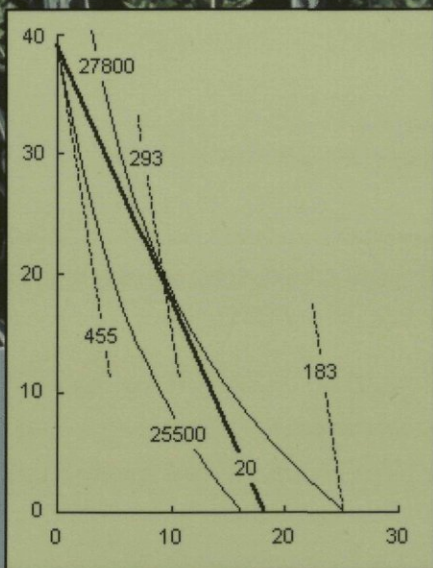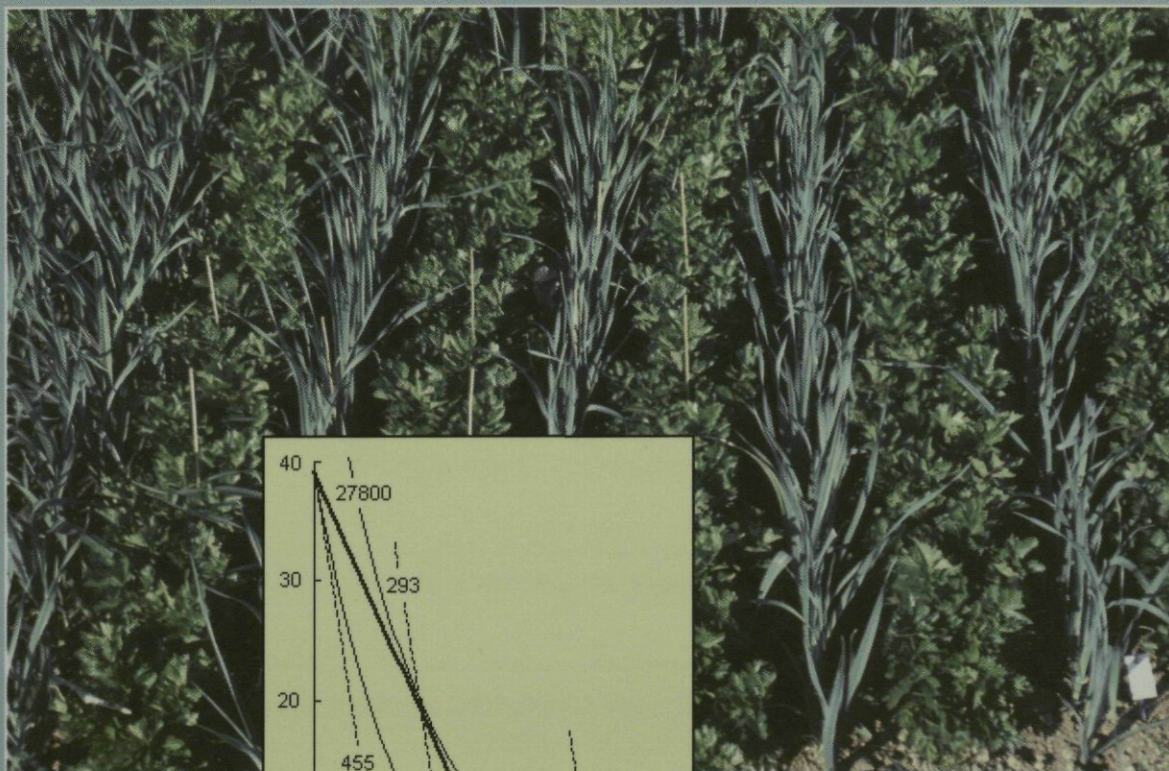Daniel T. Baumann

Competitive suppression of weeds in a leek-celery intercropping system

an exploration of functional biodiversity

Daniel T. Baumann

Competitive suppression of weeds in a leek-celery intercropping system

an exploration of functional biodiversity

Propositions

1. Intercropping of leek and celery can improve the weed suppressive ability of a leek stand while maintaining its yield potential and product quality.
   (*this thesis*)

2. The "period threshold concept" in weed management needs to be improved to include long-term effects of late-emerging weeds.
   (*this thesis*)

3. Weeds belong worldwide to the most efficient and successful organisms. We should learn from them, rather than just try to kill them.

4. Weed management strategies that strongly rely on manual weeding are not sustainable.

5. Non-chemical weed management practices can solve most weed problems.

6. The debate on the validity of additive and replacement experiments and their *analyses in competition studies is not to the point if the research objective is not* taken into account.

7. Since biodiversity exists, it is functional.

8. One man's crop can be another man's weed.

9. Admission to a PhD programme should not depend on the educational background but rather on the capability of the candidate to conduct academic research.

10. The quality of food and the way we produce it and distribute it among people is a better indicator for our civilisation than the effort put into mapping of the human genome.

11. You need an open space to reach a full expression of your mind.

Abstract

Late-emerging weeds, although not directly damaging the crop, may cause long-term weed management problems due to excessive seed production. Particularly in weak competitive crops with high quality requirements, such as leek, financial losses due to weed competition or weed management costs can be considerable.

Weed suppression by the crop is an important component of any weed management strategy. It is affected by crop characteristics and cropping systems design. Improving the weed suppression by increasing the canopy light interception is the basic concept underlying the research described in this thesis. To reduce growth and particularly the seed production of late-emerging weeds, an intercropping system was developed that combines leek with the more competitive celery.

The competitive relationships between leek and celery in the intercropping system and their interaction with *Senecio vulgaris*, which was chosen as target weed, was investigated in a series of field- and glasshouse experiments. Moreover, modelling studies, using an eco-physiological simulation model for interplant competition, were performed. Eventually, the design of the intercropping system was optimised through a combined mechanistic and descriptive modelling approach.

The competitive ability of celery was significantly higher than that of leek, owing to a more effective light interception. Therefore, the weed suppression of the intercropping system was considerably improved compared to the leek monoculture, resulting in a shorter critical period for weed control. The reproductive capacity of late-emerging *S. vulgaris* was strongly reduced in the intercropping system. Modelling studies confirmed the relatively greater competitive strength of celery compared to leek. Quantitative analysis showed that particularly differences in morphological characteristics, such as the early leaf area development, determined the differences in competitive ability between the crops. Further exploration and optimisation with a combined modelling approach allowed the design of a highly productive and profitable intercropping systems with improved weed suppressive ability.

The successful improvement of the weed suppressing ability through combination of morphological and physiological crop characteristics in a highly productive intercropping system demonstrates the functionality of enhanced biodiversity for weed management.

Keywords: leek (*Allium porrum* L.), celery (*Apium graveolens* L.) *Senecio vulgaris* L., intercropping, weed suppression, modelling, functional biodiversity.

Preface

Pablo Picasso was once asked by a fellow-guest in a restaurant to draw something, anything, on her napkin. When he refused, she offered to pay him. Picasso drew on the piece of cloth, handed it over and asked for 10'000 dollars. The lady was outraged: "But this only took you a few seconds!" "Ah! No, Madame," Picasso replied, "It is the result of many years' work!"

Similarly, this little booklet is more than just the result of a short period of intensive work. It is the culmination of almost twenty years' engagement in agricultural and life sciences. Still, I could never have finished this project without the support, encouragement and companionship of many other people.

Without Martin Kropff and Walter Müller, I would probably never have had the chance to begin this adventure. Thanks for making it possible! Appropriately, it was also Martin Kropff, together with Lammert Bastiaans, who supervised the project and guided me through the work. I very much appreciate you sharing my enthusiasm, your encouragement when I struggled, the countless stimulating discussions, constructive suggestions and critical comments and above all, your friendship.

The experiments reported in this thesis took place over a four-year period, primarily at the experimental farm "Sandhof" of the Swiss Federal Research Station for Fruit-Growing, Viticulture and Horticulture in Wädenswil, Switzerland. I wish to thank Paul Schätti and his team who ensured the quality of the experiments and assisted me many times in maintaining the plots. Many thanks also to the co-workers and summer assistants, Beni Cadalbert, Sara Doboly, Salvador Garibay, Ursina Glantz, Thomas Imhof, Marlies Klein Robbenhaar, Blanka Müller, Manuel Schneider, Claudia Seitz, Sandro Wagen and particularly Wilma van de Poll who contributed much to this thesis. Special thanks for assistance, technical solutions, discussions about practicability and on-farm research to Jürg Keller, to my knowledge the first farmer producing leek and celery in an intercropping system on a large scale. I am greatly indebted to Ernst Barben, who assisted me in the lab and kept things running when they threatened to get stuck. Thanks also to Ruedi Dössegger and his crew at MeteoSwiss for providing me with weather data.

For the theoretical work, particularly the modelling part, I spent a lot of time at the Crop and Weed Ecology and the Plant Production Systems Groups, formerly the Department of Theoretical Production Ecology at Wageningen University in The Netherlands. I wish to thank René Akanvou, Aad van Ast, Arnout van Delden, Henriette Drenth, Jan Goudriaan, Ans Hofman, Nick den Hollander, Cor Langefeld,

Table of contents

General introduction Chapter 1

General introduction

At the beginning of a new century, weed problems are still bothering millions of farmers and challenging thousands of weed scientists all over the world. Although, herbicides promised the perfect solution for weed problems eradication of weeds in agricultural production systems was not possible (Ammon and Niggli, 1990). Crop losses resulting from weeds, if not controlled, are still significantly higher than those caused by diseases and pests (Kropff and Walter, 2000). The introduction of herbicides has strongly influenced our concept of and attitude towards weed management. Weeds have been regarded as a problem that can be controlled with herbicides, rather than managed through cropping systems design. After decades of herbicide dependent plant production, farmers, extension workers, researchers as well as politicians realise that production systems reliant on herbicides are critical and in no way sustainable. Weeds can no longer be regarded as a problem resolved by curative tactics; instead integrated weed management should be seen as a component of integrated cropping systems design (Kropff and Walter, 2000; Mortensen _et al._, 2000). Weed management, in contrast to weed control, has become increasingly important as farmers strive to adopt integrated crop management. Programmes are driven by customer demand, economics and a need to recognise weeds as part of the agro-ecosystem (Leake, 1999). In this cropping systems design approach, numerous fitness-reducing and mortality events are integrated to manage weed populations where herbicides are used as a last resort, and in organic systems where no herbicides are used at all (Lotz _et al._, 1997).

Weed problems in vegetable crops

Weeds are highly efficient organisms that are able to successfully adapt to their environments. Not surprisingly, weeds benefit particularly in highly productive habitats, such as vegetable production systems, from the favourable growing conditions, which are created for the crops. Weeds can drastically limit yield and other aspects of crop performance because of their competition with the crop plants for light, moisture and nutrients. Furthermore, weeds may host pests and diseases, interfere with cultural and harvest operations, and can be a contaminant in fresh or processed produces. Weeds are therefore a chronic problem for vegetable producers and a major determinant of the production costs (Rubatzky _et al._, 1999). The development of selective and non-selective herbicides enabled producers to control weeds efficiently. The required amount of labour, which generally is a limiting factor

in vegetable production, could be reduced. Currently, vegetable production, like other high input agriculture production systems in Western Europe, has come to rely almost exclusively on curative, chemically based weed management approaches. However, the existence and development of herbicide resistance makes herbicide-dependent cropping systems increasingly vulnerable. Moreover, a widespread concern about environmental side-effects of herbicides combined with fear for public health has resulted in the banning of several herbicides in some countries and increasing pressure on farmers to reduce the use of herbicides (Matteson, 1995). This pressure will increase further, particularly for the vegetable production where the produces are sold fresh and food security is a big issue. This leads to a growing market for high-value ecologically produced vegetables, stimulating farmers to convert their production to integrated or organic farming. However, non-chemical weed control and especially the high labour requirement for hand-weeding are considered a major constraint for conversion of vegetable production to ecological farming systems (Vereijken and Kropff, 1996). Hence, weed science programmes in many European countries focus on the development of non-chemical weed control strategies with reduced labour requirement. In such strategies, labour consuming curative weed control methods are replaced by weed suppressive tactics aiming to minimise a potential weed problem and the need for direct control measures. Prevention becomes a keyword, and integrated crop management the new concept.

Intercropping as a tool to suppress weeds - Hypothesis

Intercropping, as an example of functional biodiversity, can be used to suppress weeds through niche pre-emption and resource competition (Liebman and Dyck, 1993; Teasdale, 1998). Intercropping combines two or more crops whose resource consumption characteristics are physiologically, temporally, or morphologically complementary. By combining crop species that differ in the way they use light, water and nutrients, intercropping can prevent the crops from fully competing with one another (Vandermeer, 1989). Intercrops may use a greater share of available resources and, therefore, provide improved opportunities for suppressing weeds through resource competition. Intercropping is practised in low-external input farming systems in both developing and industrial countries and can, in many cases, reduce weed density and growth more effectively than monocultures (Liebman and Dyck, 1993). Vandermeer (1989) states that the presumed mechanism of this phenomenon is that, through competition with the weed, one crop in the mixture provides an environment of reduced weed biomass for the other crop. Perhaps the

best known example of this type of weed suppression is the use of cover crops, which are solid-grown crops grown primarily to protect and cover soil between crop rows or between periods of regular crop production (Aldrich, 1984). Liebman (1986; 1988) reviewed studies of 23 crop and cover crop combinations and found that 20 of them provided significant weed suppression. While these findings with cover crops are impressive, Vandermeer (1989) states that weed suppression by combinations of two crops is more equivocal. Liebman (1986), through an extensive literature review, found that the suppressive effect of weeds was stronger in intercrops than in the monocultural components in eight cases, intermediate between monocultural components in another eight cases, and weaker than all monocultural components in two cases (Table 1.1).

Intercrops that are particularly effective at suppressing weeds capture a greater share of available resources than sole crops. Abraham and Singh (1984) found, that a grain sorghum (*Sorghum bicolor* L.) fodder cowpea (*Vigna uniguiculata* L.) intercrop intercepted more light, captured greater quantities of macronutrients, produced higher crop yields and contained lower weed densities and less weed dry matter compared with sole-cropped sorghum. Although, intercropping is only scarcely used in high-input agricultural systems, mixtures of cereals, such as barley (*Hordeum vulgare* L.), wheat (*Triticum aestivum* L.) or oats (*Avena sativa* L.) , with forage legumes, such as red clover (*Trifolium pratense* L.) or lucerne (*Medicago sativa* L.), are common in mechanised temperate farming systems and can be useful for suppressing the growth of perennial cool season weeds, such as *Elytrigia repens* L. (Dyke and Barnard, 1976).

In vegetable production systems, intercropping traditionally received much attention by applied entomologists and pathologists aiming at reducing pest numbers and diseases (Altieri and Gliessman, 1983; Latheef and Ortiz, 1983; Ryan *et al.*, 1980; Theunissen, 1994; Uvah and Coaker, 1984). In addition, intercropping has also been proposed to prevent erosion and leaching losses of mobile nutrients, such as nitrates and thus to reduce ground water contamination (Martinez and Guiraud, 1990; Muller *et al.*, 1987; Müller-Schärer *et al.*, 1992; Phatak, 1992; Shennan, 1992). The use of intercropping to suppress weeds in vegetable production was frequently suggested (Müller-Schärer and Baumann, 1993; Phatak, 1992; Wallace and Bellinder, 1992; Wiles *et al.*, 1989) but concepts proposed generally included the growth of a harvested "main" crop simultaneously with a inter-row green cover (e.g. grass or legume species) which is not harvested. Only little research has been initiated to investigate the use of two cash crops for weed suppression in a high-input vegetable production system.

Table 1.1 Strength of weed suppression effects by intercrops in which al component crops are considered "main crops" (after Liebman (1988)).

Intercrop combination	Weed suppression effects		
	Stronger than monocultures of all components	Intermediate between monoculture components	Weaker than monocultures of all components
Maize - bean	(Fleck *et al.*, 1984)	(Soria *et al.*, 1975)	
Maize - cassave	(Soria *et al.*, 1975)		
			(Soria *et al.*, 1975)
Maize - bean - cassava	(Soria *et al.*, 1975)	(Soria *et al.*, 1975)	
Maize - mung bean	(Bantilan *et al.*, 1974)		
Maize - sweet potato		(Bantilan *et al.*, 1974)	
Maize -peanut		(Bantilan *et al.*, 1974)	
Maize - sunflower	(Fleck *et al.*, 1984)		
Maize - cowpea			(Ayeni *et al.*, 1984)
Bean - cassava	(Soria *et al.*, 1975)		
Bean - sunflower	(Fleck *et al.*, 1984)		
Flax - wheat		(Arny *et al.*, 1929)	
Flax - oats		(Arny *et al.*, 1929)	
Sorghum - pigeonpea	(Shetty and Rao, 1981)	(Shetty and Rao, 1981)	
Pearl millet - peanut		(Shetty and Rao, 1981)	

Leek (*Allium porrum* L.) is one of the economically most important field vegetable crops in Europe (Benoit and Ceustermans, 1994; Brewster, 1994; Hill, 1987; Meyer and Kessler, 1990). It is especially vulnerable to weed competition and nutrient leaching due to its relatively long vegetation period, and its open canopy up to harvest. Particularly late emerging weeds receive enough light in the weakly competitive leek canopy to develop en to produce seeds. Improving the weed suppressive ability of the canopy was the basic objective and motivation for the current research, and intercropping leek with celery (*Apium graveolens* L.) was proposed to realise this goal. It was hypothesised that a leek-celery intercrop compared to a leek monoculture

- would have a faster development of the canopy leaf area and hence a faster canopy soil cover;
- would have an increased interception of incident photosynthetically active radiation (*PAR*);
- would have a shorter critical period for the weed control;

- would better suppress the growth, development and seed production of late emerging weeds;
- would at least produce the same relative total (financial) yield;
- would produce the same crop quality;
- could be fully mechanised in order to maintain the labour efficiency.

Objectives and approach

The central objective of this study was to quantitatively explain interplant competitive effects in a leek-celery intercropping system with weeds and use this knowledge to optimise the intercropping system with respect to crop performance and weed suppressive ability. For this purpose experimental and theoretical research including the use of descriptive and mechanistic modelling was combined. Competitive effects of the crop stands on natural weed populations and on _Senecio vulgaris_ L. (Common Groundsel) were studied in micro-plot and on-farm field experiments. Additionally greenhouse studies where performed to investigate the effects of competition for light on _S. vulgaris_ under controlled conditions.

To analyse crop performance, and in particular yield and quality of the component crops in the intercropping system, a descriptive regression analyses approach using an expanded version of the reciprocal yield law (Spitters, 1983b) was applied together with other methods analysing competition in replacement and additive series (De Wit, 1960; Mead and Willey, 1980; Snaydon, 1991; Vandermeer, 1989). To get quantitative insight into factors determining competitive effects between the crops and _S. vulgaris_ an eco-physiological crop model for interplant competition was used. After adaptation, the same model was used to explore the leek-celery intercropping system for a wide range of plant densities and crop ratios. A combined application of descriptive and mechanistic models was finally used to optimise and design a leek-celery intercropping system with a high yield and quality potential and improved weed suppressive ability.

Outline of the thesis

A mind-map with the chapters arranged clockwise illustrates the structure of this thesis (Fig. 1.1). The background, hypothesis and objectives of the thesis are worked out in the introductory Chapter 1. Chapter 2 gives a description of the leek-celery intercropping system. The canopy characteristics are discussed with respect to competition for light and the weed suppressive ability of the canopy. Implications for

weed control and aspects of crop performance are discussed. The effects of light competition of different crop canopies on the growth and reproductive capacity of *S. vulgaris* and implications for the management of late emerging weeds are further worked out in Chapter 3. A detailed analysis of the performance of leek and celery in the intercropping system is presented in Chapter 4. Competitive relationships, nitrogen use and efficiency and aspects of biomass production and crop quality are discussed in detail. To quantitatively identify factors determining interplant competition between leek and celery, an eco-physiological crop growth model was developed based on the model INTERCOM that served as a framework. A detailed description of the model, the morphological, phenological and physiological processes, the validation with independent data and a sensitivity analysis is presented in Chapter 5. It is shown how the model can be applied to improve the crop quality in the intercropping system. In Chapter 6, the modelling approaches as described in the previous chapters are combined and applied to design and to optimise the intercropping system. While the eco-physiological model is used to explore the system, generated data were summarised and analysed with the descriptive model. Consequences for financial yield, weed suppression and trade-offs are discussed. In Chapter 7, advantages and limitations of the leek-celery intercropping system and system features which were not discussed elsewhere are presented. Critical remarks are made with respect to a combined modelling approach for designing intercropping systems and the concept of canopy weed suppression and long-term aspects of period thresholds are discussed in more detail.
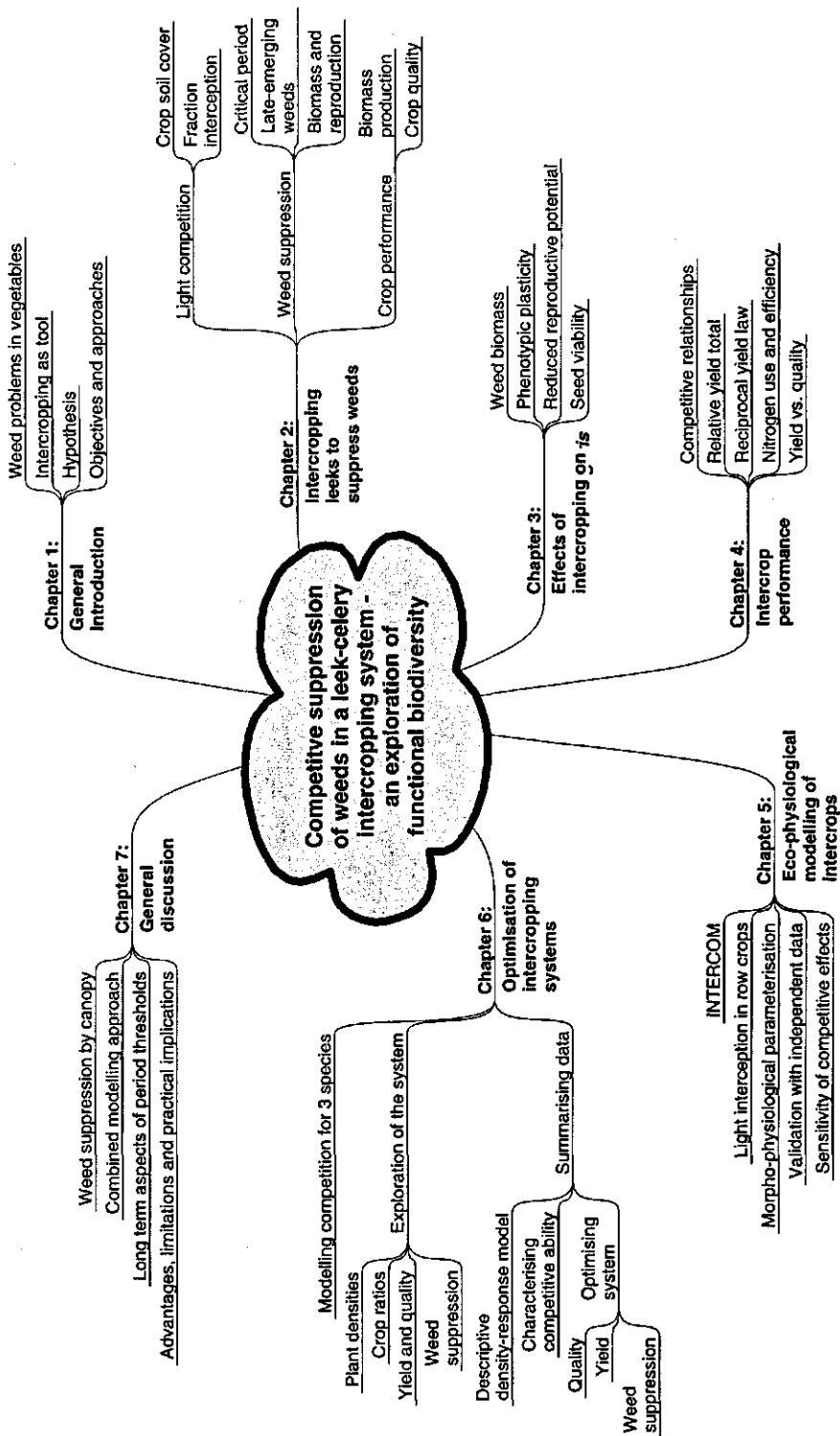
Fig. 1.1 Outline of the thesis

Intercropping leeks to suppress weeds

Chapter 2

to suppress weeds

Abstract

Many field vegetables such as leek are weak competitors against weeds, causing high costs for weed management practice. Using celery as a companion cash crop was suggested to improve the weed suppression of leek. Three field experiments were carried out to study the intra- and interspecific competition in a leek-celery intercrop with and without additional weed competition. Results from this experimental work show that intercropping of leek and celery in a row-by-row replacement design considerably shortened the critical period for weed control in the intercrop compared with the leek pure stand. The relative soil cover of weeds that emerged at the end of the critical period was reduced by 41% in the intercrop. In another experiment, the biomass of *Senecio vulgaris*, which was planted 20 days after crop establishment, was reduced by 58% in the intercrop and the number of seedlings which emerged as offspring was reduced by 98%, all reductions compared with the pure stand of leek. The relative yield total of the intercrop exceeded that of the pure stands by 10%, probably as a result of an optimised exploitation of the resources. The quality of the leek, however, was reduced. Advantages and bottlenecks of the intercrop system of leek and celery and implications for the weed control are discussed and used to identify future research needs.

Introduction

Severe weed problems in vegetable crop rotations particularly occur in crops with a weak competitive ability. Crops which are mainly sown and those with a slow juvenile development, such as carrot (*Daucus carota* L.), onion (*Allium cepa* L.) and leek (*Allium porrum L.*) are very sensitive to weed competition. As herbicides are the most common tools used to control weeds, these weed-sensitive vegetable crops strongly contribute to the high herbicide usage in vegetable production. Environmental concerns and the growing market for high value ecologically produced vegetables stimulates farmers to convert their production to integrated or organic farming, aiming to reduce or to eliminate herbicide use completely. However, non-chemical weed control and the high labour requirement for hand-weeding are considered a major constraint for conversion of vegetable production to ecological farming systems (Vereijken and Kropff, 1996). Consequently, weed science programmes in many European countries focus on the reduction of herbicide use and the development of sustainable weed control strategies in vegetable production according to the demands of integrated and organic farming systems. Farming systems research and integrated pest management have generated renewed interest in cultural control methods and these have been extended to include agro-ecosystem management. Cultural methods include some of the oldest control practices known for weed and pest control, such as crop rotation, choice of crop and cultivation technique, manipulation of the planting date and mixed cropping.

The use of polycultures (cover plants, multicropping, living mulch, trap crops) was mainly proposed to increase productivity and yield stability to improve the use of resources and to reduce damage caused by pests (Willey, 1979a; Lamberts, 1980; Coaker, 1987; Altieri, 1988; Coaker, 1988). Cover plants in field vegetables, however, may also have other advantages such as decreases in weed infestations, soil erosion, fertiliser and pesticide requirements and soil compaction together with increases in enhanced organic matter content, water infiltration and moisture and nutrient retention (Akobundo, 1980; Hartwig, 1983; Horwith, 1985).

There is some variability in the use of different terms for multiple cropping. Therefore "interplanting" is proposed by Vandermeer (1989) as a general term for growing two or more crops on the same field during the same vegetation period. In this Chapter the terms "cover crop/cover plant" is used for plants which are generally grown for soil improvement or fodder, such as grass- and clover species seeded in the inter-row space of row crops. The terms "intercrop/intercropping",

however, are used for a mixture of two cash crops where a secondary crop is simultaneously grown in the inter-row space of a main crop.

In vegetable row crops, cover plants and intercrops and weeds interfere with the main crop reducing yield through competition for light, water and nutrients. Attempts to reduce competition in interplanting systems have focused on mechanical or chemical suppression of cover plant growth, screening for less competitive mulches and variation of mulch planting dates (see Wiles _et al._, 1989 and references therein; Ammon _et al._, 1995). Based on the results of period-threshold experiments, Müller-Schärer and Potter (1991) suggested that cover plants should generally be seeded with a delay, such that they only emerge at the beginning of the second half of the growth period of the main crop. If this is met and the crop is kept weed-free during the critical period, crop yield will hardly be reduced (Potter, 1991). No adverse effects on yield were found in asparagus (_Asparagus officinalis_ L.), savoy cabbage (_Brassica oleracea_ L. var. _sabauda_ L.) (Potter, unpublished data), sweet corn (_Zea mays_ L. convar. _saccharata_ Koern) (Potter and Niggli, 1989) and leek (Müller-Schärer _et al._, 1992b) using clover (_Trifolium_ spp.) and grass species in experiments applying the concept of period thresholds. In leek, three mechanical treatments and ryegrass (_Lolium perenne_ L. cv. Elka) interseeded 5 weeks after transplanting of the crop reduced the weed cover at harvest time to a tolerable level without causing significant yield or quality loss. Additionally, there was a significant reduction of attack by _Thrips tabaci_ Lind. and a strongly reduced nitrogen loss compared with the control plots with bare soil after harvest (Baumann and Imhof, 1996). However, the introduction of a cover crop increases the ecological complexity of the cropping system demanding a more sophisticated agricultural practice. To date, growers have rejected the use of a cover crop in vegetable production because its management is too difficult, it is very laborious and it involves yield loss.

Using a secondary cash crop instead of a cover crop has been suggested to improve the weed suppression of vegetables with a weak competitive ability. Walters (1971) and Enyi (1973) stated that the more complete the soil cover provided by intercropping, the more the weed growth would be reduced by competition. While entomologists have extensively evaluated mixed cropping as a tool to reduce pest pressure, there are few investigations on the potential of intercropping to reduce weed infestations.

In this study, research focused on the improvement of the competitive ability of a leek cropping-system. Leek was chosen because of its importance in European vegetable production and its obvious problem with weed suppression. Production by the countries of the European Union (EU) reaches about 7 million tonnes per year.

Important producers are France, Belgium, The Netherlands, Spain and the UK. In Switzerland, leek is the third most important seasonal vegetable crop after lettuce and covers 360 ha per year. The average yield in the EU is 26.3 t ha^{-1}, and this varies little from country to country (Brewster, 1994). Leek, like many other *Allium* crop species, is known as a weakly competitive crop because of its slow juvenile development and the open canopy, which does not cover the soil until harvest. Consequently, weed emergence appears during the whole growing period. Weeds emerging after the critical period, which typically lasts until about 7-8 weeks after crop establishment, do not affect yield and quality of the crop, but still produce seeds causing problems in subsequent crops and may lead to problems with mechanical harvest (Müller-Schärer and Baumann, 1993).

Based on results of cover crop experiments and practical experience with the concept of period thresholds, as described by Nieto *et al.* (1968), the following hypothesis was worked out for an intercropping system with leek and celery (*Apium graveolens* L.). Replacing every second row of leek with celery improves the competitive ability of the canopy against weeds, reducing soil cover, biomass and seed production of weeds while maintaining the yield and quality of the leeks supplemented by additional celery yield. In this chapter, three experiments are described that have been carried out to test this hypothesis and to evaluate the potential of intercropping to suppress weeds in field-planted leek.

Material and Methods

Three field experiments, referred to as experiment I, II and III, were carried out on a sandy loam soil at the experimental farm "Sandhof" of the Swiss Federal Research Station for Fruit-Growing, Viticulture and Horticulture, at Wädenswil, Switzerland (47°13' N, 08°40' E). To study intra- and interspecific competition in a leek-celery intercrop a bivariate factorial design, as described by Snaydon (1991), was used for experiment I in 1996. The effect of additional weed competition was investigated in experiment II in 1996 and experiment III in 1997.

Experiment I (competition experiment with bivariate factorial design)

Bare-root transplants of leek cv. Zefa Plus with 4.4 mm thick pseudostems and a mean biomass of 0.26 g dry weight were produced in nursery beds. For celery cv. Tall Utah (F1) commercially available peat pot transplants with an average biomass of

0.43 g dry weight were used. On 30 May 1996, leek and celery were manually planted into a plant bed which was cultivated twice on the previous day using a rotary cultivator. Prior to planting, roots and leaves of the leek transplants were trimmed according to standard practice. Planting depth of leek was 8 cm, whereas celery peat pots were shallowly placed and slightly covered with soil. For accurate plant to plant distance and planting depth an adjustable hole-puncher was used.

Table 2.1 Plant densities and in-row spacing at a fixed inter-row spacing of 0.25 m for pure stands and intercrop mixtures in experiment I, 1996.

Treatment (density)	Leek		Celery	
	Density (plants m^{-2})	In-row spacing (m)	Density (plants m^{-2})	In-row spacing (m)
Leek pure stand (high)	60	0.06	0	-
Leek pure stand (medium)	40	0.10	0	-
Leek pure stand (low)	20	0.20	0	-
Intercrop (high)	30	0.06	15	0.13
Intercrop (medium)	20	0.10	10	0.20
Intercrop (low)	10	0.20	5	0.40
Celery pure stand (high)	0	-	30	0.13
Celery pure stand (medium)	0	-	20	0.30
Celery pure stand (low)	0	-	10	0.40

Inter-row spacing was 0.25 m whereas in-row spacing was dependent on plant density according to the different treatments (Table 2.1). Intercrop treatments of a bivariate factorial design (Snaydon, 1991) were designed as row-by-row replacement series. A factorial block design with 4 replicates and blocks arranged transversely to the slope (2.5%) of the experimental site was used. Plot size was 2.25 m x 2 m for treatments with non-destructive measurements and was doubled for treatments with destructive measurements where more plants for intermediate harvests were required. One week after planting, soil was treated with a tank-mixture of 1600 g a.i. ha^{-1} Pendimethalin (Stomp SC 400 g a.i. L^{-1}; Maag Agro, Dielsdorf, Switzerland) and 400 g a.i. ha^{-1} Chlorbromuron (Maloran WP 50% a.i., Novartis Agro AG, Basel, Switzerland) and a spray volume of 300 L ha^{-1}. Insecticide and fungicide treatments were applied

to avoid crop damage by thrips (*Thrips tabaci* L.), leek moth [*Acrolepiopsis assectella* (Zeller)], late blight of celery (*Septoria apicola* Speg.) and leek rust [*Puccinia allii* (D.C.) Rud.] in both experiments. Base-fertilisation was carried out according to soil analysis prior to planting with P_2O_5, K_2O and Mg to reach 60 kg P ha^{-1}, 180 kg K ha^{-1} and 30 kg Mg ha^{-1}. To avoid nitrogen deficiency, a buffer of 70 kg N ha^{-1} was maintained in the rooting zone by applying nitrogen (as 27% ammonium nitrate) as top dressings after checking the content of mineral nitrogen (NH_4, NO_3) every 10 days and additionally after heavy rainfall. To avoid water shortage, experiments were regularly irrigated based on tensiometer measurements in the field. During the growing season, the minimum and maximum diameter of the pseudostems of 5 consecutive leek plants per plot were measured weekly by digital calliper rule (Mitutoyo Digimatic Kissling AG, Switzerland). The percentage photosynthetically active radiation (*PAR*) intercepted by the canopy was measured weekly with a 0.5-m-long Sunfleck Ceptometer CEP (Decagon Devices, Pullman, WA). The fraction of *PAR* intercepted was calculated by rapidly taking 10 readings above the canopy and 10 readings below the canopy. The latter measurement was taken by placing the ceptometer perpendicularly to the plant rows and measuring a section of 0.5 m between the centres of the outside inter-row spaces within a bed. The mean of each set of 10 readings was recorded. Daily estimates of fraction *PAR* intercepted were obtained by fitting a logistic model through the measurement dates. Daily values for incoming *PAR* and cumulative intercepted *PAR* were calculated from values of total solar radiation measured at a weather station near the site, assuming that 50% of the total solar radiation was *PAR* (Goudriaan and Van Laar, 1994). At intervals of 7 days the crop soil cover was visually estimated, using a 0.5 x 0.5 m frame with a 62.5 mm x 62.5 mm grid. Biomass assessments were carried out at the planting date and at 27, 55, 89 and 105 days after crop establishment (0, 510, 984, 1599 and 1803 day-degrees (°Cd) respectively). Base temperatures of 6 °C were used to calculate the temperature sum (Brewster, 1994). Above-ground dry weight of 12 consecutive leek and 6 consecutive celery plants from the centre rows of each plot were measured. Based on minimum and maximum pseudostem diameter a linear relationship between the cross-sectional area of the pseudostem and the above-ground dry weight of the leek plants was found. This allowed the appraisal of the above-ground biomass between the destructive measurements with a high goodness-of-fit ($R^2 = 0.92$) and increased the number of values characterising the biomass development of leek in time. Crop soil cover and light interception curves were described by a logistic model (Goudriaan and Monteith, 1990) using the Genstat 5 statistical package (Payne *et al.*, 1987):

$$Y = A + \frac{C}{1 + e^{-B(X-M)}}$$ [2.1]

where Y is the fraction of soil cover or intercepted *PAR* by the canopy, A and $A+C$ are the lower and upper asymptote, the latter being the maximum soil cover or intercepted *PAR* by a canopy, M is the time when 50% of incoming *PAR* is intercepted by the canopy (F_iPAR_{50}), B is proportional to the slope at F_iPAR_{50} and X is the time in °Cd after crop establishment. A goodness-of-fit test was used to determine whether or not the model adequately described the data.

Experiment II (replacement series with additive natural weed populations)

Experiment II was set-up as bi-factorial split-plot block design with four replicates. Factors were crop stand and weed competition with three levels of each. Crop stands consisted of leek and celery pure stands with a plant density of 20 and 10 plants m^{-2}, respectively, and a row-based replacement series of the two crops (leek: 10 plants m^{-2}; celery: 5 plants m^{-2}). Each level of this factor was split by three weed competition levels including emergence of naturally occurring weeds at 4, 6 and 8 weeks after crop establishment. Crop cultivars, planting date and method, pest and disease control, fertilisation and irrigation were the same as in experiment I. Prior to the time of weed emergence, weeds were removed manually. Four blocks were arranged transversely to the slope of the experimental site. During the growing season, the minimum and maximum diameter of the pseudostems of 5 consecutive leek plants per plot were measured weekly. Relative weed soil cover was visually estimated 57 days after crop establishment. Above-ground dry weight of the crops was measured at the end of the growing season in the same way as in experiment I. Yields obtained from plots that were kept weed-free during the first 8 weeks were used as reference yields, as earlier experience indicated that the critical period for leek, being the weakest competing component crop, ends 7 weeks after crop establishment (Müller-Schärer *et al.*, 1992a). Relative yield of individual plots was calculated according to a procedure proposed by Oyejola and Mead (1982) in which the average yield of the corresponding crop stand was used as the reference yield for all replications.

Experiment III (replacement series with additive Senecio vulgaris *L. populations)*

Experiment III was established on 3 June 1997 on an experimental plot which was treated with Dazomet 58.8 g a.i. m^{-2} (Basamid Granulate 98% Dazomet, Maag Agro AG, Dielsdorf, Switzerland) 6 weeks before planting, to avoid germination of weeds. The experimental design was basically the same as for experiment II, although the factor weed competition consisted of eight levels with three replicates. Instead of the naturally occurring weeds, *Senecio vulgaris* L. (common groundsel) was planted between the crop rows every 10 days until 70 days after crop establishment. One treatment remained weed-free. Planting of bare-root leek transplants cv. Zefa Plus (4.7 mm initial diameter; 3.4 g dry weight per plant, prepared as described above) was performed using a planting machine. Commercially available peat pot celery transplants cv. Bolivar (0.23 g initial dry weight per plant) were manually planted. Two days after preparation of 1.5 m wide beds (standard practice for vegetable growing in Switzerland), the crops were planted in four rows per bed with an inter-row distance of 0.3 m. Densities of leek and celery pure stands were 18 and 9 plants m^{-2}, respectively; the intercrop was established as row-based replacement series (leek: 9 plants m^{-2}; celery: 4.5 plants m^{-2}). Seeds of *S. vulgaris* L. were pre-germinated on agar (2%) in Petri dishes and 3 days later planted attached to small agar pieces with a density of 50 plants m^{-2} (0.04 m in-row distance) between the crop rows into 10 mm deep dimples. To maximise emergence, germinating seeds were protected against heavy rain, drought and slugs during 10 days after planting by means of a cover with a cheese-cloth and Methiocarb 0.01 g a.i. m^{-2} (Mesurol Microgranulate, 1% Methiocarb, Bayer AG, Zollikofen, Switzerland). To minimise the genetic variation within the *S. vulgaris* population, a biotype, collected in The Netherlands in 1994 and inbred for four generations, was used (Wyss, 1997). During the growing season, the minimum and maximum diameter of the pseudostems of 5 consecutive leek plants per plot and interception of *PAR* (Sunfleck Ceptometer CEP, probe length 0.6 m) by the canopy were measured weekly. For *S. vulgaris* planted at 10, 20, 30 and 40 days after crop establishment, above-ground biomass and number of capitula were measured as flowering occurred, which on average was 38 days after planting of the weeds. Prior to the harvest of the crop, seedlings that had germinated as offspring of planted *S. vulgaris* were counted, using a 0.1 m x 0.1 m grid which was randomly placed three times per plot. For analysis of treatment effects ANOVA was performed using the Genstat 5 statistical package (Payne *et al.*, 1987).

