory, would be greatly enhanced when the effects of competition on storage root diameter could also be simulated. This has been achieved through the strong allometric relationship that was found between the average storage root diameter and the average storage root dry weight. The linear regression of the ln-transformed storage root dry weight on the ln-transformed storage root diameter explained nearly 90 % of the variation in the ln-transformed storage root dry weight under a wide range of conditions, *i.e.* various weed species, weed densities and weed positions. The allometric relationship between the average storage root dry weight and average storage root diameter was used to calculate a value of 25.8 g for the storage root dry weight at which the storage root diameter equals 32.5 mm.

CHAPTER 7

THE EFFECTS OF COMPETITION ON THE REPRODUCTIVE OUTPUT OF AGRICULTURAL WEEDS

B.J. Schnieders, L.A.P. Lotz, R. Rabbinge, C. Kempenaar and P.C. de Man

ABSTRACT

A study was carried out to determine for the weed species Senecio vulgaris, Solanum nigrum, and Chenopodium album: (i) to what extent intra-specific competition and/or inter-specific competition with a crop (witloof chicory, sugarbeet or maize) influences the reproductive output, (ii) which component of reproductive output is most sensitive to competition, (iii) whether the relationship between vegetative plant size and reproductive output is linear, (iv) whether there is a threshold size for reproduction, and (v) whether there is a robust relationship between plant weight and seed number, which may provide a link between competition models and models of population dynamic.

A linear relationship between vegetative plant size and total reproductive weight explained a large percentage of the variation in the total reproductive weight of S. vulgaris, S. nigrum and C. album. For all three weed species, the minimum size for reproduction was not significantly different from zero, and a constant proportion of biomass was invested into reproductive biomass.

The reduction in total reproductive weight as a consequence of increased competition, was primarily due to a lower number of seeds per plant, and to a lesser extent due to a lower individual seed weight.

The relationships between vegetative plant size and total reproductive weight, number of seeds or individual seed weight were robust for S. vulgaris, S. nigrum, and C. album, under a great range of competitive stresses. Increased competition merely reduced both the vegetative plant size and the reproductive output, but had little effect on the proportion of dry matter that was invested in reproductive output.

The effect of the relative date of emergence of weeds on the seed production differed greatly between the weed species. Plants of S. vulgaris and S. nigrum produced few seeds when emergence was 10 days or more after the witloof chicory crop. In contrast, C. album was able to produce large numbers of seeds per plant, irrespective of its relative emergence date.

Vegetative plant size is a reliable estimator of seed production of S. vulgaris, S. nigrum, and C. album, thus establishing a link between competition models and models of population dynamics. This link is useful to assess the effects of crop competitiveness on weed population dynamics, and may thus contribute to the development of weed management systems.

INTRODUCTION

The development of strategies for integrated weed management requires an accurate prediction of the effects of competition and weed control practices, on both the crop yield loss in the current year and on the future weed infestation levels. The effects of weed competition on yield loss of the crop are extensively studied, and yield losses can be predicted quite accurately using competition models (*e.g.* Kropff & Van Laar, 1993). However, the quantitative knowledge of the effects of crop competition on the reproductive output of weeds is limited (Wilson *et al.*, 1988). The reproductive output of weeds can provide the desired link between crop-weed competition models and models of weed population dynamics (Van Groenendael, 1988; Kropff *et al.*, 1993a). It is therefore important to understand how competition influences the reproductive output of weed plants.

Samson & Werk (1986) proposed a linear relationship between reproductive weight and vegetative weight. Weiner (1988a) suggested that plants must achieve a minimum size if they are to produce flowers and fruits, and that above this threshold size, a simple relationship between size and reproductive output may exist. Rees & Crawley (1989) argued that plants generally do not have threshold sizes for reproduction. Klinkamer, De Jong & Meelis (1990) showed that size-dependent reproductive effort may result from very different processes. They suggested, that when the production of the first seeds is associated with large overhead costs, the relationship between plant size and reproductive output can be described with a linear model. On the other hand, when larger plants are proportionally better pollinated or have disproportionate access to resource, a power-function may more appropriately describe the relation between plant size and reproductive output (Klinkhamer *et al.*, 1990).

Linear relationships between plant dry weight and reproductive output have been found for many weed species (Debaeke, 1988; Wilson *et al.*, 1988; Thompson *et al.*, 1991; Wright, 1993). It was suggested by Wilson *et al.* (1988) that plant dry weight may be a sufficiently reliable indicator of seed production. It is, however, important to establish the robustness of these relationships under various environmental conditions and competition situations, before they can be used to predict the population dynamics of weed species.

The objectives of the present study were to determine for the weed species *Senecio vulgaris* L., *Solanum nigrum* L. and *Chenopodium album* L.: (*i*) to what extent competition influences the reproductive output, (*ii*) which component of reproductive output is most sensitive to competition, (*iii*) whether the relationship between plant size and reproductive weight is linear, (*iv*) whether there is a threshold size for reproduction, and (*v*) whether there is a robust relationship between plant weight and seed number which may provide a link between competition models and models of population dynamics.

MATERIALS AND METHODS

Ten experiments were carried out at three locations between 1991 and 1993, to study competition between a witloof chicory (*Cichorium intybus* L. cv. Flash) crop and the weeds *S. vulgaris*, *S. nigrum* and *C. album* (Table 7.1). In the experiments, various plant densities, relative emergence dates, and spatial positions of the weed species were applied as treatments. In the greenhouse_91 experiment, three nitrogen levels (30, 60 and 120 $kg \cdot ha^{-1}$) were also applied. In the field experiments Lelystad_91, Lelystad_93 and Westmaas_93, weed species were also grown in monoculture. Reproductive output data of *C. album* were also available from four experiments carried out at Wageningen in 1993 and 1994, in which the effects of biological weed control on competition between maize (*Zea mays* L.) and *C. album*, or sugarbeet (*Beta vulgaris* L.) and *C. album* were studied (Table 7.1; Kempenaar, 1995; Kempenaar *et al.*, 1996). Seeds of the weed species were germinated on filter paper or on water agar medium (Kempenaar & Schnieders, 1995), and then transplanted into the soil to achieve a desired date of emergence, plant density and spatial position. The origin of the weed seeds varied between the years, but all seed batches originated from arable fields.

Weed plants were harvested when the seeds were ripe, but before seed shedding had started. The number of plants harvested per plot varied from 1 to 30, depending on the experimental set-up. The use of germinated weed seed at transplanting resulted in a highly synchronised development of the plants of each weed species, which ensured that all harvested plants had seeds of comparable maturity.

Analysis of variance (ANOVA, Sokal & Rohlf, 1981) was used to analyse the effects of density, emergence date, and spatial position of the weed plants, on the dry weights of total vegetative and total reproductive plant parts, the seed dry weights, and the seed numbers of weeds. Linear regression analysis was used to determine the relationships between reproductive output and vegetative plant size. A log-transformation was not performed on the data, because the residuals were consistent with the assumptions of regression analysis (Sokal & Rohlf, 1981), and because the values of the intercept would not be recoverable from log-transformed regressions, which would make interpretation of patterns much more difficult (see Samson & Werk, 1986).

Table 7.1 Summary of the experimental details of the various experiments. The relative date of emergence of the weed plants is expressed in days after the emergence date of the competing crop species. The plant density is expressed in m^{-2}, except for the greenhouse experiments where it indicates the number of plants per pot (pot size 7.6 litres, diameter 21 cm). The weed plants were positioned inside or outside the crop row in the field experiments, or at a certain distance (cm) from a target crop plant in the greenhouse experiments. The Geographical location is 5°27"E, 52°31"N for Nagele, 4°25"E, 51°50"N for Zevenbergen, and 5°40"E, 51°58"N for Wageningen. The numbers after each seed origin represent different fields.

				Weed species characteristics				Crop species	
Weed species	Expt. Nr.	Location	Year	Seed origin	Emergence date	Plant density	Spatial position	species name	Plant density
S. vulgaris	1	greenhouse	1991	Nagele 1	0	1	1.7, 3.4, 6.8	witloof	3
	2	Lelystad	1991	Nagele 1	14, 36	10	inside, outside	witloof	20
	3	Wageningen	1991	Nagele 1	0, 22, 29	7, 10, 20	inside	witloof	20
	4	greenhouse	1992	Nagele 2	0	1	1.5, 3, 6, 12	witloof	1,2,3
	5	Lelystad	1992	Nagele 2	19, 28	10, 20, 40	inside	witloof	20
	6	Westmaas	1992	Nagele 2	9, 23	10, 20, 40	inside	witloof	20
	7	Wageningen	1992	Nagele 2	10, 18	10	inside, outside	witloof	20
	8	Westmaas	1993	Zevenbergen 1	1	20, 40, 80	inside	witloof	20
	9	Wageningen	1993	Zevenbergen 1	0	20	inside, outside	witloof	20
S. nigrum	2	Lelystad	1991	Zevenbergen 2	14, 36	10	inside, outside	witloof	20
	5	Lelystad	1992	Zevenbergen 2	19, 28	10, 20, 40	inside	witloof	20
	6	Westmaas	1992	Zevenbergen 2	9, 23	10, 20, 40	inside	witloof	20
	7	Wageningen	1992	Zevenbergen 2	10, 18	10	inside, outside	witloof	20
	8	Westmaas	1993	Nagele 3	1	20, 40, 80	inside	witloof	20
	10	Lelystad	1993	Nagele 3	-2	20	inside, outside	witloof	20
C. album	7	Wageningen	1992	Zevenbergen 3	10, 18	10	inside, outside	witloof	20
	10	Lelystad	1993	Zevenbergen 3	-2	20	inside, outside	witloof	20
	11	Wageningen	1993	Wageningen 1	8	22	inside	sugarbee	11
	12	Wageningen	1994	Wageningen 1	28	2	inside	sugarbee	11
	13	Wageningen	1993	Wageningen 1	9	22	inside	maize	11
	14	Wageningen	1994	Wageningen 1	22	2	inside	maize	11

RESULTS

Linear regression of total reproductive weight on vegetative plant size (Table 7.2) explained a large percentage (93 %) of the variation in the total reproductive weight of *S. vulgaris* (Figure 7.1a) and *S. nigrum* (Figure 7.2a), and to a slightly lesser extent also of *C. album* (Figure 7.3a). The intercept of the regression line was not significantly different from zero for any of the three weed species, indicating that even very small plants of these species were able to produce reproductive structures. The slope of the linear regression line was significantly larger than zero for each of the three weed species. Within the range of plant sizes found in this data set, larger plants continued to invest a constant proportion of dry matter into reproductive structures.