Results

Light interception and soil cover (Experiment I)

The time course of the fraction of intercepted *PAR* in pure stands of leek, celery and their intercrops at various densities is shown in Figs 2.1 and 2.2. The logistic model fitted well for all data sets, and goodness-of-fit test did not reject the hypothesis of the model being appropriate to describe the data.
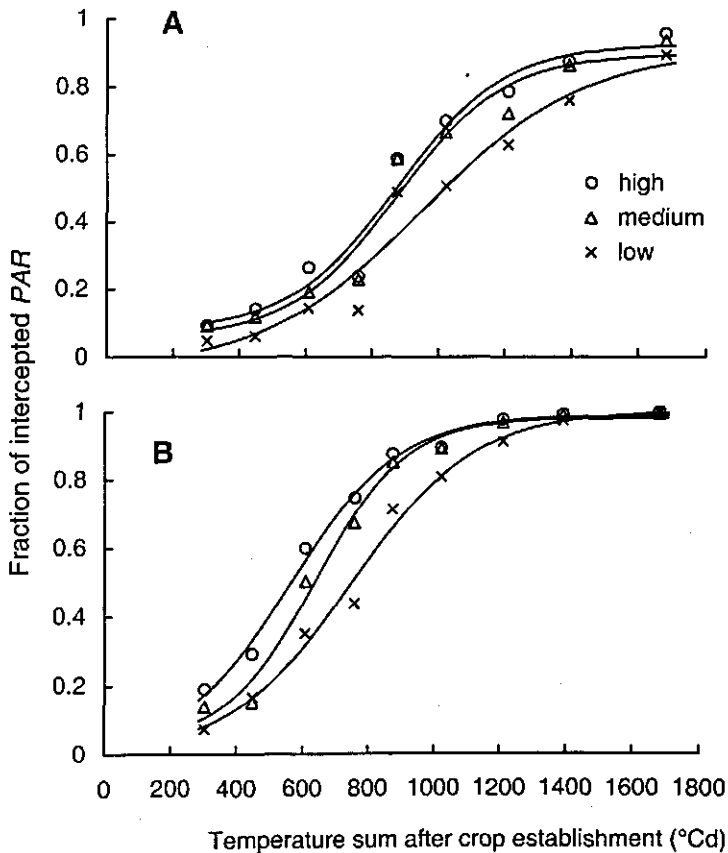
Fig. 2.1 Time course of fraction of intercepted radiation (F_iPAR) by pure stands of leek (A) and celery (B) at high (leek: 60 plants m^{-2}; celery: 30 plants m^{-2}), medium (leek: 40 plants m^{-2}; celery: 20 plants m^{-2}) and low (leek: 20 plants m^{-2}; celery: 10 plants m^{-2}) densities in 1996 (expt. I). Symbols: observed data; lines: fitted curves.
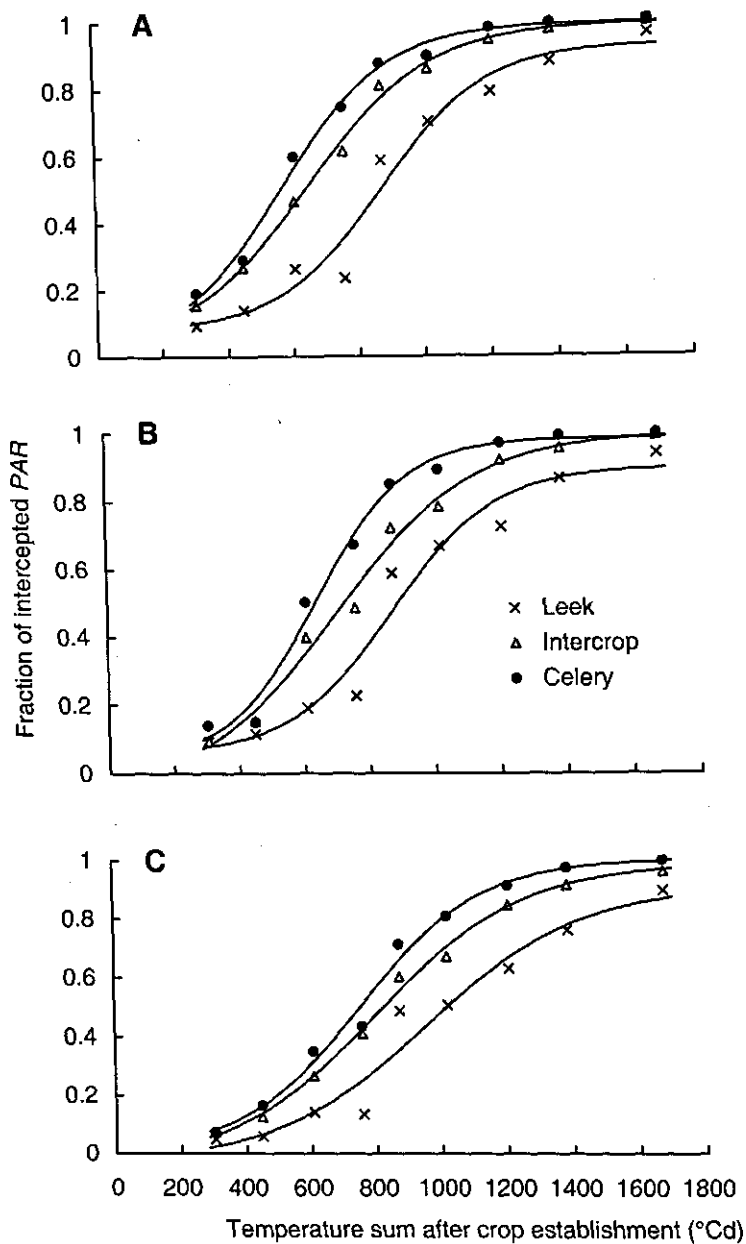
Fig. 2.2 Time course of fraction of intercepted radiation (F_iPAR) by pure stands of leek ($\times$), celery (●) and leek:celery intercrop ($\triangle$) at high (A), medium (B) and low (C) densities in 1996 (expt. I). Symbols: observed data; lines: fitted curves.

Estimated parameters for the crop stands, of which $A+C$ (maximum of intercepted _PAR_) and M (F_iPAR_{50}) showed significant differences between the canopies, are mentioned in Table 2.2. Growth of leek and celery during the first 2 weeks after transplanting (304 °Cd) was slow, partly as a result of the transplanting shock. The fraction intercepted radiation directly after transplanting was around 10% for all crop stands and remained under 20% during the first 30 days (564 °Cd), even for the highest leek density. At 30 days after transplanting, low, medium and high densities of celery pure stands intercepted 27, 37 and 50%, respectively. The canopies of the medium- and high-density intercrops reached 50% light interception (F_iPAR_{50}) significantly earlier than their corresponding pure stands of leek (Table 2.2).

Table 2.2 Estimated parameters and goodness of fit for logistic functions (eqn 2.1) of the fraction of intercepted _PAR_ in the crop stands and densities of experiment I, 1996.

Crop stands (density)	Estimated parameters				
	A	$A+C$	B	M	R^2
Leek pure stand (high)	0.11 (0.02)*	0.91 (0.02)	0.17 (0.03)	49.82 (2.3)	0.95
Leek pure stand (medium)	0.09 (0.01)	0.88 (0.04)	0.24 (0.14)	50.50 (2.4)	0.92
Leek pure stand (low)	0.01 (0.03)	0.88 (0.07)	0.22 (0.14)	53.97 (2.8)	0.82
Intercrop (high)	0.04 (0.02)	1.00 (0.01)	0.09 (0.01)	36.22 (3.0)	0.99
Intercrop (medium)	−0.04 (0.07)	1.00 (0.02)	0.09 (0.01)	39.63 (4.1)	0.99
Intercrop (low)	−0.01 (0.02)	0.99 (0.04)	0.09 (0.01)	45.94 (1.9)	0.99
Celery pure stand (high)	−0.05 (0.10)	1.00 (0.01)	0.10 (0.01)	29.72 (4.5)	0.99
Celery pure stand (medium)	0.04 (0.04)	0.99 (0.01)	0.14 (0.02)	35.56 (3.3)	0.97
Celery pure stand (low)	0.02 (0.07)	0.98 (0.02)	0.17 (0.08)	41.68 (3.5)	0.93

* Numbers in brackets are the standard errors of the mean

There were also significant differences between intercrops and leek pure stands in cumulative _PAR_, which was intercepted by the canopies in the first half of the vegetation period (Table 2.3). However, neither the latter parameter nor F_iPAR_{50} differed significantly between canopies of intercrops and celery pure stands. Intercrop canopies closed, reaching an interception of 95% of all incoming _PAR_ (F_iPAR_{95}), after 84, 74 and 68 days (1517, 1340 and 1229 °Cd) for the low, medium and high density, hence, 14, 13 and 8 days later than their corresponding celery pure stand densities, respectively. Leek pure stands, however, reached a maximum of only 88, 88 and 91% for the three densities (Table 2.2), at final harvest (1803 °Cd after crop

establishment). There was no significant difference between corresponding densities of crop stands in cumulative *PAR* that was intercepted in the second half of the vegetation period (data not shown).

Table 2.3 Cumulative intercepted *PAR* [MJ m^{-2}] in the first half of the vegetation period (until 57 days after crop establishment) by the canopies of pure stands and mixtures of leek and celery in experiment I, 1996.

Crop stand	Plant density (for densities see Table 2.1)		
	Low	Medium	High
Leek monoculture	293 (31.7)*	386 (26.9)	405 (27.7)
Leek-celery intercrop	388 (8.2)	453 (32.0)	496 (26.5)
Celery monoculture	468 (5.9)	516 (15.9)	518 (22.5)

* Numbers in brackets are the standard errors of the mean

Comparison of visually estimated crop soil cover over time showed similar differences between the three canopies (data not shown). In Fig. 2.3, the logistic fit of fraction of crop soil cover was plotted against the logistic fit of fraction of intercepted *PAR* for the medium density replacement series, in order to evaluate the usability of crop soil cover as a measure for light interception. Comparing the curves for the pure stands of leek and celery and the intercrop with the one-to-one line, representing a correlation of unity, it becomes evident that the correlation between the two parameters is dependent on the canopy and the development stage of the crops. Whereas the crop soil cover of celery pure stand described its canopy light interception reasonably, this was not the case for pure stand of leek and the intercrop. For these canopies the light interception is heavily underestimated by the vertical projection of the crop soil cover, particularly later in the growing season.

Weed suppression (Experiment II and III)

In experiment II the relative fraction of soil cover of naturally emerged weeds after different weed-free periods estimated in the middle of the vegetation period (57 days after crop transplanting) is shown in Fig. 2.4 for pure stands and the intercrop of leek and celery.

The weed flora consisted mainly of *Galinsoga* spp., *Amaranthus* spp. and *Poligonum persicaria* L. The later the weeds emerged after crop establishment, the lower was the soil cover they reached. The relative weed soil cover in the intercrop

canopy was significantly reduced only if weeds had emerged after 6 and 8 weeks, with 41% and 68% soil cover, respectively, compared with the leek pure stand. For the same treatments no significant difference in weed soil cover was found between intercropped leek and pure stand of celery. Owing to the rather small plot size, weeds were not removed until harvest of the crop, hence no biomass assessments were carried out during the growing period. By the time of final harvest, biomass of weeds was considerably reduced due to senescence and was therefore not measured.
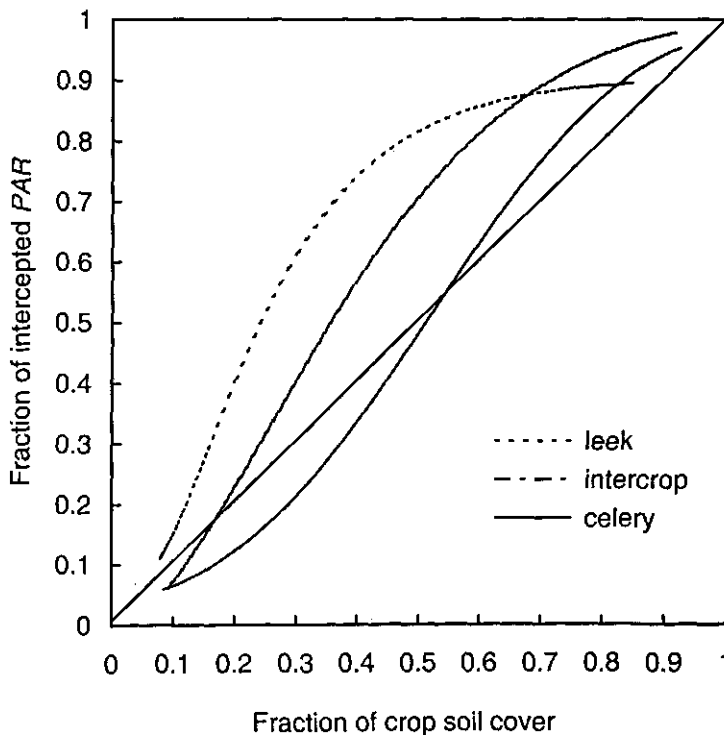
Fig. 2.3 Values from fitted curves of fractional intercepted *PAR* plotted vs. values from fitted curves of fractional soil cover in expt. I for the medium density of leek (40 plants m^{-2}), celery (20 plants m^{-2}) and the intercrop (leek: 20 plants m^{-2}; celery: 10 plants m^{-2}).

In experiment III, above-ground dry weight of *S. vulgaris* grown in intercropped leek and pure stands of leek and celery is shown in Fig. 2.5A. Biomass of *S. vulgaris* planted 10 days after crop establishment was not significantly different between the crop stands. However, for weeds planted 20, 30 and 40 days after crop establishment

biomass was reduced by 58%, 76% and 94%, respectively, in the intercrop compared with the pure stand of leek. For emergence dates of *S. vulgaris* later than 50 days no significant differences where detected and all canopies suppressed its development. There were small not significant differences in dry biomass of *S. vulgaris* between intercropped leek and the pure stand of celery.
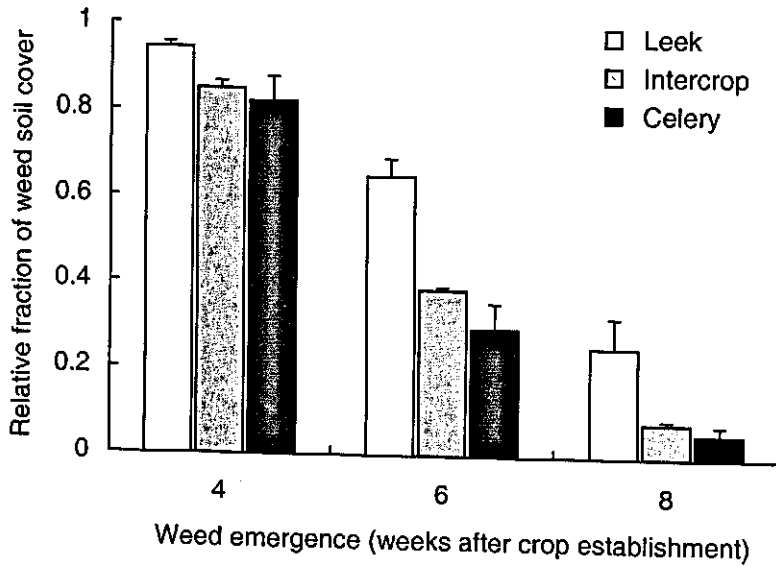
Fig. 2.4 The relative fraction of soil cover by weeds as a function of weed emergence in leek pure stand, celery pure stand and leek-celery intercrop. Vertical bars represent standard errors of means.

To study the effect of the intercrop and pure stand canopy on the reproductive potential of *S. vulgaris*, the number of capitula was counted when flowering occurred. Flower production was significantly reduced for *S. vulgaris* grown in intercropped leek and the celery pure stand compared with the leek pure stand (Fig. 2.5B). At the same time no significant difference could be found between intercrop and celery monoculture. Although even more pronounced, the same effect could be observed by counting the number of germinated *S. vulgaris* seedlings just before final harvest. Average seedling densities of almost 9500 m^{-2} were counted on individual plots of leek monoculture (Fig. 2.5C) whereas the density of seedlings under intercropped leek and the pure stand of celery remained under 450 and 70 plants m^{-2} respectively. No offspring were *S. vulgaris* had been planted later than 40 days after crop establishment in any of the crop stands.
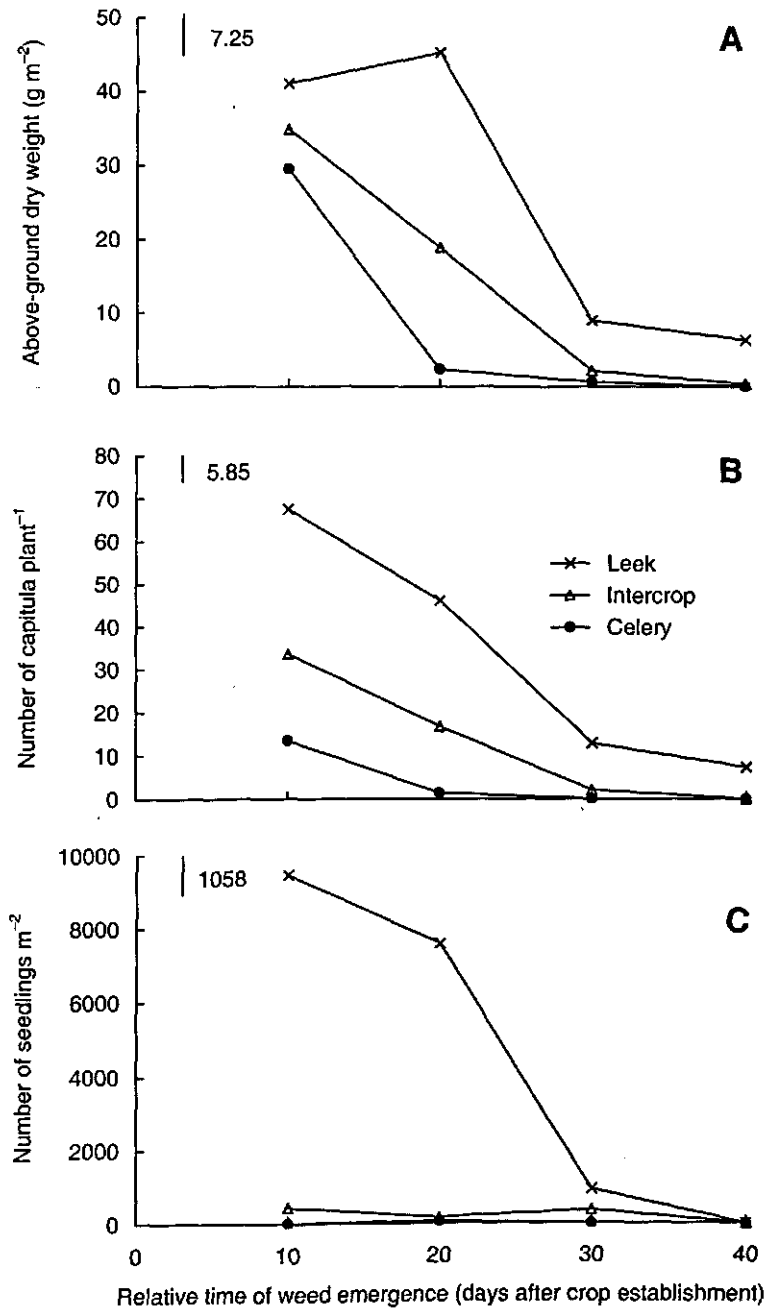
Fig. 2.5 Biomass (A), flower production (B) and the number of seedlings (C) of *Senecio vulgaris* at different times of weed emergence for leek pure stand (×), celery pure stand (●) and intercrop (Δ) in 1997 (expt. III). Vertical bars represent standard error of means.

Yield and quality of leek

Experiment II was set up to study the effect of relative time of weed emergence on weed competition. Based on these data the end of the critical period could be determined in intercrop and pure stands (Fig. 2.6).
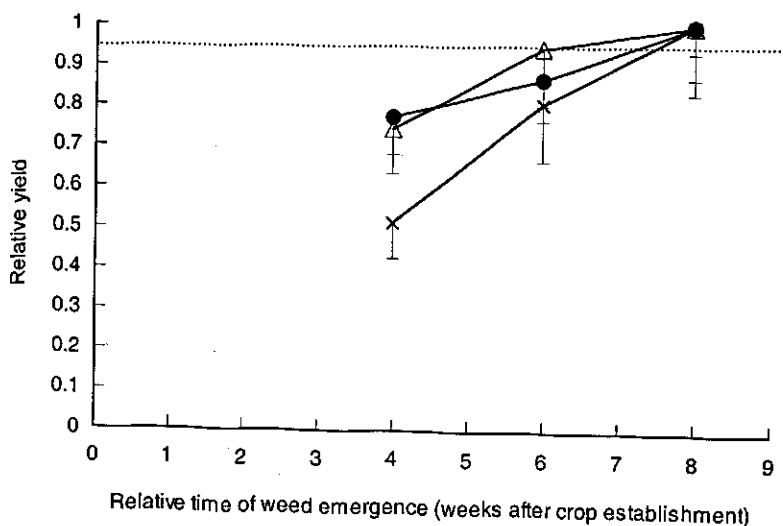
Fig. 2.6 Relative yield of leek (×), celery (●) and intercrop (Δ) at different weed-free periods from crop establishment. The dotted line indicates the end of the critical period for weed control at which yield is reduced by 5% (expt. II, 1996). Vertical bars represent standard error of means.

Yield of leek was significantly reduced with 48% when weed competition started early (no weed control from 4 weeks after transplanting onwards), whereas total yield of intercrop and celery monoculture was reduced by 25%. If yields are normalised for the weed-free treatment (in the experiment crop stands with weed control until 8 weeks after crop establishment were weed-free) and 95% of the relative maximum yield (*RY* 0.95) is defined as the acceptable yield level, the end of the critical period can be derived. For leek pure stand it was found to last until 52 days (924 °Cd) after crop establishment, whereas this was two (33 °Cd) and ten days (183 °Cd) shorter for the celery pure stand and the intercrop, respectively. Leek contributed about one-third to the total yield of the intercrop without significant differences between treatments with different weed competition. Quality of the leek crop, using a minimum diameter of the pseudostem of 20 mm for marketable leek, was affected by

intercropping and early weed competition, although the differences were not significant (Table 2.4).

Table 2.4 Percentage of marketable leek plants in pure stand of leek and leek-celery intercrop with additional weed competition from 4, 6 and 8 weeks after crop establishment (expt. II, 96).

Crop stand	Weed competition (weeks after crop establishment)		
	4	6	8 (considered weed-free)
Leek monoculture	84 (8)*	91 (9)	88 (7)
Leek-celery intercrop	53 (27)	72 (21)	78 (15)

* Numbers in brackets are the standard errors of the mean

The effect of interplanted celery on leek quality was generally greater than the effect of weed competition. Length and bleached part of the pseudostem, other quality parameters for leek, were positively affected by intercropping. This was probably due to lower light intensity in the intercrop canopy as shading by the celery plants caused leek to grow taller and producing a paler stem. Weed competition had no effect on these parameters (data not shown). Data from experiment I showed a significant reduction of 30% of the per plant weight of intercropped leek compared with its pure stand, caused by competition from celery (data not shown). However, this competitive effect appeared only in the last quarter of the growing period. Total yield of the intercrop (leeks and celery together) was, however, 30% higher than that of the pure stand of leeks (data not shown). The relative yield total (*RYT*) of the mixture was 1.1, indicating a yield advantage of the intercrop of 10% compared with the yields of the pure stands of leek and celery (Fig. 2.7).

Discussion

Leek is a weak competitor for light and therefore well-known as one of the most susceptible crops to weed competition (Niggli and Potter, 1988). It was hypothesised that the competitive ability of a leek cropping system against weeds could be improved by introduction of celery with the objective to increase the light interception of the intercrop canopy. Using celery as secondary crop, it was assumed that its properties with respect to soil cover and light interception would supplement these of leek, resulting in a higher crop canopy light interception and hence a shorter critical period for weed control for intercropped leek compared to its pure stand.
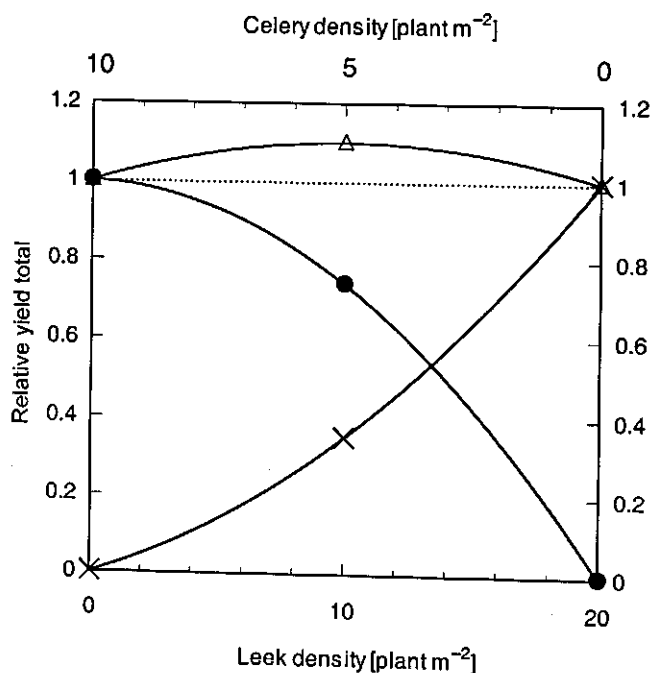
Fig. 2.7 Relation between yield of leek (×), celery (●) and intercrop (Δ) in a replacement series (expt. I, 1996).

Although the early development of leek and celery did not differ in experiment I, the relative growth rate of celery seedlings is more than 1.5 times higher than that of leek (Brewster, 1994). According to the same author, leek seedlings have an intrinsically low potential growth rate which is partly due to the narrow, upright leaf habit of leek seedlings causing a low ability to intercept radiation. Celery, however, shows a higher crop soil cover and light interception during the first weeks and its ability to suppress weeds was better in the first half of the vegetation period. As a result of the canopy architecture and a faster leaf area development celery reached complete soil cover after 11 weeks whereas leeks did not cover the soil until harvest. Owing to the morphological differences between the two crops, the effects of plant density on soil cover and light interception were more pronounced for celery than for leek. Regarding the different densities of leek-celery mixtures (Fig. 2.2), their properties with respect to competition for light seem to be dependent on the proportion of celery in the mixture rather than on the density of the single components. Whereas by doubling the leek density from 20 to 40 plants m^{-2} the time to reach 50% light interception was shortened by 3 days, intercropping 20 leek plants by 10 celery plants m^{-2} shortened this period with almost 2 weeks. Hence,

intercropping leek with celery turned out to be a better tool to increase the competitive ability of leek than increasing its density.

The relationship between crop soil cover and fraction of intercepted light (Fig. 2.3) proved to be canopy-dependent and changed in time during the growing season, indicating a strong effect of canopy architecture. For both the leek pure stand and intercrop the interception of radiation by the canopy was underestimated by the crop soil cover. Assuming competition for light to be the major competition factor, it can be concluded that crop soil cover is not suitable for defining the end of the critical period for weed control because it does not reflect the specific properties of the canopy architecture with respect to light interception. Whether or not the fraction of intercepted radiation (F_iPAR) might be used to define the end of the critical period could not entirely been shown by the experimental data . It is at least doubtful that F_iPAR can serve this objective as a single parameter since its measure is static. However, the end of the critical period defined as the status of the crop where sufficient weed suppression ability is reached also includes the leaf growth dynamics and the morphological properties of the crop. In production situations with limited water and nutrient availability, below-ground competition between crops and weeds will affect the critical period additionally.

In experiment II, no crop stand was able to suppress early germinating weeds sufficiently. However, there was a considerable reduction of the relative weed soil cover in intercropped leek and celery monoculture for weeds germinating later than 6 weeks after crop establishment. The same results were found in experiment III with _S. vulgaris_. These findings are consistent with the results of many years of research on critical periods for weed control in various vegetables crops (Müller-Schärer and Baumann, 1993). From their results (Baumann _et al._, 1993) drew the conclusion that weed control measures can be limited to the critical period without risk of yield and/or quality losses. The authors suggested, however, that late germinating weeds still produce seeds and contribute to the weed seedbank in the soil. In experiment III with _S. vulgaris_ it was shown that the flower production and the offspring of mature weed plants was considerably reduced under intercropped leek and celery pure stand compared with leek monoculture. This indicates that increasing the ability of the crop canopy to compete for light can reduce not only the biomass, but also the reproductive potential of weeds. Intercropping leek by celery proved, therefore, to be an adequate method to increase the suppressive ability of the crop canopy with respect to biomass production and reproductive potential of weeds. In both experiments no significant differences were observed between the effect of the canopies of the intercrop and the celery pure stand on the weeds. It might be

concluded that there is no distinct difference between the properties of these two canopies with respect to their suppressive ability against weeds.

Results from the replacement series experiment with natural weed infestation show that the critical period of intercropped leek lasted a shorter time than that of a leek monoculture (Fig. 2.6). Owing to its slower development and the differences of morphological properties, leek needed an additional 183 °Cd to reach the end of the critical period. This means that in practice canopy closure of an intercrop is 10-15 days earlier. Hence there is less need for an additional weed control measure which, particularly in this crop stage, can cause crop damages (mechanical treatment) or residual problems (chemical treatment).

The relative yield total diagram in Fig. 2.7 suggests that celery appeared to be a stronger competitor than leek, indicated by the convex and concave curves for celery and leek, respectively. Because the experiment was set up in such a way that no nutrient and water deficiency occurred, the observed effects are exclusively due to light competition. Celery was able to overcompensate for the yield loss of leek, resulting in a *RYT* exceeding unity. However, a real yield advantage of the intercrop appears only if the corresponding pure stands are grown at their optimal densities with respect to biomass production (Conolly, 1986). The plant density for leek in the treatment, shown in Fig. 2.7, was far below the optimal density that is normal in practice to obtain a marketable quality. Hence the 10% yield advantage of the intercrop was probably result of the optimised exploitation of the resources rather than due to a real yield advantage of the intercrop. Although no yield loss appeared in the intercrop, the quality of the leek was reduced compared with the pure stand. The non-significant reduction of marketable plants by 20%, as observed in experiment II, would not be acceptable in practice. Therefore further optimization of the system will be necessary. Simulation models for interplant competition (Kropff and Van Laar, 1993) can be helpful to determine such optima.

Conclusions

Based on the experience of many years of research on critical periods and the intercrop experiments carried out, it is concluded that intercropping can be used as a tool to improve the competitive ability of a canopy with weak suppressive characteristics. Intercropping leek with celery in a row by row replacement design increased the canopy light interception, resulting in a shorter critical period for the intercrop compared with the leek pure stand. The above-ground competitive ability

of a leek-celery intercrop is comparable to that of a pure stand of celery. According to the rule of thumb by Baumann *et al.* (1993), classifying vegetable crops in groups according to their competitive ability, intercropped leek may be considered as a strong competitor with a restricted need for weed control measures until the middle of the growing period.

The flower production and offspring of *S. vulgaris* was considerably reduced in the crop mixture, indicating a strong effect of light competition on the reproductive potential of weeds. Hence there is a low risk for extensive seed production by residual weed infestation in a leek-celery intercrop canopy.

Yield and quality of leek was negatively affected by interplanted celery, but the relative yield total of the crop mixture was not reduced.

More research is needed to extend the knowledge about the effects of an interplanted secondary crop on its main crop and the weeds. Although an effect of the improved competitive ability of the intercrop canopy on the reproductive potential of a weed species could be shown, the production and viability of weed seeds in a suppressive environment need to be studied in more detail.

Crop mixtures need to be optimised with respect to yield and quality of leek and to achieve maximum weed suppression. It is therefore necessary to gain more insight into the mechanisms of interplant competition in intercropping systems. The use of an eco-physiological model for interplant competition (Kropff and Van Laar, 1993) is suggested as a tool to investigate crop:crop and crop:weed interactions in inter-cropping systems, to optimise the crop mixtures and to improve the detection of the critical period.

Effects of intercropping on growth and reproductive capacity of late-emerging *Senecio vulgaris* L., with special reference to competiton for light

Abstract

Due to increased emphasis on long-term management of weed populations in cropping systems with a reduced reliance on herbicides, the production of seeds by weeds that emerge after the critical period for weed control is increasingly important. It was hypothesised that increased soil cover and light interception by a crop canopy would shorten the critical period for weed control and reduce growth and fecundity of late-emerging weeds. This hypothesis was tested in a series of field and glasshouse experiments in which competition for light was manipulated. *Senecio vulgaris*, an important weed in vegetable production systems, was chosen as the target plant, and canopies of pure and mixed stands of leek and celery were used to provide shade. The time course of light interception differed among the crop canopies. Increasing competition of light caused morphological changes to *S. vulgaris*, including a vertical shift in leaf area distribution. Increased shading reduced the biomass, capitula:shoot ratio, and seed production of *S. vulgaris*. However, the viability of the seeds produced by the shaded weed plants was not affected. Results indicate that intercropping can increase light interception in a weakly competitive crop such as leek and can contribute to weed suppression in a long-term strategy for weed management.

Introduction

Integrated weed management (IWM) combines preventive and curative weed control methods to address weed problems, based on ecological principles, while also addressing environmental and economic concerns. Whereas, under integrated management, herbicides may be applied as corrective measures if other weed management tactics fail to protect a crop adequately, organic farming is entirely dependent on non-chemical methods. In organically-grown crops with weak competitive ability, such as onion (*Allium cepa* L.), leek (*Allium porrum* L.) and carrot (*Daucus carota* L.), more than 400 h of hand weeding per hectare may be necessary to reach a level of weed control comparable to that obtained with herbicides (Vereijken and Kropff, 1996). Because labour-intensive methods of weed control are not sustainable, better preventive tactics, decision-making procedures, and control technology are needed (Kropff *et al.*, 1996).

Intercropping is one option for reducing weed problems through non-chemical methods (Vandermeer, 1989). Baumann *et al.* (2000) suggested that leek could be intercropped with celery (*Apium graveolens* L.) to improve weed suppression relative to a leek monoculture, whose open canopy structure permits weeds to proliferate. They found that, for an intercrop of leek and celery, light interception and soil cover were significantly increased compared with a leek monoculture, and yield loss due to weed competition was significantly reduced.

With respect to improved decision-making, application of the period threshold concept as described by Nieto *et al.* (1968) has been suggested as a tactical element for reducing herbicide use in vegetable production systems (Roberts, 1976; Zimdahl, 1980). By controlling weeds during the crop- and site-specific critical period, reductions in the yield and quality of the current crop can be avoided (Müller-Schärer and Baumann, 1993). In experiments with pure and mixed stands of leek and celery, Baumann *et al.* (2000) observed that the critical period for weed control of the intercrop was considerably shorter than that of a pure stand of leek.

Although initial results of the leek-celery intercropping system have been promising, adoption of such new cropping systems brings about other questions. Herbicides can permit the adoption of a zero-tolerance strategy against weed growth and weed seed production. However, in organic production systems, weeds emerging after the critical period may not cause direct damage to the current crop, but still produce seeds and contribute to the replenishment of the weed seedbank (Radosewich and Holt, 1984; Wilson *et al.*, 1988; Cousens and Mortimer, 1995). Since population dynamics of weeds are generally not considered in critical period

research, period threshold concepts do not account for the long-term effects caused by seed production of late-emerging weeds (Baumann _et al._, 1993).

Wallinga and Van Oijen (1997) showed that the damage threshold concept, with the threshold expressed as weed density, is defective as a tool in a long-term weed management strategy, and recommended that weed densities be kept low to maximise long-term economic returns to the farmer. In crops such as leek and onion, organic farmers often try to reduce weed seed production by controlling weeds manually after the critical period, but this is generally very labour intensive and can cause damage to the crop. Intercropping crops such as leek with a more competitive crop could help to reduce the growth of late-emerging weeds. For late-emerging weeds, however, fecundity, rather than biomass, is the main issue. The fecundity-plant size relationship is found to be relatively constant for many species (Cousens and Mortimer, 1995) and linear relationships have been proposed (Wilson _et al._, 1988; Thompson _et al._, 1991; Wright, 1993).

This chapter reports the results of two field experiments investigating the effects of pure stands and mixtures of leek and celery on growth, morphology, reproductive allocation, and seed output of late emerging _Senecio vulgaris_ L.; and three glasshouse studies of the effects of shading on the growth and reproductive capacity of _S. vulgaris_. Agronomic aspects of the leek-celery intercropping system are beyond the scope of this chapter and will be discussed later.

Material and Methods

Experiment I and II (replacement series of the two crops with additive Senecio vulgaris _in the field)_

Two field experiments, referred to as experiment I (1997) and II (1998), were carried out on a sandy loam soil at the "Sandhof" experimental farm of the Swiss Federal Research Station for Fruit-Growing, Viticulture and Horticulture, at Wädenswil, Switzerland (47°13' N, 08°40' E). These experiments examined how the relative emergence time of _S. vulgaris_ affected its biomass and reproduction when growing in pure stands and intercrops of leek and celery. Rows of _S. vulgaris_ were sown between crop rows at a density of 50 plants m^{-2}. For both experiments, a split-plot block design with three replicates was used. Cropping system (monoculture leek, monoculture celery and an intercrop of the two species) was the main-plot factor. Plant densities were 18 and 9 plants m^{-2} for leek and celery, respectively, and the

intercrop was arranged as a row-based replacement series of the two crops. The relative emergence time of *S. vulgaris* was the split-plot factor. In expt I, *S. vulgaris* was planted on seven dates, each 10 d apart, with the first planting 10 d after crop establishment. In expt II, planting occurred at five dates, each 10 d apart, starting at crop establishment. In both experiments, a weed-free plot was included, and in expt II, a monoculture of *S. vulgaris* was included.

In both experiments, the soil was treated with Dazomet at 58.8 g a.i. m^{-2} (Basamid Granulate 98% Dazomet, Maag Agro, Dielsdorf, Switzerland) six weeks before planting to prevent germination of naturally-occurring weeds. Leek and celery were planted into 1.5 m wide beds on 3 June 1997 (expt I) and 28 May 1998 (expt II) to form four rows with an inter-row distance of 0.3 m. The beds had been rotary cultivated twice on the previous day. In both experiments, bare root transplants of leek cv. "Zefa Plus" were produced in nursery beds and transplanted into the field using a planting machine. Commercially available peat pot transplants of celery cv. "Bolivar F1" (1997) and cv. "Tango F1" (1998) were transplanted manually. Prior to planting, roots and leaves of the leek transplants were trimmed according to standard practice. Planting depth of leek was 80 mm, whereas celery peat pots were placed at such a depth that there was a continuous cover of soil. Time of transplanting was taken to be the time of crop establishment.

Seeds of *S. vulgaris* were pre-germinated on agar (2%) in Petri dishes and sown three days later, attached to small agar pieces, in 10 mm deep depressions between the crop rows. Within-row distance was 40 mm, resulting in a density of 50 plants m^{-2}. To maximise emergence, germinating seeds were protected against heavy rain, drought, and slugs during the 10 d period after planting using a cheese-cloth cover and 0.01 g a.i. m^{-2} Methiocarb (Mesurol Microgranulate 1% Methiocarb, Bayer AG, Zollikofen, Switzerland). To minimise the genetic variation within the *S. vulgaris* population, a biotype, collected in The Netherlands in 1994 and inbred for four generations, was used (Wyss and Müller-Schärer, 1999). To prevent crop damage by thrips (*Thrips tabaci* Lind.), leek moth (*Acrolepiopsis assectella* [Zeller]), late blight of celery (*Septoria apicola* Speg.) and leek rust (*Puccinia allii* [DC.] Rud.), insecticide and fungicide treatments were applied in both experiments as necessary. To protect *S. vulgaris* from infection by *Puccinia lagenophorae* Cooke, a specific rust disease of common groundsel, the foliage was treated twice until run-off with Cyproconazole 0.4% v./v. (Alto 100 SL 100 g L^{-1} Cyproconazole, Novartis AG, Switzerland). Weeds that germinated in spite of the soil fumigant treatment were removed manually. Fertiliser (P_2O_5, K_2O and Mg) was applied according to soil analysis before planting to provide 60 kg P ha^{-1}, 180 kg K ha^{-1} and 30 kg Mg ha^{-1}. To

prevent nitrogen deficiency, a buffer of 70 kg N ha^{-1} was maintained in the rooting zone by applying nitrogen (as 27% ammonium nitrate) as top dressings after checking the content of mineral nitrogen (NH_4, NO_3) every 10 d and additionally after heavy rainfall. To prevent water shortage, both experiments were irrigated regularly as indicated by tensiometer measurements in the field.

Biomass and number of capitula of _S. vulgaris_ were measured in expt I at flowering, beginning 38 d after the weed was sown. In expt II, biomass and number of capitula were measured once at final harvest. Dry weight of the above-ground organs of six randomly-chosen plants per plot was measured. Samples of capitula from plants in which the pappus had just appeared were randomly taken after maturity to determine the number of seeds per capitulum. In 1997, seedlings that had germinated as offspring of planted _S. vulgaris_ were counted prior to harvesting the crop, using a 0.1 x 0.1 m grid placed randomly at three different locations per plot. Seedling counts were analysed using a generalised linear mixed model procedure in Genstat 5, assuming a Poisson distribution of the data (Keen and Engel, 1988).

The percentage of incident photosynthetically active radiation (_PAR_) intercepted by the canopy was measured weekly from 29 to 85 d after crop establishment in 1997, and 20 to 90 d after crop establishment in 1998. The fraction of _PAR_ intercepted was calculated by taking ten readings in rapid succession above the canopy and ten readings below the canopy at the soil surface using a 0.6 m long Ceptometer CEP (Decagon Devices, Pullman, Washington State, USA). The soil surface measurements were taken by placing the ceptometer at right angles to the plant rows. The mean of each set of ten readings was used in logistic models to obtain, via interpolation, daily estimates of the fraction of _PAR_ intercepted (Goudriaan and Monteith, 1990):

$$y = a + c / (1+\exp(-b\,(t-m)))$$ [3.1]

where y is the fraction of _PAR_ intercepted by the canopy, a and $a+c$ are the lower and upper asymptotes, m is the time when 50% of incoming _PAR_ is intercepted by the canopy (F_iPAR_{50}), b is proportional to the slope at F_iPAR_{50}, and t is the time in days from crop establishment. A linear model was used to describe light interception by leek and a negative exponential model (eqn [3.2]) was used to describe light interception by intercrop and celery in expt I, because early observations were lacking.

$$y = a + b\,c^t$$ [3.2]

where y is the fraction of intercepted *PAR* by the canopy, a, b, and c are parameters, and t is the time in days from crop establishment. Differences for maximum intercepted *PAR* (upper asymptote) as well as for F_iPAR_{50}, estimated for the crop stands, were tested by ANOVA after testing homogeneity of variances, using the Genstat 5 statistical package (Payne *et al.*, 1987).

Experiments III, IV, and V (leek canopies with defined light interception levels and individual potted plants of S. vulgaris*)*

In 1997, three glasshouse experiments, referred to as experiments III, IV and V, were carried out in which *S. vulgaris* was grown in pots and exposed to different light levels (0, 30, 50 and 70% of incident *PAR*). The experiments were performed in late spring (III), summer (IV) and early autumn (V) to account for different light quality at different times during the growing season. To provide the required level of shading, leek canopies of 1 m x 1 m were arranged in an open-top glasshouse using 20 cm clay pots, each containing 5 leek plants. To keep the fraction of intercepted *PAR* constant during the experiment, the density of the leek canopy was adjusted by moving the pots apart as the leek plants grew. The leek plants were protected from disease and pest attack using commercially available pesticides.

Seeds of *S. vulgaris* were germinated in 9 cm plastic pots containing a nutrient amended peat soil (Floragard TKS 2, GVZ, Zürich, Switzerland). The plants were grown in a controlled climate chamber (night/day: temperature: 23/17 °C ± 1 °C; relative humidity: 40/60%; photoperiod: 16 h d^{-1}; *PAR* flux: 260 µm m^{-2} s^{-1}) until the appearance of the first true leaves. After hardening for one day in the open-top glasshouse, 25 visually identical *S. vulgaris* plants were placed between the leek pots, such that they experienced homogeneous shading by the leek plants. To ensure natural light quality, the glass cover of the glasshouse was removed whenever the conditions allowed. Plants were treated twice until run-off with 0.4% v./v. Cyproconazole to prevent infection of *S. vulgaris* by *P. lagenophorae*. The water and nutrient requirements of the leek and *S. vulgaris* plants were met using a multinutrient fertiliser solution (FLORY 3, N:P:K:Mg=15:10:15:1.2, incl. seven micronutrients, Hauert, Grossaffoltern, Switzerland).

The dry weight of the above-ground organs and the number of capitula per plant of *S. vulgaris* were determined after the plants had reached maturity, and capitula:shoot ratio was calculated. Leaf area was determined for three separate layers: the top-, the centre- and the bottom-third of the plants. Random samples of seeds were collected over a period of 20 d from capitula in which the pappus had just

appeared. Number and weight of air-dried seeds per capitulum were determined. From the number of capitula per plant and the number of seeds per capitulum, the seed production per plant was calculated. Differences between means of treatments were tested by ANOVA, using the Genstat 5 statistical package.

Seed viability was tested by monitoring the cumulative germination of four lots of 50 seeds in an incubator under a photoperiod of 16 h d^{-1} and a light/dark temperature regime of 20 °C/15 °C. Non-linear regression techniques, fitting Gompertz curves (eqn [3.3]), were used to describe the time course of the cumulative germination (Tipton, 1984; Brown and Mayer, 1988):

$$y = a \exp[-\exp(-b\,(t-m))] \tag{3.3}$$

where y is the cumulative proportion of seeds which germinated, a is the asymptotic value of y, b is the germination rate, m is the time lag for the start of germination, and t is the time in days. After testing homogeneity of variances, ANOVA was performed on estimated parameters using the Genstat 5 statistical package.

Results

Experiments I (1997) and II (1998)

A characteristic pattern of light interception was found for each crop canopy (Fig. 3.1). The models applied fitted all data sets well ($r^2>0.95$) and residual variances were distributed homogeneously around the fitted curves (Table 3.1). In expt I, light interception by the leek monoculture increased linearly, reaching around 80% interception of _PAR_ at the time of crop harvest. In contrast, the leek-celery mixture and celery pure stand showed a steep increase from 30 d after planting onwards, approaching 100% light interception at about 70 d after planting (Fig. 3.1A). In expt II, the leek pure stand reached 50% interception of incident _PAR_ (F_iPAR_{50}) 16 d later than the intercrop, and the highest recorded fraction of intercepted _PAR_ was significantly lower than that of the intercrop. F_iPAR_{50} for the pure stand of celery was reached 8 d earlier than for the intercrop but there was no significant difference in light interception at final harvest between celery pure stand and the intercrop.

With delay in emergence of the weed the biomass of _S. vulgaris_ was progressively reduced, as a result of increased light interception by the crop canopies (Tables 3.2 and 3.3).

Table 3.1 Estimated parameters and goodness of fit for linear, negative exponential and logistic functions of the fraction of intercepted *PAR* in the crop stands and densities of experiment I (1997) and experiment II (1998).

Crop stands		Estimated parameters			
1997	Model	a	b	c	R^2
Leek pure stand	$y=ax+b$	0.01 (0.001)*	-0.32 (0.06)	–	0.96
Intercrop	$y=a+b\,c^x$	1.07 (0.070)	-2.50 (0.34)	0.96 (0.006)	0.99
Celery pure stand	$y=a+b\,c^x$	0.98 (0.020)	-4.84 (0.91)	0.93 (0.007)	0.99
1998 $y=a+c/(1+exp(-b(x-m)))$	a	$a+c$	b	m	R^2
Leek pure stand	0.06 (0.03)	0.85 (0.060)	0.08 (0.01)	56.98 (2.15)	0.98
Intercrop	-0.19 (0.09)	1.06 (0.150)	0.07 (0.02)	40.14 (1.26)	0.99
Celery pure stand	-0.23 (0.13)	0.99 (0.010)	0.08 (0.01)	31.89 (3.16)	0.99

* Numbers in brackets are standard errors of means

Table 3.2 Effect of relative time of emergence on the biomass (g m^{-2}) of stands of *Senecio vulgaris* L. 38 d after sowing into crops of leek and celery (expt I, 1997).

Crop stand	Relative time of emergence (d)			
	10	20	30	40
Leek pure stand	41.1*	45.3	9.0	6.3
Intercrop	34.9	19.0	2.2	0.4
Celery pure stand	29.6	2.3	0.6	0.04
SEM		10.25		

* The values are means of 3 observations

Table 3.3 Effect of relative time of emergence on the biomass (g m^{-2}) of stands of *Senecio vulgaris* in crops of leek and celery 90 d after crop establishment (expt II, 1998).

Crop stand	Relative time of emergence [d]					
	0	10	20	30	40	SEM
Leek pure stand	191.1*	137.3	43.0	39.4	12.1	
Intercrop	117.1	57.3	19.4	4.8	1.1	12.9
Celery pure stand	164.9	61.5	7.2	0.6	0.009	
S. vulgaris pure stand	222.1	–	–	–	–	

* Values are means of 3 observations

Weeds were less suppressed in the monoculture of leek for all dates of weed emergence than for the other crop stands, and this effect was most obvious for the later dates of emergence. In both experiments, no significant difference was detected between the intercrop and the pure stand of celery in their suppression of _S. vulgaris_.
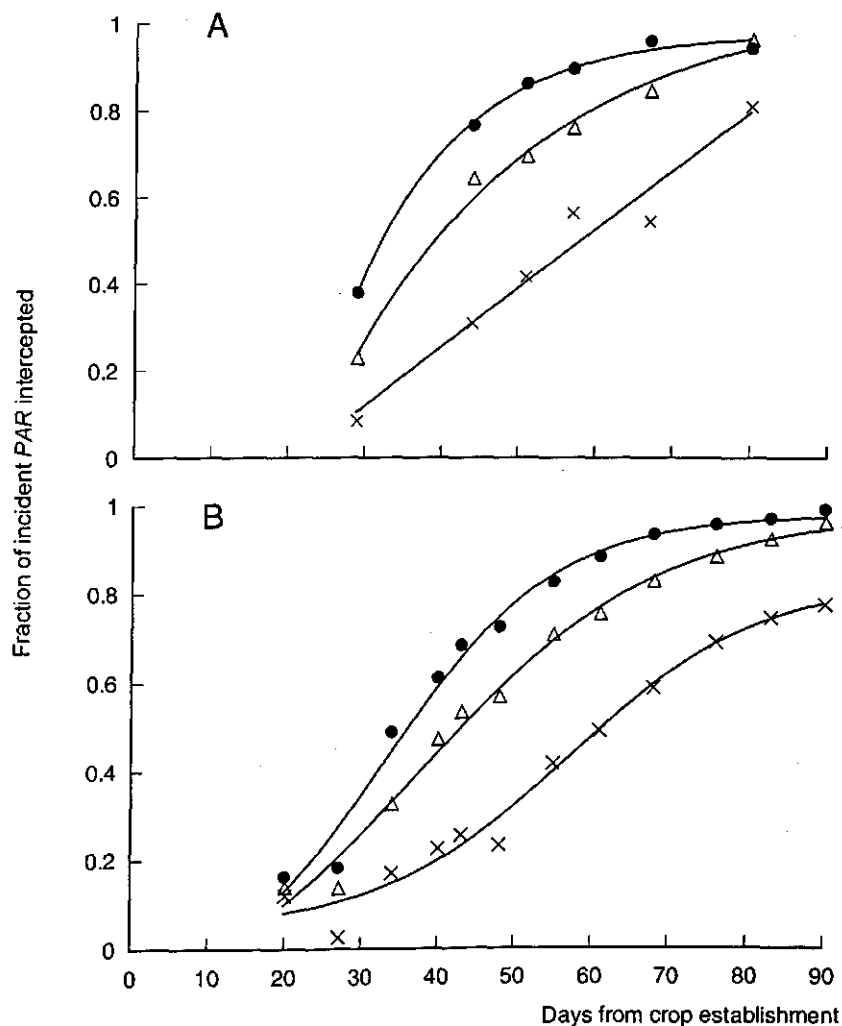
Fig. 3.1 Time courses of the fraction of incident _PAR_ intercepted by the leek pure stand (✕), the leek-celery intercrop (△) and the celery pure stand (●) in expt I, 1997 (A), and expt II, 1998 (B). Symbols are observed data; lines are fitted curves (expt I: leek = linear, intercrop and celery = negative exponential (eqn. [3.2]); expt II: all crop stands = logistic, (eqn. [3.1]).

In both experiments, competition of light reduced the number of capitula produced by *S. vulgaris* (Fig. 3.2). In expt I, in which the number of capitula was counted 48 d after crop establishment, differences between all crop stands were significant for the earliest planting date of *S. vulgaris*. Capitulum formation in plants that emerged 20 d after crop establishment was significantly reduced by the intercrop and celery pure stand compared with the leek monoculture. For later planting dates, no significant differences between cropping systems were detected.
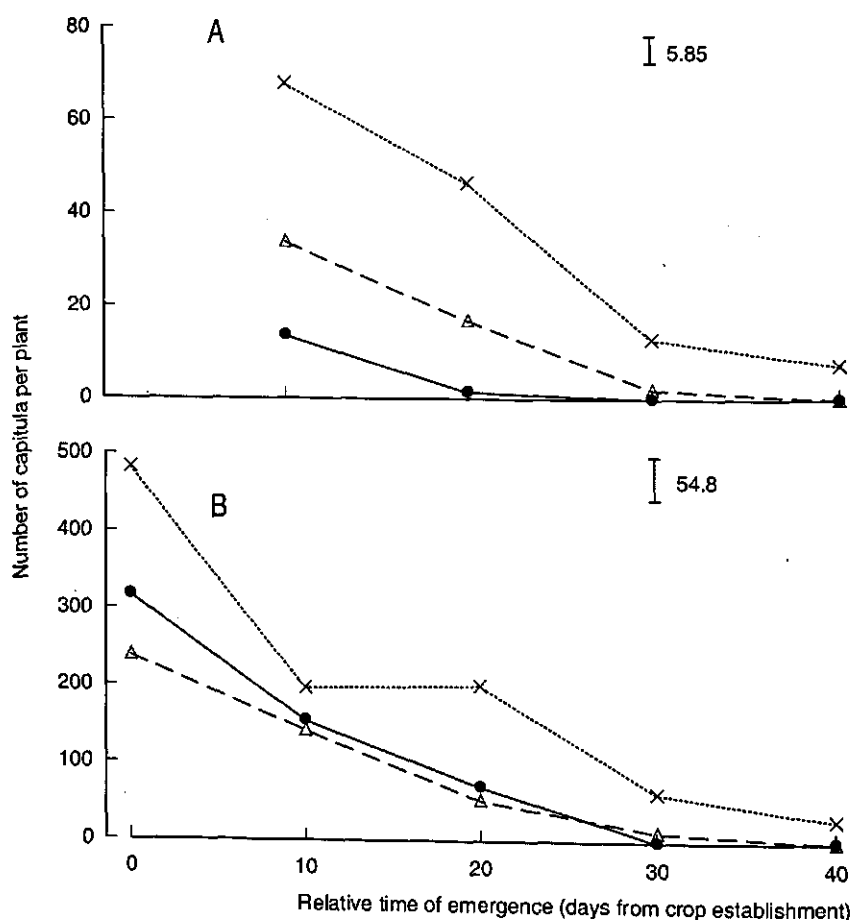
Fig. 3.2 Effects of relative time of emergence on the number of capitula per plant produced by *Senecio vulgaris* grown in the leek pure stand (···✕···), the leek-celery intercrop (--△--) and the celery pure stand (-●-) in expt I, 1997 (A), and expt II, 1998 (B). For *Senecio vulgaris* grown in monoculture (expt II), there were 600 capitula per plant. Vertical bars indicate standard errors of means.

In expt II, in which the number of capitula was counted 90 d after crop establishment, differences between crop canopies were less pronounced. For the first planting date, capitulum production was reduced significantly, compared with the *S. vulgaris* monoculture, only by the intercrop and celery pure stand. In expts I and II, the number of capitula formed by late-emerging plants (e.g. 40 d after crop establishment) in leek was reduced by 89 and 94% compared with early-emerging plants. In the intercrop and celery monoculture, no capitula were formed by late-emerging *S. vulgaris* plants (Fig. 3.2).

Crop stand had no effect on the number of seeds per capitulum that was observed for the first three planting dates of *S. vulgaris*. Only when the weed plants were planted 30 d after crop establishment in the celery monoculture and in the intercrop was the number of seeds per capitulum reduced, virtually to zero (expt II, Fig 3.3A).

Seed production of the pure stand of *S. vulgaris* was typically about 25000 seeds per plant (data not shown). In expt II, seed production per plant was reduced by 37 and 60% in competition with the leek-celery mixture and the celery monoculture, respectively, when the weeds were planted at the same time as the crop. In contrast, for the leek pure stand, no significant reduction was observed. Differences between seed production of later emerging *S. vulgaris* were less pronounced under different cropping systems, although, when the weeds emerged 20 and 30 d after crop establishment, significantly fewer seeds were produced in the intercrop and celery monoculture than in the leek monoculture (Fig. 3.3B). No interaction was detected between relative time of emergence and cropping system. Seed production of *S. vulgaris*, which was planted 30 days after establishment of leek monoculture, intercrop, and celery monoculture, was reduced by 89, 97 and 100%, respectively, relative to *S. vulgaris* sown at crop establishment.

In expt I, when *S. vulgaris* was planted 10, 20 and 30 d after crop establishment, average densities of 7807, 6267 and 770 daughter seedlings m^{-2} were found in the leek monoculture, whereas densities of 360, 138 and 304 seedlings m^{-2} were found in the intercrop. In the celery monoculture, germinating offspring were observed only in a single plot (rep 3, 20 d after crop establishment: 200 seedlings m^{-2}). Similarly, no *S. vulgaris* seedlings were observed in either of the two other crop stands if mother plants were sown 40 d or later after crop establishment.

Experiments III, IV and V (1997)

In de pot experiments, as in the field experiments, the biomass of above-ground organs of *S. vulgaris* was significantly reduced as competition for light with the crop
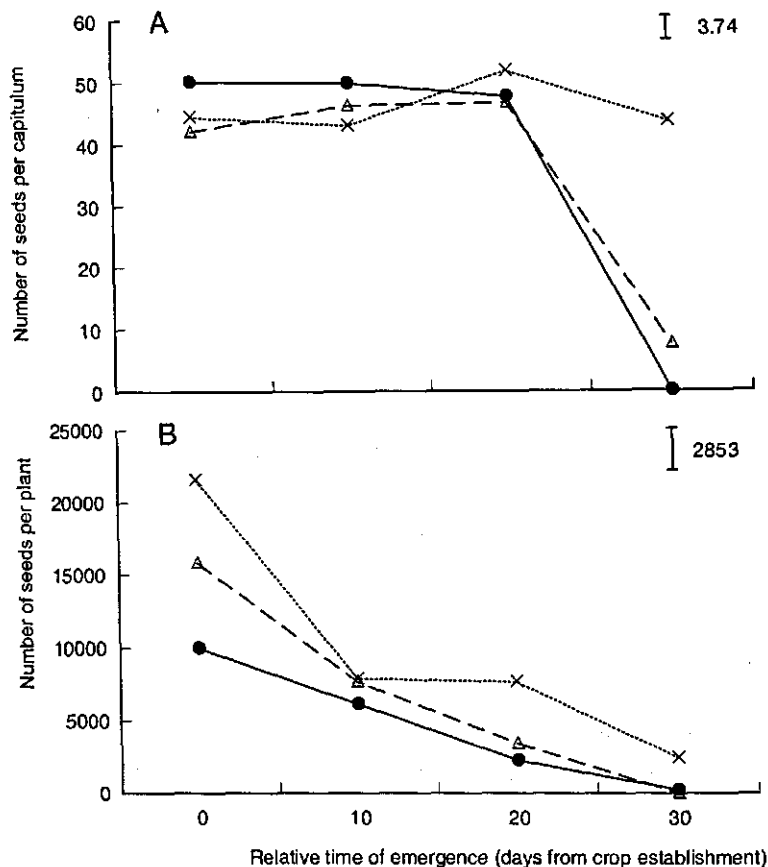
Fig. 3.3 Effects of relative time of emergence on (A) the number of seeds per capitulum and (B) on seed production per plant of *Senecio vulgaris* grown in the leek pure stand (···×···), the leek-celery intercrop (--Δ--) and the celery pure stand (-●-) in expt II, 1998. For *Senecio vulgaris* grown in monoculture, there were 51 seeds per capitula and 25173 seeds per plant. Vertical bars indicate the standard errors of mean.

increased (Fig. 3.4). Furthermore, reproductive allocation was reduced more than total plant biomass (Fig. 3.4). As a result, the capitula:shoot ratio, which can be used as a crude measure of the relative reproductive effort of the weed plants, dropped from 0.42 to 0.29 with increasing competition for light. Up to 50% shading, leaf weight was reduced only slightly, but it dropped significantly under 70% shading (Table 3.4).

Due to a near doubling in specific leaf area, the total leaf area of the plant was not changed significantly. The leaf area distribution changed as more shading occurred, with more leaf area occurring in the top-third of the canopy (Table 3.4). Moreover, the plants were taller, but stem weight did not change (data not shown).
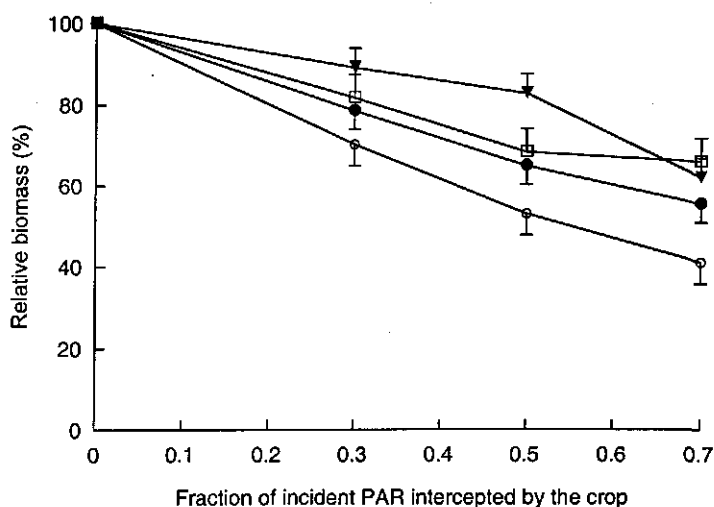
Fig. 3.4 Effects of competition for light on dry matter partitioning to leaves (▼), stems (□), capitula (○) and whole plants (●) of _Senecio vulgaris_ (expt III, 1997). Vertical bars indicate the standard errors of means.

Table 3.4 Effect of competition for light with a leek canopy on plant height, leaf weight, specific leaf area (_SLA_) and vertical leaf area distribution of plants of _Senecio vulgaris_ L. (expt III, 1997).

Plant level	Fraction of incident _PAR_ intercepted by the leek canopy				
	0	0.3	0.5	0.7	SEM
Plant height (cm)	32.90*	36.40	35.00	46.10	1.11
Leaf weight (g plant^{-1})	0.36	0.32	0.30	0.22	0.02
SLA (cm^2 g^{-1})	2.71	2.87	2.81	4.10	0.18
Leaf area (cm^2 plant^{-1})					
Top-third	6.59	7.37	4.40	18.66	1.54
Centre-third	32.53	32.48	34.61	37.22	9.48
Bottom-third	56.89	50.54	51.80	34.12	4.18
Total plant	96.01	90.39	83.89	90.00	6.55

* The values are means of 20 observations

Shading had no effect on the number of seeds produced per capitulum (Fig. 3.5B) but significant differences were found between experiments, representing the effect of season. Increasing light interception by the crop reduced the number of capitula per plant significantly, and the total number of seeds per plant was similarly reduced (Fig. 3.5A, C).
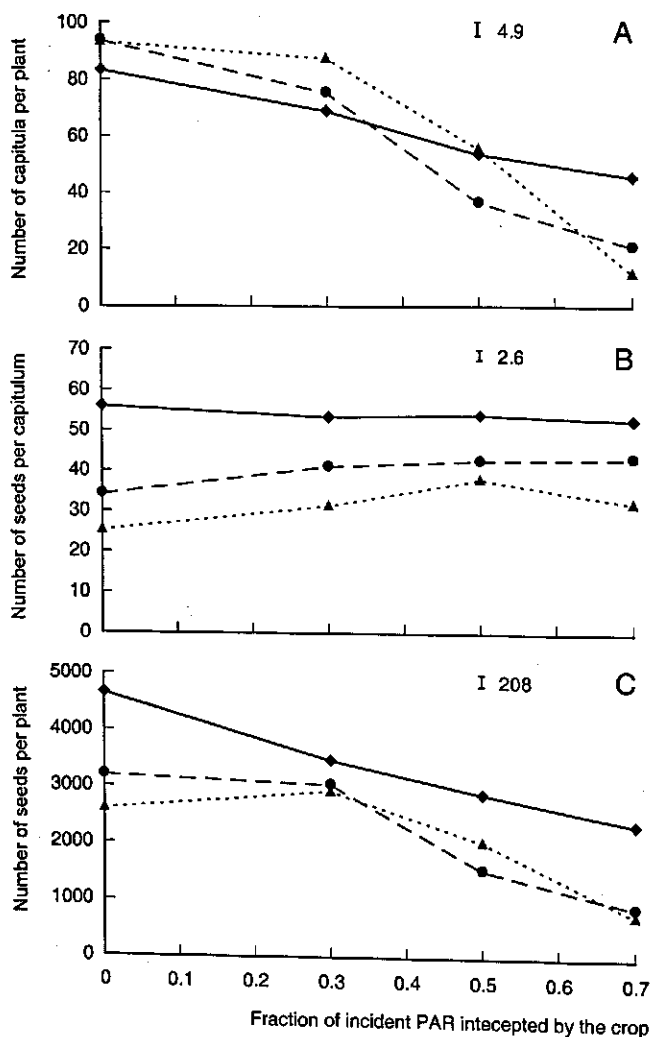
Fig. 3.5 Effect of competition for light on (A) the number of capitula per plant, (B) the number of seeds per capitulum and (C) the number of seeds per plant, of *Senecio vulgaris* in three experiments (—◆—, expt III, late spring 1997, —●—, expt IV, summer 1997, ···▲···, expt V, early autumn 1997). Vertical bars indicate the standard errors of the means.

On average, seed production in expts III, IV, and V, was reduced by 8, 36 and 64%, respectively, as light competition by the crop increased from 0 to 70%. In expt III there was a linear relationship between fecundity (number of seeds per plant) and individual plant dry weight of _S. vulgaris_ (Fig. 3.6).

Non-linear regression, using a Gompertz model, described the data from the germination tests of _S. vulgaris_ seeds well (r^2=0.97-0.99). No direct effect of the competition for light experienced by the mother plant could be detected on the viability of seeds produced. Neither the final germination percentage nor the germination rate was affected, and germination was only slightly delayed for seeds produced under intense competition for light in one experiment (Fig. 3.7).
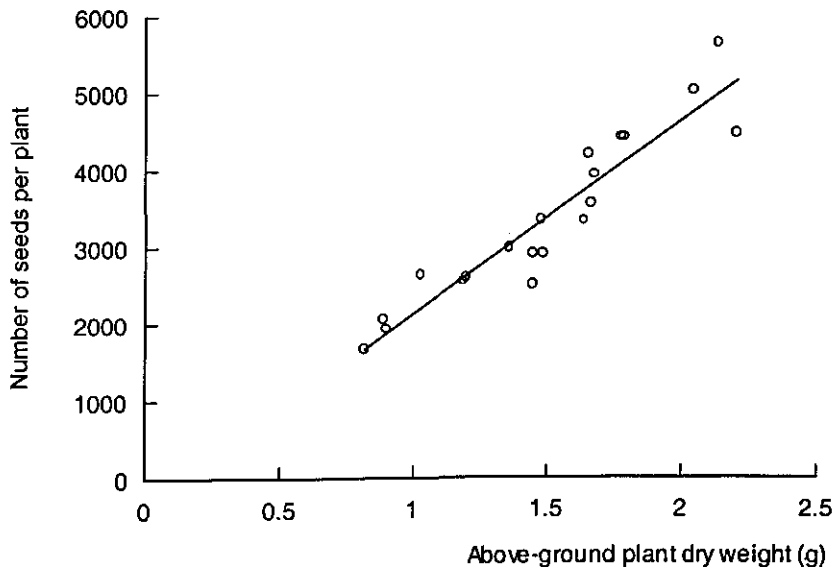
Fig. 3.6 Linear relationship between number of seeds per plant and above-ground dry weight per plant in expt III, 1997 [slope 2262.0 (SE=57.0), intercept not significantly different from zero, r^2 = 0.99).
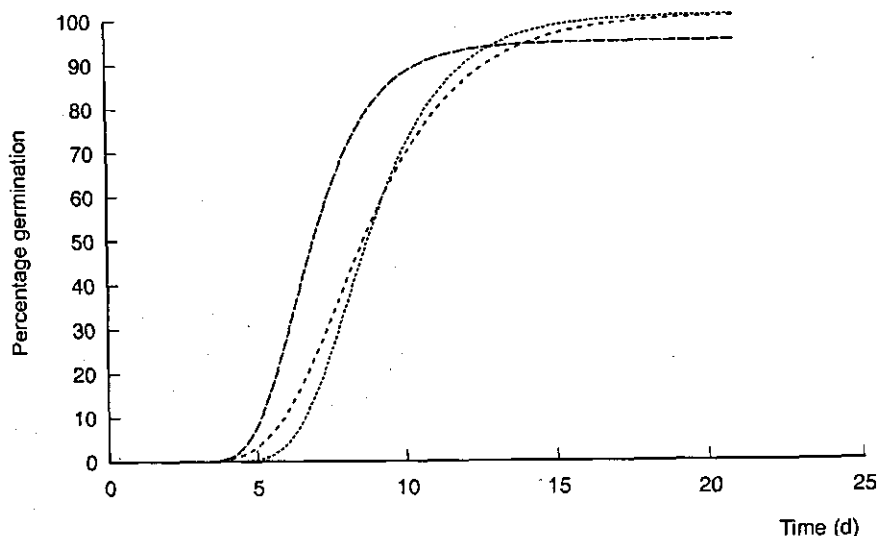
Fig. 3.7 The effects of shading of the mother plant by leek canopies (intercepting 0% [—],
30% [– –], 50% [---], and 70% [···]) on the germination of the subsequent generation of seeds
of *Senecio vulgaris*, (expt III, 1997).

Discussion

Light interception in monocultures and intercrop

The shapes of the light interception curves of the canopy of a leek-celery
intercrop reflect the faster leaf area development and more horizontal growth habit of
the celery leaves, and it explains the superior competitive ability of the intercrop
canopy compared with the leek monoculture (Fig. 3.1). Due to the faster leaf growth
and the morphology of the celery plants, suppression of *S. vulgaris* occurred
significantly earlier, thus shortening the critical period for weed control. Since the
plants were provided with unlimited water and nutrients, it can be assumed that the
suppressive effects of the crop were exclusively related to competition for light.

*Effects of competition for light on growth, morphology, seed production, and quality
of Senecio vulgaris L.*

S. vulgaris plants that emerged 20 d after crop establishment, or later, were
outcompeted by the intercrop and the celery pure stand, whereas the leek

monoculture suppressed *S. vulgaris* effectively only when the weed had been established 40 d after the crop, or later (Tables 3.2 and 3.3).

A reduction in the fecundity of *S. vulgaris* as a result of delayed emergence was found in all crop canopies, although it occurred earlier and was significantly greater in the intercrop and celery pure stand than in the leek monoculture. Schnieders (1999) described the same effect for *S. vulgaris*, *Solanum nigrum* L. and *Chenopodium album* L. when grown in competition with witloof chicory (*Cichorium intibus* L.). Other studies have shown a strong effect of the relative time of emergence on the competitive strength of a species (e.g. Lotz *et al.*, 1993; Schnieders and Lotz, 1993). Analysis of the components determining the fecundity of *S. vulgaris* shows that the decrease of seed production per plant was mainly a result of a reduced production of capitula (Figs. 3.2 and 3.5). A similar effect was reported for *Sonchus arvensis* L. by Zollinger and Kells (1991), who found that a 72% reduction in light intensity reduced capitulum production six-fold. It can be assumed from the observed effects that effective suppression of the reproductive capacity of *S. vulgaris* can be achieved if competition for light occurs during the induction of capitula. The number of seeds per capitulum remained constant under various levels of light stress and was lowered only when, under very high competition for light, capitulum formation was minimised (Fig. 3.3A).

In the glasshouse experiments, seed production of *S. vulgaris* was linearly related to plant size (Fig. 3.6). The same effects were found in the field (expt II) if seed production and plant weight from plants established at the same relative time of emergence were compared. Linear relationships between vegetative plant size and reproductive weight have been found for many species (Wilson *et al.*, 1988; Thompson *et al.*, 1991; Wright, 1993). Moreover, Schnieders (1999) reported that the relationships between vegetative plant size and total reproductive weight, number of seeds or 1000-seed weight, are very robust for *S. vulgaris*, *S. nigrum* and *C. album* under a wide range of competitive stresses and growing conditions. The model of Samson and Werk (1986) shows that reproductive effort (i.e. the ratio of reproductive weight to vegetative weight) may or may not change with plant size, depending on the value of the intercept of the regression of reproductive weight against plant size. Schnieders (1999) found, for *S. vulgaris*, that intercepts do not differ significantly from zero, as confirmed by the current study, indicating that reproductive effort does not change with plant size. Harper and Ogden (1970), also found that reproductive effort of *S. vulgaris* 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.

The partitioning of biomass to stem, leaves and capitula changed as light supply decreased (Fig. 3.4): whereas leaf biomass decreased, total leaf area remained constant and the specific leaf area doubled (Table 3.4). The amount of radiation available for photosynthesis was therefore proportional to the irradiance and not affected by reduced leaf biomass. Moreover, *S. vulgaris* was able to compensate for the reduced leaf biomass by changing the vertical leaf area distribution (Table 3.4) and possibly, by increasing the radiation use efficiency (*RUE*) because *RUE* tends to be higher at lower light levels (Goudriaan and Van Laar, 1994).

The ability of *S. vulgaris* to adjust its morphology under low light conditions shows its high phenotypic plasticity. Harper (1977) described *S. vulgaris* as an "opportunistic" plant, capable of adapting to produce seeds under a wide range of environmental conditions. Variation in number, size, and distribution of above- and below-ground plant parts reflects plastic adjustments in the allocation of assimilates (Grime, 1979). Paul and Ayres (1987) observed only small differences in the pattern of dry weight partitioning between healthy and rust-infected *S. vulgaris* plants, whereas Theaker and Briggs (1993) found that *S. vulgaris* showed a great deal of developmental flexibility and phenotypic plasticity.

Seed viability was unaffected by the light supply to the parent plants (Fig. 3.7). As part of its reproductive strategy the plant ensures the viability of seeds by forming fewer fully effective capitula. Weiner (1988) concluded that plants reduce their seed output primarily by producing fewer seeds, but also secondarily, by producing smaller seeds. A lack of plasticity in the response of seed weight to increased competition was also noted by Harper (1977). For other species, such as *C. album* and *Echinochloa crus-galli* L., a reduced germination percentage was found for seeds produced under higher competition for light (Paolini *et al.*, 1999). Smaller seeds have been associated with lower germination percentages (Weis, 1982; Lotz, 1989), lower rates of germination (Weis, 1982), lower leaf area and biomass of the seedlings (Weis, 1982; Wulff, 1986b), and a decreased competitive ability of the resulting seedlings (Wulff, 1986a). Experimental and simulation studies on crop-weed competition have shown that late emergence, and slow leaf area development during early growth stages, lower the competitive ability of weeds significantly, and hence reduce the yield loss by the associated crop (Kropff *et al.*, 1992; Kropff and Van Laar 1993). Thus, competition wit the crop may not only reduce the reproductive output of weeds, as found here for *S. vulgaris*, but may also reduce the competitive ability of their offspring. However, this was not observed in the present study of *S. vulgaris*.

So far only competition for light has been considered, as water and nutrients are not limited in high-input vegetable production systems. However, Harper and Ogden

(1970) observed a significant reduction of the biomass and fecundity of *S. vulgaris* if root competition was increased, and they considered that the reproductive strategy of *S. vulgaris* was typical for many annual weed species. There may, therefore, be possible interactions between competition for light, water and nutrients. Additional stress factors, such as pathogens attack and herbivores, may also increase the degree of stress experienced by *S. vulgaris* in competition with crops.

Competition and crop performance in a leek-celery intercropping system

Abstract

In an intercropping system with leek (*Allium porrum* L.) and celery (*Apium graveolens* L.) weed suppression is improved through increased canopy light interception. Intra- and interspecific competition in the system, however, affects the performance of the crops with respect to yield and quality. The objective of the study was to quantify intra- and interspecific competition by leek and celeriac or celery in an intercropping system. A three-year study was carried out to investigate the effects of plant density, relative proportion of component crop, spatial arrangement, and nitrogen input on biomass production, crop quality, and nitrogen use in an intercropping system with leek and celeriac or celery. Land equivalent ratios exceeding unity were found, indicating an improved resource use by the crop mixture. Relative yield totals around one showed that with respect to biomass production no yield advantage was found in the crop mixture. Analyses using a hyperbolic yield density response model showed that the competitive ability of celeriac and celery was significantly higher than that of leek. Effects of intra- and interspecific competition resulted for both crops in a reduction of the quality. Nitrogen use efficiency was generally poor in all crop stands, particularly at a high nitrogen application rate. The intercropping system needs improvement with respect to crop quality and it is suggested to apply eco-physiological crop growth models to maximise crop complementarity on one hand and competitive ability against weeds on the other hand.

Introduction

There is a resurgence of interest in intercropping systems because the advantages of intercropping[1] are by no means restricted to low-input and small-scale agricultural systems (Andrews and Kassam, 1976). Agronomists, physiologists, and ecologist are intrigued by the potential of extending resource use and the biological stability improving self regulation within integrated crop protection (ICP) in particular and integrated crop management (ICM) in general. Already in the 1970s and 1980s an increasing interest in intercropping resulted in a large number of comprehensive reviews on this topic (Francis, 1986; Papendick *et al.*, 1975; Trenbath, 1974; Vandermeer, 1989; Willey, 1979a;b; and others) and the research activities increased tremendously (Francis, 1986). Research focused mainly on resource use, and productivity but reduction in damage caused by pests were observed as well (Altieri and Liebman, 1986; Coaker, 1988; Müller-Schärer and Baumann, 1993; Imhof *et al.*, 1996). Weed management in intercrops, however, has hardly been studied to date (Moody and Shetty, 1979; Altieri and Liebman, 1986). Provided that interference between component crops is weaker than that between crops and weeds, intercropping can suppress the growth of weeds more than sole cropping (Yih, 1982). Within a larger program focusing on the use of intercropping as a cultural method to suppress weeds (Baumann *et al.*, 2000), the current study aims to investigate competition and performance of component crops in an intercropping system. The authors proposed to improve the suppressive ability of a leek canopy by intercropping it with celery. Leek, like many other *Allium* crops, is known as a weakly competitive crop due to its slow juvenile growth and the open crop canopy, which does not cover the soil until harvest. Consequently, weeds continue to emerge throughout the whole growing season causing high cost for weed management practices and, in case of insufficient control, yield and quality losses. It was assumed that the properties of celery or celeriac as companion crop with respect to soil cover and light interception would supplement those of leek. Baumann *et al.* (2000) have shown that for the intercrop a higher light interception of the crop canopy could be achieved, resulting in a better weed suppression of the intercropped leek compared to its pure stand. As a result not only weed biomass was decreased in the crop

---

[1] There is some variability in the use of different terms for intercropping. In this paper the terms "intercrop" and "crop mixture" are used synonymously for the mixture of two cash crops which are grown simultaneously on the same area. "Component crop" is used to refer to either one of the individual crops making up the intercropping situation, whereas "sole crop", "pure stand" or "monoculture" refer to a component crop being grown alone.

mixture but also the weed seed production was significantly reduced (Baumann _et al._, 1999). Light competition was recognised as the main factor promoting intercrop dominance over weeds. Canopy suppressive ability was therefore considered of critical importance in the design of effective weed management strategies in intercropping systems. To maintain intercrop yield and quality, however, complementarity in patterns of resource use must be taken into account. The goal of the study is to minimise the degree of competition between the crop species, to avoid yield and quality damage and at the same time to create a high level of competition by the intercrop to suppress the weeds. Important factors affecting competition between intercrop and weeds are the crop density and closely related to that the relative proportion of component crops as well as the spatial arrangement. Other factors, such as crop cultivars, weed community composition, herbivores, and pathogens, soil conditions and many more play an important role as well. Farmers will only accept such a system if yield and quality of the component crops will be about the same as in the sole cropping system. The practicability and possibilities for mechanisation and improved labour efficiency are critical as well for the adoption of an intercropping system by high-technology farmers, such as vegetable producers in developed countries.

In this study, intra- and interspecific competition between the component crops in a leek/celery intercropping system were analysed in multiple field experiments. In this paper the results of these experiments are presented and discussed with emphasis on yield and quality of the component crops in the intercrop system.

Material and Methods

Three field experiments, referred to as experiment I, II and III, were carried out on a sandy loam soil (Inceptisol; 17% clay, 24.5% silt, 54.2% sand, pH 7.8, 4.3% organic matter) at the experimental farm "Sandhof" of the Swiss Federal Research Station for Fruit-Growing, Viticulture and Horticulture, at Wädenswil, Switzerland (47°13' N, 08°40' E). To study intra- and interspecific competition in an intercrop system with leek-celery (or celeriac), experiments with a bivariate factorial design as described by Snaydon (1991) were conducted in 1995 (expt I) and 1996 (expt II). The effect of different nitrogen levels on interplant competition was additionally studied with a replacement series experiment in 1997 (expt III).

Experiment I and II (competition experiments with bivariate factorial design)

In 1995 and 1996, bare-root transplants of leek cv. Zefa Plus with 4.2 and 4.4 mm thick pseudostems and a biomass of 0.43 and 0.26 g dry weight, respectively, were produced in nursery beds. For celeriac and celery, commercially available peat pot transplants of cv. Monarch (F1) and cv. Tall Utah (F1) with an average biomass of 0.62 and 0.43 g dry weight were used in 1995 and 1996, respectively. On 19 June 1995, leek and celeriac were manually planted into a plant bed which was cultivated twice on the previous day, using a rotary cultivator. On 30 May 1996, leek and celery were treated the same. Prior to planting, roots and leaves of the leek transplants were trimmed according to standard practice. Planting depth of leek was 8 cm, whereas celeriac and celery peat pots were shallowly placed and slightly covered with soil. For accurate plant to plant distance and planting depth an adjustable hole-puncher was used.

Celery instead of celeriac was used in experiment II as celery in many countries is economically more important than celeriac. Though there are morphological differences between celeriac and celery leaf growth habit, relative leaf area development and other morphological parameters, largely determining light interception and hence competition, do not differ remarkably between the two variants of *Apium graveolens*.

Inter-row spacing was 0.5 m in 1995 and 0.25 m in 1996 whereas in-row spacing was dependent on plant density according to the different treatments (Table 4.1). Intercrop treatments of a bivariate factorial design (Snaydon, 1991) were designed as row by row replacement series. A factorial block design with 4 replicates and blocks arranged transversal to the slope (2.5%) of the experimental site was used. Plot size in 1995 was 3 x 4.5 m and in 1996 2.25 x 2 m. One week after planting the soil was treated with a tank-mixture of 1600 g a.i. ha^{-1} Pendimethalin (Stomp SC 400 g a.i. L^{-1}; Maag Agro, Dielsdorf, Switzerland) and 400 g a.i. ha^{-1} Chlorbromuron (Maloran WP 50% a.i., Novartis Agro AG, Basel, Switzerland) with a spray volume of 300 L ha^{-1}. Insecticide and fungicide treatments were applied to avoid crop damage by thrips (*Thrips tabaci* L.), leek moth [*Acrolepiopsis assectella* (Zeller)], late blight of celery (*Septoria apicola* Speg.) and leek rust [*Puccinia allii* (D.C.) Rud.] in both experiments. Base-fertilisation was carried out according to soil analysis prior to planting with P_2O_5, K_2O, and Mg to reach 60 kg P ha^{-1}, 180 kg K ha^{-1}, and 30 kg Mg ha^{-1}. To avoid nitrogen deficiency, a buffer of 70 kg N ha^{-1} was maintained in the rooting zone by applying nitrogen (as 27% ammonium nitrate) as top dressings after checking the content of mineral nitrogen (NH_4, NO_3) every 10 days and additionally after rainfalls over 20 mm. To avoid water shortage, the experiments were regularly irrigated based on tensiometer measurements in the field.

Table 4.1 Plant densities (plants m^{-2}) and in-row distances (m; between brackets) for plants of three intercropping experiments.

	Experiment I, 1995		Experiment II, 1996		Experiment III, 1997	
Inter-row distance	0.5 m		0.25 m		0.25 m	
Pure stands	Leek	Celeriac	Leek	Celery	Leek	Celery
	11 (0.18)	0	20 (0.20	0	18 (0.22)	0
	22 (0.09)	0	40 (0.10	0	0	9 (0.44)
	0	4 (0.50)	60 (0.67	0		
	0	8 (0.25)	0	10 (0.40)		
			0	20 (0.20)		
			0	30 (0.13)		
Mixed stands	5.5 (0.18)	2 (0.5.)	10 (0.20	5 (0.40)	9 (0.22)	4.5 (0.44)
	5.5 (0.18)	4 (0.25)	20 (0.10	10 (0.20)		
	11 (0.09)	2 (0.50)	30 (0.67	15 (0.13)		
	11 (0.09)	4 (0.25)	30 (0.67	19 (0.20)		

Biomass assessments were carried out at final harvest. Above-ground dry weight of 12 consecutive leek and 6 consecutive celery plants from the centre rows of each plot were measured after drying for 72 h at 70 °C. Relevant quality parameters for the different crops were measured. For leek this included per-plant weight, diameter and bleached part of the pseudostem and plant length. For celeriac, root weight and diameter, and for celery, weight and length of the above-ground plants were measured. Moreover, other quality related effects, such as crop injuries due to disease or pest attack were assessed.

Experiment III (replacement series with nitrogen levels), 1997

Leek cv. "Zefa Plus" and celery cv. "Ramon F1" were planted on 3 June 1997 in plant beds of 1.5 m width. Soil preparation was similar to experiments I and II. Bare root transplants of leek with 0.34 g dry weight were planted mechanically and commercial available celery peat pot transplants with a dry weight of 0.23 g were planted manually. Row distance and in-row plant distance are given in Table 4.1. Treatments consisted of two factors, crop stand and nitrogen, which were laid out as a randomised block design with four replicates. The stand included the replacement series of leek, celery, and the intercrop (Table 4.1). The levels of nitrogen were 0, 50, and 200 kg ha^{-1} of N applied as calcium ammonium nitrate with an N content of 27%.

Hereafter these nitrogen levels are denoted as N_0, N_{50} and N_{200}. N_0 was included to provoke strong competition effects, whereas at N_{200} nitrogen was meant to be available in ample supply. N_{50} was chosen to cover approximately 80% of the nitrogen demand of the crops, which was expected to give almost maximum yield (Booij, personal communication, 1997). N_{200} was manually broadcasted in three equal subsets, at planting, 42 and 64 days after planting, whereas N_{50} was split in two equal subsets, applied 42 and 64 days after planting. Fertilisation of P, K, and Mg, and the irrigation and protection of the crops against pests and diseases was similar as in experiment I and II, whereas the crops were manually kept weed free. At harvest above ground dry-weight of 6 consecutive leek and 6 consecutive celery plants from the centre row of each plot were measured.

Data analysis

For analysis of treatment effects on dry matter production and plant quality parameters ANOVA was performed using the Genstat 5 statistical package (Payne *et al.*, 1987). For comparison of means the standard errors of means (SEM) are given in each appropriate data table.