Table 7.2 Regression statistics of the linear regression analyses on the relationship $Y=a+b\cdot X$ between vegetative dry weight per plant (X, g) and total reproductive weight per plant (g), number of seeds per plant or seed weight (mg) of *Senecio vulgaris*, *Solanum nigrum*, and *Chenopodium album* (values of a and b are followed by ± S.E.).

	Intercept (a)	*P*-value	Slope (b)	*P*-value	R^2_{adj}
S. vulgaris					
reproductive weight	0.03 ± 0.05	ns	0.34 ± 0.01	<0.001	0.93
number of seeds	527 ± 269	ns	920 ± 30	<0.001	0.82
seed weight	0.09 ± 0.01	<0.001	0.007 ± 0.00	<0.001	0.38
S. nigrum					
reproductive weight	-0.02 ± 0.06	ns	0.65 ± 0.01	<0.001	0.93
number of seeds	-48 ± 137	ns	798 ± 28	<0.001	0.81
seed weight	0.95 ± 0.03	<0.001	0.02 ± 0.01	<0.01	0.05
C. album					
reproductive weight	-0.57 ± 0.61	ns	0.89 ± 0.03	<0.001	0.88
number of seeds	3614 ± 1669	<0.05	1341 ± 87	<0.001	0.69
seed weight	0.27 ± 0.01	<0.001	0.01 ± 0.00	<0.001	0.46

Linear regression of number of seeds per plant on vegetative plant size (Table 7.2) explained a large percentage of the variation (82 %) in the number of seeds of *S. vulgaris* (Figure 7.1b) and *S. nigrum* (Figure 7.2b), and to a lesser extent also of *C. album* (Figure

7.3b). The intercept of the regression line was not significantly different from zero for *S. vulgaris* and S. *nigrum*. The intercept was just significant for C. *album*, but since it is impossible for plants of zero vegetative weight to produce any seeds this must be regarded as an artefact of the regression analysis. The slope of the regression line was significantly larger than zero for each of the three weed species.

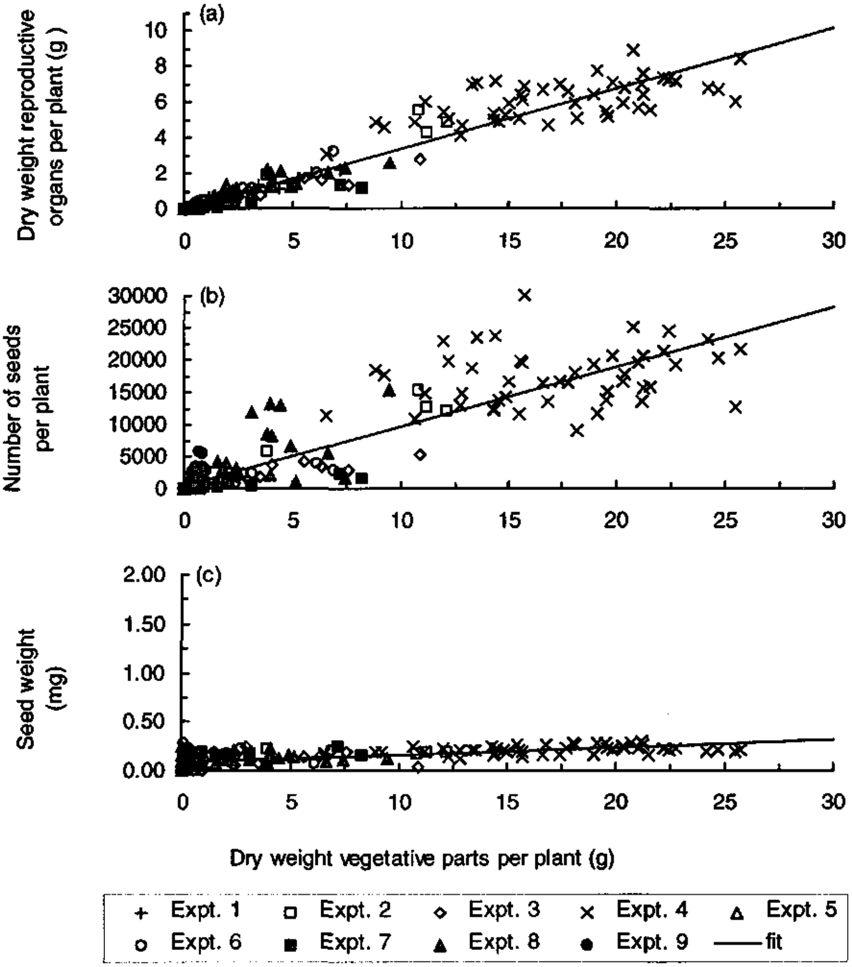

Figure 7.1 Relationships between vegetative dry weight per plant of *Senecio vulgaris* and (a) total reproductive dry weight per plant; (b) number of seeds per plant; and (c) seed weight.

Linear regression of seed weight on vegetative plant size (Table 7.2) explained only a small percentage of the variation (Maximum 46 %) in the number of seeds of *S. vulgaris* (Figure 7.1c), *S. nigrum* (Figure 7.2c), and *C. album* (Figure 7.3c). The intercept and the slope of the regression line were significantly larger than zero for each of the three weed species.

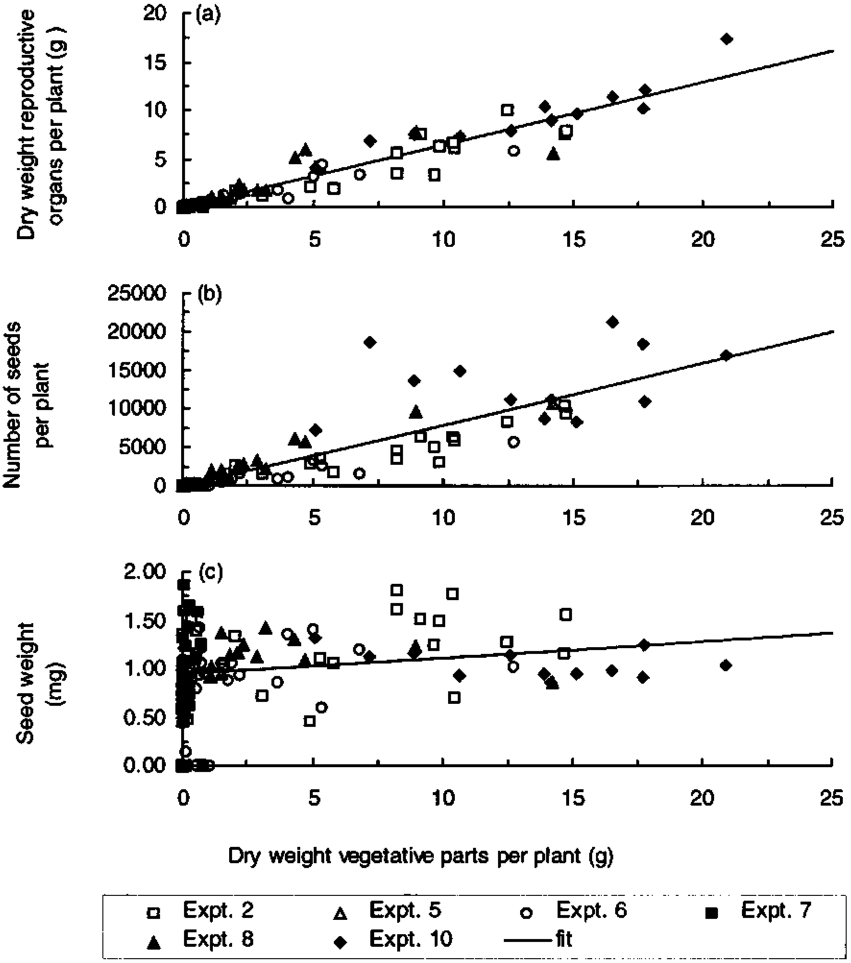

Figure 7.2 Relationships between vegetative dry weight per plant of *Solanum nigrum* and (a) total reproductive dry weight per plant; (b) number of seeds per plant; and (c) seed weight.

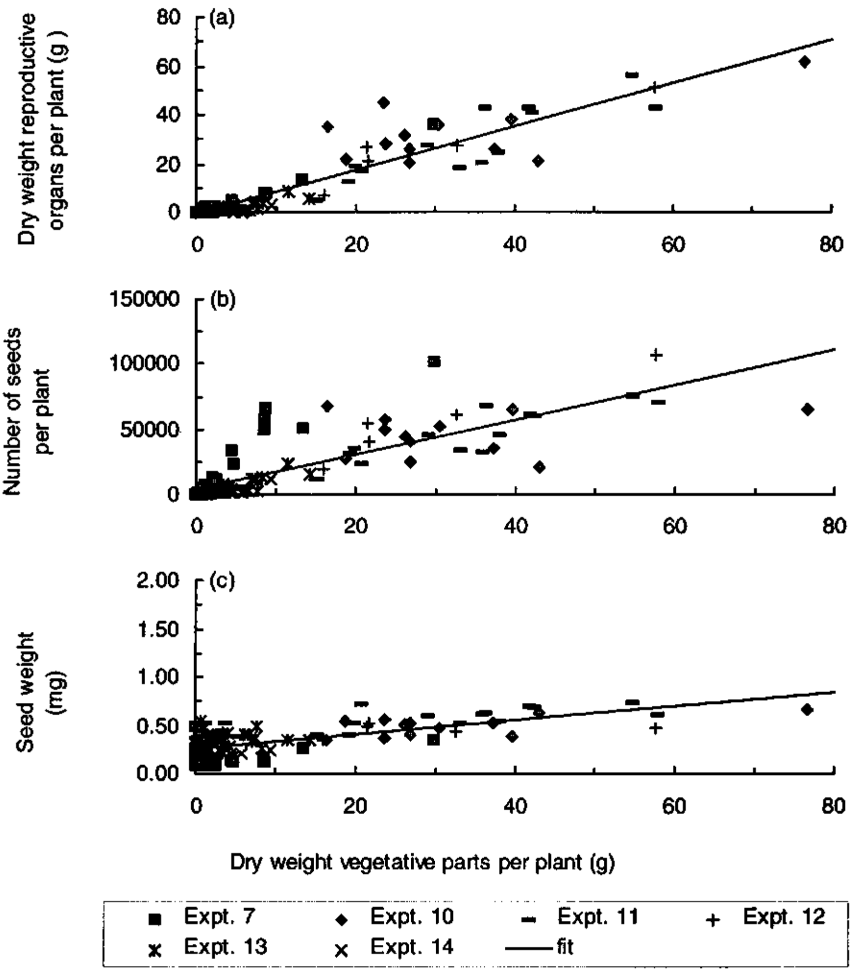

Figure 7.3 Relationships between vegetative dry weight per plant of *Chenopodium album* and (a) total reproductive dry weight per plant; (b) number of seeds per plant; and (c) seed weight.