To study competition effects between the crops and to evaluate intercrop performance, different competition functions were calculated. For experiment I that was set up to be analysed as additive series, and replacement series, the land equivalent ratio (*LER*) was calculated. The *LER*, which was first described by Mead and Willey (1980), is calculated according to the following equation:

$$LER = \frac{Y_{1,2}}{Y_{1,1}} + \frac{Y_{2,1}}{Y_{2,2}}$$

[4.1]

where *Y* is the crop yield and the suffixes 1 and 2 denote crop 1 and crop 2 in the mixture. Thus, $Y_{1,2}$ is the yield of crop 1 when grown in mixture with crop 2 and $Y_{1,1}$ is the yield of crop 1 when grown in monoculture. The *LER* characterises the performance of an intercrop by giving the relative land area under sole crops, required to produce the yields achieved in intercropping. In experiment I the *LER* was calculated for the additive series consisting of 11 leek plants m^{-2} and additional 2 and 4 celeriac plants m^{-2}, respectively.

For all experiments the relative yield total (*RYT*), as described by De Wit (1960), was calculated as it is usually used for replacement series analysis. The calculation of *RYT* is basically the same as it is for *LER* (eqn. [4.1]). But where *LER* is used to

analyse additive series, the density of each component in the mixture is identical to its corresponding pure stand, for replacement series the relative total plant density remains constant for mixture and pure stands and the proportions of the components of the mixture varies. The relative crowding coefficient (k), which is a measure for the competition experienced by crop 1 when grown in mixture with crop 2 and *vice versa*, was calculated according to De Wit (1960) as:

$$k_1 = \frac{1 - p_1}{w_{1,1} / w_{1,2} - p_1}$$ [4.2]

where p is the ratio between the density of a crop in mixture and its density in monoculture in plants m^{-2}, w is the individual plant weight of the crop in g m^{-2} and the suffixes 1, and 2 are for crop 1 and 2, respectively.

Due to critical remarks on the use and analysis of additive and replacement designs by various authors (Jolliffe *et al.*, 1984; Firbank and Watkinson, 1985; Watkinson, 1985; Connolly, 1986; Snaydon, 1991; Sackville Hamilton, 1994; and others), an alternative approach was used which was proposed by Wright (1981), Watkinson (1981), and Spitters (1983a). This approach is based on the description of biomass-density response with a rectangular hyperbola (De Wit, 1960) and aims to relate the biomass production for each species to the density of both species in the mixture. With this model the yield of a component crop in the mixture $Y_{1,2}$ is calculated by:

$$Y_{1,2} = \frac{N_1}{b_{1,0} + b_{1,1} \cdot N_1 + b_{1,2} \cdot N_2}$$ [4.3]

where N_1 and N_2 are the plant densities in plants m^{-2} of crops 1 and 2, $b_{1,0}$ is the intercept denoting the reciprocal of the virtual biomass of an isolated plant of crop 1 in plant g^{-1} and $b_{1,1}$ and $b_{1,2}$ in $m^2 g^{-1}$ are parameters for intra- and interspecific competition, respectively. Their ratio denotes the relative competitive ability between both crops with respect to the production of the first crop. A similar ratio can be calculated with respect to the production of the second crop. Based on these competition coefficients the niche differentiation index (*NDI*) can be calculated (Spitters, 1983a):

$$NDI = \frac{b_{1,1}}{b_{1,2}} \cdot \frac{b_{2,2}}{b_{2,1}}$$ [4.4]

Non-linear regression using the Genstat statistical package (Payne *et al.*, 1987) was used to estimate the parameters and their variances.

To evaluate nitrogen use by different crop stands in experiment III, the fraction nitrogen recovery (F_R) (eqn. [4.5]), the agronomic efficiency (E_A) (eqn. [4.6]) and the utilisation efficiency (E_U) (eqn. [4.7]) of nitrogen were calculated.

$$F_R = \frac{U_F - U_0}{N_F}$$
[4.5]

$$E_A = \frac{Y_F - Y_0}{N_F}$$
[4.6]

$$E_U = \frac{Y_F - Y_0}{U_F - U_0}$$
[4.7]

where U_F is the uptake of N in kg ha^{-1} when the amount N_F of fertiliser-N in kg ha^{-1} is applied and U_0 is the corresponding uptake when no N is applied. Moreover Y_F and Y_0 are the yield in kg ha^{-1} at the corresponding fertiliser-N rates. Analogous to the calculation of *RYT*, the relative total nitrogen uptake (*RNT*) was calculated as the sum of the quotients between nitrogen uptake of a crop in mixture and in monoculture.

Results

The duration of the growth period was 105 days for experiments I and II in 1995 and 1996 and 90 days for experiment III in 1997. With a 3-year average temperature during the growing period of about 17 °C, cumulative precipitation of 500 mm, and an average daily global irradiation total of 17.2 MJ m^{-2}, the weather conditions were typical for the location in all years. Crop growth was not affected by unusual climate events such as exceptional drought, wetness, or hailstorms.

Experiment I, 1995

A significant density response for dry matter production was found for pure and mixed stands of leek and celeriac (Table 4.2). Doubling the density in the pure stands

increased the yield with 48 and 61% for leek and celeriac respectively. The highest total dry matter production was achieved with the pure stand of leek at 22 plants m^{-2} (837 g m^{-2}), whereas celeriac in its lowest plant density gave the lowest biomass production (359 g m^{-2}). Replacing leek by celeriac plants did not increase total biomass production. However, replacing half of the celeriac plants by 5.5 or 11 leek plants m^{-2} increased total biomass production by 37 and 61% respectively, compared to celeriac pure stand.

Table 4.2 Plant density and above ground biomass in pure stands and mixtures of leek and celeriac (Experiment I; Wädenswil, Switzerland, 1995).

Density (plants m^{-2})		Above-ground biomass (g m^{-2})		
Leek	Celeriac	Leek	Celeriac	Total
11	0	566	-	566
22	0	837	-	837
5.5	2	288	203	492
5.5	4	257	279	536
11	2	408	169	577
11	4	408	302	710
0	4	-	359	359
0	8	-	577	577
SEM (d.f.=15)*		38.8	45.8	52.8

* SEM = standard error of means (degrees of freedom)

The ratio of the indices for intra- and interspecific competition (Table 4.3) as calculated by non-linear regression using eqn. [4.3] was 0.3 for leek whereas it reached 3 for celeriac, indicating a higher relative competitive ability for celeriac than for leek. For the mixed stand of 11 leek and 4 celeriac plants m^{-2} a _LER_ of 1.56 was found, whereas the _RYT_ for the same mixture was 1.01 (Table 4.4) and a _NDI_ of 0.95 was calculated (Table 4.3). _RYT_'s of different mixtures did not differ significantly (SED=0.12) neither did the crowding coefficients (k) for leek (SEM=0.11) and celeriac (SEM=0.22) (Table 4.4), indicating that the two crops did not experience competition from one another. This is also visualised by the almost straight lines for leek and celeriac in the replacement series diagram (Fig. 4.1A). Doubling the leek density in the pure stand resulted in a significant reduction of the per plant weight and pseudostem diameter (Table 4.5). These quality parameters were not significantly affected in mixtures at the same leek density with added celeriac plant. In all mixtures

Table 4.3 Estimates and standard errors of intercept (b_{10}), intraspecific (b_{11}), and interspecific (b_{12}) competition for leek and celery and niche differentiation index (NDI; eqn. [4.4]) in experiment I (Wädenswil, Switzerland, 1995) and II (Wädenswil, Switzerland, 1996).

	1995				1996			
	Leek		Celery		Leek		Celery	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
b_{10}	0.01282	0.00267	0.00848	0.00267	0.00950	0.00175	0.00081	0.00085
b_{11}	0.00062	0.00015	0.00069	0.00040	0.00077	0.00005	0.00084	0.00006
b_{12}	0.00201	0.00066	0.00023	0.00022	0.00359	0.00032	0.00019	0.00004
b_{11}/b_{12}	0.3		3.0		0.2		4.4	
r^{2}*	0.92		0.8		0.97		0.91	
NDI	0.95				0.97			

* adjusted r^2

Table 4.4 Land equivalent ratio (LER), relative yield total (RYT) and relative crowding coefficient (k) for mixtures of leek and celery in experiment I (1995), II (1996) and III (1997); all experiments in Wädenswil, Switzerland.

Experiment		Plant density (plants m^{-2})		LER	RYT	k	
		Leek	Celery			Leek	Celery
I (1995)		11	2	1.19	1.07	0.95	1.21
		11	4	1.56	1.01	0.95	1.10
II (1996)		10	5	-	1.1	0.53	2.91
		20	10	1.1	1.0	0.49	1.91
		30	15	-	1.0	0.62	1.78
III (1997)	N_0	9	4.5	-	0.98	0.37	2.42
	N_{50}	9	4.5	-	0.97	0.39	2.19
	N_{200}	9	4.5	-	0.89	0.44	1.41

leek reached the quality requirements of the market. Leek in mixtures grew significantly taller, whereas the bleached part of the pseudostem tended to be longer at higher plant densities. Root weight and diameter of the celeriac was significantly lower when plant density was doubled from 4 to 8 plants m^{-2}. There was, however, no difference between pure stand and mixtures for root weight and diameter and the quality requirements of the market were met. For other effects reducing crop quality,

such as symptoms of diseases and pests, no significant differences where found between the treatments.
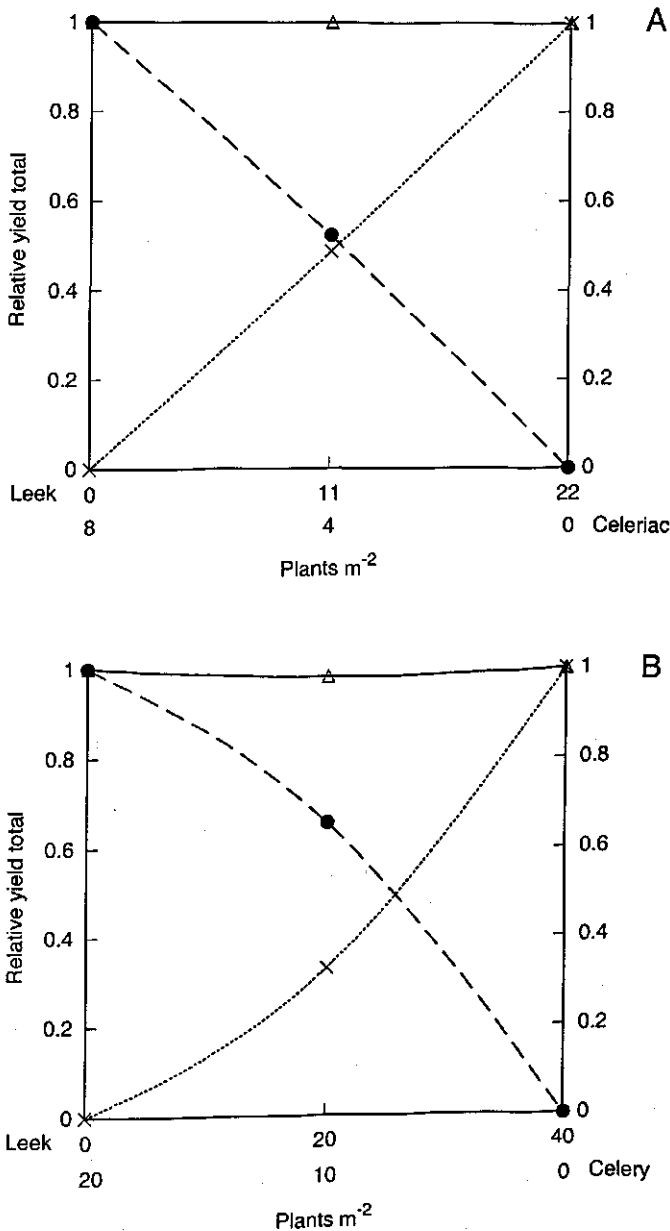
Fig. 4.1 Replacement series diagrams with relative yield totals (*RYT*) for leek, celeriac and celery, and their intercrop in experiment I, 1995 (A) and experiment II, 1996 (B).

Table 4.5 Plant density and quality parameters in pure stands and mixtures of leek and celeriac (Experiment I; Wädenswil, Switzerland, 1995).

Density (plants m^{-2})		Leek				Celeriac	
Leek	Celery	Per plant weight (g)	Diameter stem (mm)	Plant length (cm)	Bleached part of stem (cm)	Root weight (g plant^{-1})	Root diameter (mm)
11	0	51.4	33.4	51.1	5.8	-	-
22	0	38.1	28.9	49.9	6.3	-	-
5.5	2	52.4	35.6	68.9	5.8	54.9	109
5.5	4	46.7	34.9	65.6	5.8	39.2	96
11	2	37.1	28.6	69.6	6.5	46.7	105
11	4	37.1	30.6	63.2	5.9	38.4	94
0	4	-	-	-	-	52.2	106
0	8	-	-	-	-	42.6	94
SEM (d.f.=15)*		3.23	1.0	2.9	0.3	3.56	1.9

* SEM = standard error of means (degrees of freedom)

Experiment II, 1996

In 1996 again a significant density response was found for leek and celery pure stand (Table 4.6). As much higher plant densities where chosen than in 1995 for both crops, the biomass production tended to an asymptotic value at the highest plant density. In contrast to 1995, the highest total biomass production was achieved with the highest plant density of the celery pure stand, whereas the lowest density of leek pure stand had the lowest production. Replacing leek by celery instead of doubling leek density resulted in a production increase that on average was 8% higher. Doing the same for celery reduced the yield advantage by 6%. The ratio of the intra- and interspecific competition coefficients was 0.2 for leek and 4.4 for celery (Table 4.3). The replacement series diagram (Fig. 4.1B) shows the differences in competition, which the two crops experienced, from each other. The concave and convex curves for leek and celery are more pronounced in 1996 than in 1995, which is also reflected by the significantly differing crowding coefficients (Table 4.4). For the mixture of 20 leek and 10 celery plants m^{-2} a *LER* of 1.1, a *RYT* of 1.0 (Table 4.4) and a *NDI* of 0.97 (Table 4.3) was calculated. In spite of mutual effects between the crops the biomass production of the mixture was not reduced. Per plant weight of leek and diameter of

Table 4.6 Plant density and above-ground biomass in pure stands and mixtures of leek and celery (Experiment II; Wädenswil, Switzerland, 1996).

Density (plants m^{-2})		Above-ground biomass (g m^{-2})		
Leek	Celery	Leek	Celery	Total
20	0	809	-	809
40	0	995	-	995
60	0	1080	-	1080
10	5	279	780	1059
20	10	328	728	1056
30	10	379	686	1065
30	15	414	768	1182
0	10	-	1047	1047
0	20	-	1109	1109
0	30	-	1200	1200
SEM (d.f.=18)*		41.7	69.7	63.1

*SEM = standard error of means (degrees of freedom)

the pseudostem responded strongly to plant density and replacement of leek by celery (Table 4.7). Doubling the density of leek from 20 to 40 plants m^{-2} in the pure stand caused a reduction in plant weight of 38%, and stem diameter just reached the minimum quality requirements of 20 mm. For the lowest leek density similar results were achieved by replacing half of the leek plants with 5 celery plants m^{-2}. At the highest leek density and for the other mixtures the quality requirements of the market were not reached. As in 1995, leek grew higher with increasing plant density and in mixed stands the bleached part of the pseudostem tended to be longer than in pure stands.

For the lowest plant density of celery, the reduction in individual plant weight was 17% lower when 20 leek plants were added per m^2 instead of doubling the density of celery. Replacing celery plants by twice as many leek plants resulted in an increase in the celery plant weight of 49, 31, and 28% for the lower, medium and higher plant density of celery, respectively. There was no significant response of plant length or any other quality related parameter of celery on plant density or intercropping with leek.

Table 4.7 Plant density and quality parameters in pure stands and mixtures of leek and celery (Experiment II; Wädenswil, Switzerland, 1996).

Density (plants m^{-2})		Leek				Celery	
Leek	Celery	Per plant weight (g)	Diameter stem (mm)	Stem length (cm)	Bleached part of stem (cm)	Plant weight (g plant^{-1})	Plant length (cm)
20	0	40.4	26.7	28.0	7.7	-	-
40	0	24.9	21.4	29.5	7.7	-	-
60	0	18.0	17.6	29.8	7.5	-	-
10	5	27.9	22.1	29.6	8.0	155.9	82.8
20	10	16.4	16.8	31.7	8.5	72.8	77.0
30	10	12.6	14.9	30.6	7.9	68.6	78.9
30	15	13.8	14.9	34.1	8.5	51.2	79.0
0	10	-	-	-		104.7	82.6
0	20	-	-	-		55.5	81.8
0	30	-	-	-		40.0	81.3
SEM (d.f.=18)*		1.8	0.7	1.3	0.4	6.9	2.5

*SEM = standard error of means (degrees of freedom)

Experiment III, 1997

A significant response to crop stand and nitrogen and the interaction was found for leek and celery yield (Table 4.8). Highest production was achieved with celery grown in monoculture (926 g m^{-2}), which at the highest nitrogen level produced 55% more above-ground biomass than the pure stand of leek. The total biomass production of the mixture was intermediate. The production of celery was also significantly higher than that of leek when no nitrogen was applied. *RYT*'s and crowding coefficients for all N-levels, as shown in Table 4.4, are comparable to those found in 1996. The total relative nitrogen uptake (*RNT*) for the replacement series at the three nitrogen levels is shown in Fig. 4.2. Nitrogen uptake of celery was significantly higher than that of leek for the N$_0$ and N$_{200}$ treatments, but it did not differ at the N$_{50}$-level (Fig. 4.3). As a result the fraction of nitrogen recovery (*F$_R$*) by the celery pure stand was lower at N$_{50}$ than for leek and the mixed stand, whereas it was similar for all crop stands for the higher N-level (Table 4.9). All crop stands used the lower nitrogen rate significantly more efficiently than the higher one; moreover the agronomic efficiency (*E$_A$*) was higher for the celery pure stand than for leek and
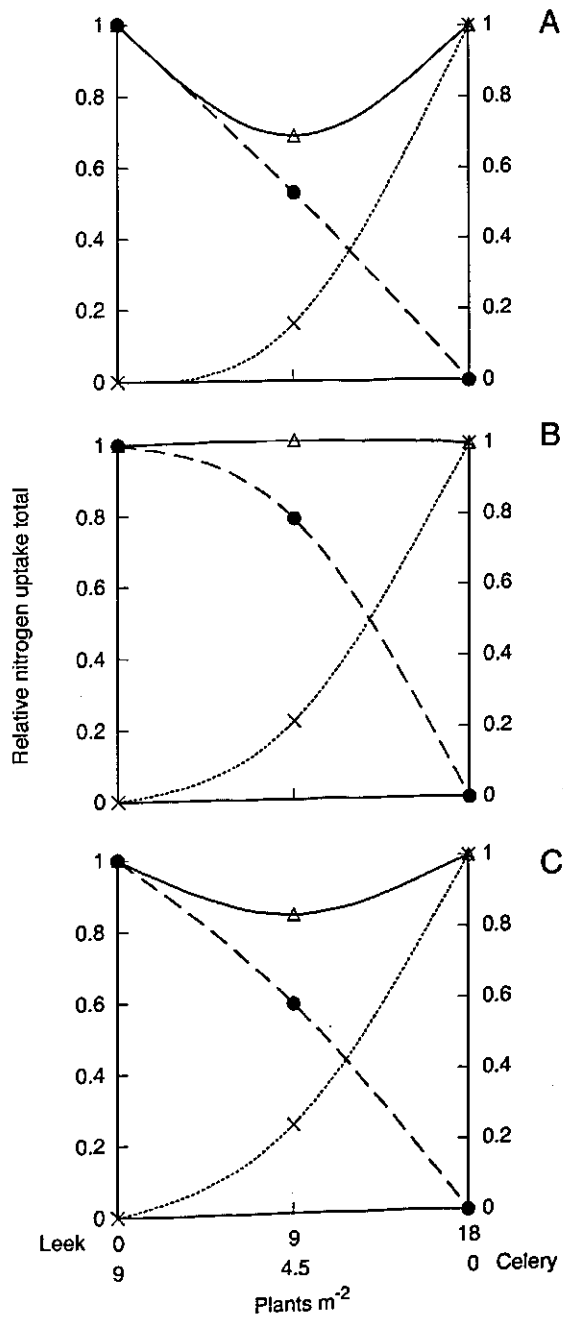
Fig. 4.2 Replacement series diagrams with relative nitrogen uptake totals (*RNT*) for leek, celeriac, and celery, and their intercrop at nitrogen fertiliser rates of 0 (A), 50 (B), and 200 (C) kg ha^{-1} in experiment III, 1997.

the crop mixture at both nitrogen levels. Even though N-recovery for the celery pure stand at the N_{50}-level was significantly lower than that of the leek pure stand and the crop mixture, its increase in biomass production compared to the unfertilised treatment was not different from that of the other crop stands.

Table 4.8 Plant densities, dry matter production and per-plant weight at different nitrogen levels (kg ha^{-1}) for pure stands and a mixture of leek and celery (Experiment III; Wädenswil, Switzerland, 1997).

Density (plants m^{-2})			Per-plant weight (g plant^{-1})		Dry matter production (g m^{-2})		
Leek	Celery	N-level	Leek	Celery	Leek	Celery	Total
18	0	0	16.8	-	302	-	302
		50	27.6	-	497	-	497
		200	33.2	-	597	-	597
9	4.5	0	9.0	62.4	81	281	361
		50	15.4	102.5	140	462	601
		200	20.3	120.3	183	541	724
0	9	0		44.1	-	397	397
		50		74.6	-	671	671
		200		102.9	-	926	926
SEM (d.f.=24)*			1.6	3.1	25.9	20.2	31.6

*SEM = standard error of means (degrees of freedom)

Table 4.9 Fraction recovery (F_R), agronomic efficiency (E_A) and utilisation efficiency (E_U) for nitrogen by leek and celery grown in pure stands and mixtures at different N levels (Experiment III; Wädenswil, Switzerland, 1997).

Crop stand	N-level	Leek			Celery			Intercrop		
	(kg ha^{-1})	F_R	E_A	E_U	F_R	E_A	E_U	F_R	E_A	E_U
Pure stand	50	0.76	0.39	0.49	0.47	0.55	1.30	-	-	-
	200	0.46	0.15	0.32	0.54	0.27	0.49	-	-	-
Mixture	50	0.21	0.12	0.57	0.63	0.36	0.69	0.85	0.48	0.65
	200	0.13	0.05	0.38	0.33	0.13	0.39	0.47	0.18	0.39
SEM (d.f.=9)*		0.07	0.05	0.06	0.13	0.13	0.12	0.07	0.05	0.09

*SEM= standard error of means for crop stand x N-level interaction (degrees of freedom); SEM within the same N-level (d.f.=15): F_R=0.12, E_A=0.05, E_U=0.09

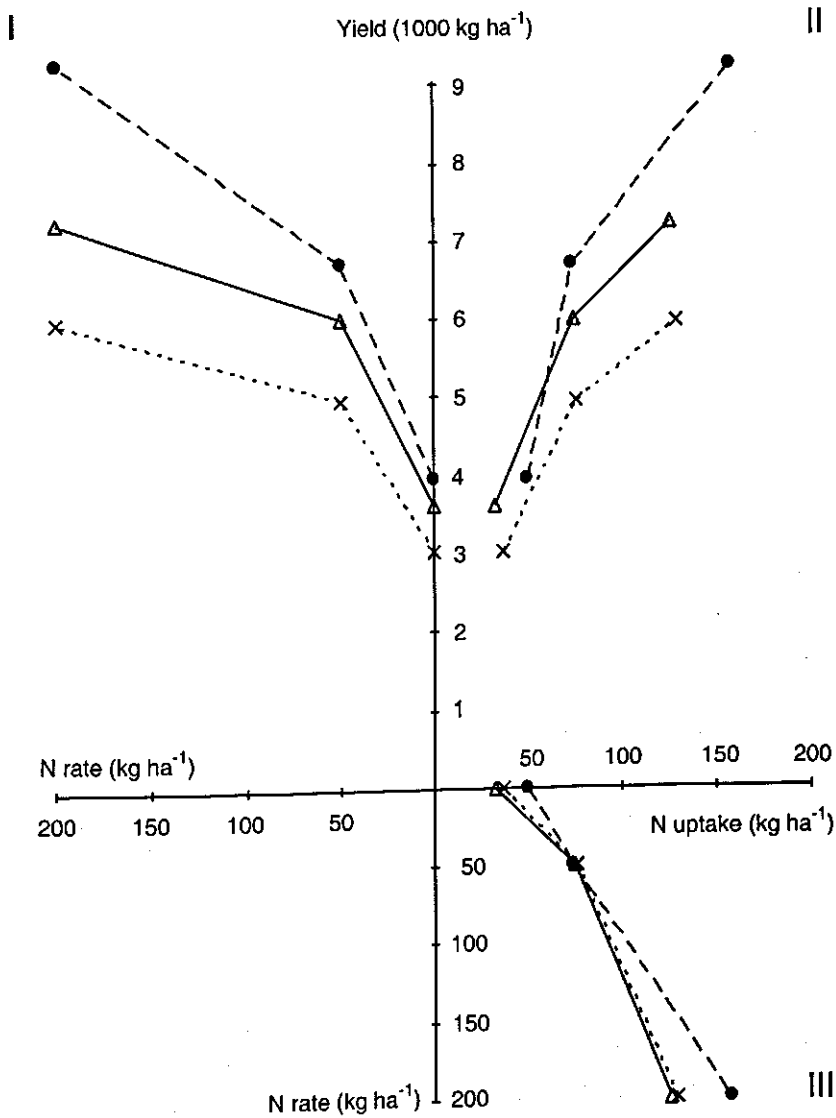**Fig. 4.3** Quadrant diagram with response of yield to N rate (I), relation between yield and N uptake (II), and response of N uptake to N rate (III) for leek and celery monoculture, and their intercrop in experiment III, 1997.

This resulted in significantly higher utilisation efficiency of nitrogen (E_U) by celery at the N_{50} level. The utilisation efficiency of all crop stands was lower at the N_{200} level compared with the N_{50} level. Again celery used nitrogen significantly better than leek if grown in monoculture. A considerably higher recovery and agronomic efficiency was found for leek and celery if grown in monoculture as compared with the crops grown in mixture. The utilisation efficiency, however, was higher for leek and lower for celery if grown in mixture.

Discussion

Biomass production

The strong density response which was found for the yield of leek monoculture in experiments I and II indicates that leek, if grown at densities used in practice, is far from reaching the asymptotic value of maximum biomass production as described by Holliday (1960). The highest biomass production (Brewster (1994) reports 107 t ha^{-1}) could be usually achieved with 50-60 plants m^{-2}, but to produce large leeks for the market, densities of 15-20 plants m^{-2} are used. In the current study a maximum yield of 108 t ha^{-1} was harvested in experiment II at 60 plants m^{-2}. Plant densities as they are used in practice, produce about 75% of the potential biomass. The response of celery yield to plant density was less pronounced if densities were higher than 10 plants m^{-2}. In practice, plant density of celery varies from 5 to 27 plants m^{-2}, but densities are generally not higher than 15 plants m^{-2} (Rubatzky *et al.*, 1999). The same author reported a maximum celery yield plateau of around 150 t ha^{-1} which the current study reached in 1996 at a plant density of 20 plants m^{-2}. Celery, like leek, is grown in lower densities than required in practice for optimum biomass production. Reasons are quality requirements, mechanical weed control and a lower risk for disease incidence due to a more favourable microclimate.

Analysis of the additive series gave land equivalent ratios exceeding unity, indicating an intercrop advantage and hence an apparent increase in resource use efficiency by the crop mixture (Table 4.4). Since both pure stands with which the mixture was compared were not grown at densities where maximum yield was achieved, the resources were not entirely used. It is therefore correct to conclude that the crop mixture improved the resource use but it is impossible to distinguish a true yield advantage from a density effect; higher yields could also have been achieved by increasing the densities of the pure stands. Because of possible

differences in population response of the component crops in a crop mixture, Huxley and Maingu (1978) pointed out that calculations of yield advantages should only be made between intercrop and sole crop at their respective optimum populations. This can be shown by comparing the results of the replacement series analysis and the hyperbolic model approach for the 1995 and 1996 experiments. From the replacement series analyses one would conclude that in 1995 no competition occurred between leek and celeriac in the crop mixture (Fig. 4.1A and Table 4.4) whereas in 1996, when plant densities were higher, replacement series diagrams (Fig. 4.1B) and the corresponding k values (Table 4.4) indicate a strong competitive effect of celery on leek. Analysis applying non-linear regression using the model of Spitters (1983a) (eqn. [4.3]), however, shows that in both years the celeriac and celery were more competitive than leek (Table 4.3). The replacement series analysis for the 1995 experiment did not detect differences in competitive ability between the crops because the crowding coefficient k does not distinguish between intercrop competition and a density effect. Competitive effects did not (1995) or only partly (1996) appear because crop densities were lower than the optimum density. Parameters for intraspecific (b_{11}) and interspecific (b_{12}) competition, as calculated in eqn. [4.3], however, exclude density effects and give a true estimate of the competitive ability of the crops for both experiments.

Crop quality

It would be insufficient if merely biomass productivity would be considered to analyse the performance of crop mixtures. Particularly for vegetable crops quality plays a predominant role on the market and must therefore be part of the evaluation.

Quality parameters of leek responded strongly to either changes in plant density (intraspecific competition) or replacement of leek by celery (interspecific competition). Plant density together with planting date, transplant size and cultivar are the most important factors determining the quality of a leek crop (Brewster, 1994). The strong response of per-plant weight and pseudostem diameter of leek to intraspecific competition is the main reason that leek is generally produced in four to six times lower plant densities than would be required for maximum biomass production. Another reason for spacious row distances is to facilitate mechanical weed control and other crop maintenance measures.

In experiment I, the effect of doubling leek density on per-plant weight and pseudostem diameter was about the same as replacing leek by celeriac. The same results were found in 1996, though the competitive effects of celery were stronger

and leek quality was more affected by interspecific than by intraspecific competition. Positive effects of intercropping were, however, found for plant length and the bleached part of the pseudostem, which are also quality parameters (Tables 4.5 and 4.7). Light competition by celeriac and celery caused leek to grow higher and to produce a longer white stem in the mixed stand.

For celeriac, doubling the plant density from 4 to 8 plants m^{-2} caused a significant reduction of root weight and diameter but increased the yield by 60%. Smaller roots generally meet the requirements of the fresh market, however, large roots with a small ratio between surface area and root weight are required for post-harvest processing in the canning industry. In 1996 per-plant weight of celery was also reduced with increasing plant densities and intraspecific competition was considerably higher than interspecific competition from leek (Table 4.3). As for celeriac and leek, the experiments demonstrate that although higher plant densities may increase the total yield, the trade-off might be that marketable yield is reduced. If celery is to be blanched, even wider spacing is needed to enable banking of soil against plants, or for use of other light excluding materials. Alternative to blanching are closely spaced plantings that cause a certain level of self-blanching.

In the intercrop systems with leek and celeriac/celery the latter received a larger proportion of the resources. Assuming root competition was excluded, as intended by the experimental set-up of experiments I and II, differences in competition between the two crops were mainly due to their abilities to capture and use the light. Increasing canopy light interception was the desired goal to improve the competitive ability versus weeds. This target was reached by intercropping leek with celery or celeriac (Baumann *et al.*, 2000). At the same time, however, crop quality is reduced if total plant density and celery density in particular exceeds the density to achieve optimal crop quality. To improve the quality of the component crops and the suppressive ability of the crop mixture against weeds the intercropping system needs optimisation.

Resource use

Leeks as well as celeriac/celery are biennial plants. During the vegetative phase, in the first year, growth of leaf blades, leaf sheaths (leek), petiole (celery), and roots (celeriac) take place. The reproductive organs usually develop during the second year. For vegetable production leek, celeriac, and celery are harvested in the first year. The major part of the nitrogen is taken up during 5-7 weeks before harvest (Booij *et al.*, 1996; Zink, 1963), hence there is a high nitrogen requirement for both

crops in this period. Moreover, very little biomass is produced during the first month of growth. Consequently, little nitrogen is absorbed during the early growth phase (Rubatzky *et al.*, 1999; Van der Werf *et al.*, 1996). Booij *et al.* (1996) for leek and earlier McNeal and Pratt (1978) for celery reported low fertiliser recoveries, particularly at higher nitrogen rates. Rubatzky *et al.* (1999) stated that the inefficient nitrogen uptake of celery is a result of the relatively shallow and inefficient root system. The low nitrogen utilisation of leek was explained with a combination of shallow rooting and the time course of the nitrogen demand of the crop (Smit *et al.*, 1996). Studies on the use of soil resources and nitrogen in particular have shown that nitrogen uptake often is greater by intercropping (Dalal, 1974; Liboon and Harwood, 1975; and others). This has very often been claimed as the basic cause of yield advantages, but usually it is impossible to determine whether greater nutrient uptake was either the cause or the effect of greater biomass production. In experiment III neither nitrogen uptake nor yield of the mixture was greater than that of celery pure stand (Fig. 4.3). Comparing relative nitrogen uptake total *RNT* (Fig. 4.2) with relative yield total *RYT* (Table 4.4) as suggested by Hall (1974), it can be seen that the exploitation of nitrogen by the intercrop is poor at N_0 (*RNT* = 0.69 vs. *RYT* = 0.96). Whereas the N-uptake of celery was proportional to plant density, the uptake of leek was very low, probably due to the retarded development of the plants. When additional nitrogen was applied, leek could hardly profit because it was outcompeted by celery. At N_{50} the high uptake rate of celery compensated for the low uptake rate of leek resulting in a *RNT* of 1.01. At N_{200} the N-uptake by leek remained low due to intraspecific competition and at the same time celery apparently reached a maximum uptake, resulting in incomplete compensation and consequently a reduced *RNT*. A generally higher nitrogen recovery and agronomic efficiency for celery in the mixed stand confirm these findings (Table 4.9). Due to the high interspecific competition, the agronomic efficiency for leek was very low, whereas the utilisation of nitrogen taken up (E_U) was still comparable to that of celery. Hence, with respect to nitrogen and probably also other soil resources there is no indication for facilitation due to spatial nutrient complementarity. The results show that in the intercropping system higher nitrogen rates cannot compensate for interspecific competition, particularly with respect to effects on leek quality. Whereas biomass is at least partly compensated by celery, leek quality remains low because retarded leek plants are not able to capture soil resources even if the availability is increased.

Improving intercropping advantages is a matter of maximising the degree of complementarity between the component crops and minimising inter-crop competition (Willey, 1979a). Analyses of the experiments show that celery (or

celeriac) generally was dominant in the mixture whereas leek was dominated. This is a result of a better ability of celery to capture light and soil resources, or a combination of the two. Willey and Roberts (1976) emphasised that light was probably the most important factor since it is lost if it is not instantaneously intercepted by the crop. An improved light interception is the intrinsic objective of the currently studied leek-celery intercrop system. Baumann *et al.* (2000) found that the course of light interception during the growing period for the crop mixture follows that of celery pure stand and differs significantly from that of leek grown in monoculture. Regarding the canopy architecture of the crops it is reasonable to assume that celery with its more horizontal leaves has a better ability to capture light than leek does. Moreover, leek seedlings have an intrinsically low potential growth rate which is partly due to the narrow, upright leaf habit causing a low ability to intercept radiation (Brewster, 1994). Due to the morphological difference of the crops, a spatial complementarity with respect to light interception can be assumed in a leek-celery crop mixture. In addition resource use might be more efficient by celery than by leek.

Planting, maintenance, and harvesting

Parallel to the experiments described above, leek and celery were grown as monocultures and intercrop on a larger scale under conditions as usual in practice. On these fields the practicability and in particular mechanical planting, crop maintenance, and harvesting were evaluated. Planting was carried out with a commercially available Bärtschi-Accord planting machine (BÄRTSCHI-FOBRO AG, Hüswil, Switzerland) equipped with alternately mounted planting elements for bare root transplants (leek) and for peat pot transplants (celery). Weed control during early crop stages was exclusively carried out by mechanical equipment combined with nitrogen top dressing. An inter-row hoe with goosefoot shares mounted on a tool carrier with a combined in-row fertiliser spreader was used (BÄRTSCHI-FOBRO AG, Hüswil, Switzerland). Leek and celery were harvested mechanically using a commercially available Simon leek lifter (JAMPEN, Münschemier, Switzerland). Planting, harvesting and tilling operations could be carried out at normal operating speed and without any technical difficulties. The quality of the work was judged as highly satisfactory by the farmers, who provided their fields for these trials. It was their conclusion that leek and celery can be produced as an intercrop using common machinery without any technical difficulties.

Improvement of the intercrop

Optimising the crop performance in an intercrop system is a question of maximising complementarity and minimising the competition between the two component crops (Willey, 1979a). Intercrop performance can be improved with respect to temporal and spatial complementarity and also by improving the compatibility of genotypes used as components of the mixture (Willey, 1979b). Staggering the relative planting time of the crops would be an example to account for temporal differences in resource use by the crops. Studies at the International Rice Research Institute (Anonymous, 1973) and by Osiru and Willey (1976) showed increasing yield advantages due to staggered sowing of the component crops. For the leek-celery intercrop system, staggering planting time could possibly improve crop performance, as the temporal resource requirement of the crops is very similar. However, planting times would have to differ substantially, which would make it impossible to plant and harvest the crop mechanically and hence would reduce the acceptability of the system in practice.

It is obvious that the space allocated to the component crops is directly related to the resources available for the crops. Within a certain range of plant densities yield is, however, not affected as for example well known from row-spacing experiments of cereals (De Wit *et al.*, 1979). For leek and celery, the present study showed that there is a significant response of per-plant weight to plant density. Regarding the objective of the intercrop system to improve the light interception of the canopy compared to leek pure stand, a dense and homogeneous mixture of the component crops would be ideal. From a point of view of practicability, a plant mixture beyond a row-based replacement design is, however, not realistic. Hence, optimisation of the spatial arrangement should focus on row distance and in-row distance between plants. In this optimisation process, practicability and options for mechanisation should be taken into account. The proportion of the component crops in mixture is closely linked to the spatial arrangement. Replacement series at different densities have shown that there is a strong response of plant weight on population pressure on one hand and proportion of the component crops in the mixture on the other hand. It was shown that the carrying capacity (b_{10}/b_{11}) and the interspecific competition (b_{12}) are different for leek and celery. It can therefore be concluded that optimisation with respect to total plant density and the ratio between the density of the component crops can contribute to an improved complementarity of the crops in the mixture.

Another possibility is the selection of suitable genotypes for the crop mixture. As stressed by Willey (1979b) and authors cited therein, it seems likely that this

offers just as much scope for crop performance improvement as it does in sole cropping. The objectives of selection can simply be stated as the selection that minimises inter-crop competition and maximises complementary effects. With respect to improved spatial and temporal complementarity, information is needed about eco-physiological characteristics determining intra- and interspecific competition of a specific genotype. Important factors affecting the competitive ability of species and genotypes are the leaf area dynamics, plant height, root growth dynamics, and resource use efficiency (Kropff and Van Laar, 1993).

Extensive field research using suitable experimental designs and appropriate statistical analysing methods can help to improve the performance of intercrops with respect to yield and quality. Eco-physiological crop growth models simulating interplant competition can help to find the most suitable combinations of genotypes, spatial arrangements and relative planting times (Kropff and Van Laar, 1993). Based on simulation studies, the most promising intercrop combinations could be identified before field experimentation was initiated, and experimentation could be limited to the most promising combinations, thus reducing experimental costs. Moreover, simulation studies can help to detect traits making species and genotypes most suitable for use in intercrops.

Analysing crop yield
and plant quality in an
intercropping system using
an eco-physiological model
for interplant competition

Baumann D.T., Bastiaans L., Goudriaan, J.,
Van Laar, H.H., Kropff M.J., 2001

Abstract

An eco-physiological model was used to improve understanding of interplant competition based on physiological, morphological and phenological processes. The model was parameterised based on characteristics of the plants in monocultures and its performance was evaluated for the crop mixtures using experimental data from different growing seasons. A light interception routine accounting for row-geometry was compared to a routine assuming a homogeneous horizontal leaf area distribution. The models simulated the light distribution among the species equally well. The production of the two crops in the mixture was accurately simulated using parameter values based on monoculture growth characteristics. Morphological characteristics of the species such as the relative growth rate of leaf area during early growth and specific leaf area largely determined the competitive strength of the species. Dry matter production of the species, particularly if grown in mixture, was highly sensitive to maximum plant height and radiation use efficiency. Celery was found to be a stronger competitor than leek and clear responses of quality characteristics to plant density in monoculture and mixtures were observed. The model was used to determine ranges of plant densities that enable the intercropping system to meet current quality standards of the component crops.

Introduction

Intercropping, or growing two or more crops in association, which is widely applied in developing countries, plays a minor role in high input agriculture (Mead and Riley, 1981; Vandermeer, 1989; Willey, 1979b and others). However, recently, intercropping gained an increasing interest in an attempt to substantiate functional biodiversity for agricultural production and to reduce pesticide use. In the seventies and eighties, intercropping research focused mainly on increased productivity (Papendick *et al.*, 1975; Trenbath, 1974; Vandermeer, 1989; Willey, 1979a,b) whereas more recently several reviews and studies rather emphasised the pest suppressing potential of intercrops (Müller-Schärer and Baumann, 1993; Altieri, 1994; Mineau and McLaughlin, 1996; Den Belder *et al.*, 2000). A number of recent studies addressed weed problems and potential solutions offered by intercropping systems (Baumann *et al.*, 2000; Bulson *et al.*, 1997; Liebman and Davis, 2000; Solaimalai and Selvam, 1998). Several of the above-mentioned authors suggested intercropping specifically as a tool for pest and weed management in organic farming and minor crops. Particularly for the vegetable production for the fresh market there is an increasing need for efficient non-chemical weed management techniques because of a rapid decline in registered herbicides on one hand and consumer concerns about pesticide residuals on the other hand.

Baumann *et al.* (2000) suggested intercropping of the poorly competitive leek (*Allium porrum* L.) with celery (*Apium graveolens* L.) to suppress growth and seed production of weeds. The authors found a reduced biomass and reproductive potential for weeds in the intercropping system compared to leek in a pure stand. They related this effect to the increased canopy light interception and hence improved competitive ability of the mixed stand. However, although the relative yield total of the mixture was equal to the monocultures, negative effects on yield and particularly quality of leek were found, caused by intercropped celery. As intercropping was identified as a useful tool for weed suppression, additional studies were initiated to analyse and explain crop interference in a leek-celery intercropping system. Besides a descriptive regression approach, Spitters (1990) proposed an eco-physiological approach using mechanistic models for the analysis of interplant competition in species mixtures. He defined interplant competition as the interaction between plants in which they restrict each others growth by capturing growth-limiting resources (e.g., light, water and nutrients). Consequently, the competition process is described in terms of the distribution of the growth-limiting factors over the species in the mixture and utilisation of these resources for dry matter

production. For a potential production situation, where water and nutrients are available to the crops in ample supply, crop growth is determined by radiation, temperature and the species characteristics (De Wit and Penning de Vries, 1982). With respect to competition for light, morphological and physiological characteristics of species growing in mixtures are determinants for competition effects. Based on the eco-physiological characterisation of competing species, mechanistic models, as initially developed by Spitters and Aerts (1983) and Kropff *et al.* (1984) and further developed, evaluated and fully documented by Kropff and Van Laar (1993) provide insight into the processes underlying competition effects observed. For intercropping systems this methodology is extremely usefull, as empirical methods and experimentation are limited due to systems complexity and the large number of options that can be altered in the system.

The objective of this study was to improve the understanding of crop growth in a species mixture and to gain insight into competitive interactions between crops based on physiological, morphological and phenological processes of the species. Special emphasis was put on the canopy architecture of the row-by-row intercrop and its implications for simulation of the light distribution within the canopy. The final target was the application of the model for optimisation of intercrop performance, in which apart from yield quantity, particular attention is given to quality aspects of the produce.

In the present paper, a short description of the model structure is given with special attention to the light capture procedures in row-canopies. The estimation procedure of the eco-physiological parameters required for model parameterisation is explained and model performance evaluated. Finally, the results of a simulation analysis of the effects of several morpho-physiological species characteristics on competitive interactions within the intercropping system are presented.

Material and Methods

Models to describe interplant competition in mixtures of species have been described by many authors (e.g., Cousens, 1985; De Wit, 1960; Kropff and Spitters, 1991; Kropff and Van Laar, 1993; Shinozaki and Kira, 1956; Spitters, 1983a). However, to study and understand the underlying mechanisms of competition as it occurs in intercropping systems an explanatory model is needed. Based on eco-physiological crop growth models, the model INTERCOM for interplant competition was developed (Kropff and Van Laar, 1993). INTERCOM, dynamically simulates the competition

process based on underlying processes and as such provides an excellent framework to evaluate plant interference in intercropping systems. In the current study, this framework was used as a tool to analyse the specific processes and plant characteristics which determine the competition within a leek-celery intercropping system. In this way, it served as a basis for design and optimisation of this intercropping system.

Model structure for horizontally homogeneous canopies

The competition model INTERCOM of which the general structure as a relational diagram is shown in Fig. 5.1 was used to simulate the growth of the crops in monoculture and mixture. Under favourable growing conditions, where light, temperature, and species-specific characteristics determine the growth of a plant community, plants compete primarily for light (Kropff and Van Laar, 1993). From the leaf area indices (*LAI*) of the species the light profile within the canopy and the fraction of intercepted light is calculated. In INTERCOM, the net daily growth rate is calculated based on the CO_2 assimilation and the respiration requirements for maintenance of each species. In the current study, a simplified version of INTERCOM was used, in which dry matter production was based on intercepted radiation and an average radiation use efficiency (*RUE*) rather than on detailed computations of CO_2 assimilation and respiration. This procedure is based on the generally observed linear relationship between cumulative light interception and dry matter growth as found for many crops if grown in potential production situation (Monteith, 1969; Williams *et al.*, 1965). The growth rate of the species is then calculated as

$$G_i = RUE_i \cdot I_{A,i} \qquad [5.1]$$

where G_i is the growth rate of species i (g dry matter [m^{-2} ground] d^{-1}), RUE_i the average radiation use efficiency of species i (g dry matter [J^{-1}] d^{-1}), $I_{A,i}$ the daily total photosynthetically active radiation (*PAR*) absorbed by species i (J [m^{-2} ground] d^{-1}).

The dry matter produced is partitioned among the various plant organs, using partitioning coefficients that are introduced as a function of the phenological development stage of the species. Phenological development rate is tracked in the model as a function of ambient daily average temperature. During an early growth phase, when no light competition occurs, leaf area as calculated from daily average
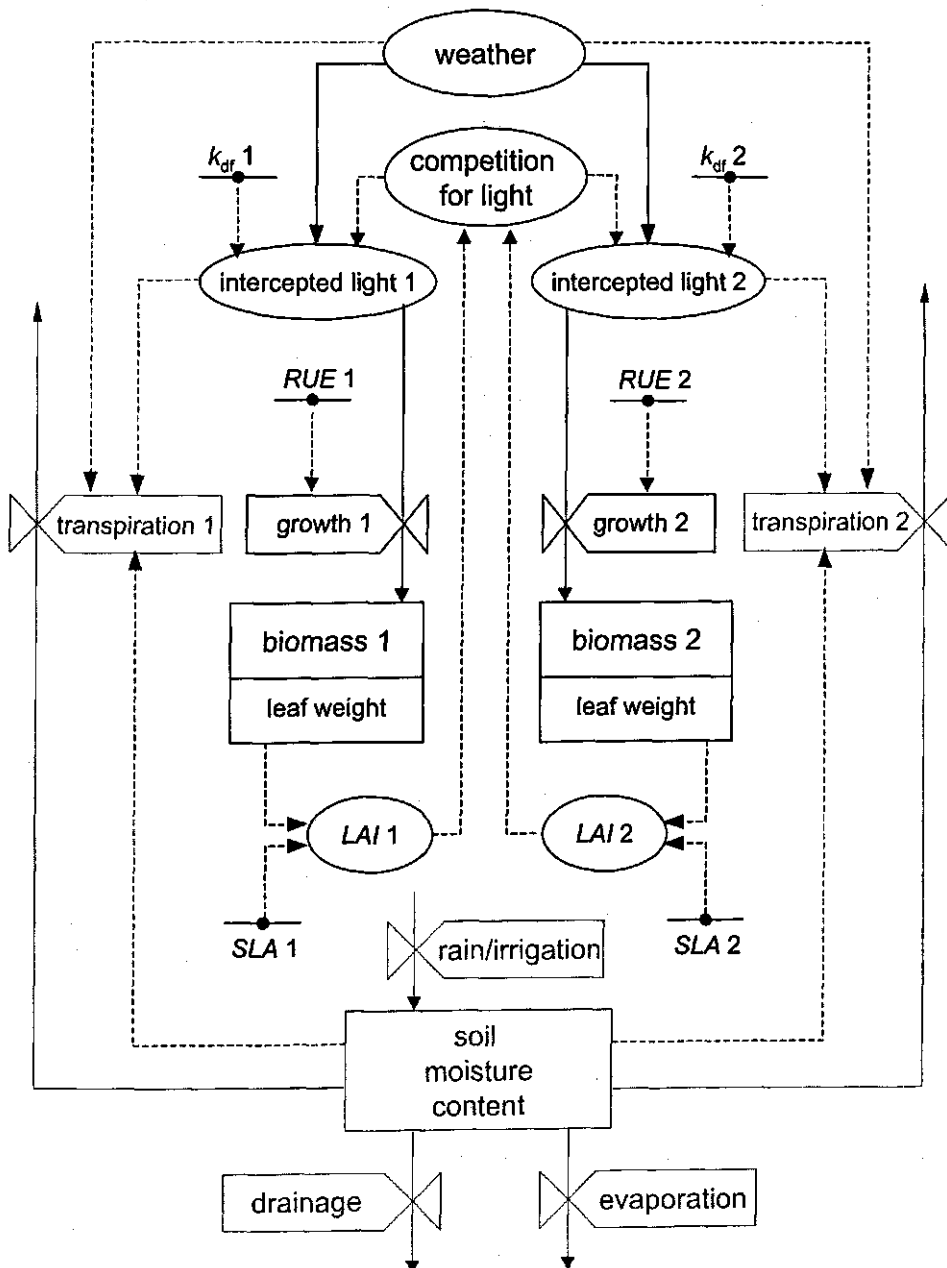
Fig. 5.1 General structure of the eco-physiological model for interplant competition (INTERCOM, redrawn after Kropff and Van Laar, 1993). Brightened processes are implemented in the model but not considered for the current study. For abbreviations of parameters see Table 5.2.

temperature increases exponentially. As the crops start to compete for light, the increase in leaf area begins to depend on the increase in leaf weight as given by the specific leaf area (*SLA*, [m^2 leaf] [kg^{-1} leaf]). Integration of daily growth rates of the organs and the balance between leaf growth and senescence rates provided the time course of *LAI* and dry weight in the growing season.

To simulate competition for light between species within a crop mixture the growth models of the competing species were linked through subroutines that account for the distribution of light. The amount of incoming photosynthetically active radiation (*PAR*, wavelength 400-700 nm) is calculated as 50% of the global daily solar irradiation, which is an input into the model. Incoming radiation is partly reflected by the canopy and the remaining fraction is potentially available for absorption by the canopy. Radiation fluxes attenuate exponentially within a canopy as a function of the cumulative *LAI* counted from the top downwards, according to Beer's law

$$I_L = (1 - \rho)\, I_0 \, \exp(-k\,L) \qquad\qquad [5.2]$$

in which I_L the net *PAR* flux at depth L in the canopy (the height in the canopy above which *LAI* equals L) (J [m^{-2} ground] s^{-1}), ρ the reflection coefficient of the canopy, I_0 is the amount of incoming radiation at the top of the canopy (J [m^{-2} ground] s^{-1}), k the extinction coefficient for *PAR*. and L the cumulative *LAI* counted from the top of the canopy downwards ([m^2 leaf] [m^{-2} ground]).

A distinction was made between diffuse skylight and direct sunlight and the radiation fluxes were calculated as described by Kropff and Van Laar (1993) and references cited therein. The extinction coefficient for direct radiation was calculated from the solar angle and the scattering coefficients according to Goudriaan (1977). The extinction coefficient for diffuse light k_{df} was input into the model.

Expressed per unit leaf area, the rate of absorption at any depth can be found by taking the derivative of eqn. [5.2] with respect to the cumulative *LAI* in the canopy:

$$I_{A,L} = -\frac{dI_L}{dL} = k(1 - \rho)I_0\exp(-k\,L) \qquad\qquad [5.3]$$

where $I_{A,L}$ is the radiation absorbed at depth L in the canopy (J [m^{-2} leaf] s^{-1}). The daily total radiation absorption I_A by a species can be determined by integration.

In crop mixtures competition for light is related to efficiency of resource capture and hence the light absorption characteristics of the species. These are determined by leaf angle distribution, leaf thickness, *LAI*, and the vertical leaf area density profile. Leaf thickness and leaf angle distribution are implicitly accounted for in the radiation extinction coefficient, and leaf area is directly included in the calculation of light interception (eqn. [5.2] and [5.3]). The vertical leaf area density profile was specified in INTERCOM by combining the plant height development with a parabolic pattern of vertical leaf area distribution against relative height (Tetio-Kagho and Gardner, 1988). Other functions such as a rectangular or more skewed leaf area distribution can be used as well (Graf *et al.*, 1990; Cavero *et al.*, 2000).

In the model the leaf canopy was separated into a large number of leaf layers, and light absorption was calculated for each leaf layer starting from the top. The distribution of absorbed light over the species within each layer is done to the share of leaf area weighted by the extinction coefficient as described by Kropff *et al.* (1984). In a canopy with mixtures of species, eqn. [5.2] can be rewritten as

$$I_h = (1 - \rho)\, I_0 \, \exp\!\left(-\sum_{j=1}^{n} k_j\, L_{h,j} \right) \qquad\qquad [5.4]$$

where I_h is the net flux (*PAR*) at height h (J [m^{-2} ground] s^{-1}), and $L_{h,j}$ is the cumulative *LAI* of species j above height h ([m^2 leaf] [m^{-2} ground]). The leaf areas ($L_{h,j}$), weighted by the extinction coefficients (k_j), are summed over the $j=1,...,n$ plant species in the mixed vegetation. Similar to a monoculture situation, the light absorbed by species i at height h in the canopy ($I_{a,h,i}$, J [m^{-2} leaf] s^{-1}) is obtained by taking the derivative of eqn. [5.3] with respect to the cumulative *LAI*:

$$I_{A,L} = -\frac{\mathrm{d}I_{h,i}}{\mathrm{d}L_i} = k_i\,(1 - \rho)\, I_0 \exp\!\left(-\sum_{j=1}^{n} k_j\, L_{h,j} \right) \qquad\qquad [5.5]$$

Light competition in row crop canopies

Through the procedure described above, the standard approach in INTERCOM accounts for differing heights between species within a mixed canopy. It assumes, however, that the mixture of the species is horizontally homogeneous. As in the current study the intercrop system of leek and celery is grown in a row-by row replacement design the need to account for the row canopy structure in the model had to be explored. Therefore, a modified version of the row canopy model

INTERROW as described by Schnieders (1999) was used. Modules simulating the distribution of the light in the canopy account for the vertical and horizontal variation in light capture by the competing species based on a model developed by Gijzen and Goudriaan (1989). In the module, canopy space was divided into a series of rectangular boxes with indefinite length each representing a crop row. Within each box, the leaf area of a species was assumed to be parabolically distributed over height. The canopy dimensions are defined by the row dimensions of each species, by the intra-specific row distance, which in the intercrop system is constant, and by the relative spatial position of rows of the two species. The height and width of the rows, and the leaf area within them, may change in time, all of which need to be defined or simulated. The module distinguishes direct and diffuse radiation. Diffuse radiation comes from all directions and direct radiation changes with the solar angle during the day. When a light beam enters the canopy, it can directly fall on the bare soil between the rows or enter a specific row. Within the row, a part is absorbed by the leaves of the species and a part is transmitted either to the adjacent row or to the soil under the row. The light absorption thus depends on the size of the plants, the leaf area density in the row, the distance between the rows, the orientation of the row and the position of the sun. For a detailed description of the INTERROW module the authors refer to Gijzen and Goudriaan (1989) and Schnieders (1999).

To evaluate the effect of row canopy architecture of the intercropping system on light interception of the component crops, simulations with INTERCOM assuming a horizontally homogeneous leaf area distribution were compared with simulations using the INTERROW light interception module.

Water and nutrients

Because water was not limiting in the experimental system, competition for water was not considered in the current study, though INTERCOM includes a water balance allowing simulation of effects of water shortage on growth and competition processes. Neither competition for nitrogen or other nutrients was subject of the study because it is assumed that in the highly developed vegetable production systems, as they are common in Western Europe, irrigation and ample supply of nutrients are common practice.

Although light competition may affect growth and development of below-ground plant organs through dry matter partitioning of the biomass and morphological plasticity of a plant, root growth was not considered in the model because the radiation use efficiency was determined from experimental data in which only above

ground dry matter was taken into account. In production situations with limited water and nutrient supply, however, the growth and efficiency of the root system is of key importance. It is obvious that in such cases interplant competition is strongly affected by the ability of the roots to capture below ground resources necessitating an adaptation of the model.

Experiments for parameterisation and validation

Parameter values were derived from field experiments and compared with values from literature. Two field experiments, referred to as experiments I and II, were carried out in 1996 and 1998 at two different sites in Switzerland. Experimental details are given in Table 5.1. In both experiments treatments consisted of pure and mixed stands of leek and celery designed as row by row replacement series. In experiment I, the density of the component crops was included as an additional factor into the experimental design. Factorial block designs were used for both experiments. In experiment I, bare root transplants of leek and commercially available peat pot transplants of celery were planted manually into a plant bed which was cultivated twice on the previous day. In experiment II, transplanting was performed mechanically after a rotary cultivation treatment directly before planting. Base fertilisation was carried out according to soil analysis prior to planting with P_2O_5, K_2O and Mg to reach 60 kg ha^{-1} P, 180 kg ha^{-1} K and 30 kg^{-1} Mg. To avoid nitrogen deficiency, in experiment I a buffer of 70 kg ha^{-1} N was maintained in the rooting zone by applying nitrogen (as 27% ammonium nitrate) as top dressings after checking the content of mineral nitrogen (NH_4, NO_3) every 10 days and additionally after heavy rainfalls. In experiment II, top dressings of N were applied to the crop rows with every mechanical weeding which was carried out every 10 days until canopy closure. To avoid water shortage, the experiments were regularly irrigated based on tensiometer measurements in the field. Crop protection measures were carried out according to common practice and weeds were controlled mechanically.

In both experiments, plants were harvested at regular intervals throughout the growing period. At each harvest, samples were dissected into various plant organs, dried at 72 °C and weighed. In leek, the point where the edges of the outermost leaves ensheathing the pseudostem cross was used as a criterion to separate leaves and pseudostem. The minimum and maximum diameter of the pseudostem, of which the average is used as quality parameter for leeks, was measured weekly 5 cm above the base of the pseudostem. Roots were removed where they attach to the stem. In celery petioles, leaf blades and tap roots were separated. As leek and celery are

biennial plants they do not form reproductive organs in the first year. The area of green leaf blades was measured with an electronic planimeter (LI-3100, LI-COR Inc. Lincoln, Nebraska). Dead leaves that fell off were collected, dried and weighed.

Table 5.1 Details of field experiments with monocultures and mixtures of leek (*Allium porrum* L.) and celery (*Apium graveolens* L.) conducted in 1996 and 1998.

Experiment	I	II
Year	1996	1998
Experimental site	Wädenswil (Switzerland)	Dättlikon (Switzerland)
	47°13'N, 08°40'E	47°32'N, 08°36'E
Altitude	487 m	434 m
Soil type	Sandy loam soil	Loam soil
Cultivars		
Leek	Zefa Plus	Pandora
Celery	Tall Utah	Ramon
Planting date	30 May	10 June
Harvest date	12 September	15 September
Row distance (m)	0.25	0.30
Plant densities (plants m^{-2})		
Monoculture leek	L_L=20, L_M=40, L_H=60	25
Monoculture celery	C_L=10, C_M=20, C_H=30	11
Intercrops leek:celery	I_L=10:5, I_M=20:10, I_H=30:10	12.5:5.5
Gross plot size (m)	2x4.5	1.5x4.5
Net plot size	1x2	0.6x0.6
Number of replicates	4	3

The percentage *PAR* intercepted by the canopy was measured weekly under diffuse light conditions with a Ceptometer CEP (Decagon Devices, Pullman, WA). The fraction of *PAR* intercepted was calculated by rapidly taking 10 readings above the canopy and 10 readings below the canopy. The latter measurement was taken by placing the ceptometer perpendicular to the plant rows and measuring a section of 0.5 m between the centres of the outside inter-row spaces within a bed. The mean of each set of 10 readings was recorded. With the same frequency the vertical projection of the crop soil cover was visually estimated using a 0.5 x 0.5 m frame with a 62.5 x 62.5 mm grid.

Validation of the model and sensitivity analysis

As parameterisation and calibration of the model was based on data from pure stand treatments of the medium density of leek and celery, simulation runs were performed for the other crop densities of pure stands and mixtures of experiment I and II to validate the model. Only treatment and experiment specific inputs, such as plant density and weather data were varied between the simulation runs. In a first step, simulation runs were performed with measured *LAI* as input to exclude confounding effects of the feedback between plant growth and leaf area development on the simulation of light capture and biomass production. In a second step, the simulation of leaf area development was included according to the procedure described by Kropff and Spitters (1992). Results of both simulation steps were evaluated by comparing simulated with observed biomass production.

To study the effect of a the most important species parameters on the competition process, simulation runs were done in which the original parameter values were increased and decreased by 5%, respectively. Runs were carried out for pure stands with plant densities of 40 and 20 plants m^{-2} for leek and celery, respectively, as well as for the corresponding intercrop. Run characteristics where kept constant except for the parameter under study. In the crop mixture, the response of the above-ground dry matter production was calculated for both component crops after changing the parameters for either of the crops independently. The relative sensitivity of the dry matter production to a 5% decrease and 5% increase of a specific parameter was calculated as the proportion of change of yield and parameter change meaning that for a relative sensitivity of 1.0 dry matter production changes proportionally with the parameter.

Results

Model parameterisation

The parameter values used for the eco-physiological characterisation of leek and celery are summarised in Table 5.2. The values were mainly derived from pure stand treatments with medium density ($L_M = 40$ leek plants m^{-2}; $C_M = 20$ celery plants m^{-2}) of experiment I except for plant height. In experiment I, plant height was only measured in the laboratory, whereas modelling requires observations on actual height in the field. Therefore, field observed data of experiment II were used.

Table 5.2 Summary of the parameter estimates for leek and celery.

Description	Symbol	Unit	Value Leek	Value Celery	details in Figure
Light extinction coefficient	k_{df}	$m^2\,m^{-2}$	0.8-0.44	0.44-0.8	5.2
Radiation use efficiency	RUE	$g\,DM\,MJ^{-1}$ of PAR	2.4	2.2	5.3
Base temperature for development	T_b	°C	2	2	–
Maximum temperature for development	T_m	°C	23	23	–
Partitioning coefficients	pc				5.4
Initial leaf area per plant	LA_0	$m^2\,plant^{-1}$	0.002	0.005	5.5
Relative growth rate of leaf area	$RGRL$	$[°Cd]^{-1}$	0.0033	0.0039	5.5
Specific leaf area	SLA	$m^2\,leaf\,kg^{-1}$ leaf	6.9-12.1	9.6-21.7	5.6
Leaf senescence parameter	R_s	–	–	–	5.4
Height increment parameter	H_m	m	0.69	0.65	5.7
Relative growth rate of height	s	$[°Cd]^{-1}$	0.00026	0.00032	5.7

Light interception (k_{df}) The extinction of direct solar radiation varies with solar elevation (Goudriaan, 1977). Under a uniform overcast sky all radiation is diffuse making the extinction coefficient for diffuse radiation (k_{df}) independent of solar elevation. Therefore, k_{df} was used as a model parameter. The model accounts for the effects of solar angle for direct radiation. The light extinction coefficient for diffuse radiation was estimated from measurements of the light interception and the _LAI_ using eqn. [5.2]. Extinction coefficients between 0.4 and 0.8 were found in pure stands of leek and celery during the growing period (Fig. 5.2). Whereas in an early growth phase leek had a high k_{df} value this was not the case for celery. Due to the slow development and the erect leaf habit, k_{df} values of leek decreased and remained low compared to those of celery that showed a steady linear increase.
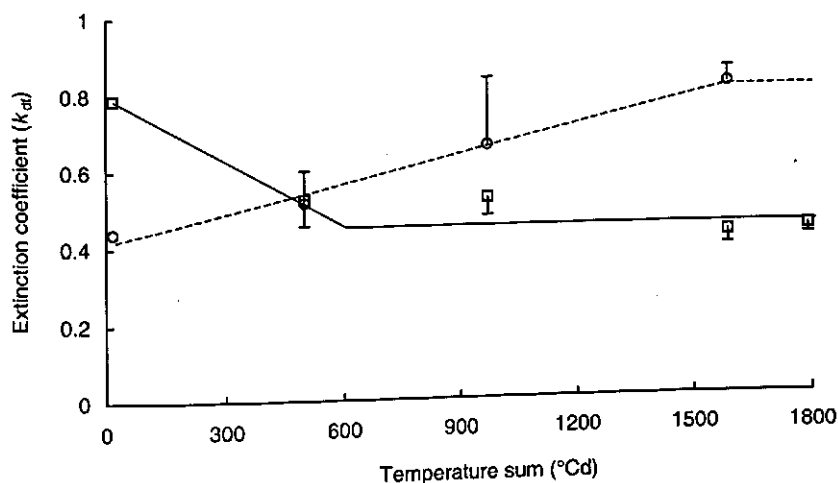
Fig. 5.2 Extinction coefficient (k_{df}) as a function of the temperature sum after crop establishment for leek (□) and celery (○) measured in pure stands (treatment L_M and C_M, resp.) in experiment I, 1996. Vertical bars are standard errors, drawn lines indicate the relationships used in the model.

Radiation use efficiency _(RUE)_ The average radiation use efficiency was estimated as the slope of the linear regression of dry matter production on cumulative radiation intercepted by the crop. For leek and celery _RUE_ values of 2.4 and 2.2 g dry matter MJ^{-1} _PAR_ were found, respectively, in experiment I (Fig. 5.3). The _RUE_ found for leek was similar to the value reported by Booij _et al._ (1996).

Phenological development Phenological development is mainly determined by the temperature sum after establishment of the crop. The temperature sum was calculated

on the basis of daily average temperature. For leek and celery a base temperature (T_b) of 2 °C was used, below which no development occurs, and a maximum temperature (T_m) of 21 °C above which the development rate is not further accelerated by increasing temperature. In the literature T_b values between 0 and 5.9 °C are reported for leek and many other temperate vegetable species (Angus *et al.*, 1981; Brewster, 1994).
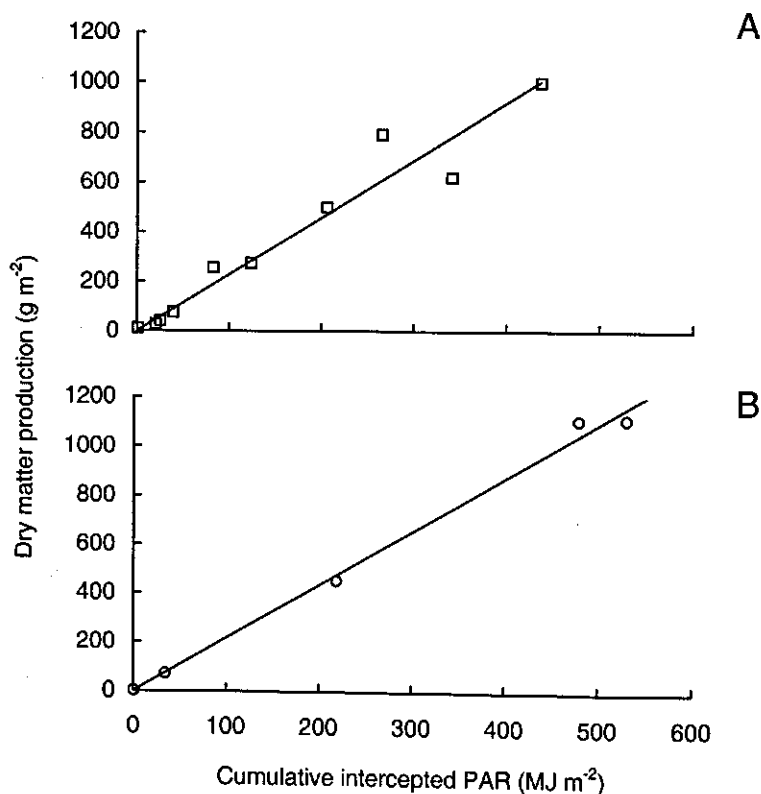
Fig. 5.3 Relationship between cumulative intercepted photosynthetically active radiation (C_iPAR) and dry matter production of leek (A) and celery (B) in pure stands (treatment L_M and C_M, resp.) in experiment I, 1996. Linear regression is applied to determine the radiation use efficiency (*RUE*) which is given by the slope of the regression line (with SE between brackets):Leek: RUE=2.28(±0.126)•C_iPAR, r^2=0.94; Celery: RUE=2.17(±0.054)•C_iPAR, r^2=0.99.

Dry matter partitioning In the model, the total daily dry matter increase was partitioned to the various plant organs as a function of the developmental stage. The partitioning pattern was derived by analysing the fractions of new dry matter

production allocated to the plant organs between subsequent harvests. The instantaneous partitioning between the different shoot organs is shown in Fig. 5.4. The dry matter distribution patterns in the various treatments of the experiments corresponded closely with each other.
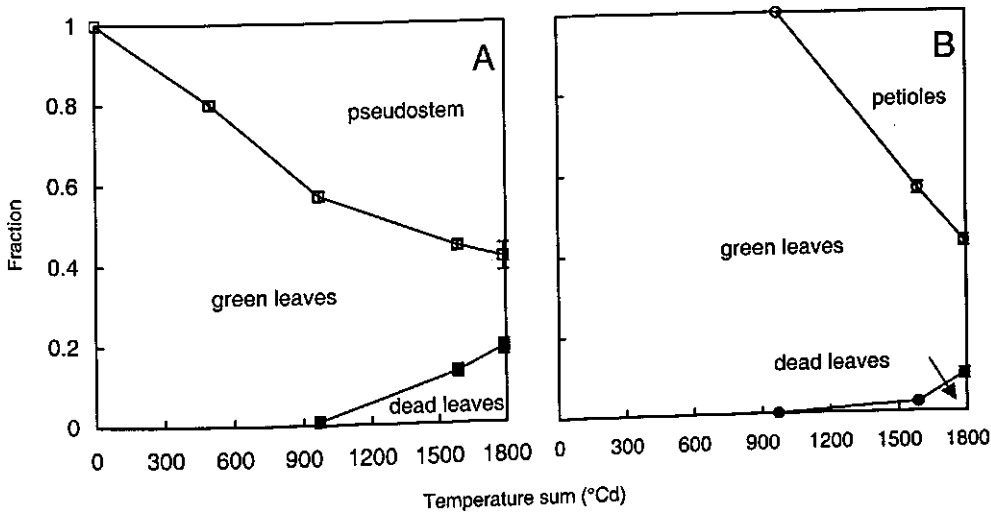
Fig. 5.4 The partitioning of dry matter among the various shoot organs as a function of temperature sum after crop establishment for leek (A) and celery (B) in pure stands (treatment L_M and C_M, resp.) in experiment I, 1996. Vertical bars are standard errors.

Leaf area During the early growth phase when no light competition occured, leaf area increased approximately exponentially over time. By plotting the per plant leaf area against the temperature sum after crop establishment an exponential relationship was obtained (Fig. 5.5) defined by a relative leaf area growth rate (_RGRL_) and the apparent leaf area (_LA₀_) at crop establishment. A significantly higher _RGRL_ and LA_0 was found for celery compared to leek, indicating the lower potential leaf area growth rate of leek as it was also reported by Brewster (1994).

After this early exponential phase, leaf area growth was simulated by multiplying the leaf dry weight increase by the specific leaf area (_SLA_) of the newly formed leaves. _SLA_ was plotted in Fig. 5.6 as a function of the development stage expressed in °Cd. The values measured in experiment I corresponded with findings of
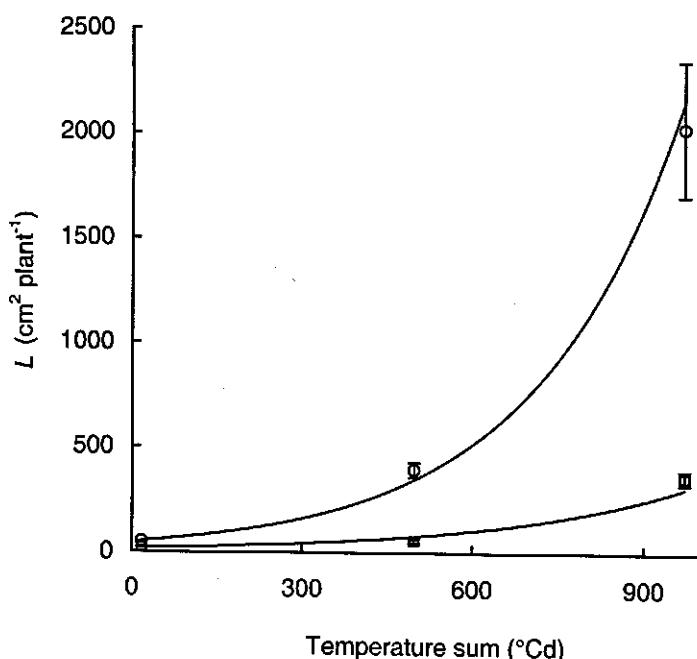
Fig. 5.5 Relationship between temperature sum (*ts*) after crop establishment and leaf area per plant (*L*) for leek (□) and celery (O) in pure stands (treatment L_M and C_M, resp.) in experiment I, 1996. Vertical bars are standard errors. Parameter estimates with SE in squared brackets:

Leek: L_{ts}=18.5[±1.14] exp(0.0029[±0.0003] *ts*); r^2=0.96;

Celery:L_{ts}=50.7[±1.05] exp(0.0039[±0.0003] *ts*); r^2=0.99.

Van der Werf *et al.*(1996) for leek. The decrease in leaf area due to senescence was estimated based on the weight of dead leaves which was measured in experiment I (Fig. 5.4). An exponential reduction of the leaf area was assumed and a relative death rate was derived from the measurements in order to calculate the resulting net growth rate of the leaf area.

Plant height The time course of plant height was described by a linear function of temperature sum after crop establishment (Fig. 5.7). The maximum height did not differ significantly between the crops within the same year. A generally lower maximum height for leek and celery was found in experiment II compared to experiment I, probably due to the wider row spacing in experiment II (see Table 5.3).
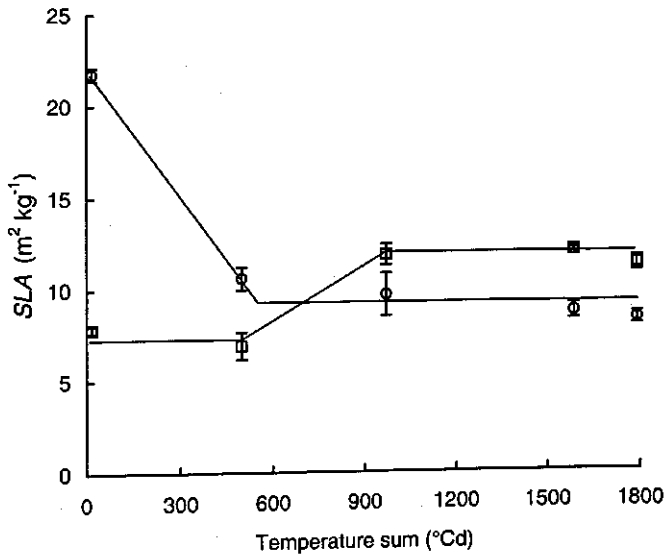
Fig. 5.6 Specific leaf area of leaves (*SLA*) as a function of temperature sum (*ts*) after crop establishment for leek (□) and celery (○) in pure stands (treatment L_M and C_M, resp.) in experiment I, 1996. Vertical bars are standard errors, drawn lines indicate the relationships used in the model.
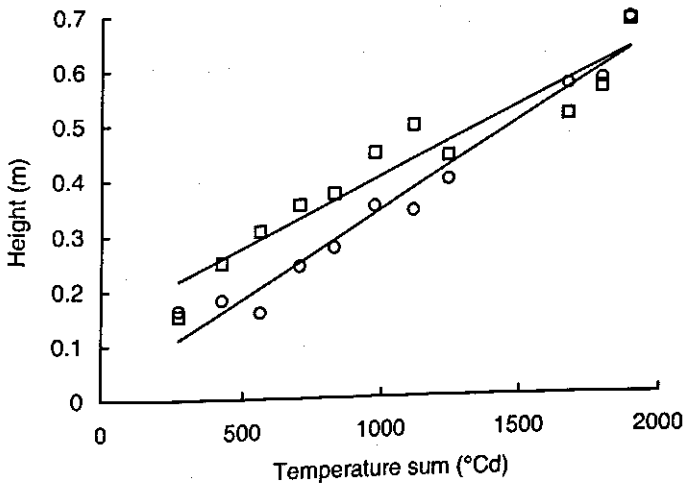
Fig. 5.7 Plant height (*H*) as a function of temperature sum(*ts*) after crop establishment for leek (□) and celery (○) in pure stands (treatment L and C, resp.) in experiment II, 1998. Parameter estimates with SE in brackets: Leek: H_{ts}=0.00026(±0.00003) *ts* + 0.15(±0.03); r^2=0.91; Celery: H_{ts}=0.00032(±0.00002) *ts* + 0.023(±0.02); r^2=0.96.

Weather Differences in average daily temperature and global radiation between the two experimental seasons are shown in Fig. 5.8. The cumulative global radiation during the growth period differed less than 1% between the two years whereas the temperature sum in the same period was 8% higher in 1998 compared to 1996. During the early growth phase there was a period of higher temperature and radiation in 1996. In the last third of the growing period, however, radiation was higher in 1998. During both years the water supply was kept at an optimal level by irrigation based on tensiometer measurements. Therefore, it was assumed that no water deficit occurred during the growing period.
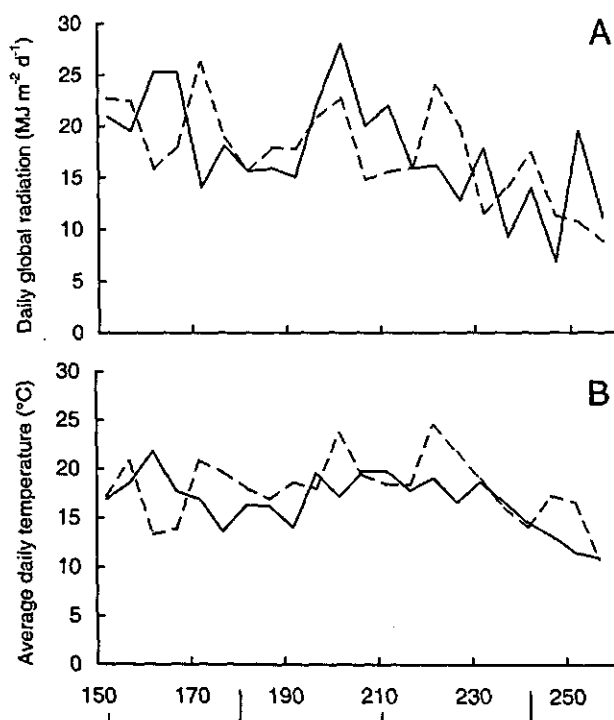
Fig. 5.8 Time course of daily global radiation (A) and average daily temperature (B) in the growing season of 1996 (—) and 1998 (---).

Canopy structure effects

To evaluate the effect of the row structure of the canopy on the fraction intercepted light by the pure and mixed stands of the component crops, the results of simulation runs carried out with the INTERROW module were plotted against the fraction intercepted light simulated by INTERCOM (Fig. 5.9). A high degree of

agreement was found between the two models for both crop stands indicating that the simulated radiation interception by the two crops was not significantly affected by the canopy structure. For leek and celery a deviation from the 1:1 line of 2.7% (SE=0.02) and 0.4% (SE=0.007) was found for the pure stands while for the mixtures this was 3.5% (SE=0.016) and 2.9% (SE=0.012), respectively.
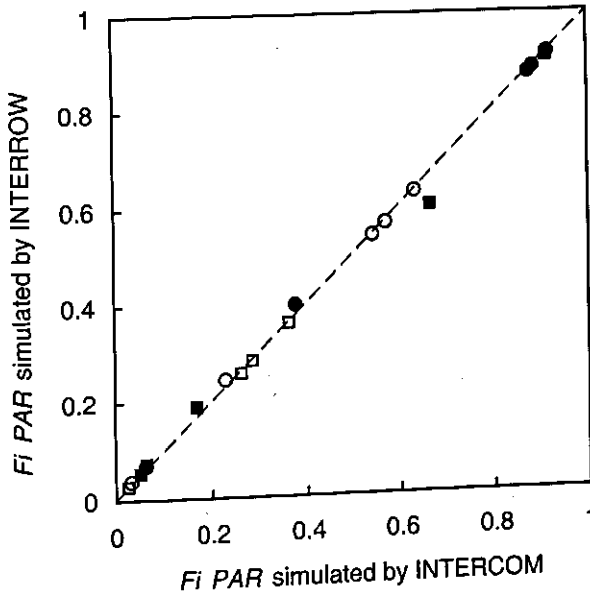
Fig. 5.9 Simulation of the fraction of intercepted photosynthetically active radiation (F_iPAR) assuming a homogeneous horizontal leaf area distribution in the canopy (INTERCOM) vs. simulation of F_iPAR when accounting for the row structure of the canopy (INTERROW). Squared symbols represent leek, circles represent celery, closed symbols represent pure stands, open symbols represent component species grown in mixture. The dashed line indicates the 1:1 line.

Biomass production

Growth data for pure and mixed stands of leek and celery for experiments I and II are given in Table 5.3. The dry matter production of celery grown in monoculture in both experiments was considerably higher than that of leek for the corresponding plant densities. In experiment I a density response was found for the monoculture crops though this was more pronounced for leek than for celery. In the mixed stands this response was not significant. Production of leek in mixture was about one third

Table 5.3 Growth data for leek (*Allium porrum* L.) and celery (*Apium graveolens* L.) in monocultures and mixtures. Dry weight of above-ground plant organs and pseudostem diameter are given for the final harvest; maximum leaf area index (*LAI*) and maximum height of the species are given for the total growing season.

Experiment	Experiment I, 1996									Experiment II, 1998		
Treatment	L_L	C_L	L_M	C_M	L_H	C_H	I_L	I_M	I_H	L	C	I
Leek density (plants m^{-2})	20	–	40	–	60	–	10	20	30	25	–	12.5
Dry matter production (t ha^{-1})	7.3 a*	–	8.8 b	–	9.6 b	–	2.8 c	3.3 c	3.8 c	6.8 a	–	3.4 b
Pseudostem diameter (mm)	26.7 b	–	21.4 c	–	17.6 d	–	22.1 b	16.8 ab	14.8 a	26.6 a	–	21.8 b
Maximum LAI	6.2 d	–	5.2 c	–	3.6 ab	–	n.m.	3.4 b	5.0 c	6.1 a	–	3.1 b
Maximum plant height (m)	0.69 a	–	0.73 a	–	0.73 a	–	0.73 a	0.79 a	0.76 a	0.69 a	–	0.65 a
Celery density (plants m^{-2})	–	10	–	20	–	30	5	10	10	–	11	5.5
Dry matter production (t ha^{-1})	–	10.4 a	–	11.0 a	–	12.0 a	7.8 b	7.3 b	6.9 b	–	8.1 a	5.7 b
Maximum LAI	–	n.m.‡	–	5.6 a	–	n.m.	n.m.	3.7 b	2.8 c	–	4.5 a	3.4 a
Maximum plant height (m)	–	0.73 a	–	0.72 a	–	0.71 a	0.73 a	0.67 a	0.69 a	–	0.69 a	0.74 a

* Means within rows, for each year, followed by different letters are significantly different at $P>0.05$, as determined by analysis of variance
‡ n.m. = not measured

of that in monoculture whereas for celery this increased from 57 to 75% with decreasing plant density. In 1998, the biomass production of leek and celery was 7 and 22% lower compared to similar densities of the same crop in 1996.

Quality parameters of leek and celery were affected by crop density in much a similar way than biomass production. At the highest leek density the diameter of the pseudostem dropped below the required minimum of 20 mm for marketable leek plants and the same occurred in mixed stands with medium and high crop densities in 1996. For celery the per plant fresh weight which should reach at least 0.25 kg ranged between 0.5 and 1.4 kg for decreasing densities at an average dry matter content of 7.3%. In 1998, leek and celery in all treatments reached the quality standards of the market.

The leaf area index of leek and celery was measured 90 days after transplanting (1570 °Cd), except for low and high density monoculture of celery and the low density mixture, as reduced plot size for these treatments did not allow destructive measurements. Visual estimation of crop soil cover indicated that canopy closure for celery in the lowest density was reached after about 1400 °Cd whereas leek crops irrespective of density never reached canopy closure (Fig. 5.10).
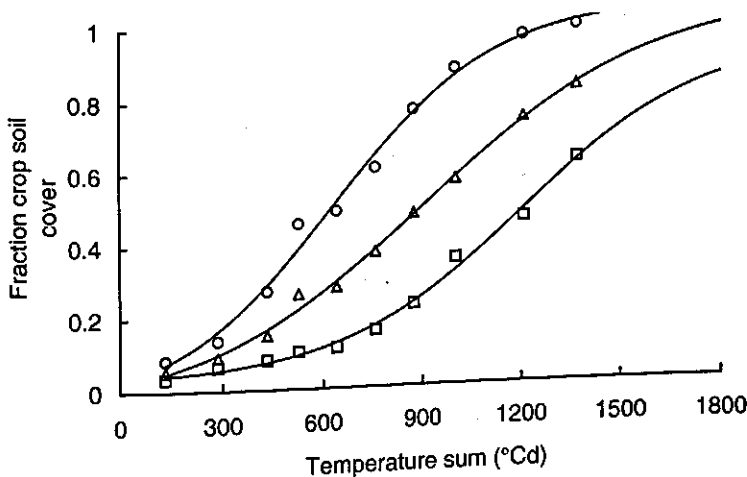
Fig. 5.10 Time course of the fraction of crop soil cover (*Fc*) for pure stands of leek (40 plants m^{-2}; ×) and celery (20 plants m^{-2}; ○) and the corresponding crop mixture (△) fitted by the logistic function *Fc=a/*(1+exp(−*b* (*ts−m*))). Estimates of parameters with SE in brackets for leek monoculture: *a* = 0.91(±0.03), *b* = 0.0037(±0.0009), *m* = 1212(±157), r^2 = 0.99; for celery monoculture: *a* = 1.0(±0.15), *b* = 0.0041(±0.0009), *m* = 629(±47.2), r^2 = 0.99 and for the intercropping system: *a* = 1.0(±0.20), *b* = 0.0029(±0.0007), *m* = 913(±66.9), r^2 = 0.99.