The linear regressions showed that the relationships between vegetative plant size and total reproductive weight, number of seeds or 1000-seed weight were very robust under the broad range of growing conditions and competitive stresses. The various levels of competitive stress were caused by the broad range of plant densities, relative emergence dates and plant positions, that were provided by the 14 experiments on crop-weed competition. Firstly, the origin of the seeds (see Table 7.1 for the origin of the seeds used in a particular experiment) did not affect the relationships between vegetative plant size and reproductive output. The data points for each seed origin appeared to be nicely scattered around the regression lines of Figures 7.1, 7.2 and 7.3. Linear regression of total reproductive weight on vegetative plant size, performed separately on the data of each of the seed origins, showed that none of the intercepts were significantly different from zero. The slopes of the regression lines of each origin did not deviate more than 10% from the slopes of the overall regression lines. Secondly, growing *S. vulgaris* plants at various nitrogen application rates in the greenhouse experiment of 1991, did not alter the relationship between vegetative plant size and total reproductive weight (Figure 7.4; Y = 0.12 + 0.30*X for the nitrogen treatments vs. Y = 0.03 + 0.34*X, for the rest of the data points). The intercepts were not significantly different from zero, and the slopes of both regression lines were almost identical. Reducing the nitrogen application rate from 120

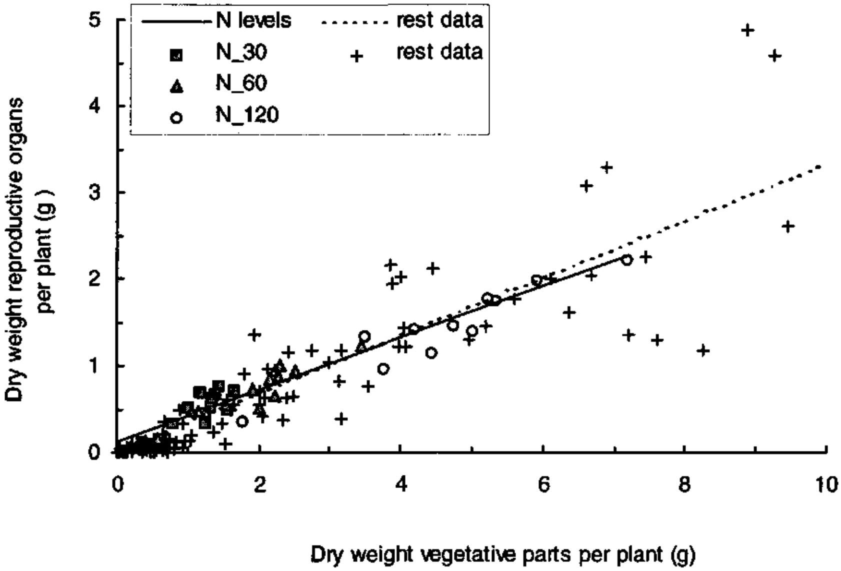

Figure 7.4 Effect of nitrogen application rate on the relationship between vegetative dry weight (g) and total reproductive dry weight (g) per plant of *Senecio vulgaris* in experiment 1. The symbols and lines represent the data points and the regression lines, respectively.

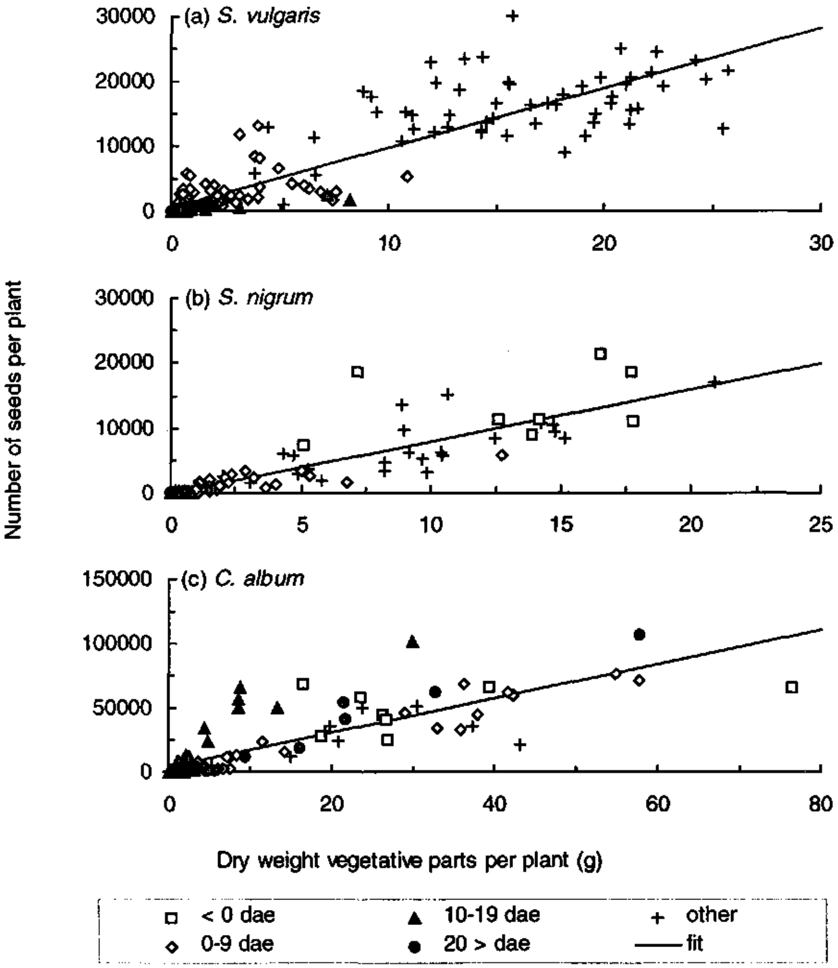

Figure 7.5 Effects of relative date of emergence of the weed plants (in days after emergence of the crop plants, dae) on the seed production of (a) *Senecio vulgaris*; (b) *Solanum nigrum*; and (c) *Chenopodium album*. Data points of weed plants grown in monoculture, of *S. vulgaris* plants grown in the greenhouse (Figure 7.5a, see text) and of *C. album* plants infected with *Ascochyta caulina* (Figure 7.5c, see text) are plotted using the + symbol.

kg·ha^{-1} to 60 and 30 kg·ha^{-1} created a situation of increased nitrogen shortage, and thus increased the competition for nitrogen between the plants in a pot. This reduced the vegetative plant size, but the total reproductive weight was reduced proportionally. Thirdly, the crop species that *C. album* competed with, appeared to have little or no effect on the relationships between vegetative plant size and reproductive output of *C. album* (Figure 7.3). Competition with maize reduced the vegetative plant size of *C. album* to a greater extent than competition with witloof chicory or sugarbeet, but the relationships between the vegetative plant size and reproductive output remained largely intact.

For weed management purposes it is essential to understand the effects of crop-weed competition on the number of seeds produced per plants, because this may determine to a large extent the future weed infestation levels. Analysis of the data from the field experiments of all species revealed that the emergence date of weed plants relative to that of the crop plants (dae, in Figure 7.5), had the largest effect on the vegetative plant size of the weeds, much more so than the effects of plant density or plant position (data not shown). Figure 7.5 shows that the relationship between vegetative plant size and the number of seeds per plant was not affected by the relative date of weed emergence. Furthermore, Figure 7.5 shows that the effect of the relative emergence date of weeds on the number of seeds per plant differed greatly between species. For example, *S. vulgaris* plants emerging 10 days or more after plants of a witloof chicory crop produced very few seeds per plant (Figure 7.5a). To an even greater extent this can also be concluded for *S. nigrum* (Figure 7.5b), which produces even lower numbers of seeds than *S. vulgaris* plants when emerging 10 days or more after plants of a witloof chicory crop. In contrast, *C. album* plants were able to produce large numbers of seeds, irrespective of their date of emergence relative to the crop (Figure 7.5c).

Data from a biological weed control experiment showed that in a sugarbeet crop (which has a crop structure very similar to that of witloof chicory), a moderate infestation of C. *album* with the fungus *Ascochyta caulina* greatly reduced the competitive ability of *C. album*. This ensured that the vegetative plant size of *C. album* remained small. Consequently, the number of seeds per plant was negligible. (Figure 7.6). When *C. album* was grown in a maize crop, a slight infestation with the mycoherbicide was sufficient to greatly reduce the seed production. Linear regression on data of *C. album* infected with *Ascochyta caulina* (Figure 7.6; $Y = -64 + 1348*X$ for the infected *C. album* plants) also showed that the relationship between number of seeds per plant and vegetative plant size of *C. album* (see Table 7.2) is not changed by the biological weed control treatment.

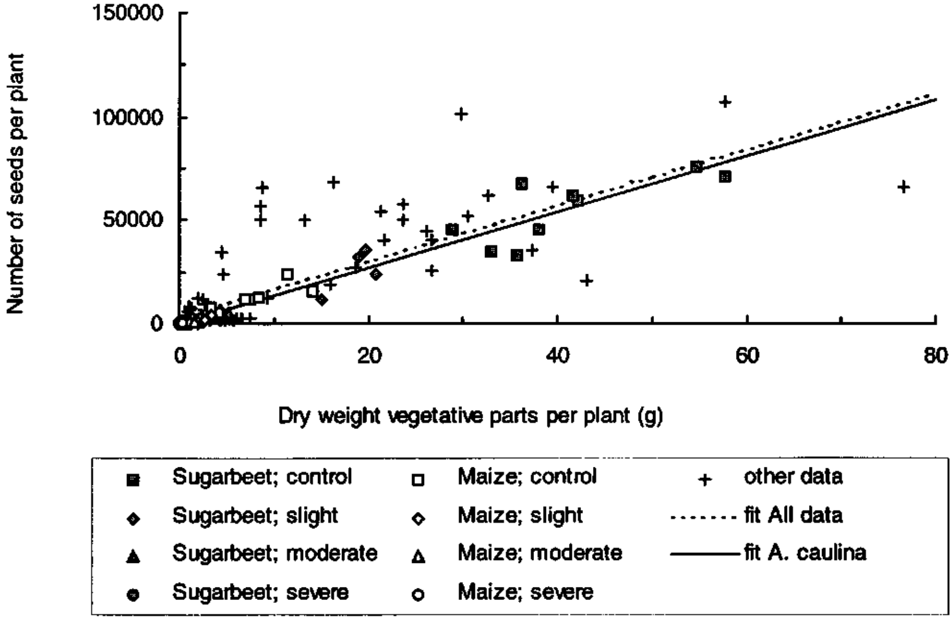

Figure 7.6 Effect of a weed management action (*i.e.* foliar application of a spray containing spores of *Ascochyta caulina*) on the seed production of *Chenopodium album*. (experiments 11 and 13; original data published in Kempenaar *et al.*, 1996). The terms "slight", "moderate" and "severe" refer to the severity of *Ascochyta* infestation as measured in the experiments. The data points from all other experiments with *C. album* are plotted using the + symbol.