Maximum plant height was similar for both crops, though it was lower in 1998 than in 1996. Plants tended to grow higher in denser stands, but this effect was not significant. Height growth for both crops could be well described by a linear function (Fig. 5.7).

Model evaluation

Simulation runs either using observed *LAI* as input or dynamically simulating leaf area development were evaluated using independent experimental data. Results for the high density leek pure stand in experiment 1 are shown as an example in Fig. 5.11. The simulation with *LAI* as input deviated only 1% (SE=0.03) from the 1:1 line. Simulation of the run including the leaf area development, resulting in a slight overestimation of the biomass, was considered acceptable.
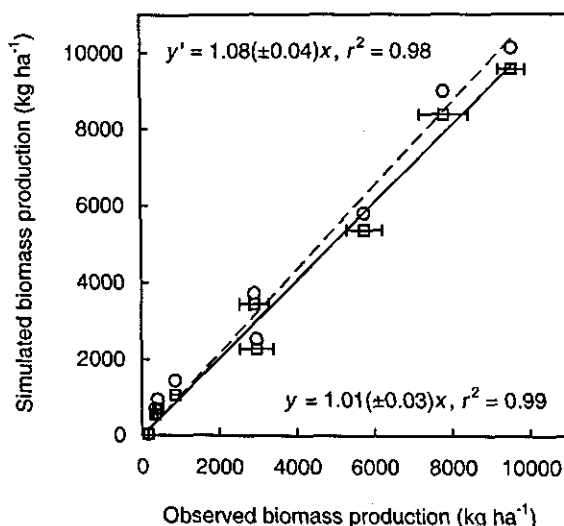
Fig. 5.11 Simulated and observed biomass production for leek monoculture with 60 plants m^{-2} (expt 1, 1996). The solid line shows the relation between simulated and observed data when measured *LAI* was used as model input; the dashed line represents the relation when *LAI* was simulated. The slope (with SE in brackets) of the linear functions given for the regression lines indicates the deviation of the simulation from the 1:1 line. Horizontal bars are standard errors of observed yield measurements.

Using this model the course of the biomass production of leek and celery grown in pure and mixed stands could be adequately simulated for 1996 and 1998 (Fig. 5.12).
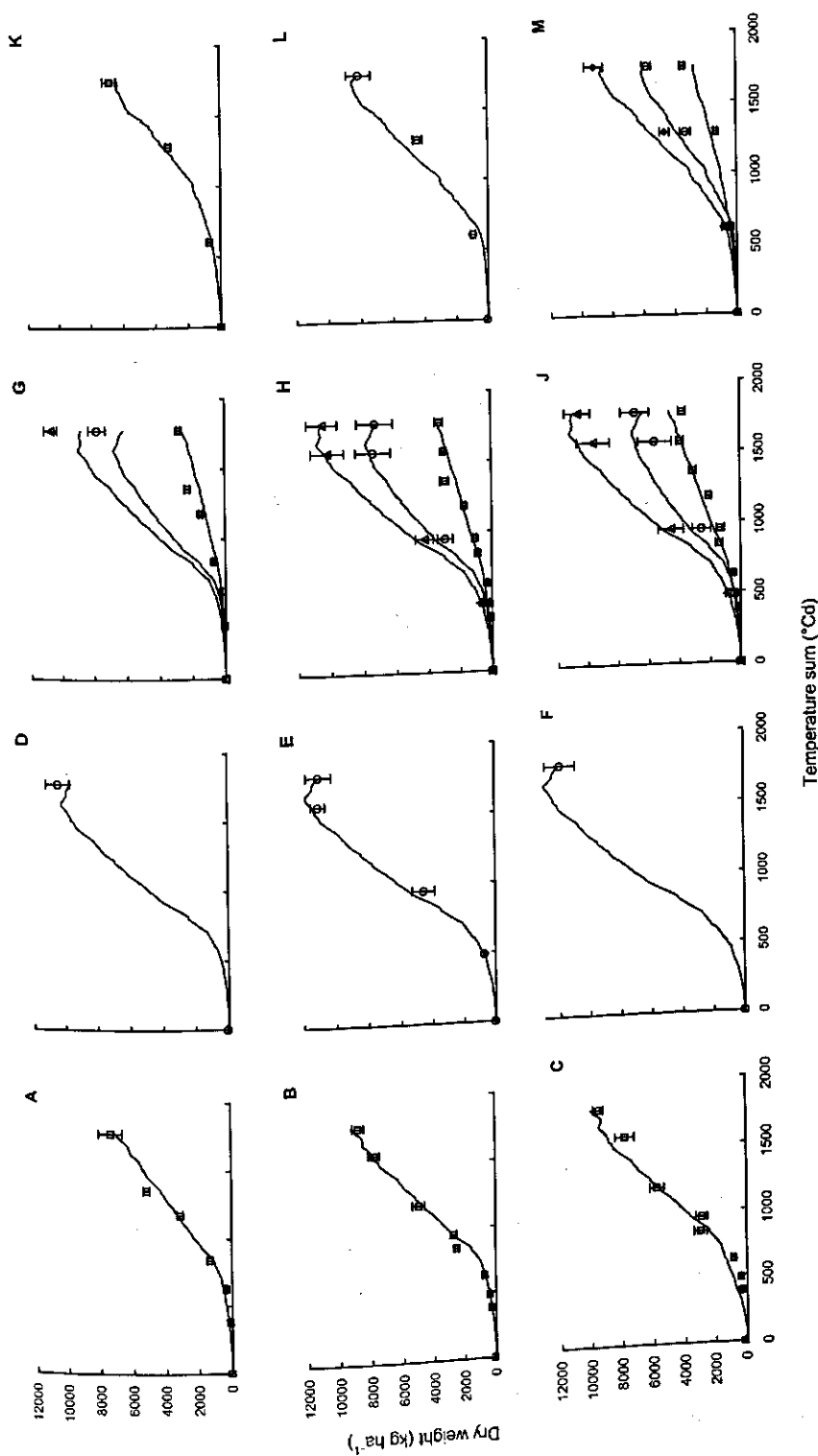
Fig. 5.12 Time course of observed (symbols) and simulated (lines) dry weights of leek (squares), celery (circles) and total biomass of the intercropping system (triangles). A-C are low, medium and high densities of leek monocultures, D-F are low, medium and high densities of celery monocultures and G-J are corresponding densities of crop mixtures, all for the 1996 growing season. Observed data shown in B (leek) and E (celery) where used for model calibration. Simulated and observed crop yields for 1998 are shown in K and L for leek and celery monoculture, respectively, and in M for the corresponding crop mixture. Vertical bars are standard errors.

Celery production in the lower plant density was underestimated in 1996 for the pure stand (8%) and for the mixture (26%), possibly due to an increased death of leaves in stands with a lower plant density. In 1998 the celery and leek production tended to be slightly overestimated for the second intermediate harvest (1293 °Cd) and for the final harvest leek production was slightly underestimated by the simulation.

To evaluate the effect of density and ratio of the crops in the mixed stand on crop quality, relevant characteristics were calculated based on the results of the simulation runs. For leek the diameter of the pseudostem was calculated based on the observed linear relationship between the logarithm of per plant biomass and pseudostem diameter as found in intermediate and final harvests for all crop stands and density treatments in experiment I (Fig. 5.13).
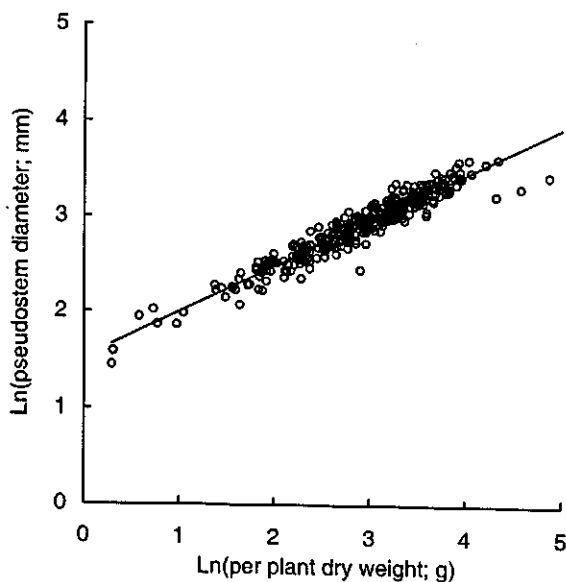
Fig. 5.13 Relationship between the natural logarithms of diameter of the pseudostem (D) and per plant dry weight (W) of leek. A linear regression line was fitted through the data of all treatments and intermediate measurements of experiment I, 1996 and regression parameters with their standard errors were estimated: ln W=0.478(±0.008) ln D + 1.52(±0.023); r^2=0.92.

Per plant dry weight of celery was transformed into fresh weight using the average dry matter content of 7.3% observed in experiment I. The results of simulation runs with different plant densities and crop ratios in the mixture are plotted in Fig. 5.14 and compared with data which were measured in experiment I.
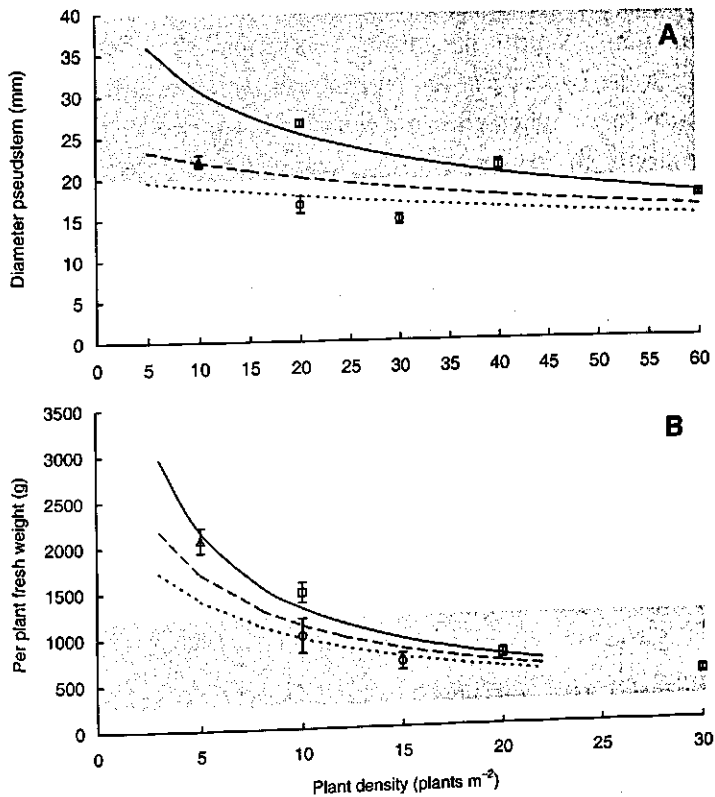
Fig. 5.14 Simulated (lines) and observed (symbols) quality parameters as a function of plant density for (A) leek monoculture (solid line and □), a mixture with 5 celery plants m^{-2} (dashed line and Δ) and a mixture with 10 celery plants m^{-2} (dotted line and O). (B) celery (solid line and □), a mixture with 10 leek plants m^{-2} (dashed line and Δ) and a mixture with 15 leek plants m^{-2} (dotted line and O). Vertical bars are standard errors; the grey area represents the quality requirements of the market.

Sensitivity analysis

Values for the relative sensitivity of the crops in pure and mixed stands are shown in Fig. 5.15. The simulated dry matter production of leek and celery was most sensitive to a change in radiation use efficiency. Per percent increase in *RUE* a 1.4 and 1.3% production increase resulted for leek and celery pure stands respectively. This more than proportional response was even more pronounced in the intercrop situation. In the intercrop the adverse competition effects on the companion crop were not the same for leek and celery. The competitive effect of celery on leek was about twice as high as the inverse competitive effect. The response of the pure

stands to the morphological parameters was remarkably smaller and not very different between the two crops. The pure stands were not affected by the heights and the response to an increased extinction coefficient was negligible. In the mixed stand the sensitivity to the morphological parameters differed clearly between the crops. Whereas leek responded more than proportional to an increased maximum height this was not the case for celery. On the other hand increasing the height for celery caused a considerable yield loss for leek, whereas the reverse effect was not found. The effect of a change of the parameters for early leaf growth ($RGRL$ and LA_0) was comparable for leek and celery, though increasing $RGRL$ for celery resulted in strong negative response of the leek dry matter yield. The same was the case if the specific leaf area of celery was increased. Leek was much more sensitive to an increase of the light extinction coefficient than celery. Again leek yield responded negatively proportional to a change of the k_{df} value of celery whereas the inverse effect was less pronounced.
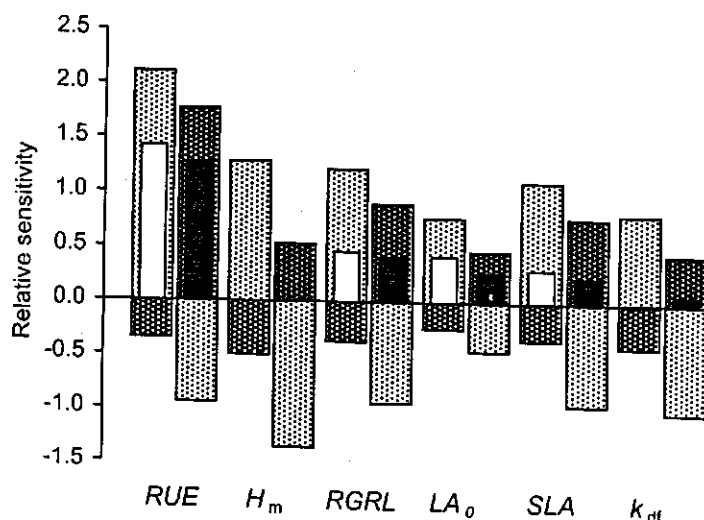
Fig. 5.15 Relative sensitivity of simulated dry matter production of leek and celery to physiological and morphological plant parameters. Sensitivity was based on differences in dry matter production obtained with simulations in which the parameter was consecutively changed with −5% and +5% of the original value. White and light grey bars represent changes for leek grown in monoculture and mixture respectively; black and dark grey bars correspond with celery monoculture and mixture. Positive responses are due to an increase of the parameter for the same crop whereas negative responses are caused by an increase of the parameter for the competing crop. For parameter abbreviations see Table 5.2.

Discussion

Canopy structure effects

The competition model INTERCOM is based on an eco-physiological crop growth model. The procedures to simulate the physiological processes for the two species in the intercropping system are basically the same as they are used for a monoculture situation (Kropff *et al.*, 1992). Competition between the two component crops is simulated at the interface between the growth process and the resource pool. INTERCOM simulates competition for light and water, moreover modules for nitrogen are available (Kropff and Van Laar, 1993). The model can be adapted for different levels of detail for individual growth processes and hence provides an excellent framework to study specific characteristics of competitive interactions within plant communities. In the current study, competition for water and nutrients was not considered as it was assumed that in high-input vegetable production systems in Western Europe irrigation and an ample supply of nutrients is common practice. A simple approach described by Kropff and Van Laar (1993) based on Williams *et al.* (1965) and Monteith (1969) was used to calculate dry matter production based on average radiation use efficiency replacing the computations of daily rates of CO_2 assimilation and respiration processes. As the study focused on the optimisation of the intercropping system with respect to radiation utilisation and weed suppression, emphasis was put on the detailed simulation of light capture in the intercropping situation. Thereby the row structure of the canopy demanded special attention and the model INTERROW for intra- and interspecific competition in row crops, as described by Schnieders (1999) was used to simulate the light distribution within the intercrop canopy. The INTERROW module was based on an earlier model for light distribution and photosynthesis in single-species row crops and accounts for the row geometry and its consequences for light absorption within an intercrop canopy (Gijzen and Goudriaan, 1989). They concluded that the effect of the row structure on light interception was small when the path width between the rows was in the order of $\leq 30\%$ of the row height. This was confirmed by the current study where only in the very early growth stage of the crops the interrow space was larger than 30% of the plant height. Simulation results of INTERCOM, which assumes a horizontally homogeneous leaf area distribution, were compared with results produced by INTERROW (Fig. 5.9). Deviations found between the results of the two models ranged between 0.4 and 3.5% for the individual crops and crop stands. It was, therefore, concluded that for the simulation of light capture by leek

and celery there is no necessity to specifically account for the row geometry in the cropping system. Since for INTERROW a number of additional parameters, such as the azimuth of the sun and the width of the row and the interrow space in time is required, it was decided to use the standard INTERCOM module for the simulation of light competition in the intercropping system. Simplified procedures and a reduced number of parameters improve the transparency of the calculation routines and hence serve the robustness of the model. This was also advocated by Spitters (1990) which in this context cited Ockham's razor "multiplicity ought not to be posited without necessity" (William of Ockham, 14th century).

Model performance for crop mixtures

INTERCOM parameterised for the pure stands of leek and celery was able to simulate dry matter production of pure and mixed stands quite accurately for various densities of the component crops (Figs. 5.11 and 5.12). Remarkable deviations of simulated from measured data occurred particularly for the low celery density in 1996. It was observed that particularly in the mixed stand with the lowest celery density leaf senescence was lower compared to that in the medium density, which was used to calibrate the model. Increased senescence in the higher densities might have been the result of bacteria rot (*Erwinia* spp.) which occurred more frequently after canopy closure probably due to a more humid microclimate.

Using the physiological and morphological characteristics that were assessed from the monocultures of the two crops, growth and production of leek and celery in mixed stands was closely simulated using weather data of two different years. None of the parameters required an adjustment for simulation of the intercropping situation.

Quantification of physiological and morphological characteristics of leek and celery, combined with subsequent model analysis, showed that differences in competitive ability between the two crops were mainly due to differences in early leaf growth rate (*RGRL*) and initial leaf area (*LA$_0$*). Differences between specific leaf area (*SLA*) and light extinction properties (*k$_{df}$*) were less important whereas the maximum height (*H$_m$*) and the radiation use efficiency (*RUE*) hardly differed between the two crops (Table 5.3).

Sensitivity analyses showed that both crops were more sensitive to parameter changes if grown in the mixed stand compared to the monoculture. In the intercrop situation, leek was generally more sensitive than celery to parameter changes of either leek or celery. Both crops responded in the pure and the mixed stand more than

proportional to an increase in radiation use efficiency. As mentioned above, _RUE_ determined in experiment I did not differ between leek and celery. Moreover the value found for leek was similar to that determined by Booij _et al._ (1996), who conducted their experiments under different conditions with another cultivar. A comparison of a range of important agricultural crops showed that under optimal growth conditions and with closed canopies the potential growth rates of the crops do not differ considerably (Sibma, 1968). Under sub-optimal conditions (e.g., shortage of water and/or nutrients), however, the relative growth rate (_RGR_) can be reduced. As the maximum photosynthetic rate per unit of leaf area is related to the nitrogen concentration in the leaf, _RGR_ is directly related to the nitrogen content in the plant (Lambers _et al._, 1989; Van Keulen _et al._, 1989). Booij _et al._ (1996) found a very weak response of the leek dry matter production rate to nitrogen, particularly during early growth. For celery, Stark _et al._ (1982) reported an increase in the early season growth rate when more nitrogen was applied but a weak response to high nitrogen rates at a later stage. It can, therefore, be concluded that, if water and nutrients are sufficiently available, the possibilities to effectuate a further increase in radiation use efficiency by crop management practices seem to be limited.

The morphological parameters were identified as the most important factors determining differences in competitive ability between the crops. Similar conclusions for situations where competition is mainly for light were drawn by Rooney (1991) and Kropff _et al._ (1992). Sensitivity analysis confirmed these findings as for the morphological parameters disproportional responses were found for the intercrop situation and for leek in particular. An increase in H_m, _RGRL_, _SLA_ and to a lesser extent k_{df} and LA_0 resulted in an increase in leek yield. A distinct negative response of leek resulted from an increase in the same parameters for celery. On the other hand, the competitive effects on celery due to a change in the morphological properties of leek were less pronounced. Differences in competitive ability between leek and celery can mainly be explained with the different abilities of the crops to capture radiation. _RGRL_ was thereby recognised as the most important parameter showing significant differences between leek and celery. Leek, like many other _Allium_ crops, is known as a weak competitor due to its slow leaf development, particularly in the early growth stages. Brewster (1994) related the relative growth rates of leek and celery to that of onion and found values for different leek varieties ranging from 0.8 to 0.89 whereas _RGRL_ of celery was 1.37 times that of onions. Consequently, leaf area and hence soil cover of celery increases faster, resulting in an earlier canopy closure compared to leek (Fig. 5.10). Another parameter affecting early leaf development is the initial leaf area. In experiment I, LA_0 differed significantly

between the crops (Fig. 5.5). The same was true for the leaf area ratio of the transplants, which in this stage was similar to the SLA as the sprout consisted only of leaves and roots were disregarded. Although leeks showed the least response to LA_0, among the various morphological parameters, the importance of this parameter is that it can easily be manipulated. Early growth of leek and celery can be affected by using conditioned transplants. To favour initial conditions for leek growth in an intercropping system strong leek and moderatly sized celery transplants can be used, which will result in a more balanced growth pattern of the two crops during early growth.

Whereas during early growth the leaf area development is sink limited and temperature dependent (Horie *et al.*, 1979), in later stages leaf area increment is increasingly limited by assimilate supply as a result of an increasing amount of growing points, stem growth and mutual shading of leaves (Kropff and Van Laar, 1993). After reaching an LAI of 1, leaf area development is dependent on the daily increment of the leaf weight and directly proportional to SLA. Differences in SLA between the crops gradually reduced in time, though they remained significant (Fig. 5.6). Van der Werf *et al.* (1996) compared the components of the relative growth rate of leek and Brussels sprouts and found that differences in RGR between these crops were mainly due to differences in SLA, whereas differences between net assimilation rates or leaf weight ratios were marginal. Similar results were reported for a wider range of species by various authors who stated that differences in RGR are highly correlated with differences in SLA and less with differences in biomass partitioning or net assimilation rate (Garnier, 1992; Poorter and Remkes, 1990; Poorter *et al.*, 1990; Van der Werf *et al.*, 1993; Van der Werf, 1996).

The extinction coefficient (k_{df}) for diffuse radiation, which was used as input to the model, was calculated based on measurements of light absorption and LAI using eqn. [5.2]. Except for the early growth phase k_{df} of leek remained low whereas that of celery increased during the growing period (Fig. 5.2). It can be expected that the ability of leek to capture light is lower due to the more erect growth habit of leek compared to celery. The difference in light extinction contributes to the explanation of the competitive ability between leek and celery, though it was less important than the dynamics of early leaf growth. From the sensitivity analysis it can be seen that particularly leek responded about proportional or negative proportional to an increase in k_{df} for leek and celery, respectively. As celery already reaches a high k_{df} its sensitivity to a change is low.

In the sensitivity analysis, a strong response of leek and to a lesser extent of celery to the maximum plant height was found. In the experiments H_m did, however,

not differ between the crops (Table 5.3, Fig. 5.7). Non significant differences of H_m between the two experimental seasons were observed which could have been the result of either the slightly differing row spacing, the different varieties that have been used, the varying growth conditions or a combination of all. The fact that specifically leek responded very sensitively to a change in H_m leads to the conclusion, that plant height, for example through adequate cultivar choice, could be used as a tool to affect interspecific competition between leek and celery. Another suggestion is to use celeriac (*Apium graveolens* var. *rapaceum*) instead of celery in the crop mixture as for celeriac leaf growth tends to be shorter, less erect and exhibits a more open growth habit than for celery (Rubatzky *et al.*, 1999).

Optimisation of the intercropping system

The experimental results show that for leek and celery there is a significant response of dry matter production and crop quality to plant density (Table 5.3). This was true for the pure stands but in particular for the intercropping system. Competition studies analysing replacement series of leek and celery have shown that with respect to competitive ability leek is inferior to celery (Baumann *et al.*, 2000). In the same study, it was also found that the ability of the intercropping system to suppress weeds was significantly better compared to a leek monoculture. However, implementing intercropping into a weed management strategy will only be adopted by vegetable producers if this cropping system does not have a major drawback compared to traditional monoculture cropping systems.

When agricultural cropping systems are optimised the focus is mainly on yield and quality. In vegetable production especially the latter plays an important role, as product quality is decisive for a ready sale. A product quality according to the standards required from the market is, therefore, a precondition for the performance of a cropping system. Because of that quality parameters such as pseudostem diameter of leek and per plant fresh weight of celery have been implemented into the model as output variables. Although calculation of these parameters is based on empirical data and therefore entirely descriptive, it allows evaluating the model results in a comprehensive way. In this way, the model can be used as a tool to optimise the cropping system with respect to crop quality. Simulation runs for increasing plant densities and mixtures with various proportions of crops demonstrate the quality response of leek and celery if grown in an intercropping compared to monoculture system (Fig. 5.14). For leek monoculture densities producing marketable leek plants ranged from <5 to 44 plants m^{-2}. In an intercropping

system with 5 celery plants m^{-2} the maximum leek density to produce an acceptable yield was found at 21 leek plants m^{-2} whereas when 10 celery plants m^{-2} were added no marketable leek could be produced anymore. Celery, although its per plant weight showed a strong response to plant density, was less sensitive to additional leek plants and the quality requirements of the Swiss vegetable market were easily met. It could be shown that celery is clearly more competitive than leek as it was already demonstrated by the sensitivity analysis for the physiological and morphological parameters. Willey (1979a) stated for intercropping in general that optimising the crop performance is a question of maximising complementarity and minimising competition between the two component crops. The same holds for the leek-celery intercropping system as presented in this study. An explanatory model based on eco-physiological characteristics of the competing species was used as a tool to quantify and explain competitive interactions between the component crops. Moreover options and targets for improvement of the intercropping system were identified. Adapted and validated for different conditions (e.g., crops, sites, weather conditions, etc.) the model provides an excellent tool to optimise intercropping systems for vegetable production.

Intercropping system optimisation for yield, quality and weed suppression combining mechanistic and descriptive models

Abstract

Intercropping leek (*Allium porrum* L.) with celery (*Apium graveolens* L.) was recognised as a useful option to reduce growth and reproductive potential of weeds in leek production while maintaining productivity. Optimisation of the intercropping system with respect to crop yield, quality of the produce, and weed suppressive ability was, however, needed. This study used combined modelling approaches for analysis and optimisation of an intercropping system for high-quality production of leek and celery with a reduced need for direct weed control measures. An adapted version of the eco-physiological model for interplant competition INTERCOM was used to simulate biomass production of leek, celery, and the weed *Senecio vulgaris* L. for a wide range of crop densities and different relative times of weed emergence. The result of the simulations were summarised using a descriptive hyperbolic yield-density model, which than allowed evaluation of the intercropping system in terms of productivity, product quality and weed suppressive ability.

In a weed-free mixture, the competitive ability of celery was six times higher than that of leek. With respect to late-emerging *S. vulgaris*, the relative competitive ability of leek was 5.4 times lower than that of celery. Replacing two leek plants of a leek monoculture by one celery plant resulted in almost 20% biomass reduction of late-emerging *S. vulgaris*. Crop mixtures with a leek density of about 20 plants m^{-2} and a leek:celery ratio of 2 proved to be the optimum intercropping system, given the current price ratios. Compared to leek monoculture profitability was maintained, whereas particularly late-season weed suppressive ability was greatly improved, resulting in reduced weed seed production.

Introduction

Recently, a number of studies addressed intercropping as an option for an integrated weed management strategy, particularly in low-external input farming systems (Caporali *et al.*, 1998; Itulya and Aguyoh, 1998; Liebman and Davis, 2000; Rana and Pal, 1999; Schoofs and Entz, 2000). Effects of crop diversification on weeds have been reviewed a.o. by Liebman and Dyck (1993); Liebman and Ohno (1998) and Teasdale (1998). As an example of functional biodiversity, intercropping leek (*Allium porrum* L.) with celery (*Apium graveolens* L.) showed various beneficial effects, such as the reduction of weeds and pests, and an improved resource capture, while cropping practices were not hampered (Baumann *et al.*, 2000; Baumann *et al.*, 2001b). Celery improved the weed suppressive ability of the canopy by increasing its light interception. As a result, incoming radiation was captured more efficiently by the intercrop canopy and less radiation was available for germination and growth of weeds. However, the strong relative competitive ability of celery in the intercropping system resulted in a loss of leek quality as stem diameter was reduced to less than 20 mm (market criterion) (Baumann *et al.*, 2001b). The authors, therefore, concluded that optimisation of the intercropping system with respect to crop quality and weed suppressive ability was needed for successful implementation of the intercropping system and suggested the application of eco-physiological simulation models to optimise the system. Earlier Kropff and Van Laar (1993) already advocated the use of modelling to develop and optimise weed management systems with respect to cost effectiveness and minimisation of environmental effects.

Eco-physiological crop growth models can be very effective to evaluate and develop complex systems, such as multi-species plant communities (Kropff and Van Laar, 1993). Based on physiological, morphological, and phenological processes such models provide insight into the competitive relationships of the system. These models facilitate the exploration of complex systems without extremely extensive field experimentation to investigate all options in a wide range of conditions. Empirical models and regression techniques can help to analyse the final outcome of competition trials and to describe plant interference in cropping systems. Approaches to describe interplant relationships have been developed for a long time and helped to improve understanding of competitive effects between crops, and crops and weeds (De Wit, 1960; Kira *et al.*, 1953; Shinozaki and Kira, 1956). The current study attempts to combine a mechanistic and descriptive modelling approach to optimise the system. The well evaluated eco-physiological model provides the necessary insight into the processes and plant characteristics determining mutual

competitive effects and allows generating a large number of data sets for a wide range of densities and environments. Subsequent application of a descriptive model to the generated data sets can help to summarise the results, to calculate the relative competitive ability of the system components, and to describe yield and product quality of the component crops in relation to plant density and mixing ratios.

The main aim of this study was to optimise an intercropping system of leek and celery, with respect to yield and quality, while improving the weed suppression. Moreover it was the objective to evaluate the use of combined modelling approaches for analysis and design of an intercropping system. The use and feasibility of the modelling approaches will be discussed and conclusions will be drawn with respect to profitability and weed suppressive ability of a leek-celery intercropping system.

Material and Methods

Model description

The eco-physiological competition model INTERCOM (Kropff and Van Laar, 1993) was used as a framework to simulate interplant competition in a leek-celery intercropping system. The model was simplified with respect to physiological processes but included a detailed simulation of competition for light (Chapter 5). Because water and nutrients were available in ample supply in the experimental system, competition for these resources was not included in this version of the model. The competition model was parameterised using experimental data from pure stands of the crops. Validation with independent data showed that the model simulated growth in both monocultures and mixtures accurately. For a detailed description of the model, the eco-physiological characteristics of the crops and the underlying experiments the authors refer to Chapter 5. To study the growth of _S. vulgaris_ and its effect on intercrop performance the model was extended to include this weed species. Parameter values were derived from field experiments and additionally from earlier studies carried out by Schnieders (1999), and are summarised in Table 6.1. The model was validated with independent data from monocultures and mixtures of the three species collected in two field experiments, which were carried out in 1997 and 1998.

Table 6.1 Summary of the parameter estimates used for parameterisation of the model INTERCOM for leek, celery and *Senecio vulgaris*.

Description	Symbol	Unit	Value Leek[1]	Celery[1]	S. vulgaris
Light extinction coefficient	k_{df}	$m^2\ m^{-2}$	0.8-0.44	0.44-0.8	0.45[2]
Radiation use efficiency	RUE	g DM MJ^{-1} of PAR	2.4	2.2	2.1[3]
Base temperature for development	T_b	°C	2	2	2[2]
Maximum temperature for development	T_m	°C	23	23	23[2]
Initial leaf area per plant	LA_0	$m^2\ plant^{-1}$	0.002	0.005	0.00014[2]
Relative growth rate of leaf area	$RGRL$	[°Cd]$^{-1}$	0.0033	0.0039	0.01[2]
Specific leaf area	SLA	m^2 leaf kg^{-1} leaf	6.9-12.1	9.6-21.7	5.0-22.5[2]
Height increment parameter	H_m	m	0.69	0.65	0.45[3]
Relative growth rate of height	s	[°Cd]$^{-1}$	0.00026	0.00032	0.00008[3]

[1] Chapter 5; [2] Schnieders, 1999; [3] expt. II, 1998, Switzerland

Field experiments I and II (replacement series of leek and celery with additive S. vulgaris)

Two field experiments, referred to as experiment I (1997) and II (1998), were carried out on a sandy loam soil (Inceptisol; 17% clay, 24.5% silt, 54.2% sand, pH 7.8, 4.3% organic matter) at the "Sandhof" experimental farm of the Swiss Federal Research Station for Fruit-Growing, Viticulture and Horticulture, at Wädenswil, Switzerland (47°13' N, 08°40' E). The experiments were set up to examine the effect of pure and mixed stands of leek and celery on the biomass and reproduction of *S. vulgaris* in relation to its relative time of emergence in the crops. Rows of *S. vulgaris* were sown between crop rows at a density of 50 plants m^{-2}. For both experiments, a split-plot block design with 3 replicates was used. Crop system (monoculture leek, monoculture celery and intercrop of the two species) was the main plot factor. Plant densities were 18 and 9 plants m^{-2} for leek and celery, respectively, and the intercrop was arranged as a row based replacement series of the two crops. The relative emergence time of *S. vulgaris* was the split-plot factor. In experiment I, *S. vulgaris* was planted at seven times, each 10 days apart, with the first planting at 10 days after crop establishment. In experiment II, planting occurred at five times, each 10 days apart, starting at crop establishment. In both experiments, a weed-free plot was included. In experiment II, a monoculture of *S. vulgaris* was included which was used to generate data for model parameterisation. A comprehensive description of the experimental details of the two experiments is given in Baumann *et al.* (2001a).

Data analysis

After validation of the model, the performance of pure and mixed crop stands with and without *S. vulgaris* were simulated for Swiss environmental conditions. Plant density for leek was varied between 0 to 25 plants m^{-2}, and plant density of celery was varied between 0 and 20 plants m^{-2}. Plant density of *S. vulgaris* remained constant at 50 plants m^{-2} at a relative emergence time of 0, 10, 20, 30 and 40 days after crop establishment. Simulation runs were conducted with weather data of 1997 and 1998 from Wädenswil, Switzerland for all combinations of crop densities with and without *S. vulgaris*. Biomass production and per-plant weight of the species after a growing period of 88 and 92 days for 1997 and 1998, respectively, were output of the model. For leek the diameter of the pseudostem, which is used as quality parameter, was calculated based on the per-plant weight, as a high correlation (r^2=0.92) between the dry weight of above-ground organs and pseudostem diameter was found in earlier experiments (Chapter 5). For celery the per-plant fresh weight was calculated

based on an average dry matter content of 7.3%, which was found in experiment I and II, and did not differ significantly between the various treatments. For *S. vulgaris* seed production was estimated based on the established linear relationship between per-plant dry weight and number of seeds per plant (Baumann *et al.*, 2001a; Schnieders, 1999).

Biomass production of *S. vulgaris* in the intercrop was expressed relative to its biomass production in leek monoculture. The effect of progressively replacing leek by celery in the mixture on *S. vulgaris* biomass was than analysed with a hyperbolic function using celery density as an explanatory variable (Cousens, 1985):

$$RY = 1 - \frac{a N_C}{1 + a N_C / m}$$ [6.1]

where RY is the relative yield of *S. vulgaris* (as biomass fraction of its biomass in leek monoculture), N_C is the plant density of celery (plants m^{-2}), a is a parameter describing the effect of replacing the first leek with celery (m^2 plant^{-1}), and m is the maximum relative yield loss of *S. vulgaris* in intercropping.

To analyse the crop performance of the intercropping system, the relative yield total (*RYT*) was calculated according to (De Wit, 1960) for all replacement series of the simulated crop stands:

$$RYT = \frac{Y_{LC}}{Y_{LL}} + \frac{Y_{CL}}{Y_{CC}}$$ [6.2]

where Y is the crop yield (kg ha^{-1}) and the suffixes L and C denote leek and celery, respectively. Thus, Y_{LC} is the yield of leek when grown in mixture and Y_{LL} is the yield of leek when grown in monoculture. Y_{CL} and Y_{CC} are the corresponding yields for celery in mixture and monoculture, respectively.

Additionally, the relative competitive ability of the crops was analysed using an approach proposed by (Spitters, 1983a; Watkinson, 1981; Wright, 1981). This approach is based on the notion that the biomass-plant density response can be described by a rectangular hyperbola (De Wit, 1960; Spitters, 1983a). The model relates the biomass of each species to the density of both species in the mixture and the yield Y (g m^{-2}) of a component crop can be calculated by:

$$Y_{1,2} = \frac{N_1}{b_{1,0} + b_{1,1} N_1 + b_{1,2} N_2}$$ [6.3]

where N_1 and N_2 are the plant densities (plants m^{-2}) of crop 1 and 2, $b_{1,0}$ is the intercept denoting the reciprocal of the virtual biomass of an isolated plant of crop 1 (plant g^{-1}), and $b_{1,1}$, and $b_{1,2}$ (m^2 g^{-1}) are parameters for intra- and interspecific competition, respectively. The ratio of these last two parameters denotes the relative competitive ability (_RCA_) between both crops with respect to the production of the first crop. A similar ratio was calculated with respect to the production of the second crop. Based on the coefficients for intra- and interspecific competition of leek and celery the niche differentiation index, _NDI_, was calculated (Spitters, 1983a):

$$NDI = \frac{b_{L,L}}{b_{L,C}} \cdot \frac{b_{C,C}}{b_{C,L}} \qquad\qquad [6.4]$$

The same approach was used to analyse interplant competition in a system with three components leek, celery, and _S. vulgaris_ by expanding eqn. [6.3] with an additional parameter to account for the third species:

$$Y_{L,C,S} = \frac{N_L}{b_{L,0} + b_{L,L}\,N_L + b_{L,C}\,N_C + b_{L,S}\,N_S} \qquad\qquad [6.5]$$

where $Y_{L,C,S}$ is the yield of leek (L) in presence of celery (C) and _S. vulgaris_ (S) (g m^{-2}) and N_L, N_C and N_S are the plant densities of leek, celery and _S. vulgaris_, respectively. Dividing yield by plant density of corresponding species result in the per-plant weight, which was used to derive crop quality parameters and seed production for _S. vulgaris_:

$$W_{L,C,S} = \frac{1}{b_{L,0} + b_{L,L}\,N_L + b_{L,C}\,N_C + b_{L,S}\,N_S} \qquad\qquad [6.6]$$

where $W_{L,C,S}$ is the per plant dry weight (g plant^{-1}).

Optimisation of the intercropping system

To optimise the intercropping system, crop mixtures corresponding in either quality, yield, or weed suppressive ability were determined. For this purpose, eqn. [6.5] was rewritten to obtain an expression for plant density of celery (N_C). Isolines with equal biomass production of each of the components of the mixture were than determined by fixing crop yield (_Y_) and calculating the corresponding celery density

(N_C) for a range of leek densities. A similar procedure was followed for per-plant dry weight using eqn. [6.6] after converting quality parameters for leek and celery, and seed production for *S. vulgaris* into per-plant dry weight. Isolines for total biomass production of the intercrop were calculated in an identical way. Here the equation in biomass production of leek and celery were first added, after which the combined equation was rewritten to obtain an equation for N_C. Accordingly, the total financial yield, Y_T, of the mixture was calculated as:

$$Y_T = \frac{P_L \, N_L}{b_{L,0} + b_{L,L} \, N_L + b_{L,C} \, N_C} + \frac{P_C \, N_C}{b_{C,0} + b_{C,C} \, N_C + b_{C,L} \, N_L} \qquad [6.7]$$

where P is the price of the product received by the farmer (€ kg^{-1}), the other parameters are denoted as indicated for eqn. [6.3] and the suffixes L and C are for leek and celery, respectively. Rewriting eqn. [6.7] for N_C, which results in a quadratic equation, allowed calculation of isolines for crop stands with equal financial yield. For the calculation, average prices achieved by farmers over a five-year period between 1993 and 1998 where used (Spigt and Janssen, 1997). The crop stand with the highest financial gross return was detected by determining the point where the Y_T-isoline and the minimum quality isoline for leek touch. This was established by introducing the equation for the minimum quality isoline into the equation of the Y_T-isoline, which resulted in a new equation. Calculating the celery density for which the first derivative of this combined equation equals zero allowed than to determine the crop densities of the optimal mixture. The sensitivity of the yield and crop densities to a 5% change of the prices was tested.

Results

Model performance

The model was calibrated based on data from monocultures of the crops using data from field experiments carried out in 1996 and 1998 (Chapter 5). Calibration for *S. vulgaris* was based on experimental data from 1998 (Exp. II) and from literature (Schnieders, 1999). For the evaluation of the model, independent data sets from two field experiments were used and dry matter production could be simulated adequately for leek monoculture and mixture in 1997 and 1998 (Fig. 6.1A). For celery, simulations with 1998 weather data underestimated the observed biomass production in the mixed stand compared to observed data in experiment II (Fig. 6.1B). For other crop
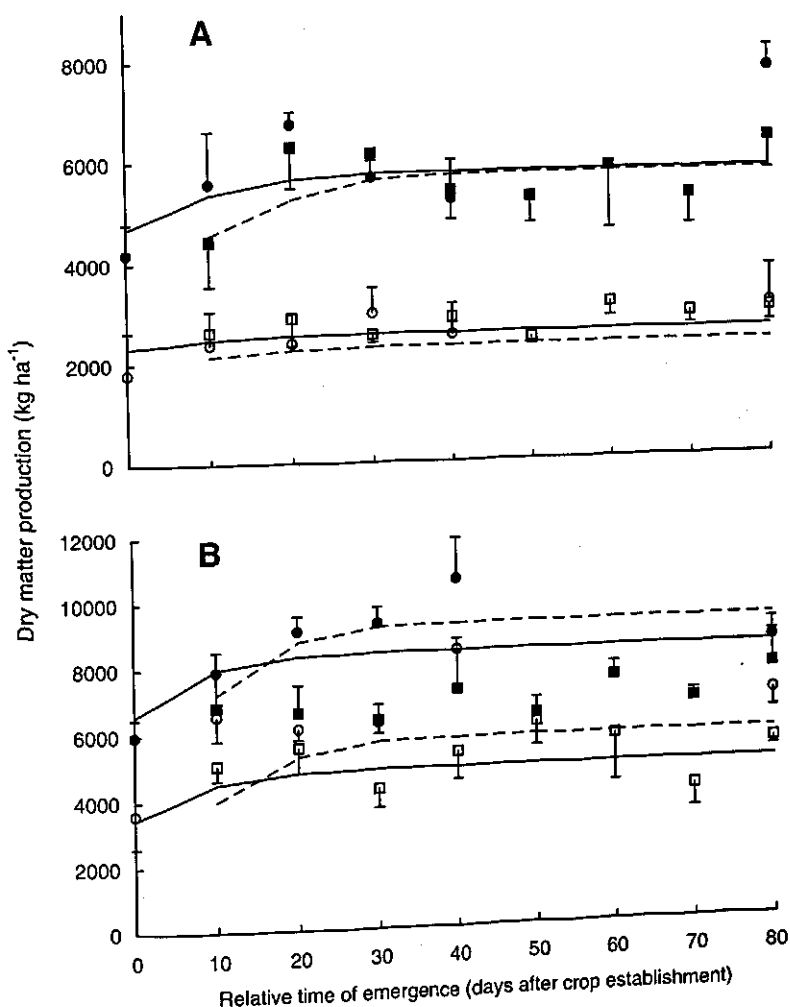
Fig. 6.1 Observed (symbols) and simulated (lines) shoot dry matter of leek (A) and celery (B) at harvest in monoculture (closed symbols) and mixture (open symbols) as affected by the relative time of emergence of *Senecio vulgaris*. Results of 1997 (expt. I; squares; dashed lines) and 1998 (expt. II; circles; solid lines). Error bars are standard errors of means.

stands simulation of celery production was acceptable in both years. Standard errors for celery dry matter production in the experiments were high in both years. The model simulated *S. vulgaris* biomass in all crop stands very accurately (Fig. 6.2) for 1998. The model could not be evaluated for the 1997 data, because *S. vulgaris* had been infected by *Puccinia lagenophorae* Cook., which caused early senescence and a strong reduction of the biomass. Biomass of *S. vulgaris* was more reduced in all
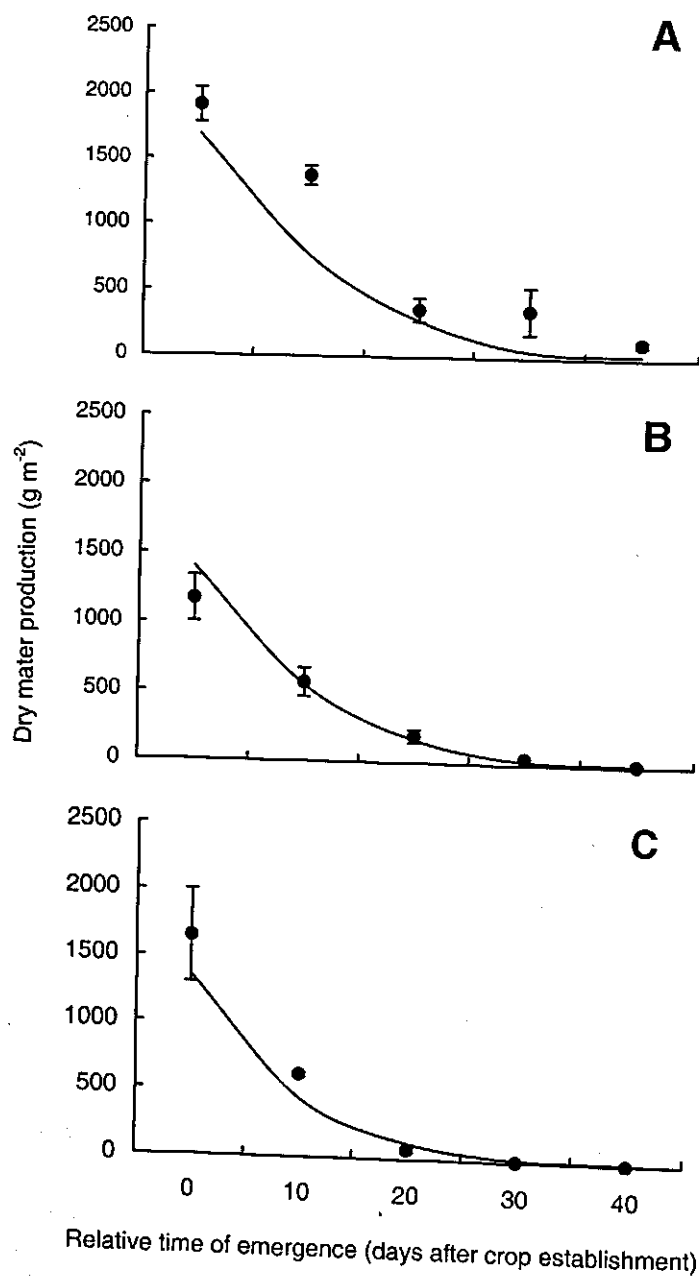
Fig. 6.2 Observed (symbols) and simulated (lines) shoot dry matter of *Senecio vulgaris* grown in leek monoculture (A), leek-celery intercrop (B), and celery monoculture (C) as affected by the relative time of emergence. Error bars are standard errors of means.

crop stands when the plants emerged later than the crop. Biomass was more reduced in the crop mixture and celery monoculture compared to leek monoculture particularly for early dates of emergence.

Relative competitive ability

Parameter estimates for non-linear regression of density-yield relationships for simulated competition results using eqn. [6.3] are given in Table 6.2. Under weed-free conditions the competitive ability of celery, was about 3 times higher than the competitive ability of leek both with respect to celery and leek production (Fig. 6.3A). If *S. vulgaris* was introduced in the intercrop at the time of crop transplanting, both *RCA*'s were slightly changed (about 15%) to the benefit of leek. For later planting dates of *S. vulgaris* the relative competitive ability of both crops differed less than 3% from that of the weed-free mixture.

For the weed-free mixture of leek and celery a niche differentiation index (*NDI*) of 1.45 was calculated (eqn. [6.4]), indicating a slight complementarity in capture and/or use of light for leek and celery. *NDI* for leek and *S. vulgaris* ranged between 2 and 5, whereas *NDI*'s between 1.7 and 3.2 where found for celery and *S. vulgaris*, depending on the relative time of emergence of the weed.

When *S. vulgaris* was planted together with the crops, 12 plants of *S. vulgaris* were found equally competitive with either one leek or one celery plant. For later planting dates of *S. vulgaris* the ratio between the relative competitive ability of celery versus *S. vulgaris* and leek versus *S. vulgaris* with respect to the productivity of the respective crops (RCA_{CS}/RCA_{LS}) increased linearly reaching a value of 5.4 when *S. vulgaris* was introduced as late as 40 days after crop establishment (Fig. 6.3B). The large differences in competitive strength between leek and celery with respect to *S. vulgaris* was also reflected in RCA_{SC} and RCA_{SL} which differed markedly for the early plantings of *S. vulgaris* (Fig. 6.3C).

The relative yield total (*RYT*) of the intercrop (eqn. [6.2]) ranged from 1.0 and 1.03 over a wide range of densities of the two crops and was not affected by introduction of *S. vulgaris* (Fig. 6.4A). The relative biomass of *S. vulgaris* was reduced when the proportion of celery density was increased in the mixture (Fig. 6.4B). The response function could be well described with a rectangular hyperbola using eqn. [6.1] irrespective of the relative emergence time of *S. vulgaris* ($r^2 = 0.99$). Parameter estimates are given in Table 6.3. Replacing two leek plants m^{-2} of the monoculture with one celery plant resulted in a 2.9% biomass reduction of *S. vulgaris*, when planted together with the crops.

Table 6.2 Estimates and standard errors of the parameters for density response functions of simulated biomass production (eqn. [6.5]) in a leek-celery intercropping system with *Senecio vulgaris* introduced at different times relative to crop establishment. Adjusted r^2-values were ≥0.99 for all estimates.

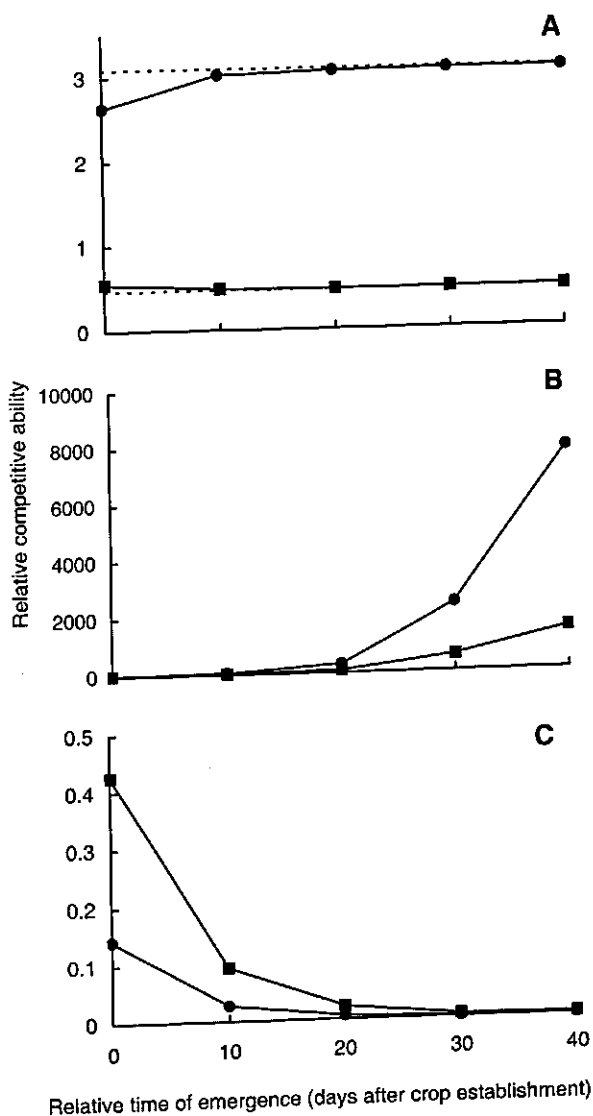| Crop	Relative time of emergence for *S. vulgaris* (days after crop establishment)									
	0		10		20		30		40	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Leek										
b_{L0}	$1.69\ 10^{-2}$	$3.20\ 10^{-4}$	$1.51\ 10^{-2}$	$2.65\ 10^{-4}$	$1.41\ 10^{-2}$	$2.69\ 10^{-4}$	$1.36\ 10^{-2}$	$2.76\ 10^{-4}$	$1.36\ 10^{-2}$	$2.78\ 10^{-4}$
b_{LL}	$9.28\ 10^{-4}$	$1.59\ 10^{-5}$	$9.33\ 10^{-4}$	$1.32\ 10^{-5}$	$9.57\ 10^{-4}$	$1.33\ 10^{-5}$	$9.76\ 10^{-4}$	$1.37\ 10^{-5}$	$9.79\ 10^{-4}$	$1.38\ 10^{-5}$
b_{LC}	$1.70\ 10^{-3}$	$1.81\ 10^{-5}$	$1.93\ 10^{-3}$	$1.69\ 10^{-5}$	$2.04\ 10^{-3}$	$1.82\ 10^{-5}$	$2.08\ 10^{-3}$	$1.94\ 10^{-5}$	$2.09\ 10^{-3}$	$1.96\ 10^{-5}$
b_{LS}	$7.98\ 10^{-5}$	$3.21\ 10^{-6}$	$3.22\ 10^{-5}$	$2.67\ 10^{-6}$	$1.08\ 10^{-5}$	$2.73\ 10^{-7}$	$1.72\ 10^{-6}$	$2.82\ 10^{-6}$	$6.70\ 10^{-7}$	$2.84\ 10^{-6}$
Celery										
b_{C0}	$3.90\ 10^{-3}$	$4.02\ 10^{-5}$	$3.79\ 10^{-3}$	$1.70\ 10^{-5}$	$3.69\ 10^{-3}$	$1.65\ 10^{-5}$	$3.65\ 10^{-3}$	$1.71\ 10^{-5}$	$3.65\ 10^{-3}$	$1.72\ 10^{-5}$
b_{CC}	$7.41\ 10^{-4}$	$2.71\ 10^{-6}$	$7.55\ 10^{-4}$	$1.10\ 10^{-6}$	$7.65\ 10^{-4}$	$1.06\ 10^{-6}$	$7.68\ 10^{-4}$	$1.10\ 10^{-6}$	$7.69\ 10^{-4}$	$1.10\ 10^{-6}$
b_{CL}	$2.81\ 10^{-4}$	$1.84\ 10^{-6}$	$2.50\ 10^{-4}$	$7.60\ 10^{-7}$	$2.50\ 10^{-4}$	$7.30\ 10^{-7}$	$2.50\ 10^{-4}$	$7.60\ 10^{-7}$	$2.50\ 10^{-4}$	$7.70\ 10^{-7}$
b_{CS}	$6.10\ 10^{-5}$	$4.80\ 10^{-7}$	$1.20\ 10^{-5}$	$1.90\ 10^{-7}$	$2.50\ 10^{-6}$	$1.80\ 10^{-7}$	$3.20\ 10^{-7}$	$1.90\ 10^{-7}$	$9.80\ 10^{-8}$	$1.90\ 10^{-7}$
S. vulgaris										
b_{S0}	$5.61\ 10^{-2}$	$1.32\ 10^{-3}$	$5.90\ 10^{-2}$	$2.21\ 10^{-3}$	$6.02\ 10^{-2}$	$1.16\ 10^{-3}$	$8.99\ 10^{-2}$	$5.40\ 10^{-4}$	$1.08\ 10^{-1}$	$4.37\ 10^{-4}$
b_{SS}	$2.58\ 10^{-3}$	$2.17\ 10^{-5}$	$2.72\ 10^{-3}$	$4.04\ 10^{-5}$	$2.50\ 10^{-3}$	$2.12\ 10^{-5}$	$2.54\ 10^{-3}$	$9.04\ 10^{-6}$	$2.32\ 10^{-3}$	$6.93\ 10^{-6}$
b_{SL}	$6.05\ 10^{-3}$	$7.70\ 10^{-5}$	$2.91\ 10^{-2}$	$3.56\ 10^{-4}$	$1.11\ 10^{-1}$	$1.12\ 10^{-3}$	$5.86\ 10^{-1}$	$6.15\ 10^{-3}$	1.00	$1.21\ 10^{-2}$
b_{SC}	$1.81\ 10^{-2}$	$1.29\ 10^{-4}$	$9.88\ 10^{-2}$	$1.20\ 10^{-3}$	$4.24\ 10^{-1}$	$7.60\ 10^{-3}$	2.95	$9.03\ 10^{-2}$	5.69	$2.28\ 10^{-1}$

Fig. 6.3 Effect of relative time of emergence of _Senecio vulgaris_ (50 plants m^{-2}) on relative competitive ability of (A) leek versus celery with respect to leek production (■; $b_{1,1}/b_{1,2}$) and celery versus leek with respect to celery production (●; $b_{2,2}/b_{2,1}$), dotted lines indicate the relative competitive ability of the weed free mixtures ; (B) leek versus _S. vulgaris_ with respect to leek production (■; $b_{1,1}/b_{1,3}$) and celery versus _S. vulgaris_ with respect to celery production (●; $b_{2,2}/b_{2,3}$) ; and (C) _S. vulgaris_ versus leek with respect to production of _S. vulgaris_ (■; $b_{3,3}/b_{3,1}$) and _S. vulgaris_ versus celery with respect to production of _S. vulgaris_ (●; $b_{3,3}/b_{3,2}$).
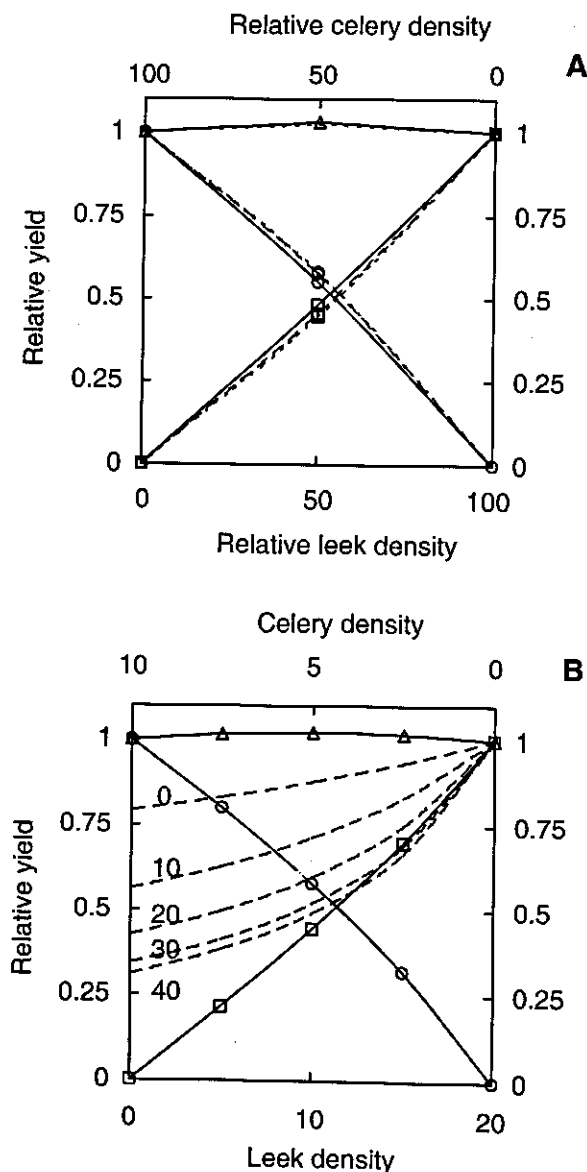
Fig. 6.4 Replacement series diagram with relative yields of leek monoculture (□), leek-celery intercrop (Δ) and celery monoculture (○) for (A) three crop densities; leek:celery = 40:20 (—); 20:10 (---); and 10:5 (⋯) plants m^{-2}; and (B) one crop density (leek:celery=20:10) and the yield of *S. vulgaris* grown in crop mixture expressed relative to its yield in leek monoculture for various relative times of emergence (0, 10, 20, 30, and 40 days after crop establishment).

This reduction percentage, represented by the initial slope of the hyperbolic curve, increased steadily for later dates of introduction, finally reaching 19.3% if *S. vulgaris* emerged 40 days after crop establishment (Table 6.3).

Table 6.3 Parameter estimates and standard errors for the hyperbolic function (eqn. [6.1]) describing the response of *S. vulgaris* biomass expressed relative to the biomass in leek monoculture to plant density of celery in a leek-celery intercropping system. Parameter *a* describes the effect of replacing the first leek with celery (m^2 plant^{-1}), and *m* is the maximum relative yield loss of *S. vulgaris* in intercropping.

Relative time of emergence	Parameter estimates				r^2
(days after crop establishment)	*a*	SE	*m*	SE	
0	0.029	0.00025	0.70	0.0176	0.99
10	0.082	0.00037	0.94	0.0065	0.99
20	0.133	0.00075	1.0	0.0059	0.99
30	0.176	0.00148	1.0	0.0075	0.99
40	0.193	0.00072	1.0	0.0032	0.99

Isolines for crop quality, yield, and weed biomass

Isolines for crop stands with equal quality were calculated using the hyperbolic competition model, which was fitted to the simulated data for leek (Fig. 6.5A) and celery (Fig. 6.5B). For leek, the diameter of the pseudostem was used as quality parameter and isolines for diameters ranging between 15 and 30 mm were calculated. A minimum pseudostem diameter of 20 mm is required for marketable leek plants in many European countries (Brewster, 1994). For celery, isolines for the per-plant fresh weight are given. Market requirements range between 0.25 kg and 1 kg or more, larger plants being used for industrial processing.

A second set of isolines indicates crop stands with equal yield levels for leek (Fig. 6.5C) and celery (Fig. 6.5D). For both crops the slopes of the isolines differed six-fold if the yield level was tripled. In combining isolines for yield with the isoline for an acceptable leek quality, a solution space indicating crop stands with acceptable quality and high yields could be determined. Isolines for crops stands with equal total yield could be drawn by adding leek and celery yield (Fig. 6.6A). The highest biomass production was achieved with celery monocultures.

Financial rather than physical yield determines solutions with the highest economic value. Isolines for total financial yield were calculated using eqn. [6.6] and

average prices of 0.35 € kg^{-1} and 0.19 € kg^{-1} for leek and celery, respectively. By combining isolines for financial yield with the quality isoline for leek the mixture with the highest financial yield could be determined (Fig. 6.6B). With a crop mixture of 19 leek and 9.4 celery plants m^{-2}, indicated by the point where the isoline for financial
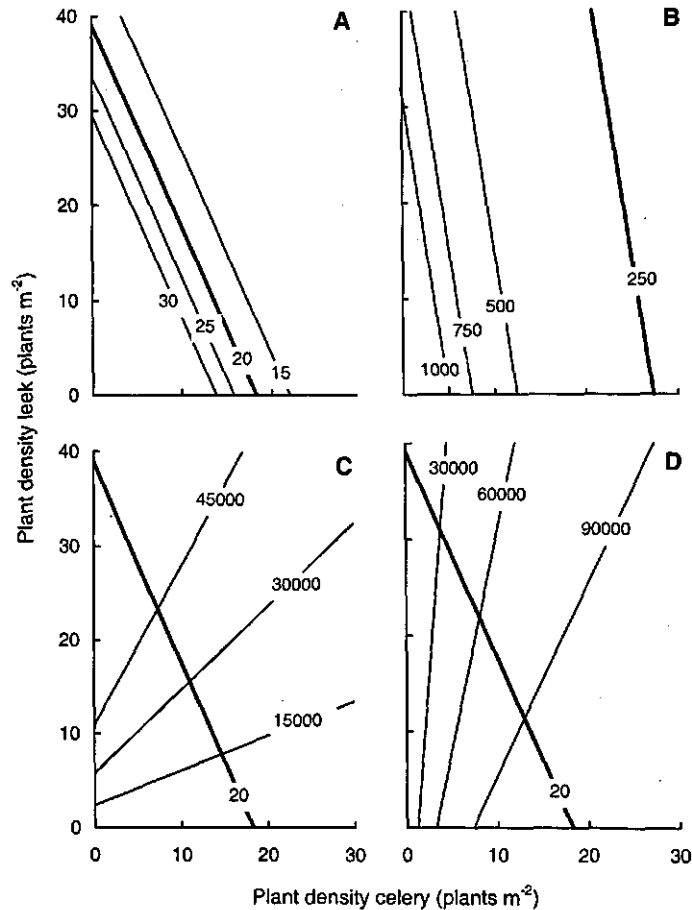

Fig. 6.5 Isolines for crop stands producing (A) leek with similar pseudostem diameters (mm); (B) celery with similar per-plant fresh weight (g); (C) similar leek yield (kg fresh weight ha^{-1}); and (D) similar celery yield (kg fresh weight ha^{-1}). In compound Figs. C and D the quality isoline for leek given by a minimum pseudostem diameter of 20 mm is included.

yield touches the leek quality isoline, a financial yield of € 27 854 could be achieved. This yield was 7% higher than the maximum financial yield that could have been achieved with a leek monoculture and 9% higher than a maximum financial yield of a celery monoculture with a per-plant fresh weight of 730 g which is equal to the per-

plant fresh weight achieved in the optimum intercrop. Increasing the price for either leek or celery by 5% while keeping the price of the other crop constant resulted in a 2.5% and 3% increase of the financial yield for leek and celery, respectively. Decreasing the prices in the same way by 5% caused a yield reduction of 2% and 2.6% for leek and celery, respectively. The optimal leek and celery density was more sensitive to altering the leek price than to altering the celery price.
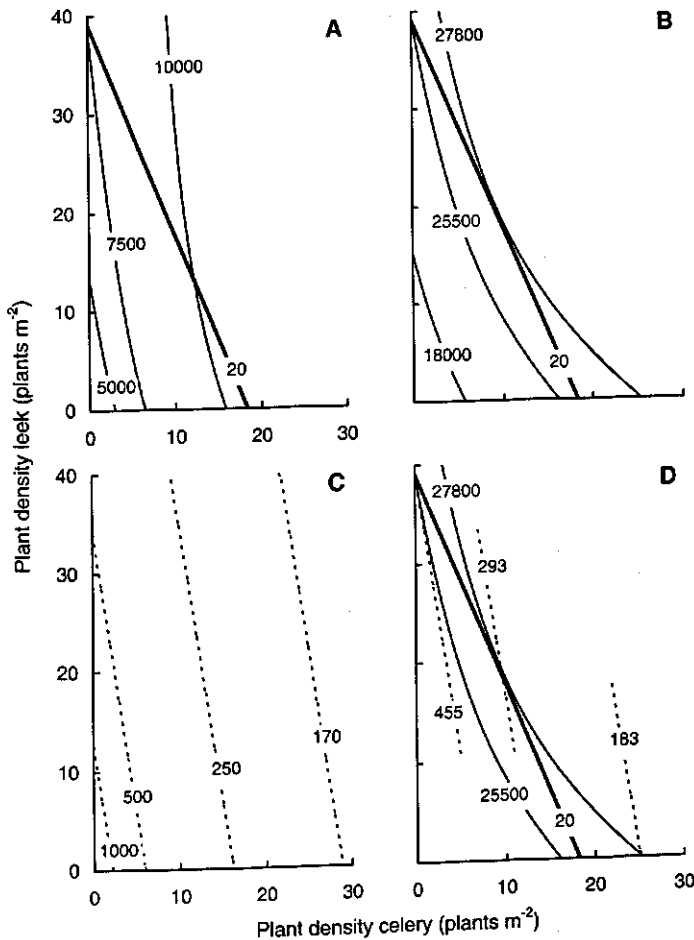
Fig. 6.6 Isolines for crop stands with (A) similar total biomass production (kg dry matter ha^{-1}); (B) similar total financial yield (€ ha^{-1}); and (C) similar seed production by initially 50 _Senecio vulgaris_ plants m^{-2} (seeds m^{-2}). Compound figure (D) combines isolines for financial yield, minimum required leek pseudostem diameter, and seed production of _S. vulgaris_. The isoline for minimum required leek pseudostem diameter of 20 mm is also included in compound figure A and B.

The effect of the crop systems on the reproductive potential of 50 *S. vulgaris* plants m^{-2}, which were introduced 40 days after crop establishment, is shown by the isolines with equal production of *S. vulgaris* seeds m^{-2} in Fig 6.6C. The slope of the curves reflects the five to six times higher sensitivity of *S. vulgaris* to competition by celery compared to leek. To reduce the seed production of 50 initial *S. vulgaris* plants m^{-2} from 500 to 250 seeds m^{-2}, a 2.7 times increase of plant densities was required in the crop stands. A similar effect was achieved when for a given crop stand the initial *S. vulgaris* density was reduced from 50 to 18.5 plants m^{-2}. When *S. vulgaris* emerged 30 instead of 40 days after crop establishment seed production was about 5.6 times higher or, in other words, if the weed free period was extended from 30 to 40 days seed production of *S. vulgaris* was reduced with 82%.

Combining isolines for financial yield, leek quality, and *S. vulgaris* seed production created a solution space including crop mixtures with high yield level, quality production and high suppressive ability for *S. vulgaris* (Fig. 6.6D). The maximum financial yield did not coincide with highest suppressive ability. The latter could be further increased with increasing numbers of celery in the mixture, which, however, will cause a dramatic reduction of financial yield as quality criteria for leek will not be met anymore. Seed production of *S. vulgaris* could be reduced by 38% by growing a celery monoculture at density of 25 plants m^{-2} which would produce plants with a per-plant fresh weight of about 500 g and result in the same financial return as the highest yielding crop mixture. The highest yielding leek monoculture, on the other hand, resulted not only in an 7% lower financial return than the highest yielding mixture, it also caused a *S. vulgaris* seed production, which was 35% higher (Fig. 6.4D). Similar comparisons could be made for yield, quality and levels of weed suppression between other crop stands.

Discussion

Modelling weed growth in monoculture and intercrop systems

Calibration of the model INTERCOM for two crops and one weed species demonstrated the growing complexity of interplant competitive relations if species richness in the system is increased. Morphological characteristics such as plant height, and leaf area dynamics, which in the weed-free crop mixture proved to be determinant for competition (Chapter 5), were critical for the simulation of weed growth in the intercropping system. Adaptations to the model had to be made with respect to early leaf area development, which is often temperature determined (Horie

_et al._, 1979). The transition from sink-limited to source-limited simulation of leaf area development was erratic, since transition from one state to the other is predetermined and abrupt. This might be improved by explicitly simulating sink and source size for each species independently followed by the determination of the most limiting factor. The model underestimated the biomass production of celery in the crop mixture in 1998 (expt. II; Fig. 6.1B) whereas the two other species were simulated accurately. This was possibly the result of a different response of the leaf morphology (e.g. higher _SLA_) of celery if grown in mixture compared to monoculture. The model, parameterised for monoculture, was not able to account for these adaptations occurring in the mixture. As the effect of _S. vulgaris_ on the crops (Fig. 6.1) and inversely the effect of the crops on _S. vulgaris_ (Fig. 6.2) was well simulated for the other crop stands in both years the model performance was considered acceptable.

Competitive relations between leek, celery, and S. vulgaris

Differences between the relative competitive ability (_RCA_) for leek and celery found with model analysis, confirmed results found in earlier experiments with a leek-celery intercropping system (Baumann _et al._, 2001b). Only small yield advantages were detected for crop mixtures if _RYT_ was calculated over a wide range of crop densities (Fig. 6.4A). In the simulated data sets, a near-balanced competitive relation was reached with a leek:celery ratio of about 2.0, which was also found in earlier experiments with a leek-celery intercropping system (Baumann _et al._, 2001b). As the response of relative yield to mixing ratio is dependent on total density in a replacement design, it does not reflect the proper relative competitive ability of the crops if they are not grown at a density where the total yield reaches the asymptote on the density-yield response curve (Connolly, 1986). The niche differentiation index (_NDI_) defined by (Spitters, 1983a), reflects the true degree of niche differentiation. The _NDI_ calculated for the weed-free crop mixture slightly exceeds unity, indicating complementarity in light capture between the crops. In earlier experiments, _NDI_'s around 1.0 were found and it was concluded that no complementarity in resource capture occurred between leek and celery (Baumann _et al._, 2001b).

S. vulgaris affected the competitive relation between leek and celery only when emerging at the time of crop establishment. Celery, which is more competitive than leek, was more affected by early emerging _S. vulgaris_ (Fig. 6.3A). Probably due to the transplanting shock and a retarded early development (Rubatzky _et al._, 1999), celery was more susceptible to early weed competition than leek. The latter could profit from the reduced competitive ability of celery, which was reflected by the higher

RCA_{LC} in the weedy situation compared to RCA_{LC} in the weed-free crop stand. This illustrates the complexity of mixtures with more than two species; competition relations between the first two species were mediated through the introduction of a third and levels of change was affected by the time of introduction of the third species. The initial size advantage of the transplanted crops resulted in a weak response of the crops to later sown *S. vulgaris*, which had to germinate from seeds. After an equal competitive advantage of leek and celery over *S. vulgaris*, when the weed was introduced at transplanting of the crop, RCA_{CS} increased much faster than RCA_{LS} with later times of weed introduction, reflecting the faster leaf area development of celery and the better ability to intercept light compared to leek (Chapter 5). As a result a negative response of *S. vulgaris* biomass to the proportion of celery in the mixture was found (Fig. 6.4B). Cousens (1985) demonstrated that a yield loss – weed density relationship could be well described using a rectangular hyperbolic function (eqn. [6.1]). In the current study, it was observed that this rectangular hyperbola could be equally well used to relate the reduction in *S. vulgaris* biomass to the proportion of celery in the crop mixture.

The degree of *S. vulgaris* biomass reduction was not only affected by celery density but to an even larger extent by the time of emergence of the weed relative to the crops (Table 6.1). Weed density and difference in between time of crop and weed emergence were earlier found to be critical for the predication of yield loss due to weed competition (Cousens, 1987; Kropff and Spitters, 1992; Kropff *et al.*, 1984). Moreover, the relative time of emergence between crops and weeds is crucial for "period thresholds" which predicts when, rather than if, weeds need to be controlled to prevent yield and quality losses (Dawson, 1986). Period thresholds, however, are generally based on expected yield reduction in current crops and do not account for seed production of late emerging weeds which may cause considerable problems in subsequent crops (Cousens and Mortimer, 1995). The experiments and simulation studies showed that the replacement of a few leek plants by celery in the crop stand contributed already considerably to the improvement of the suppressive ability of the cropping system particularly with respect to late emerging weeds (Table 6.1). At the same time leek yield and quality could be maintained (Fig. 6.5). Because of the improved competitive ability of the intercrop canopy, the critical period for weed control of the intercrop will be reduced compared to leek monoculture (Baumann *et al.*, 2000). Though weeds emerging early in the season still require direct control measures, the current study indicates that it is likely that compared to a leek monoculture the number of required weed control treatments to obtain a successful weed control strategy will be lower in a leek-celery intercropping system.

The high _NDI_'s between late emerging _S. vulgaris_ and leek as well as celery indicate the distinct phenotypic plasticity of _S. vulgaris_ which was also described by Harper (1977) and Theaker and Briggs (1993). In experiments where _S. vulgaris_ was exposed to light stress an upwards shift of the vertical leaf area distribution and an increased stem elongation was observed, while _LAI_ was maintained through an increase in specific leaf area (Baumann _et al._, 2001a). Such morphological adaptations enable the plant to improve the light capture and reproduce even if light availability is reduced. The simulation model, parameterised for the monoculture, does not account for morphological adaptations, such as stem elongation, increase of _SLA_, or shift of the vertical leaf area distribution that are caused by increased competition (Cavero _et al._, 2000). More insight in the principles underlying plasticity and the environmental conditions regulating morphological adjustments, are required to improve the explanatory value of the model.

Simulation runs with crop densities as used in practice showed that late germinating _S. vulgaris_ might still produce up to 1000 seeds m^{-2} in a leek monoculture (Fig. 6.6C). In crop mixtures with 6 celery plants, seed production could be reduced by 50% due to increased light competition. Although, only _S. vulgaris_ was considered in this study, similar effects of increased light competition were found for other species such as _Solanum nigrum_ L., _Chenopodium album_ L. and _Echinochloa crus-galli_ L. (Lotz _et al._, 1993; Paolini _et al._, 1999; Schnieders, 1999).

Optimisation of the intercropping system

Insight in the competitive relations between crops and weed enabled the optimisation of the system with respect to financial yield and weed suppressive ability. Crop quality plays a predominant role, as it is critical for the profitability of the system. For leek and celery there is a strong response of quality parameters to intra- and interspecific competition (Baumann _et al._, 2001b). For celery, quality requirements depend on whether the produce is used for industrial processing, convenience food or the fresh market. Leek pseudostem diameter proved to be the limiting factor for crop quality in the intercropping system. Therefore, the crop density combinations that represented the isoline for leek plants with a pseudostem diameter of 20 mm delimits the solution space for profitable mixed stands (Figs 6.5 and 6.6). Although, high biomass yields can be achieved with high proportions of celery in the mixture (Fig. 6.6A) producing leek is more profitable as its price is higher than that of celery. A large yield gap was found between the calculated maximum financial yield and the yield level obtained with plant densities as used in practice. In

practice lower densities are usually planted to ensure high plant quality and to enable efficient and labour-saving cultivation and harvesting. Particularly leek is generally grown at row distances between 0.5 and 0.75 m. For high plant densities (e.g. >30 plants m^{-2}), in-row spacing would need to be between 4 and 6 cm, which would increase the plant-to-plant variability and would result in a higher proportion of undersized plants (Brewster, 1994). Therefore, limitations for the spatial arrangement of the crop directed by the cultivation practices as well as the use of below optimal densities that meet the risk perception of the farmer have to be taken into account.

Depending on whether the intercropping system is compared with a monoculture production of leek or celery, a double advantage or a trade-off between financial yield and weed suppression arises. For leek production, the yield advantage of an intercropping system is combined with a reduction of *S. vulgaris* seed production. If celery production is considered, a monoculture with the same yield as a mixture suppresses *S. vulgaris* better (Fig. 6D). In this study, leek was the crop of interest, due to its economic potential in many European countries and the weak competitive ability against weeds. It was shown that high quality leek can be produced at a high yield level in an intercropping system with celery, which in the same time has distinct advantages with respect to the suppression of weeds.

Conclusion

A combined approach using mechanistic and descriptive models for analysis and optimisation of an intercropping system of leek and celery proved to be very effective. A new version of the model INTERCOM enabled accurate simulation of biomass production, product quality and weed seed production for monocultures and mixtures. Application of a descriptive regression model for summarising the simulation results was very effective and facilitated optimisation of the intercropping system. It is concluded that this combined modelling approach enlarges the potential of mechanistic crop growth and competition modelling to be used in the optimisation and design of cropping systems.

The study showed that functional biodiversity, as represented by the intercropping system, can contribute to the improvement of the economical potential of a highly developed agricultural production system. In the same time, the sustainability of the production system could be improved by reducing the need for labour and cost intensive direct weed control measures and environmental exposure

to potentially harmful chemicals. It can be concluded that intercropping systems, such as the currently studied leek-celery mixture, have a high potential for organic and low-external input agriculture.

General discussion Chapter 7

General discussion

In the research described in this thesis, interplant competition in a leek-celery intercropping system were quantitatively analysed. Additionally, competitive interactions between the model-weed *Senecio vulgaris* and the crops in the monocultures and the mixture were investigated. The analysis combined modelling studies with experimental research. This chapter discusses the new insights obtained into competition phenomena in an intercropping system and their implications for the application of intercropping in horticultural practice. Specific attention is given to methodological aspects.

Improving weed suppression by increasing canopy light interception

The primary goal of weed control practices is to obtain the greatest possible reduction in weed competition without adversely affecting crop performance. Hence, weed management activities are weed-centred, while the crop is protected. However, the crop has an important role in a weed management strategy and should not be dismissed as just a passive element (Grundy *et al.*, 1999). Crop plants can suppress weed development through interplant competition. The intensity of weed suppression depends principally on morphology and growth rate of the crop but allelopathic effects might also be important (Putnam, 1986). Morphological characteristics of the plant are one category of factors affecting the canopy architecture. Plant spacing, cultivar choice and other aspects will also influence the level of weed suppression by a canopy (Christensen and Rasmussen, 1994). Basically this idea suggests that weed-suppressive ability is a canopy characteristic which is partly determined by species-specific traits but also to a large extent by cropping-systems design. Consequently, the canopy rather than the crop should be considered when new options for weed management are explored. Strong differences in radiation interception between canopies of monocultures and crop mixtures of leek and celery were observed. The amount of radiation available for germination and growth of weeds was significantly lower in the crop mixture compared to the leek monoculture (Baumann *et al.*, 2000). Weed suppressive ability of the intercrop canopy was improved by the prostrate-growing celery, which filled the gaps between the erect-growing leek. Moreover, canopy closure occurred significantly earlier due to the higher relative growth rate of the leaf area (*RGRL*), which was found for celery (Chapter 5). Identifying plant traits which determine competitive ability was proposed as a first step in breeding for competitive cultivars (Bastiaans *et al.*, 1997). Similarly,

knowledge about morphological characteristics of crop species could be used to design intercropping systems with improved weed competition. INTERCOM proved to be a useful tool for determining the relative importance of morphological characteristics for weed suppressive ability (Kropff and Van Laar, 1993). The sensitivity analysis presented in Chapter 5 showed that morphological characteristics, which led to early ground cover and height development, were the most important traits for crop competitive ability. It is this type of knowledge that might lead to the identification of suitable crop combinations with a high potential for weed suppression.

Modelling competition effects in an intercropping system

To reach meaningful conclusions with respect to the effects of competition in an intercropping system, a quantitative understanding of the underlying processes is essential. Empirical study of all relevant combinations for a wide range of conditions is not realistic and for experimentation at the process level, appropriate methodologies are often missing. Eco-physiological simulation models can be used to link field-level observations of competitive effects to underlying physiological and morphological processes, and thus enhance understanding of interplant competition (Kropff and Van Laar, 1993). The studies, described in Chapter 6, demonstrate the advantage of combining experimental research with modelling. Responses of plants to intra- or interspecific competition measured in replacement series with leek and celery were analysed using (descriptive) regression models. It was observed that celery was much more competitive than leek. Further analysis with a mechanistic (eco-physiological) competition model showed that celery was more competitive because of its morphological characteristics, which enable the plant to capture more radiation, particularly during early growth. Another example of a successful combination of an eco-physiological competition model and experimentation is described by Schnieders (1999). A higher yield loss, occurring if cabbage (*Brassica oleracea* L.) was planted into an established cover of *Trifolium subterraneum* after 3 weeks instead of 6 weeks could not be explained by experimental data only. Analysis using an eco-physiological model showed that the leaf area index of early sown *T. subterraneum* was already declining when the cabbage was transplanted after 6 weeks, which resulted in less severe competition for light and thus a smaller yield loss of cabbage. These and other examples demonstrate that modelling together with experimentation offers a powerful tool for competition research and the development of improved weed management strategies.

Light interception by row crops

Competition models, such as the model INTERCOM, generally account for different heights between competing species, but they assume a horizontally homogenous distribution of the species mixture. In the current study, however, the intercropping system of leek and celery was grown in a row-by-row based replacement design. Therefore, the need to account for the row canopy architecture in the simulation of light capture by the species had to be explored. For this purpose, a light interception module was developed, based on an earlier model for light distribution and photosynthesis in single-species row crops (Gijzen and Goudriaan, 1989). Simulation of the light interception using simple model (which does not account for the row structure) compared to simulations using the adapted row crop model showed small deviations between the light capture of the single species ranging between 0.4 and 3%. These results are in line with the findings of Gijzen and Goudriaan (1989), who found that the effect of the row structure of the canopy on the light interception was small when the path width between the rows was $\leq$ 30% of row height.

Modelling weed growth under severe competition: Phenotypic plasticity

Adaptation of species to a new or changed habitat may occur in two ways: by genetic differentiation and phenotypic plasticity. _S. vulgaris_ is predominantly autogamous with outcrossing rates rarely exceeding 1% (Hull, 1974). Genetic differentiation of _S. vulgaris_ has been studied either by comparison of plants from various natural sites (Abbott, 1976a,b) or by comparing plants from a single site (Briggs and Block, 1992). Leiss (2000) studied phenotypic plasticity and genetic differentiation of _S. vulgaris_ and found that plants growing in ruderal habitats were genetically different from plants growing in agricultural habitats, with the latter having a larger leaf area and higher reproductive output. Moreover, plasticity of reproductive characters in response to nutrients was found to be genetically different among different families of _S. vulgaris_ in the agricultural habitat. In the current study, a genetically uniform _S. vulgaris_ biotype showed a high phenotypic plasticity by adjusting its morphology to the lower light conditions as they occur in an intercrop canopy compared to a leek pure stand. Leiss (2000), in her study, found genetic diversity for _S. vulgaris_ in the agricultural habitat, not the case in a ruderal habitat. Similar results were found for _Stellaria media_ L. (Sobey, 1987), whereas for other species, such as _Solanum ptycanthum_ (Hermanutz and Weaver, 1996) and

Xanthium strumarium (Blais and Lechowicz, 1989), no genetic differentiation between nutrient-rich natural and nutrient-poor ruderal habitats were detected.