DISCUSSION

The linear regression of total reproductive weight on vegetative plant size explained a large percentage of the variation in the total reproductive weight of *S. vulgaris*, *S. nigrum*, and *C. album*. The intercepts of the relationships between vegetative plant size and total reproductive weight were not significantly different from zero, indicating that the minimum size for reproduction was zero or very low. Thus, these results appear to support Rees & Crawley (1989) who argued that plants generally do not have threshold sizes for reproduction. The results also appear to disagree with Weiner's (1988a) suggestion that plants must achieve a minimum size if they are to produce flowers and fruits. However, if the minimum plant size for reproduction is very small, measurement errors may make it difficult to show a statistically significant threshold. Visual observations made during the experiments, indicated a small but definite minimum size for reproduction. These observations revealed that weed plants showed a strong phenotypic plasticity in the struggle for light, such that very small plants often managed to produce one long thin stem, with two or three leaves and one flower at the top of the crop canopy, which may or may not produce seeds. Those long thin stems were not able to bear the weight of the leaves and reproductive organs without the support of the neighbouring crop plants. However, when the weed plants were unable to reach the top of the crop canopy, they usually did not survive. Kropff & Van Laar (1993) also described a strong phenotypic plasticity for *C. album*, such that plants could obtain a large height under very unfavourable conditions. The slope of the relationship between vegetative plant size and total reproductive weight was significantly larger than zero for each of the three weed species, indicating that a constant proportion of biomass was allocated into reproductive biomass. Linear relationships between vegetative plant size and reproductive weight have been found for many species (Debaeke, 1988; Wilson *et al.*, 1988; Thompson *et al.*, 1991; Wright, 1993). It must be kept in mind that total reproductive weight consists of a seed component and a "seed supporting" component. Thus, a low positive total reproductive weight does not necessarily mean a positive seed weight, but may merely reflect the formation of one flower by a very small plant. The relationships presented in this study were established using only those plants with mature seeds before seed shedding had commenced. Using plants with immature seeds or with some seeds already shedded will result in an underestimated reproductive output.

The relationships between vegetative plant size and total reproductive weight, number of seeds or 1000-seed weight were very robust for *S. vulgaris*, *S. nigrum*, and *C. album*, under a great range of competitive stresses and growing conditions. Growing the 3 species under various ranges of competitive stress, *i.e.* at various relative emergence dates, nitrogen application rates, plant densities or plant positions inside a crop species, had no effect on the proportion of dry matter that was invested in reproductive output. Increased competition merely reduced both the vegetative plant size and the reproductive output. This is in agreement with Thompson *et al.* (1991), who also showed linear relationships between reproductive and vegetative weights, especially when size differences were primarily due to competition. The relative emergence dates of the weed species had the strongest effect on the vegetative plant size and reproductive output. Other studies also showed a strong effect of the relative date of emergence on the competitive strength of a species (*e.g.* Schnieders & Lotz, 1993; Lotz *et al.*, 1993). The spatial position and density of the weed plants, generally had very little effect on vegetative plant size and reproductive output of the weeds. Other research showed strong density effects (*e.g.* Watkinson, 1980), but in our experiments the range of densities was probably too small to show effects. The relationship between number of seeds per plant and vegetative plant size of *C. album* was not changed by a by biological weed control treatment, in which the fungus *Ascochyta caulina* was used as the biological agent.

The model of Samson & Werk (1986) shows that the reproductive effort (*i.e.* the ratio of reproductive weight and vegetative weight) may or may not change with plant size, depending on the value of the intercept of the regression of reproductive weight on plant size. The intercepts of the regressions of total reproductive weight on vegetative plant size were not significantly different from zero for *S. vulgaris*, *S. nigrum* or *C. album*, thus indicating that the reproductive effort should not change with plant size. This is in agreement with Harper & Ogden (1970), who found that the reproductive effort of *Senecio vulgaris* L. was maintained at the same level over a seven-fold difference in total plant weight, and that the reproductive effort was reduced only under extreme stress conditions. An increase in reproductive effort of *C. album* with increasing competitive stress, as reported by Szente *et al.* (1993) was not found in this study.

The decrease in total reproductive weight as a consequence of smaller vegetative plant sizes, *i.e.* as a consequence of increased competition, was primarily due to a lower number of seeds per plant, and to a lesser extent due to a lower seed weight. It appears that the seed weight is a more conservative plant characteristic than the number of seeds per plant. This relatively non-plastic response of seed weight to increased competition was also reported by Harper (1977). Weiner (1988a) also concluded that plants reduce their seed output primarily by producing fewer, and, secondarily, by producing smaller seeds. Decreased seed size has been associated with a decreased germination percentage (Lotz, 1989; Weis, 1982), a decreased germination rate (Weis, 1982), a lower leaf area and biomass of its seedlings (Weis, 1982; Wulff, 1986b), and a decreased competitive ability of its seedlings (Wulff, 1986a). Experimental and simulation studies on crop-weed competition have shown that a late emergence and a slow leaf area development in the early growth stages, strongly reduce the competitive ability of weeds, and hence reduce the yield loss of the crop (Kropff *et al.*, 1992; Kropff *et al.*, 1993b). Thus, crop competition may not only reduce the reproductive output of *S. vulgaris*, *S. nigrum* and *C. album*, as was found in this study, but may also reduce the competitive ability of its offspring.

The results of this study showed that the effect of relative date of emergence on seed production differed greatly between the weed species, which has consequences for weed management strategies. *S. vulgaris* and *S. nigrum* produced few seeds per plant when emerging 10 days or more after the witloof chicory crop, and probably do not need to be controlled for reasons of future weed infestation. In contrast, *C. album* was able to produce large numbers of seeds per plant, irrespective of its relative date of emergence. Therefore, within the range of relative dates of emergence available in this data set, *C. album* plants need always to be controlled for reasons of future weed infestation, especially when grown in crops such as witloof chicory and sugarbeet.

The development of strategies for integrated weed management requires an accurate prediction of the effects of competition and weed control practices, on both the yield loss in the current year and on the future weed infestation levels. When dry matter production is related to number of seeds, a valuable link between crop-weed competition models and models of weed population dynamics can be established. The relationships between vegetative plant size and reproductive output of *S. vulgaris*, *S. nigrum* and *C. album* were very robust under a great range of competitive stresses and growing conditions, thus establishing a valuable link between competition models and models of population dynamics.

CHAPTER 8

GENERAL DISCUSSION

The main objective of this thesis was to:

> *quantitatively explain the effects of spatial arrangements, emergence dates, plant densities, and physiological and morphological characteristics of competing species in a canopy with a row structure, on growth and dry matter production of those species.*

This quantitative knowledge is essential to evaluate in an early stage in the growing season:

(1) the yield loss that may be caused by weed competition,
(2) the effects of weed control practices on this yield loss, and
(3) the effects of weed control practices on the reproductive output of weeds and the consequences for subsequent crops.

This chapter discusses the increased quantitative knowledge obtained of inter-specific competition in row crops, and the methodological advances that were made during this study. The results are discussed with respect to various crop husbandry practices that can be implemented, such that a good crop yield and crop quality can be obtained, and that the reproductive output of the weeds can be minimised.

Quantitative insight into competition in row crops achieved in this study

Effects of spatial arrangements of weeds on dry matter production

Results from pot experiments showed that when a low prostrate growing witloof chicory was competing primarily for light with a tall erect growing *S. vulgaris* plant, the growth of the witloof chicory plant was reduced more when the *S. vulgaris* plant was at shorter distance (Chapter 2). When resource competition was shifted from being primarily for light, towards becoming more for nitrogen, the effects of position of the *S. vulgaris* plant on the dry weight of the witloof chicory plant became less pronounced (Chapter 2). The results from the pot experiments were consistent with the findings of other studies that competition for light is primarily asymmetric (Watkinson *et al.*, 1983, Weiner, 1985, 1986, 1988b) and that competition for nitrogen is primarily symmetric (Weiner, 1985, 1986, 1988b; Weiner & Thomas, 1986; Tollenaar, 1992).

None of the experimental and simulation results of the field experiments did show effects of inter-specific competition on either plant nitrogen levels or soil water levels (Chapter 4), which was an indication that competition in these field experiments was primarily for light. Under these circumstances effects of spatial position of weed plants on the growth of witloof chicory would be expected. Indeed, experimental results showed small effects of spatial position of weeds on the storage organ dry weight of witloof chicory, which were accurately simulated by the model INTERROW.

Model analysis showed that a large plant height, fast initial growth and a long leaf area duration of weeds were more influential in determining the effect of weed competition on the storage organ dry weight of witloof chicory, than spatial position of weeds (Chapter 4 and Chapter 6). This is consistent with results from the pot experiments (Chapter 2), which indicated that the effects of spatial weed position on dry matter production of witloof chicory were more pronounced for weed plants which are approximately of the same height as witloof chicory, than for weed plants which grow much higher.

Model analysis also showed that decreasing the row spacing will result in the highest dry matter production, if the height growth of weeds can be controlled or if the emergence date of weeds can be delayed (Chapter 3). Other research also showed that decreasing the row spacing is more effective in preventing yield loss in row crops, if the weeds have smaller height (Légère & Schreiber, 1989) or are emerging later (Teasdale & Frank, 1983) than the crop. Board & Harville (1992) found increased light interceptions at narrower row spacings, which resulted in an increased dry matter production of soya bean.

Effects of emergence dates of weeds on dry matter production

Experimental data and model analysis showed that weeds emerging more than approximately one week after witloof chicory, caused little or no reduction in dry matter production of witloof chicory (Chapter 4 and Chapter 6). A long period between emergence of witloof chicory and the weeds, ensured that witloof chicory obtained a strong competitive position, such that it could easily outcompete the weeds. Other research (*e.g.* Kropff & van Laar, 1993) also found that the emergence date of weeds is a very important factor in determining the yield loss caused by weeds. Thus, all weed control decisions must ensure that weeds emerging up to at least one week after the witloof chicory crop are removed, to limit yield loss to acceptable levels.

Effects of plant density of weeds on dry matter production

Reductions in storage root dry weight of witloof chicory of more than 50% were recorded at relatively low weed densities (20 pl.m^{-2}), but only when weeds emerged early (Chapter 4 and Chapter 6). An increase in weed density to 40 or 80 pl.m^{-2} increased the yield reduction, although the added effect of a higher weed density was not as large as the effect of the first 20 pl.m^{-2}. Spitters *et al.* (1989) and Kropff & van Laar (1993) also reported large yield reduction at low weed densities, and a small added effect of increased weed density, especially when weed emergence was early.

Effects of weed species on dry matter production

Of the three weeds studied, *C. album* which grows very tall and positioned its leaf area above the crop canopy caused the highest yield reductions of witloof chicory (Chapter 4 and Chapter 6). *S. nigrum* appeared to be a strong competitor only when its date of emergence was earlier than that of witloof chicory (Chapter 4 and Chapter 6). Due to its high base temperature for growth, *S. nigrum* needs time to get established. Consequently, S. *nigrum* can only cause high yield reductions when it has time to develop before competition starts. *S. vulgaris* showed a very strong juvenile growth, and thus has the potential to be a strong competitor (Chapter 4 and Chapter 6). However, the leaf area duration of *S. vulgaris* is very short compared to the other two weed species, and after senescence these *S. vulgaris* plants will not further increase the yield loss of witloof chicory (Chapter 4 and Chapter 6).

Effects of weed competition on plant size and marketable yield

Results from pot experiments showed that the spatial position of a tall erect growing *S. vulgaris* plant could affect the variability in plant weight of witloof chicory. When competition was primarily for light, a S. *vulgaris* plant growing at a shorter distance caused a greater reduction in plant weight of the target witloof chicory plant while at the same time it had a smaller effect on the plant weights of the other witloof chicory plants in the pot, thus increasing the variability in plant weight of witloof chicory (Chapter 2). When competition was shifted from being primarily for light towards becoming more for nitrogen, *i.e.* becoming more symmetric, the effects of competition with *S. vulgaris* on the variability of plant weight of witloof chicory disappeared (Chapter 2). It has been reported that a great variability in root sizes of a witloof chicory crop has negative effects on the ripening of the roots and the chicon quality (Anonymous, 1989, Van Kruistum *et al.*, 1993).

In the growing of the storage roots for chicon production, not only the total yield but also the diameter of the roots is important. The economic value of storage roots with diameters of 25-32.5 mm, 32.5-45 mm, and >45 mm, was 0.015, 0.078, and 0.069 Dfl. per root, respectively (Van Kruistum *et al.*, 1997). Results from field experiments showed that competition with weeds decreased the storage root diameter, and increased the percentage of storage roots with a diameter smaller than 32.5 mm. Storage roots below a diameter of 32.5 mm are of little economic value, because they do not contain sufficient redistributable carbohydrates to produce a chicon of good quality (Anonymous, 1989; Van Kruistum *et al.*, 1997). The magnitude of the reductions in storage root diameter due to competition with weeds, depended on the size of the weed biomass (expressed as leaf area index), and on the timing and duration of the weed competition within the growing season. Plants of all weed species but especially *C. album* plants, could intercept a disproportionally large part of the incoming radiation. As a result, *C. album* caused a greater reduction in storage root dry weight and storage root diameter than *S. vulgaris* or *S. nigrum*. At the end of the growing season, the number of storage root with a diameter smaller than 32.5 mm could be as high as 95 %.

Models for crop-weed competition are usually based on dry matter calculations for the "average plant" (Kropff & van Laar, 1993), but the above results showed that the actual yield loss due to weed competition can be much greater than suggested by the reduction in dry weight. A strong allometric relationship was found between the average storage root diameter and the average storage root dry weight, explaining nearly 90 % of the variation in storage root dry weight. This relationship can be incorporated in simulation models such as INTERROW. This would greatly enhance the usefulness of the models in the study of the effect of crop-weed competition and in the development of weed management strategies in witloof chicory.

Effects of competition on reproductive output of weeds

Linear relationships were found between vegetative plant size and reproductive weight of *S. vulgaris*, *S. nigrum*, and *C. album* (Chapter 7). The relationships between vegetative plant size and total reproductive weight or number of seeds were robust for these three weed species, under a great range of competitive stresses. Increased competition primarily reduced the number of seeds per plant, and to a lesser extent the individual seed weight. Increased competition reduced both the vegetative plant size and the reproductive output, and had little effect on the proportion of dry matter that was invested in reproductive output. It was concluded that vegetative plant size is a reliable estimator of seed production of *S. vulgaris*, *S. nigrum*, and *C. album*, thus establishing a link between competition models and models of population dynamics. This link is useful to assess the effects of crop competitiveness on weed population dynamics, and will thus contribute to the development of weed management systems.

Methodological advances achieved in this study

Because, so many factors influence the outcome of crop-weed competition (Van Heemst, 1985; Radosevich, 1987; Kropff & van Laar, 1993), a system-analytical approach was adopted, in which experimental studies and simulation studies were performed side by side.

Pot experiments were carried out at the start of the project, to obtain a better understanding of the effects of spatially explicit inter-specific competition for resources between plants (Chapter 2). It was shown that when competition was primarily for light, the growth of witloof chicory was increasingly reduced when a *S. vulgaris* plant was growing at a shorter distance. Descriptive neighbourhood models gave the best fit to the data, when only density of neighbour plants was included in the model. The neighbourhood models did not give an improved fit when spatial arrangement or size of neighbour plants were included in the model. Deterministic eco-physiological models of competition for light, water and nutrients were available (*e.g.* Spitters & Aerts, 1983; Kropff & van Laar, 1993; Graf *et al.*, 1990; Wilkerson *et al.*, 1990). These models assume that the horizontal distribution of leaves is homogeneous (Kropff & Lotz, 1992a, 1992; Schnieders & Lotz, 1993), which made them unsuitable to analyse the effects of spatial plant arrangement on competition (Schnieders & Lotz, 1993). To analyse intra-specific and inter-specific competition in canopies with a row structure, a model (INTERROW) was developed (Chapter 3). In the model, special attention was given to the simulation of light interception by each species, taking into account the distribution of leaf area over the soil area, the row dimensions, the orientation of the rows, and the relative position of rows of different species.

The simulation of light interception inside a canopy with a row structure was consistent with measured light interception data. The model INTERROW simulated peaks of light interception that corresponded with the position of rows, and lower light interception levels in between the rows early in the growing season. A complete closure of the canopy at small row spacings and consequently a 100 % light interception was also correctly simulated, as well as a less complete canopy closure and a less than 100 % light interception at larger row spacings. This showed that the mechanisms of light interception in a row canopy were correctly incorporated in the model INTERROW.

The model INTERROW adequately simulated competition between witloof chicory and the weeds *S. vulgaris*, *S. nigrum*, and *C. album* under a wide range of conditions (Chapter 3 and Chapter 4). Model analysis found small effects of spatial position of weeds on dry matter production, consistent with experimental results. The experimental results alone, could not explain the effect of the spatial position of weed plants on the reduction of storage root dry weight. Model analysis showed that when the weed plant height is greater than that of witloof chicory and the leaf area duration is large, the yield reduction will be greatest when weeds are growing in between the crop rows. However, when the weed plant height is greater than that of witloof chicory, but the leaf area duration is very short, the yield reduction will be greatest when weeds are growing inside the crop rows. Model analysis also showed that a large plant height, fast initial growth and a long leaf area duration of weeds were more influential in determining the effect of weed competition on the storage organ dry weight of witloof chicory, than spatial position of weeds. Model analysis also showed that decreasing the row spacing will result in the highest dry matter production, if the height growth of weeds can be controlled or if the emergence date of weeds can be delayed

To test whether the model INTERROW could be successfully used to explain competition in other multi-species systems, a data set on the effects of intercropping on the dry matter production of white cabbage and *T. subterraneum* or *T. repens* was analysed with the model (Chapter 5). The combined use of the model INTERROW and experimental data did have added value. The experiment data alone could not explain why *T. subterraneum* sown 3 weeks before the transplanting date of cabbage caused greater yield loss of cabbage than *T. subterraneum* sown 6 weeks before the transplanting date. Model analysis showed that the leaf area index of early sown *T. subterraneum* was already in decline when the cabbage was transplanted, which resulted in less severe competition for light and thus a smaller yield loss of cabbage. Model analysis also showed that mowing *T. subterraneum* at a temperature sum between 400 and 600 °C·d after emergence minimised the reduction in dry weight of cabbage due to competition. Mowing at this stage reduced the plant height, leaf area and biomass of *T. subterraneum* to such extent, that the ability of *T. subterraneum* to capture light resources was greatly reduced. Model analysis further showed that reduction in cabbage head dry weight due to competition with *T. subterraneum* will be very small, when a *T. subterraneum* variety with very low plant height will be used as cover crop.

It is concluded that the model INTERROW is a powerful tool that was used to gain a deeper knowledge of the effects of spatial arrangements, emergence dates, plant densities, and plant characteristics of competing species in a canopy with a row structure, on growth and dry matter production of those species.

Possible implementation of the results to improve crop competitiveness and weed management practices

Smaller row spacing

Witloof chicory is often grown at large row widths, to enable the use of adjusted potato harvesters to harvest the witloof chicory roots. Narrowing the row spacing may appear an obvious way to increase the soil cover and light interception early in the growing season, thus increasing the competitive ability of the witloof chicory crop. Experimental results showed that growing witloof chicory at a smaller row spacing, while total plant density of witloof chicory remained unchanged, did not reduce the yield loss caused by weed competition, in a situation where weeds were able to grow vigorously due to an early emergence date (Chapter 4). Model analysis showed that attempts to increase the competitiveness of crops by decreasing the row spacing, such that a more uniform spatial arrangement is obtained, is not a valuable weed management strategy when weeds succeed in growing to at least the same height as the crop (Chapter 3).

Row orientation

If it is necessary to use wide row spacings, model analysis showed that the row orientation that gives maximum dry matter production under Dutch conditions (52° N) is approximately NorthWest - SouthEast (Chapter 3). Model analysis showed that dry matter production of witloof chicory in monoculture with row orientation NorthWest - SouthEast could be more than 10 % larger than that of witloof chicory in monoculture with row orientation SouthWest - NorthEast. These findings agree with Mutsaers (1980), who found that for northern latitudes the row orientation giving the maximum light interception in row crops was approximately NorthWest - SouthEast. The simulation analysis also showed that the row orientation had little influence on the competitive effects of weeds on the dry matter production of witloof chicory. Thus, changing the row orientation does not change the competitiveness of the crop.

Weed emergence date

Early emerging weeds caused great yield losses of witloof chicory (Chapter 4). The effects of plant arrangement and plant density on the outcome of competition were small compared to the effects of the emergence date. Both experimental and simulation results showed that weeds emerging up to at least one week after the witloof chicory crop must be removed to limit yield losses to acceptable levels.

Growth temperature

Experimental and simulation results suggested that high initial growing temperatures may be essential for witloof chicory to establish a strong competitive position, especially when weeds emerge later than the crop (Chapter 4). With respect to the development of new weed management methods which take into account crop husbandry measures to increase the crop competitiveness, this implies that witloof chicory should be sown when soil and air temperatures are sufficiently high to ensure a quick establishment of the crop. Model analysis showed that an increase in air temperature increases the dry matter production of witloof chicory, when grown in monoculture. Model analysis also showed that early emerging weeds caused a great reduction in dry matter production of witloof chicory, especially at higher air temperatures. One practical way of increasing the temperature is to cover the soil with a "bio-degradable" plastic. If an increase in temperature is the only effect of covering the soil with "bio-degradable" plastic, then it may increase the growth and competitiveness of witloof chicory if early emerging weeds can be controlled. A total soil cover by "bio-degradable" transparent plastic will enhance growth of both crop and weeds, and may therefore increase the yield loss caused by weeds. A soil cover by "bio-degradable" non-transparent plastic with holes through which the crop plants can grow, will allow the crop plant to profit from the higher temperatures while inhibiting the growth of weeds underneath the plastic. Further practical research will show if the use of "bio-degradable" plastic is indeed a viable method to increase growth of witloof chicory and decrease the yield loss caused by weeds.

Final remarks

INTERROW is a model for inter-specific competition that explicitly takes into account the row structure of the crop (Chapter 3). This thesis showed that the model was able to accurately explain competition between witloof chicory and weeds (Chapter 4 and Chapter 6), and between white cabbage and clover species sown as cover crop (Chapter 5). Model analyses have helped to explain experimental results and were used to generate recommendation about growing crops in such a way that yield losses due to weeds or cover crop are minimised.

This thesis also found that robust linear relationships existed between vegetative plant weight and reproductive plant weight of weed species (Chapter 7), and that a strong allometric relationship existed between the average storage root diameter and the average storage root dry weight of witloof chicory (Chapter 6). These relationships can be included in the model INTERROW to enable the model analysis of the effects of crop-weed competition on the population dynamics of weeds and the marketable yield of witloof chicory crops.

It is concluded that the model INTERROW is a powerful tool that was used to gain a deeper knowledge of the effects of spatial arrangements, emergence dates, plant densities, and plant characteristics of competing species in a canopy with a row structure, on growth and dry matter production of those species.

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SUMMARY

Weed control is a key issue and a major cost factor in producing most agricultural crops. Despite all weed control efforts, the average yield losses due to weeds are estimated at 7.5 % and 25 % in developed and developing countries, respectively. Without weed control, even very low weed densities can cause yield losses of up to 100 % in vegetable crops with incomplete canopy closure, such as witloof chicory.

Weed control has been dominated by the use of herbicides for the last three decades. Increasing concerns about the effects of herbicides on the environment, the quality of food, the widespread development of herbicide resistance in weed species, and the necessity to reduce costs of inputs, has highlighted the need to reassess our present weed control methods. The development of new weed control methods requires a comprehensive understanding of the processes underlying the outcome of crop-weed competition. Plant growth and inter-plant competition are complex phenomena, that are governed by various biological, environmental and proximity factors. The quantitative insight into the effects of all these interacting factors on the outcome of inter-plant competition, can be provided by systems analysis using experimental studies and process-based models side by side.

This thesis reports on studies carried out to quantitatively explain the effects of spatial arrangements, emergence dates, plant densities, and physiological and morphological characteristics of competing species in a canopy with a row structure, on the growth of those species. Witloof chicory (*Cichorium intybus* L.) was selected as the main "model crop", and the effects of competition with *Senecio vulgaris* L., *Solanum nigrum* L., or *Chenopodium album* L., on dry matter yield and marketable yield were quantified. A model for inter-specific competition, that explicitly takes into account the row structure of the crop, was developed and validated for competition between witloof chicory and associated weeds. White cabbage (*Brassica oleracea* var. capitata), in which *Trifolium repens* L. or *Trifolium subterraneum* L. were grown as cover crops, was selected as a second "model system", to evaluate the ability of the model to correctly simulate the effects of competition in other multi-species associations.

The effects of spatial plant arrangements and type of resource competition on growth of the prostrate growing witloof chicory and the erect growing *S. vulgaris*, were studied in two pot experiments (Chapter 2). In these experiments the non-competitive factors (*e.g.* seed weight and site homogeneity), the neighbourhood arrangements and the type of resource competition were controlled, which allowed us to gain a more accurate understanding of the effects of spatially explicit competition on plant growth. When

resource competition was primarily for light (*i.e.* asymmetric), the dry weight of a target witloof chicory plant was reduced more when a *S. vulgaris* plant grew at a shorter distance. The position of a *S. vulgaris* plant also affected the uniformity in dry weight of all the witloof chicory plants in the pot. The dry weight of the *S. vulgaris* plant was not affected by its position. When resource competition was shifted from being primarily for light (*i.e.* asymmetric) towards becoming more for nitrogen (*i.e.* more symmetric), the effects of the position of the *S. vulgaris* plant on the dry weight of the target witloof chicory plant and on the uniformity in dry weight of the witloof chicory plants became less pronounced or were absent. Neighbourhood models were fitted to the data, and the best fits were obtained when only the density of neighbours was included in the measure of competition pressure. The analysis of variance showed clear effects of spatial arrangements on the outcome of competition, whereas the neighbourhood model fits did not improve when spatial arrangements were included in the measure of competition. A possible explanation for this discrepancy may be that the substantial effects of the presence of the *S. vulgaris* plant masked the effects of the spatial position of the *S. vulgaris* plant. Also, the way that the effects of spatial arrangements were incorporated in the models may have been inadequate.

A model (INTERROW) for intra-specific and inter-specific competition in a canopy with a row structure, is described (Chapter 3). In the model, special attention has been given to the simulation of light interception by each species, taking into account the distribution of leaf area over the soil area, the row dimensions, the orientation of the rows, and the relative position of rows of different species. The simulation of light interception inside a canopy with a row structure was consistent with measured light interception data. A first test of the model, showed that the simulated effects of intra-specific and inter-specific competition on dry matter production of witloof chicory and *S. vulgaris* matched the experimental data. Model analysis showed that attempts to increase the competitiveness of crops by providing a more uniform spatial arrangement (*i.e.* using a smaller row spacing), is not a valuable weed management strategy if weeds succeed in growing to at least the same height as the crop. When it is necessary to use wide row spacings, the row orientation that gives maximum dry matter production under Dutch conditions (52 °N) is approximately north west - south east.

The effects of spatial plant arrangements, plant densities, and emergence dates, on competition between witloof chicory and *S. vulgaris*, *S. nigrum* or *C. album* were studied in field experiments (Chapter 4). The model INTERROW was tested on its ability to accurately describe the outcome of competition under a wide variety of conditions. Strong reductions of the storage root dry weight of witloof chicory due to competition with *S. vulgaris*, *S. nigrum* or *C. album*, were found to be primarily caused by an early emergence of the weeds, and to a lesser extent by weed density and weed position. The model INTERROW accurately simulated the growth of all species, both in monocultures and in mixtures, under a wide range of conditions. The model simulated the effects of spatial position of weeds on the storage root dry weight, consistent with the experimental results. Model analysis showed that weeds emerging up to at least one week after the witloof chicory crop must be removed to limit the yield loss to acceptable levels. Witloof chicory has a high base temperature (6 °C) for growth and development. With respect to the development of new weed management methods which take into account crop husbandry measures to increase the crop competitiveness, this implies that witloof chicory should be sown when soil and air temperatures are sufficiently high to ensure a quick establishment of the crop. Model analysis showed that an increase in air temperatures increases the dry matter production of witloof chicory when grown in monoculture. However, model analysis also showed that early emerging weeds caused a great reduction in dry matter production of witloof chicory, especially at higher air temperatures. It was suggested that a soil cover with "bio-degradable" non-transparent plastic with holes through which the crop plants can grow, will allow the crop plant to profit from higher temperatures while inhibiting growth of weeds underneath the plastic.

The model INTERROW was successfully employed to study competition between white cabbage (*Brassica oleracea* L. var. *capitata*) and two clover species (*Trifolium repens*, and *Trifolium subterraneum*), that were used as cover crops (Chapter 5). The model INTERROW simulated smaller reductions in cabbage dry weight when competition occurred with *T. subterraneum*, relative to competition with *T. repens*. This could be explained by the smaller plant height and consequently lower competitive ability of *T. subterraneum*, relative to *T. repens*. The model INTERROW correctly simulated a higher yield loss of cabbage due to competition, when the emergence date of *T. subterraneum* was closer to the transplanting date of cabbage. The leaf area index of early sown *T. subterraneum* was already in decline when the cabbage was transplanted, which resulted in less severe competition for light in the early growth stages and consequently a smaller reduction in cabbage dry matter production. A model analysis showed that when *T. subterraneum* was mown at a temperature sum between 400 and 600 °C·d after emergence, the reduction in dry weight of cabbage due to competition would be minimised. Mowing at this stage reduced the plant height, leaf area and biomass of *T. subterraneum* to such extent, that the ability of *T. subterraneum* to capture light resources was greatly reduced. The model analysis further showed that reduction in cabbage head dry weight due to competition with

T. subterraneum will be very small, when a *T. subterraneum* variety with very low plant height will be used as cover crop.

The effects of weed competition on the weight and diameter of the individual storage roots of witloof chicory were quantified, and evaluated with respect to the use of 'dry weight based' competition models in the study of crop-weed competition (Chapter 6). Competition with *S. vulgaris* , *S. nigrum* or *C. album* reduced the storage root dry weight between 10 and 75 % and the storage root diameter between 9 and 44 %. The magnitude of the reductions in total plant dry weight, storage root dry weight and storage root diameter due to competition with weeds, depended on the leaf area of the weed biomass, and on the timing and duration of the weed competition within the growing season. The percentage of storage roots with a diameter smaller than 32.5 mm was greatly increased by weed competition and was found to be as high as 95 %, when the emergence of the weed plants occurred very shortly before or after the emergence of the witloof chicory plants. These roots have little economic value, because they do not contain sufficient redistributable carbohydrates to produce a chicon of good quality. This indicates that the actual yield loss caused by weed competition can be much greater than expected from the reduction in storage root dry weight. Models for crop-weed competition are usually based on dry matter calculations for the "average plant". This study showed that actual yield loss due to weed competition can be much greater than suggested by the reduction in dry weight alone. The usefulness of these models in the study of the effects of crop-weed competition and in the development of weed management strategies in witloof chicory, would be greatly enhanced when the effects of competition on storage root diameter could also be simulated. This has been achieved through the strong allometric relationship that was found between the average storage root diameter and the average storage root dry weight.

The effects of competition with a crop (witloof chicory, sugarbeet or maize) on the relationship between plant weight and seed number of weeds, which may provide a link between competition models and models of population dynamics was carried out (Chapter 7). A linear relationship between vegetative plant size and total reproductive weight explained a large percentage of the variation in the total reproductive weight of *S. vulgaris*, *S. nigrum* and *C. album*. For all three weed species, the minimum size for reproduction was not significantly different from zero, and a constant proportion of biomass was invested into reproductive biomass. The reduction in total reproductive weight as a consequence of increased competition, was primarily due to a lower number of seeds per plant, and to a lesser extent due to a lower individual seed weight. The relationships between vegetative plant size and total reproductive weight, number of seeds or individual seed weight were robust for *S. vulgaris*, *S. nigrum*, and *C. album*, under a great range of competitive stresses. Increased competition merely reduced both the vegetative plant size and the reproductive output, but had little effect on the proportion of dry matter that was invested in reproductive output. The effect of the relative date of emergence of weeds on the seed production differed greatly between the weed species. Plants of *S. vulgaris* and *S. nigrum* produced few seeds when emergence was 10 days or more after the witloof chicory crop. In contrast, *C. album* was able to produce large numbers of seeds per plant, irrespective of its relative emergence date. Vegetative plant size is a reliable estimator of seed production of *S. vulgaris*, *S. nigrum*, and *C. album*, thus establishing a link between competition models and models of population dynamics. This link is useful to assess the effects of crop competitiveness on weed population dynamics, and may thus contribute to the development of weed management systems.

Chapter 8 discusses the increased quantitative knowledge about inter-specific competition in row crops that were obtained, and the methodological advances that were made during this study. The results are discussed with respect to new or improved crop husbandry practices that can be implemented, such that a good crop yield and crop quality can be obtained, and that the reproductive output of the weeds can be minimised. INTERROW is a model for inter-specific competition that explicitly takes into account the row structure of the crop. It is a powerful tool that helps in gaining a deeper knowledge of the effects of spatial arrangements, emergence dates, plant densities, and plant characteristics of competing species in a canopy with a row structure, on growth and dry matter production of those species. This thesis showed that the model was able to accurately explain competition between witloof chicory and weeds, and between white cabbage and clover species sown as cover crop. Model analyses have helped to explain experimental results and were used to generate recommendations about planting crops and performing weed control measures, in such a way that yield losses due to weeds or cover crop are minimised. This thesis found that robust linear relationships existed between vegetative plant weight and reproductive plant weight of weed species, and that a strong allometric relationship existed between the average storage root diameter and the average storage root dry weight of witloof chicory. These relationships can be included in the model INTERROW to enable the model analysis of the effects of crop-weed competition on the population dynamics of weeds and the marketable yield of witloof chicory crops.

SAMENVATTING

De beheersing van onkruiden is van essentieel belang in de productie van de meeste landbouwgewassen en brengt grote kosten met zich mee. Ondanks de uitvoering van onkruidbeheersingsmaatregelen, wordt het gemiddelde opbrengstverlies ten gevolge van onkruiden geschat op 7.5 % en 25 % voor respectievelijk ontwikkelde en ontwikkelings landen. Zelfs bij lage onkruiddichtheden kunnen opbrengstverliezen oplopend tot 100 % voorkomen in vollegronds-groentegewassen met een open gewasstructuur, zoals bijvoorbeeld witlof.

Het gebruik van herbiciden heeft gedurende de laatste decennia een dominante rol gespeeld in de onkruidbeheersing. Toenemende bezorgdheid over de effecten van herbiciden op het milieu en de voedselkwaliteit, de toenemende ontwikkeling van onkruidresistentie tegen herbiciden, en de noodzaak om de inputkosten te reduceren, heeft geleid tot een noodzakelijke herwaardering van de huidige methoden van onkruidbeheersing. Een grondige kennis van de processen die het verloop van de gewas-onkruid concurrentie bepalen is noodzakelijk voor het ontwikkelen van nieuwe methoden voor onkruidbeheersing. Groei en concurrentie tussen planten is een complexe zaak, die wordt gestuurd door vele biologische, milieu- en standplaats-factoren. Kwantitatief inzicht in de effecten van al deze interactieve factoren op het verloop van de concurrentie tussen planten kan worden verkregen via systeem-analyse, waarbij experimenteel onderzoek wordt gecombineerd met proces-georïenteerde modellen.

Dit proefschrift beschrijft onderzoek naar een kwantitatieve verklaring van de effecten van ruimtelijke plantverbanden, opkomstdata, plantdichtheden, en fysiologische en morfologische planteigenschappen van elkaar beconcurrerende soorten in een gewas met een rijenstructuur, op de groei van deze soorten. Witlof (*Cichorium intybus* L.) is geselecteerd als "model gewas". De effecten van concurrentie met *Senecio vulgaris* L., *Solanum nigrum* L., of *Chenopodium album* L., op de ontwikkeling van droge stof en marktbaar produkt zijn gekwantificeerd. Een concurrentiemodel, waarin de rijenstructuur van een gewas is ingebouwd, was ontwikkeld en getest voor concurrentie tussen witlof en de bijbehorende onkruiden. Als tweede modelsysteem is witte kool (*Brassica oleracea* var. capitata) met als ondergroei *Trifolium repens* L. of *Trifolium subterraneum* L. gekozen. Dit tweede modelsysteem is gebruikt om de bruikbaarheid van het model ter verklaring van concurrentie-effecten in andere multi-soort situaties te testen.

De effecten van ruimtelijke plantverbanden en van verschillende concurrentietypen, op de groei van de rozetvormige witlof en de hoog opgroeiende klein kruiskruid (*S. vulgaris*), werden bestudeerd in twee potexperimenten (Hoofdstuk 2). De plantverbanden, het concurrentietype, en anderse factoren zoals homogeniteit van de grond en zaad, kunnen worden geconditioneerd in potexperimenten. Dit maakt het mogelijk om de effecten van ruimtelijke plantverbanden op de plantengroei zeer accuraat te bestuderen. De reductie van het drooggewicht van een "doel"-witlofplant was groter wanneer de afstand tot de *S. vulgaris* werd verkleind, en de concurrentie voornamelijk om licht (asymmetrische concurrentie) ging. De positie van de *S. vulgaris* plant had ook effect op de uniformiteit in drooggewicht van alle witlofplanten in een pot. Het drooggewicht van de *S. vulgaris* plant zelf, werd niet beïnvloed door de positie van de *S. vulgaris* plant. Wanneer de concurrentie verschoof van concurrentie om licht (asymmetrisch concurrentie) naar concurrentie om stikstof (symmetrische concurrentie), dan was het effect van de positie van de *S. vulgaris* plant kleiner of zelfs afwezig. "Neighbourhood" modellen werden gefit op de data. De beste fits werden verkregen, wanneer alleen de plantdichtheid van de buurplanten werden gebruikt als maat voor de concurrentiedruk. De variantieanalyse liet duidelijke effecten van ruimtelijke plantverbanden op het concurrentieverloop zien, terwijl de fits met de "Neighbourhood" modellen geen verbetering toonden, wanneer ook de plantverbanden werden gebruikt in de maat voor de concurrentiedruk.

Een model (INTERROW) voor concurrentie in een gewas met een rijenstructuur werd beschreven in Hoofdstuk 3. In het model is speciale aandacht gegeven aan de wijze waarop de lichtonderschepping door elk soort wordt gesimuleerd. Hierbij zijn de distributie van het bladoppervlak, de dimensies van de rijen, de rijorientatie, en de relatieve positie van rijen van verschillende soorten, in beschouwing genomen. De gesimuleerde lichtonderschepping in een rijengewas kwam goed overeen met de experimentele data. De gesimuleerde effecten van intra-specifieke en inter-specifieke concurrentie op de droge stofproductie van witlof en *S. vulgaris*, weken niet af van de experimentele data. Een modelstudie liet zien dat verhoging van de concurrentiekracht van een gewas door middel van een uniformere plantverdeling, bijvoorbeeld door het gebruik van geringere rijafstanden, geen voordeel opleverde indien de onkruiden dezelfde planthoogte als het landbouwgewas konden bereiken. Indien het noodzakelijk is om grote rijafstanden te gebruiken, dan wordt de grootste droge-stofproductie onder Nederlandse omstandigheden (52 °N) bereikt bij een rij-oriëntatie Noordwest - Zuidoost.

De effecten van ruimtelijke plantverbanden, plantdichtheden en opkomstdata, op de concurrentie tussen witlof en de onkruiden *S. vulgaris*, *S. nigrum* of *C. album* werden bestudeerd in veldexperimenten (Hoofdstuk 4). Het model INTERROW is getoetst op de nauwkeurigheid waarmee het verloop van de concurrentie onder een grote variatie van omstandigheden, kon worden beschreven. Het drooggewicht van witlofwortelen werd sterk gereduceerd als gevolg van concurrentie met *S. vulgaris*, *S. nigrum* of *C. album*, vooral bij een vroege opkomst van de onkruiden. De invloed van onkruiddichtheid en positie van het onkruid op het drooggewicht was minder groot. De groei van alle soorten, zowel in monocultuur als in de mengsels, werd nauwkeurig gesimuleerd onder een grote variatie van omstandigheden. Het model simuleerde geringe effecten van de onkruidpositie op het drooggewicht van de witlofwortelen, wat overeenkwam met de experimentele resultaten. Een modelstudie liet zien dat onkruiden met een opkomstdatum tot een week na de opkomst van een witlofgewas, moeten worden bestreden om het opbrengstverlies te beperken. Witlof heeft een hoge basistemperatuur (6 °C) voor groei en ontwikkeling. Voor de ontwikkeling van nieuwe onkruidbeheersing-maatregelen, die gebruik maken van teeltmaatregelen ter verhoging van de concurrentiekracht, betekent dit dat witlof pas gezaaid moet worden wanneer de bodem- en luchttemperatuur hoog genoeg is voor een snelle begingroei van het witlofgewas. Modelstudies lieten zien dat een verhoging van de luchttemperatuur de droge-stofproductie van witlof in monocultuur vergrootte, maar ook dat vroeg opkomende onkruiden een groot opbrengstverlies veroorzaakten, vooral wanneer de temperatuur was verhoogd. Het bedekken van de bodem na het zaaien met een folie van afbreekbaar plastic verhoogd mogelijkerwijs de temperatuur en kan daardoor de groei en concurrentiekracht van witlof verhogen, zodat vroeg opkomende onkruiden beheerst kunnen worden. Het gebruik van een ondoorzichtige afbreekbare plastic folie met plantgaten waardoor de witlofplanten kunnen groeien, laat de witlofplanten profiteren van de hogere temperaturen terwijl de onkruiden door het plastic worden onderdrukt.

Het model INTERROW werd gebruikt bij een onderzoek naar de concurrentie tussen witte kool (*Brassica oleracea* L. var. *capitata*) en twee soorten klaver (*Trifolium repens* en *Trifolium subterraneum*) die als ondergroei waren gezaaid (Hoofdstuk 5). Het model INTERROW simuleerde op een correcte wijze een geringer opbrengstverlies van kool ten gevolge van concurrentie met *T. subterraneum*, wat verklaard kon worden door een geringere planthoogte en daardoor een geringer concurrentievermogen van *T. subterraneum* vergeleken met *T. repens*. Het model simuleerde op een correcte wijze een groter opbrengstverlies van kool ten gevolge van concurrentie, wanneer de opkomstdatum van *T. subterraneum* dichter bij de plantdatum van kool lag. Het bladoppervlak van de vroeg gezaaide *T. subterraneum* was al aan het afnemen ten tijde van de plantdatum van de kool, wat resulteerde in een geringere lichtconcurrentie in de vroege groeifase en dus een geringer opbrengstverlies van kool. Een modelstudie liet zien dat maaien van *T. subterraneum* wanneer een temperatuursom van 400 - 600 °C·d was bereikt, resulteerde in een minimalisering van het opbrengstverlies van kool door concurrentie. Maaien rond deze tijd, verlaagde de planthoogte, het bladoppervlak en de biomassa van *T. subterraneum* dusdanig dat het vermogen van *T. subterraneum* om licht te onderscheppen sterk werd gereduceerd. De modelstudie liet verder zien dat het opbrengstverlies van kool als gevolg van concurrentie met *T. subterraneum* erg klein is, wanneer een *T. subterraneum* cultivar met geringe planthoogte wordt gebruikt als ondergroei-gewas.

De effecten van onkruidconcurrentie op het gewicht en de diameter van individuele witlofwortelen werden gekwantificeerd, en geëvalueerd met betrekking tot het gebruik van "droge-stof" modellen in de bestudering van gewas-onkruidconcurrentie (Hoofdstuk 6). Het drooggewicht van witlofwortelen werd gereduceerd met 10 to 75 %, en de worteldiameter met 9 tot 44 %, als gevolg van concurrentie met *S. vulgaris* , *S. nigrum* or *C. album*. De grootte van de onkruidbiomassa (uitgedrukt in bladoppervlak) en de timing en duur van de onkruidconcurrentie, bepaalde de mate waarin het drooggewicht en de worteldiameter werd gereduceerd. Onkruidconcurrentie vergrootte het percentage wortelen met een diameter kleiner dan 0.03 m, tot zelfs 90 % wanneer de opkomstdata van de onkruiden en witlof nagenoeg gelijk waren. Deze witlofwortelen zijn te klein om te gebruiken voor de witloftrek, dus het opbrengstverlies veroorzaakt door concurrentie kan groter zijn dan verwacht op basis van de droge stofopbrengst van witlofwortelen. Concurrentiemodellen zijn meestal gebaseerd op de berekening van het drooggewicht van de "gemiddelde" plant. De bruikbaarheid van deze modellen ter bestudering van de effecten van concurrentie en de ontwikkeling van onkruidbeheersingsmethoden in witlof kan worden verhoogd, indien het mogelijk is om ook de effecten van concurrentie op de worteldiameter te simuleren. De allometrische relatie tussen de diameter en drooggewicht van de "gemiddelde" witlofwortel die is gevonden in dit onderzoek, kan worden ingebouwd in het model, zodat de effecten van concurrentie op de worteldiameter kunnen worden bestudeerd.

De effecten van concurrentie tussen gewas (witlof, suikerbiet of mais) en onkruid (*S. vulgaris, S. nigrum* of *C. album*) op de reproductie van de onkruiden werden bestudeerd (Hoofdstuk 7). Een sterke lineaire relatie werd gevonden tussen het vegetatieve en het totale generatieve plantgewicht, voor de drie onkruiden. Het minimum vegetatieve plantgewicht vereist voor reproductie was niet significant verschillend van nul, en een constante fractie van de biomassa werd geinvesteerd in generatieve biomassa. De afname in het totale generatieve plantgewicht als gevolg van concurrentie, werd vooral veroorzaakt door een geringer aantal zaden per plant en in mindere mate door een lager gewicht per zaad. De relatie tussen het vegetatieve plantgewicht en het totale generatieve gewicht, het aantal zaden of het gewicht per zaad, was geldig voor zeer verschillende groeiomstandigheden. Een toenemende concurrentiedruk verkleinde zowel het vegetatieve als het generatieve plantgewicht, maar had geen invloed op de verdeling van de droge stof naar de generatieve plantorganen. De zaadproductie van de onkruiden werd beïnvloed door de relatieve opkomstdatum van de onkruiden. Er was een groot verschil in effect tussen de onkruidsoorten. *S. vulgaris* en *S. nigrum* planten produceerden weinig zaden wanneer de onkruidplanten meer dan 10 dagen na de witlofplanten opkwamen. *C. album* planten waren in staat om grote hoeveelheiden zaden te vormen, ongeacht de relatieve opkomstdata. Het vegetatieve plantgewicht bleek een goede indicator te zijn van de zaadproductie, voor zowel *S. vulgaris*, *S. nigrum*, als *C. album*. Hiermee is een link gelegd tussen concurrentie-modellen en populatie-dynamische modellen die gebruikt kunnen worden om het effect van gewasconcurrentie op de populatie-dynamica van onkruiden te bestuderen. Deze relatie kan ook een bijdrage leveren aan de ontwikkeling van beheerssystemen voor onkruiden.

In Hoofdstuk 8 worden de nieuwe kwantitatieve inzichten over concurrentie in rijengewassen, alsmede de methodologische vorderingen gemaakt tijdens deze studie, bediscussieerd. De resultaten worden besproken met betrekking tot nieuwe of verbeterde teeltmethoden die kunnen worden ingevoerd, om de opbrengst en kwaliteit te verbeteren en de zaadproductie van onkruiden te minimaliseren. Het model INTERROW bleek een krachtig hulpmiddel, dat is gebruikt om het inzicht in de effecten van ruimtelijke plantverbanden, opkomstdata, plantdichtheden en planteigenschappen, op het verloop van concurrentie in rijengewassen te vergroten. Dit proefschrift heeft laten zien dat het INTERROW model de effecten van concurrentie tussen witlof en onkruiden, en tussen witte kool en klaversoorten, nauwkeurig kan simuleren. Modelstudies hebben bijgedragen aan het verklaren van de experimentele data. Modelstudies zijn gebruikt om aanbevelingen te genereren, met betrekking tot het nemen van teeltmaatregelen die het opbrengstverlies door onkruidconcurrentie minimaliseren. Verder werden sterke relaties gevonden tussen het vegetatieve en generatieve plantgewicht van onkruiden, en tussen de worteldiameter en het wortelgewicht van witlof. Deze relaties kunnen worden ingebouwd in het INTERROW model, zodat de effecten van gewas-onkruid concurrentie op de populatiedynamica van onkruiden en op de marktbare witlofopbrengst kunnen worden gesimuleerd.

CURRICULUM VITAE

Bert Schnieders werd geboren op 20 augustus 1964 te Ter Apel. In 1982 behaalde hij het Atheneum-B diploma aan de Rijksscholengemeenschap te Ter Apel. In 1988 werd het doctoraalexamen voor de studierichting Landbouwplantenteelt aan de Landbouwuniversiteit te Wageningen behaald. De doctoraalfase bestond uit de afstudeervakken Theoretische Teeltkunde, Akkerbouw, Onkruidkunde en Plantenfysiologie en een stage bij de vakgroep Crop Science van de University of Guelph in Canada. Van mei 1990 tot mei 1994 werkte hij als toegevoegd onderzoeker bij het Instituut voor Agrobiologisch en Bodemvruchtbaarheidsonderzoek (AB-DLO); het daar verrichtte onderzoek heeft geresulteerd in dit proefschrift. Van juni 1994 tot december 1996 werkte hij op het Oak Park Research Centre te Carlow (Ierland), waar hij als Post-Doc onderzoek verrichtte naar de effecten van kooldioxide (CO_2) en ozon (O_3) op de groei en ontwikkeling van zomertarwe. Van december 1996 tot en met maart 1997 werkte hij als onderzoeker bij de vakgroep Botany van de Trinity College Dublin te Ierland aan de modellering van de effecten van klimaatsverandering en luchtverontreiniging op de groei van gewassen. Sinds juli 1997 is hij in dienst bij Ericsson Expertise Ireland, waar hij als "software engineer" werkt aan het ontwikkelen van netwerkfuncties voor mobiele telecommunicatiesystemen.

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