Applying a mechanistic approach to understand interplant competition, as it was used in this study, requires the determination and quantification of the genetic variation in eco-physiological and morphological traits between species. It is this variation that causes differences in competitiveness of species. The model can then be used to integrate these characteristics and to simulate competitive processes. To account for effects of phenotypic plasticity, additional feedback mechanisms are required in the model. The importance of such feedback mechanisms was shown by Kropff and Van Laar (1993) who found that the height development of *C. album* was reduced due to competition by sugar beet (*Beta vulgaris* L.) but that due to strong phenotypic plasticity the stem grew very thin resulting in plants that still overtopped the sugar beets. To account for this effect of phenotypic plasticity in the model, the impact of competition on height development was simulated, by introduction of a maximum specific stem length at a given height of the weed based on experimental data. Similar effects were found for *Datura stramonium* L. that adapted its specific leaf area and specific stem length considerably if grown in competition with maize (*Zea mays* L.) (Cavero *et al.*, 2000). After introducing a procedure accounting for this morphological response to increased shading, simulation of competition was improved. Similar effects of phenotypic plasticity were also found for *S. vulgaris* in the current study. The ability of weeds to adapt their morphology if grown in competition with crops needs to be simulated explicitly by models such as INTERCOM. As the scientific base of our insight in phenotypic plasticity is limited in-depth research is required to obtain qualitative and quantitative understanding of phenotypic plasticity in crop-weed competition.

Combined use of mechanistic and descriptive models for optimisation

In this thesis, descriptive yield-density response models and a mechanistic eco-physiological crop growth model for resource competition were iteratively used for analysis, evaluation and finally optimisation of the leek-celery intercropping system. This combined use of descriptive and mechanistic models showed how a modelling approach, together with experimental work, was used in a step-by-step analysis to explore the relations in the system and finally to determine the optimal systems design (Fig. 7.1). A similar way of linking research activities, at different scales and with different methodologies, was proposed earlier by Kropff and Lotz (1992). The level of complexity increases from monocultures to intercropping systems and even
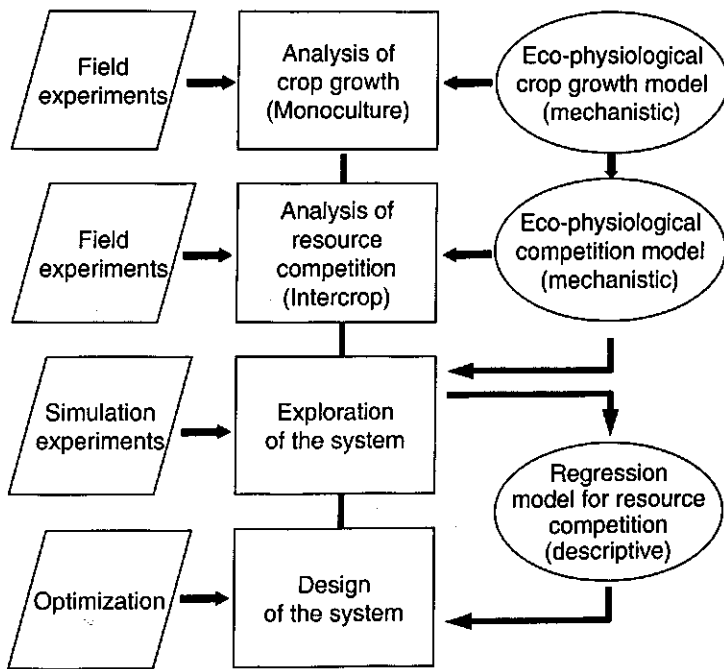
Fig. 7.1 Schematic indication of how to use descriptive regression models for resource competition and mechanistic eco-physiological competition models in combination with field experimentation step-by-step to design and optimise a cropping system.

more if, additionally, a weed species is introduced. Generally, there is a trade-off between complexity and robustness of an eco-physiological model. This was avoided by adapting the level of detail in the model, dependent on the relevance of the process with respect to competition. For the leek-celery intercropping system, morphological, rather than physiological processes were found to determine the competition between the crops. Therefore, a detailed computation of the light distribution between the crops, accounting for the specific geometry of the row canopy, was developed, while the photosynthesis processes were consolidated by simulating growth using radiation use efficiency (Chapter 5). INTERCOM proved to be an excellent framework, allowing such adaptation without the need for major changes in the programme structure.

The data set generated in the simulation experiment was summarised using a descriptive regression model for resource competition (Spitters, 1983a), which then allowed evaluation of the intercropping system in terms of productivity, crop quality

and weed suppressive ability (Chapter 6). This combined modelling approach allowed analysis, exploration and design of a complex intercropping system, which would have been impossible with experimentation only.

Long-term aspects of intercropping systems for weed management

The use of period thresholds in integrated weed management systems to predict when, rather than if, weeds must be controlled to prevent yield losses was proposed by Dawson (1986). The period threshold concept was worked out for various vegetable crops under Swiss conditions (Baumann *et al.*, 1993; Potter, 1991) and was laid down in the guidelines for integrated vegetable production in Switzerland, which are mandatory for more than 80% of Swiss vegetable producers (Anonymous, 1995). In practice, seed production of late-emerging weeds and difficulties with mechanical harvesting are the main reasons to extend weed control beyond the critical period. To prevent late emerging weeds producing seeds Potter (1991) and Baumann *et al.* (1993) suggested to extend the critical period in non-competitive crops, such as leek and onion, by extending the minimum weed-free period with 3 to 4 weeks. This recommendation was based on short-term empirical research, where seed production of late-germinating weeds, weed dispersal within the crop rotation and aspects of population dynamics were not explicitly considered. The current study aimed to understand and quantify the response of a weedy annual plant to increased light competition as experienced by late-emerging weeds in crops and more competitive intercrops (Baumann *et al.*, 2001a). It was shown that increased light competition reduced biomass production and the capitula:shoot ratio and consequently seed production of *S. vulgaris*. Although, the inflow of newly produced seeds into the seed bank could be determined, the experimental set-up did not allow conclusions to be drawn with respect to the population dynamics of the weed. Additional research will be necessary to gather information about the effect of competition on the main processes determining the population dynamics of particularly late germinating weeds. Fig. 7.2 depicts a schematic representation of a simple model of population dynamics of annual weeds as described by Spitters (1989) and Kropff *et al.* (1996). The long-term consequences of weed management strategies can be evaluated by using models for weed population dynamics. For instance, from effects of damage thresholds on long-term development of weed populations it was shown that economic benefits for various threshold values depend on initial densities and the number of years for which economic benefits are calculated (Cousens, 1987; Vleeshouwers and Streibig, 1988). The frequency of control measures, however, was

found to be independent on the level of the applied damage threshold (Wallinga and Van Oijen, 1997). Although, the effect of crop competition on weed reproductive capacity is well known, few studies have dealt with the effects of period thresholds on the population dynamics of weeds. Apart from the weed seed production, there are various processes regulating the population density of weeds that are affected by time of emergence and crop competition through factors influencing seed losses (e.g. predation, germination (e.g. loss of viability), and survival (e.g. reduced *RGRL*). Quantifying the effect of these factors on population dynamic processes will help to assess the risk for extensive seed production by weeds that are not removed if the short-term period threshold is applied. Inclusion of the dynamics of weed populations and particularly the seed production of late emerging weeds renews the concept of the period threshold and makes it more interesting for practical application because both short and long term aspects are taken into account.
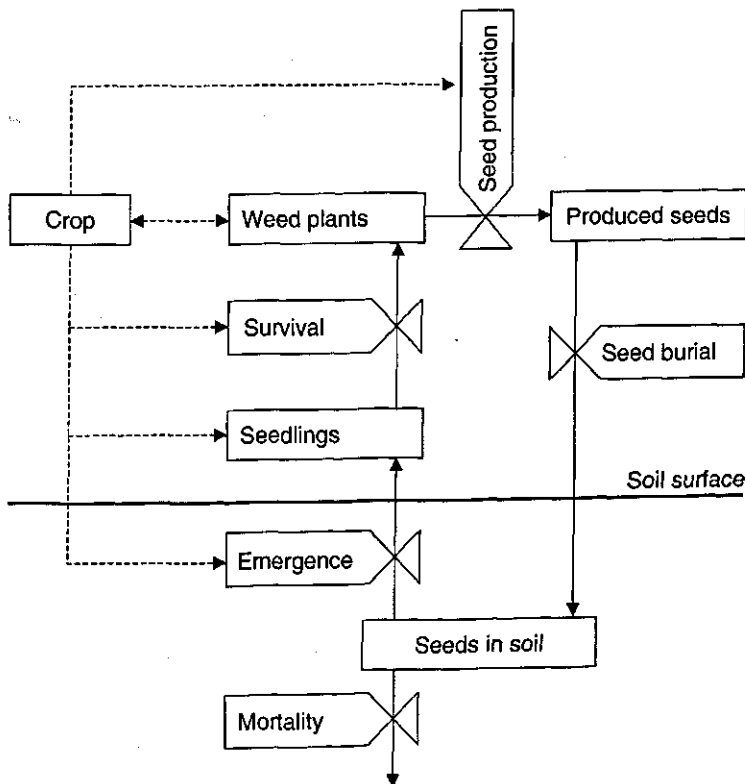

Fig. 7.2 Schematic representation of a population dynamics model for weeds. Broken arrows indicate processes where crop and weeds interact (after Kropff and Lotz, 1992).

Intercropping leek and celery: advantages, limitations, and practical implications

Intercropping is generally not considered as a feasible system in high-input horticulture and agriculture in Western Europe. Although, many advantages of intercropping systems might have been recognised by farmers and extension workers, difficulties with mechanisation and hence the high labour requirement reduced the applicability of intercropping until now to allotment gardens and labour-intensive farming systems in the tropics. The current work demonstrates, however, that intercropping leek and celery combines high profitability with many advantages that intercrops have above monocultures. The improved resource capture and suppression of weeds by the intercropping system is discussed extensively in this thesis. In the following paragraph, aspects of the leek-celery intercropping system not mentioned elsewhere are discussed with respect to the practical applicability of such a system.

Pests Another advantage of the leek-celery intercropping system is the reduction of attack by *Thrips tabaci* Lind. (Dobolyi *et al.*, 1996). The authors found a significant reduction of the numbers of *T. tabaci* on leek if intercropped with celery, compared to the untreated leek monoculture. In other experiments, the *T. tabaci* population on intercropped leek was not reduced, but there was less damage by the pest. In field experiments with leek intercropped by *Lolium perenne* L., significantly less *T. tabaci* were found on leek plants compared to monocropped leek (Imhof *et al.*, 1996). In experiments with leek intercropped by *Trifolium fragiferum* L., *T. tabaci* on intercropped leek was consistently lower compared to monocropped leek (Den Belder *et al.*, 2000). From these studies, the authors concluded that the host-plant quality was the underlying cause for the reduced number of adult *T. tabaci*. Although, the mechanisms of *T. tabaci* suppression were not studied in detail for a leek-celery intercrop, the results of the above mentioned field experiment suggest that similar effects as found by Den Belder *et al.* (2000) could play a role.

Diseases Infection of leek by leek rust [*Puccinia allii* (DC) Rud.] is related to the attack by *T. tabaci* because the resulting leaf damage facilitates the infection process. Leek rust incidence was found to be slightly reduced if leek was intercropped by *T. subterraneum* (Theunissen and Schelling, 1996).

White Tip Disease (*Phytophthora porri*) can become prevalent after heavy rainfalls late in summer. It was observed that a soil cover with straw or intercropping clover and/or grass species reduced that disease almost completely (Embrechts and Pijnenburg, 1991). Spores of *P. porri* are transported to the leaves attached to soil

particles with water splashing up during heavy rainfall. A soil cover prevents water from splashing up and hence avoids infection by _P. porri_. Although not studied in detail, a similar effect may be expected from the more complete soil cover in a leek-celery intercropping system.

Several mechanisms may reduce disease severity in genetically diverse plant populations (Garrett and Mundt, 1999; Wolfe, 1985). Increased distance between plant genotypes, which dilutes inoculum of a given pathogenic race as it is dispersed between compatible host varieties, has been considered the most important mechanism contributing to disease reduction in variety mixtures (Wolfe, 1985). Moreover, there is an immunisation process among mixed plants and morphological differences may physically block spore dispersal and/or alter wind patterns compared. with monocultures (Zhu _et al._, 2000). On the other hand, a more humid microclimate might be created through the introduction of celery into the leek monoculture. This might promote certain diseases. For example, in one of the experiments, bacterial soft rot (a complex of _Erwinia_ spp. and _Pseudomonas_ spp.) caused early senescence of celery (Chapter 5).

VA-mycorrhiza It was observed that roots of leek and celery were colonised by vesicular-arbuscular (VA) mycorrhiza fungi (Table 7.1). Their significance for various crops was reviewed by (Stribley, 1990). Leek, like other _Alliums_, has thick, little-branched roots, which gives them a low ratio of root length to shoot weight. Moreover, they also lack root hairs. Through colonisation by VA-mycorrhiza, phosphate uptake in particular can be considerably increased.

Table 7.1 Percentage colonisation of roots by VA-mycorrhiza 70 and 92 days after transplanting (DAT) for leek and celery grown in pure and mixed stands at different nitrogen levels ($N_0 = N_{min}$; $N_{50} = 50$ kg ha^{-1}; $N_{200} = 200$ kg ha^{-1}), expt. III, 1997.

Crop	Stand	70 DAT			92 DAT	
		N_0	N_{50}	N_{200}	N_0	N_{200}
Leek	pure	20	20	15	31	32
	mixture	-	-	-	22	32
Celery	pure	29	24	14	21	16
	mixture	-	-	-	21	9
SEM (d.f.)*			3.7 (15)			3.3 (21)

* SEM = standard error of means (degrees of freedom)

Furthermore, mycorrhiza may also increase the uptake of micronutrients. However, vegetables are generally grown on soils of high nutrient status, and in such conditions, the significance of mycorrhizal fungi might be limited.

Mechanisation The practice of intercropping in mechanised agriculture becomes difficult when modern machines are used for planting and harvesting. Vandermeer (1989) compared the problems in harvesting intercrops mechanically with the difficulty to mechanically harvest tomato, an operation which used to be regarded as close to lunacy. Given that the first mechanical tomato harvester appeared in the field in California in 1958, Vandermeer (1989) rejected the assertion that the same could not be realised for intercrops, where the technical problems are frequently less complicated. Probably the major impediment to mechanically harvesting intercrops is an economical, rather than a technical one (Erbach and Lovely, 1976). In case of the leek-celery intercropping system, planting, tillage operations, mechanical weed control and harvesting could be carried out using commercially available machinery (Baumann *et al.,* 2001b). Depending on soil type, planting techniques of leek (deep planting), type of transplants used and other factors, adaptation of machinery might be necessary. It can be concluded that mechanisation does not form a major impediment for the application of a leek-celery intercropping system.

Cultivation method The cultivation method (plain field or raised beds) and the row spacing imply a number of aspects to be considered in a leek-celery intercropping system. Apart from crop density and ratio, which was comprehensively discussed in Baumann *et al.* (2001b), row spacing affects yield, crop quality and husbandry practices. Wider row spacing facilitates mechanical weed control and harvesting and is necessary if leek is to be ridged for longer white stems or celery is to be blanched with light-excluding materials (Rubatzky *et al.*, 1999). Closer row spacing improves weed suppression and causes a certain level of self-blanching, which can be preferable for leek and celery. Closer row spacing, however, is likely to be more conducive to the incidence of diseases and pests. Moreover, row spacing and cultivation method have implications for the proportion of leek and celery produced. Systems with four rows on a raised bed, often used in Switzerland, yield the same proportions of leek and celery. Other proportions can be produced with three rows on a raised bed, a system that is currently gaining popularity. The choice of system is usually determined by the available on-farm mechanisation and the sales potential of leek and celery. The relatively lower sales volume of celery has been found to be detrimental to the introduction of intercropping systems in Switzerland.

Crop rotation Crop rotation is another aspect to be considered if a leek-celery intercropping system is applied. Simultaneous growth of an _Allium_ and an _Umbelliferae_ crop implies limitations for crop rotation. There are a number of soil born pathogens, such as _Fusarium oxysporum, Pythium_ spp., _Rhizoctonia solani_, and _Sclerotium rolfsii,_ which attack leek and celery. Moreover, nematodes, such as _Ditylenchus dipsaci, Meloidogyne_ spp. and _Pratylenchus_ spp., can cause considerable damage. The possibility of greater incidence of pests and diseases where reported by Pinchinat _et al._ (1975). However, no problems with soil-born diseases or pests where found in a 4-year single rotation with a sorghum (_Sorghum bicolor_ L.) and pigeonpea (_Cajanus cajan_ L.) intercropping system (ICRISAT, 1983). In highly-productive agricultural systems, which often have narrow crop rotations, intercropping will probably not contribute to a reduction of soil born diseases and pests. However, since intercropping is not widely used in such production systems, information about rotational effects are sparse.

Plant production in intercropping systems always results in a reduced yield for the main crop compared to monoculture systems, simply because the production area used to grow the intercrop is not available to produce the main crop. Nevertheless, enhanced functionality of biodiversity in crop mixtures makes intercropping interesting as a tool in integrated crop production, particularly in integrated weed management. Lower labour requirement resulting from the reduced need for direct weed control in an intercropping system has a direct impact on the economic result. If the advantages of intercropping can be realised by mixing two cash crops, as demonstrated with the leek-celery intercropping system, it could lead to an economic breakthrough for intercropping in the high-input agricultures of developed countries.

Summary
Samenvatting
Zusammenfassung
Résumé

Summary

Field vegetables with weak competitive ability against weeds, such as leek, require labour-intensive weed management practices and thereby cause high production costs. If the period threshold concept is applied, it is possible to restrict direct weed control measures to the critical period for weed control. However, the period threshold concept generally does not account for the long-term effects caused by weed seed production: late-emerging weeds that are not controlled if the period threshold concept is applied contribute to the replenishment of the weed seed bank, causing potential problems in subsequent crops. Leek, like onion and fennel, are crops that maintain an open canopy, allowing late-emerging weeds to grow substantially and to produce seeds. Therefore, these are considered as crops with a high risk of weed contamination in the crop rotation, causing potential problems in long-term weed management.

Weed management practices, particularly direct weed control measures, are weed-centred, aiming to protect the crop from competition for light, water and nutrients. However, the weed suppressing function of the crop can be used deliberately as an important component of a weed management strategy. The crop characteristics (e.g. through cultivar choice) and the cropping systems design (e.g. plant density and spatial arrangement) are the most important options to improve the competitive ability of the canopy. For weak competitive crops with high quality requirements these options are limited. Therefore, it was hypothesised that combining crops with low competitive ability, such as leek, with a more competitive crop would lead to improved suppression of growth and seed production of weeds.

In Chapter 1, various advantages of intercropping systems are outlined, mainly based on the experience with labour-intensive agricultural systems in the tropics. On the strength of these perceptions, hypotheses for a weed suppressive intercropping system including two cash crops were developed. The objectives and the general approach are explained and an outline of the thesis is given.

In Chapter 2, a description is given of the design of the intercropping system in which celery was introduced as a companion cash crop to improve the weed suppression of leek. To study the intra- and interspecific competition in a leek-celery intercropping system, two field experiments were carried out with and without additional weed competition. Light interception measurements in pure and mixed stands of leek and celery showed that the intercrop and the celery monoculture captured the light faster and to a larger extent than the leek monoculture. The shape

of the light interception curve of the intercrop canopy reflects the faster leaf area development and the more horizontal growth habit of the celery leaves.

The effect of interplant competition on the growth and fecundity of *Senecio vulgaris* (Common groundsel), an important weed in vegetable production systems, was additionally investigated in a series of field and glasshouse experiments (Chapter 3). Due to the faster leaf growth and the morphology of the celery, suppression of *S. vulgaris* occurred significantly earlier in the intercropping system compared to the leek pure stand, thereby shortening the critical period for weed control. Increasing competition for light caused morphological changes, reduced the biomass, the capitula:shoot ratio and the seed production of particularly late-emerging *S. vulgaris*, while the viability of the seeds was not affected.

To quantify intra- and interspecific competition by leek and celeriac or celery in an intercropping system, three field experiments were carried out including treatments which allowed analysis of additive and replacement design series. Effects of plant density, relative proportion of component crop, spatial arrangement and nitrogen input on biomass production, crop quality, and nitrogen use where analysed, using a descriptive hyperbolic yield-density response model (Chapter 4). Quantification of the intra- and interspecific competition in the intercropping system showed that the competitive ability of celery (and celeriac) was significantly higher than that of leek. Land equivalent ratios (*LER*), calculated from analyses of additive series, exceeded unity indicating an improved resource use by the crop mixture. Relative yield totals (*RYT*), deviated from analysis of replacement designs, and niche differentiation indices (*NDI*), which are a result of the hyperbolic yield-density analyses, did not exceed one. It was therefore concluded that with respect to biomass production, no true yield advantage occurred in the intercrop and that the increased *LER* was the result of a density effect. Effects of intra- and interspecific competition resulted in a reduction of the quality for both crops.

An eco-physiological simulation model was used to quantitatively explain interplant competition in the intercropping system based on underlying physiological, morphological and phenological processes. A detailed description of the model is given in Chapter 5. After parameterisation and calibration of the model for leek and celery in monoculture, the model performance was evaluated for the crop mixtures, using experimental data from two different growing seasons. The validation showed that the growth and competition effects between the two crops in the intercropping system were simulated adequately. The model analysis indicated that differences in morphological parameters such as early leaf area development and the extinction coefficient are critical factors determining the competitive relations

between leek and celery. Adaptation of the eco-physiological competition model allowed simulating quality of leek and celery and seed production of _S. vulgaris_ based on the biomass production of the plants for a wide range of plant densities, component crop ratios and different relative times of weed emergence. The resulting data confirmed that the relative competitive ability of leek with respect to _S. vulgaris_ was considerably lower than that of celery. Previous to the validation of the model a light interception routine accounting for the row-geometry of the intercropping system was compared to a simulation procedure assuming a homogeneous horizontal leaf area distribution. Deviations found between the results of the two routines were ≤ 3.5% for the individual crops and crop stands. It was concluded, therefore, that there is no need to specifically account for the row geometry in the cropping system for the simulation of light capture by the crops.

In Chapter 6, a combined modelling approach (descriptive and mechanistic) for analysis and optimisation of an intercropping system with respect to crop yield, quality and weed suppressive ability was applied. Crop mixtures with a leek density of about 20 plants m^{-2} and a leek:celery ratio of about 2:1 proved to be highly productive and profitable at current price levels, while the weed suppressive ability of the mixture was greatly improved compared to the leek monoculture.

In Chapter 7, the concept of improved weed suppression through increased canopy light interception is further explored. Moreover, methodological aspects of modelling competition and the use of a combined mechanistic and descriptive modelling approach are discussed. Finally, implications for the practical implementation of intercropping systems in high-input agriculture, such as long-term weed management aspects and other advantages and limitations are discussed.

Combining morphological and physiological characteristics of two species in an intercropping system to improve the suppressive ability of the canopy against weeds is an example of the functionality of enhanced biodiversity in a high-input agricultural production system.

Samenvatting

Vollegrondsgroente-gewassen met een gering onkruidonderdrukkend vermogen, zoals bijvoorbeeld prei, vergen arbeidsintensieve onkruidbeheersingsmaatregelen en veroorzaken dientengevolge hoge productiekosten. Uitgaande van het concept van de kritieke periode kan de directe bestrijding van onkruiden beperkt blijven tot een deel van het groeiseizoen. Aangezien er in dit concept geen rekening gehouden wordt met lange termijn effecten veroorzaakt door zaadproductie, kunnen laat opkomende onkruiden tot een verhoging van de zaadbank leiden en daarmee tot problemen in toekomstige gewassen. Vooral in gewassen waarin de rijen niet of pas laat in het seizoen sluiten, zoals bijvoorbeeld in prei, uien en knolvenkel, bestaat er een verhoogd risico op vervuiling van het bouwplan met onkruiden.

Onkruidbeheersingsmaatregelen, en met name de directe bestrijding, zijn op het onkruid gericht en hebben tot doel het gewas voor concurrentie om licht, water en nutriënten te behoeden. Daarnaast kan de onkruidonderdrukkende werking van het gewas zelf als een belangrijke component van een onkruidbeheersingsstrategie worden ingezet. Gewaseigenschappen (via bijvoorbeeld rassenkeuze) en de inrichting van het teeltsysteem (via bijvoorbeeld zaai- of plantdichtheid en rijafstand) zijn de belangrijkste opties om de concurrentiekracht van een bladerdek te verhogen. Bij matig concurrentiekrachtige gewassen, waarbij tevens hoge eisen gesteld worden aan de individuele plantgrootte, zijn de mogelijkheden in dit opzicht beperkt en daaruit werd het idee geboren om via introductie van een tweede, meer competitief gewas de onkruidonderdrukkende werking van het gewasdek te verbeteren.

In Hoofdstuk 1 wordt een overzicht gegeven van verschillende voor- en nadelen van het bedrijven van mengteelt, waarmee met name in arbeidsintensieve teeltsystemen in tropische landen veel ervaring is opgedaan. Op basis hiervan werden ideeën voor een teeltsysteem met twee hoog salderende gewassen uitgewerkt. In het laatste deel van het hoofdstuk wordt aangegeven tot welke specifieke doelstellingen dit heeft geleid en op welke wijze het onderzoek vervolgens is opgezet. Ten slotte wordt een overzicht gegeven van de opzet van het proefschrift.

In hoofdstuk 2 wordt vervolgens een beschrijving gegeven van het teeltsysteem dat centraal staat in dit proefschrift, en waaraan de eerder genoemde ideeën zijn getoetst en verder ontwikkeld: een prei-gewas met daaraan toegevoegd bleekselderij als tweede gewas ter verhoging van het onkruidonderdrukkend vermogen. Bovendien worden in dit hoofdstuk een tweetal veldproeven met mono- en mengteeltsystemen beschreven, waarbij in enkele objecten tevens de onkruidconcurrentie nader werd onderzocht. Uit metingen van de lichtonder-

schepping in monocultuur en mengteelt van prei en bleekselderij bleek dat de mengteelt, evenals de selderij-monocultuur, in korte tijd een aanzienlijk hogere lichtonderschepping bereikt dan een prei-monocultuur. Deze verschillen in de licht-onderscheppingscurves weerspiegelen de snellere bladoppervlakte-ontwikkeling en de meer laterale bladgroei van selderij ten opzichte van prei.

Het effect van gewasconcurrentie op de groei en het reproductievermogen van *Senecio vulgaris* (klein kruiskruid), een belangrijk onkruid in de vollegronds-groenteteelt, werd nader onderzocht in een serie kasexperimenten en veldproeven (Hoofdstuk 3). Als gevolg van de snellere bladgroei en de afwijkende morfologie van selderij werd *S. vulgaris* significant vroeger onderdrukt in de selderij-monocultuur en in de mengteelt, waardoor de kritieke periode voor de onkruidbestrijding beduidend korter was dan in de prei-monocultuur. Door de verhoogde lichtconcurrentie in het gewas werd de onkruid biomassa verminderd en naam bovendien de gewichtsverhouding tussen bloemkopjes en spruit af. Zodoende werd de zaadproductie van met name laat opgekomen *S. vulgaris* planten op twee manieren gereduceerd. De kiemkracht van de geproduceerde onkruidzaden werd echter niet negatief beïnvloed.

Drie veldproeven, met daarin een zodanige keuze van de behandelingen dat het experiment zowel volgens de principes van een additief ontwerp als die van een vervangingsexperiment kon worden geanalyseerd, werden uitgevoerd om de intra- en interspecifieke concurrentieverhoudingen tussen prei en selderij in een mengteeltsysteem te kwantificeren. Daarbij werden de plantdichtheid, het relatieve aandeel van elk van de twee gewassen, de ruimtelijke verdeling en het stikstofniveau gevarieerd en de effecten hiervan op biomassaproductie, gewaskwaliteit en stikstofbenutting vastgesteld. Bij de analyse van de concurrentieverhoudingen werd als uitgangspunt gehanteerd dat het verband tussen opbrengst en dichtheid bij planten veelal goed beschreven kan worden met behulp van een rechthoekige hyperbool (Hoofdstuk 4). Uit de analyse kwam naar voren dat de concurrentiekracht van bleek-(en knol-)selderij significant groter was dan die van prei. Analyse op basis van de objecten die tezamen een additief ontwerp vertegenwoordigden leverden een land equivalent ratio (*LER*) groter dan één op, wat er op duidt dat in de mengteelt de aanwezige hulpbronnen efficiënter werden benut. Analyse op basis van objecten die tezamen een vervangingsontwerp vertegenwoordigden leverden echter een relatief opbrengsttotaal (*RYT*) van één op. Terwijl de meer algemene analyse met de rechthoekige hyperbool waarvoor geen specifieke proefopzet vereist is een niche diffentiatie index (*NDI*) opleverde die niet significant afweek van één. Op basis van deze laatste twee bevindingen werd afgeleid dat in deze mengteelt, onder de gegeven

omstandigheden, van een echt opbrengstvoordeel geen sprake is en dat dientengevolge de verhoogde *LER*-waarde aan een dichtheidseffect kan worden toegeschreven. Overigens bleek de concurrentie in de mengteelt, met name bij hoge totale plantdichtheden, een negatief effect te hebben op de kwaliteit van beide gewassen.

Een eco-fysiologisch simulatiemodel werd gebruikt om de effecten van concurrentie in het mengteeltsysteem kwantitatief te verklaren op basis van de onderliggende morfologische, fysiologische en fenologische processen. Een gedetailleerde beschrijving van het model staat weergegeven in Hoofdstuk 5. Monocultures van prei en selderij werden gebruikt om het model te parameteriseren en te calibreren, waarna het concurrentiemodel gevalideerd werd op basis van proeven uitgevoerd in twee verschillende jaren. De validatie maakte duidelijk dat het model uitstekend in staat is de groei en concurrentie van beide gewassen in de mengteelt adequaat te simuleren. Modelanalyse toonde vervolgens aan dat verschillen in morfologie, en met name de verschillen in vroege bladontwikkeling en extinctiecoëfficiënt, bepalend zijn voor de concurrentieverhoudingen tussen beide gewassen. Door het eco-fysiologische concurrentiemodel enigszins aan te passen werd het mogelijk op basis van de biomassaproductie de gewaskwaliteit van prei en selderij te simuleren. Bovendien maakte de toevoeging aan het model van *S. vulgaris* als derde soort het mogelijk de onkruid-zaadproductie te simuleren, waarna simulaties werden uitgevoerd voor een groot aantal plantdichtheden en verschillende relatieve opkomsttijdstippen van het onkruid. De modelstudies bevestigden dat de relatieve concurrentiekracht van prei ten opzichte van *S. vulgaris* beduidend kleiner is dan de concurrentiekracht van selderij.

Voorafgaand aan de validatie van het model werd een vergelijking gemaakt tussen de oorspronkelijke lichtonderscheppingsmodule, waarbij een homogene verdeling van bladoppervlak in het horizontale vlak verondersteld werd, en een alternatieve procedure, waarbij expliciet rekening gehouden werd met de rijenstructuur van de mengteelt. De verschillen tussen de resultaten van de twee routines waren doorgaans ≤ 3.5% voor de individuele gewassen en teeltsystemen. Op basis van deze resultaten werd geconcludeerd dat voor de simulatie van de lichtonderschepping van het onderhavige teeltsysteem geen rekening gehouden hoeft te worden met de rijenstructuur van het gewas.

In Hoofdstuk 6 werden de resultaten van de simulatie met het mechanistische model, uitgevoerd voor een uitgebreide reeks totale plantdichtheden en mengverhoudingen tussen prei en selderij, samengevat met behulp van een eenvoudig beschrijvend model. De op deze wijze hanteerbaar gemaakte resultaten

werden vervolgens gebruikt voor een optimalisatie van het mengteelsysteem naar opbrengst, kwaliteit en onkruidonderdrukkend vermogen. Gewasmengsels met een totale plantdichtheid van 20 planten m^{-2} prei en een prei:selderij verhouding van ongeveer 2:1 bleken de hoogste productie van kwalitatief goede prei en selderij op te leveren en daarmee tevens de hoogste financiële opbrengst bij de actuele prijzen te bewerkstelligen. Bovendien was het onkruidonderdrukkend vermogen van deze mengteelt aanzienlijk verbeterd ten opzichte van dat van een prei monocultuur .

Het concept van een verbeterde onkruidonderdrukking door via een mengteelt een verhoogde lichtonderschepping van het bladerdek te bewerkstelligen wordt in Hoofdstuk 7 breder uitgewerkt. Methodologische aspecten die bij het modelleren van concurrentie naar voren kwamen en het gebruik van een gecombineerde toepassing van mechanistische en beschrijvende modellen worden kritisch bediscussieerd. Tenslotte wordt aandacht besteed aan diverse aspecten die bij praktijkinvoering van mengteeltsystemen in intensieve landbouwproductiesystemen een rol zouden kunnen spelen.

De succesvolle realisatie van een verbeterd onkruidonderdrukkend vermogen, door de morfologische en fysiologische eigenschappen van twee gewassoorten in een mengteeltsysteem te combineren, geeft aan dat ook op het gebied van de onkruidbeheersing een verhoogde biodiversiteit functioneel kan zijn.

Zusammenfassung

Freilandgemüsearten mit geringer Konkurrenzkraft gegenüber Unkräutern, wie zum Beispiel Lauch, erfordern arbeitsintensive Unkrautregulierungsmethoden und erhöhen damit die Produktionskosten. Bei Anwendung des Konzeptes der zeitbezogenen Schadensschwelle, können direkte Unkrautbekämpfungsmassnahmen auf die kritische Periode für Unkrautkonkurrenz beschränkt bleiben. Da das Konzept der zeitbezogenen Schadensschwelle jedoch langfristigen Auswirkungen der Verunkrautung keine Rechnung trägt, führt die Samenbildung von spätkeimenden Unkräutern, die bei Anwendung dieses Konzeptes toleriert werden, zu einer Erhöhung des Unkrautsamenvorrates im Boden und damit potentiell zu Problemen in Folgekulturen. Lauch, Zwiebeln aber auch Fenchel sind Kulturen, die den Bestand erst spät oder überhaupt nicht schliessen. Spätkeimende Unkräuter können sich dadurch ungehindert entwickeln und Samen produzieren. Solche Kulturen tragen deshalb eher zu einer Verunkrautung der Fruchtfolge bei und damit zu Problemen bei der langfristigen Unkrautregulierung.

Unkrautregulierungsmassnahmen, insbesondere die direkte Bekämpfung, richten sich gegen Unkräuter, mit dem Ziel die Kultur vor Konkurrenz um Licht, Wasser und Nährstoffen zu schützen. Das Vermögen einer Kultur Unkräuter zu unterdrücken kann jedoch gezielt als wichtige Komponente der Unkrautregulierungsstrategie eingesetzt werden. Neben den Eigenschaften der Kulturpflanze (z.B. durch die Sortenwahl) gehört die Gestaltung des Anbausystems (z.B. via Pflanzdichte und Pflanzenverband) zu den wichtigsten Möglichkeiten, um die Konkurrenzkraft eines Pflanzenbestandes zu erhöhen. Bei Kulturen mit schwacher Konkurrenzkraft, für die zudem aus Qualitätsgründen hohe Einzelpflanzengewichte angestrebt werden, sind diese Möglichkeiten beschränkt. Deshalb wurde die folgende Hypothese aufgestellt: Der Mischanbau von Kulturen mit schwacher Konkurrenzkraft, wie zum Beispiel Lauch, mit konkurrenzkräftigeren Arten führt zu einer stärkeren Unterdrückung des Wuchses und der Samenproduktion von insbesondere spät auflaufenden Unkräutern.

Im Kapitel 1 sind verschiedene Vorteile von Mischkultursystemen, wie sie vor allem in arbeitsintensiven Anbausystemen tropischer Länder genutzt werden, zusammengefasst. Aufgrund dieser Erkenntnisse wurden Hypothesen für ein Mischkultursystem mit zwei Gemüsekulturen und erhöhter Unkrautunterdrückung entwickelt. Im weiteren werden die Zielsetzungen und der Forschungsansatz sowie die Struktur der Dissertation erläutert.

Im Kapitel 2 wird das Mischkultursystem beschrieben, in dem Stangen- (oder Knollen-) sellerie als Partnerkultur zusammen mit Lauch angebaut wird, um die Unkrautunterdrückung des Pflanzenbestandes zu verbessern. Es wurden zwei Feldversuche durchgeführt, um die intra- und interspezifische Konkurrenz im Lauch-Sellerie Mischkultursystem mit und ohne zusätzlichem Unkrautbesatz zu untersuchen. Messungen der Lichtabsorption in den Mono- und Mischkultur-beständen von Lauch und Sellerie zeigten, dass die Mischkultur wie auch der reine Selleriebestand, verglichen mit dem Lauchbestand, in kürzerer Zeit eine höhere Lichtmenge absorbieren konnte. Dabei war der zeitliche Verlauf der Licht-absorptionskurve der Mischkultur durch die schnelle Blattflächenentwicklung und die horizontale Wuchsform der Sellerieblätter bedingt.

In einer weiteren Serie von Feld- und Gewächshausversuchen wurde der Konkurrenzeinfluss der verschiedenen Kulturbestände auf das Wachstum und Reproduktionsvermögen von *Senecio vulgaris* (Gemeines Kreuzkraut), ein Problemunkraut des Freilandgemüsebaus, untersucht (Kapitel 3). Aufgrund der schnelleren Entwicklung der Blattfläche und der morphologischen Eigenschaften von Sellerie wurde *S. vulgaris* durch die Mischkultur deutlich früher unterdrückt als durch den reinen Lauchbestand. Dadurch ergab sich eine Verkürzung der kritischen Periode für Unkrautkonkurrenz. Zunehmende Lichtkonkurrenz durch die Kultur führte zu folgenden morphologischen Veränderungen: Reduktion der Biomasse, Abnahme des Verhältnisses zwischen Blütenkopf- und Sprossgewicht und Verminderung der Samenproduktion von insbesondere spätkeimenden *S. vulgaris* Pflanzen. Die Keimfähigkeit der Samen wurde hingegen nicht beeinflusst.

In drei weiteren Feldversuchen wurden die Einflüsse der intra- und interspezifischen Konkurrenz auf Lauch und Knollen- oder Stangensellerie in einem Mischkultursystem quantifiziert. Die Versuchsanordnung wurden so gewählt, dass sowohl eine Analyse der additiven Verfahren (additive series) wie auch eine solche der substituiven Verfahren (replacement series) vorgenommen werden konnte. In diesen Versuchen wurde der Einfluss der Pflanzdichte, der relativen Proportion der einzelnen Kulturen in der Mischung, der räumlichen Anordnung der Pflanzen sowie des Stickstoffniveaus auf die Ertragsleistung, Qualität und den Nutzungsgrad des verabreichten Stickstoffs erhoben. Grundlage der Analyse der Konkurrenz-verhältnisse war die Tatsache, dass der Zusammenhang zwischen Bestandesdichte und Ertrag von Pflanzen oft mit Hilfe einer quadratisch hyperbolischen Funktion beschrieben werden kann (Kapitel 4). Aufgrund der Quantifizierung der Konkurrenzverhältnisse zeigte sich, dass die Konkurrenzkraft von Sellerie signifikant höher war als jene von Lauch. Die Analyse der additiven Verfahren ergab „Land

Equivalent Ratios" (*LER*) die eins überstiegen, was auf eine verbesserte Nutzung der Ressourcen hinweist. Die relativen Ertragstotalen (Relative Yield Totals, *RYT*), wie sie anhand der substituiven Verfahren berechnet werden konnten, und die „Niche Differentiation Indices" (*NDI*), die sich aus der Analyse mit dem hyperbolischen Modell ableiten liessen, überstiegen den Wert eins nicht. Dies liess die Schlussfolgerung zu, dass die Mischkultur in Bezug auf Biomassenproduktion keinen eigentlichen Ertragsvorteil gegenüber den Monokulturen aufwies und, dass der höhere *LER*-Wert die Folge einer suboptimalen Pflanzdichte war. Bei beiden Kulturen war die Qualität infolge intra- und interspezifischer Konkurrenz reduziert.

Mit Hilfe eines öko-physiologischen Simulationsmodells wurden die Konkurrenz-verhältnisse im Mischkultursystem, basierend auf den physiologischen, morpho-. logischen und phänologischen Prozessen, quantitativ erklärt. Das Simulationsmodell ist in Kapitel 5 ausführlich beschrieben. Nach der Parameterisierung und Kalibrierung des Modells für Lauch und Sellerie unter Monokulturbedingungen, wurden die Simulationen für die Mischkultur Situation mit Hilfe von Versuchsdaten zweier Jahre evaluiert. Die Validierung des Modells zeigte, dass sowohl Wachstum wie Konkurrenz zwischen den beiden Kulturen adäquat simuliert werden konnte. Die Modellanalyse ergab, dass vor allem Unterschiede zwischen morphologischen Parametern, wie frühe Blattflächenentwicklung und Lichtextinktionskoeffizient, für die Konkurrenzverhältnisse zwischen Lauch und Sellerie in der Mischkultur bestimmend waren. Eine Anpassung des Modells erlaubte es die Qualität für Lauch und Sellerie und die Samenproduktion von *S. vulgaris* auf Basis der Einzelpflanzengewichte für eine grosse Anzahl Pflanzdichten, Mischungsverhältnisse der Kulturen und relativen Auflaufzeitpunkten des Unkrautes zu simulieren. Diese Daten bestätigten, dass die relative Konkurrenzkraft von Lauch gegenüber *S. vulgaris* erheblich geringer war als jene von Sellerie. Vor Evaluation des Modells wurde ferner eine Routine zur Simulation der Lichtabsorption, die der Reihenstruktur der Mischkultur Rechnung trägt, mit einer einfacheren Simulationsmethode verglichen. Letzterer liegt eine homogene horizontale Blattverteilung im Pflanzenbestand zugrunde. Die Abweichungen zwischen den Resultaten der beiden Simulationsmethoden lagen für die einzelnen Kulturen und Pflanzenbestände unter 3.5%. Aus diesen Erkenntnissen wurde geschlossen, dass keine Notwendigkeit besteht die Reihenstruktur bei der Simulation der Lichtabsorption durch die Kulturen speziell zu berücksichtigen.

Kapitel 6 beschreibt die Anwendung eines kombinierten Ansatzes, bei dem für den Entwurf und die Optimierung einer Mischkultur bezüglich hoher Ertrags- und Qualitätsleistung sowie verbesserter Unkrautunterdrückung sowohl deskriptive wie mechanistische Modelle eingesetzt wurden. Die grosse Datenmenge der Simulations-

analysen wurde mittels eines einfachen beschreibenden Modelles zusammengefasst, so dass das Mischkultursystem in Bezug auf Ertrag, Qualität und Unkrautunterdrückung optimiert werden konnte. Mit Hilfe dieses Vorgehens konnte gezeigt werden, dass Kulturmischungen mit einer Pflanzdichte von ca. 20 Pflanzen m^{-2} für Lauch und einem Dichteverhältnis von Lauch und Sellerie von etwa 2:1 eine hohe Produktivität erreichen, die beim aktuellen Preisniveau auch eine hohe Rentabilität aufweisen. Gleichzeitig war die Unkrautunterdrückung durch die Mischkultur gegenüber jener eines reinen Lauchbestandes wesentlich besser.

Kapitel 7 geht unter anderem näher auf das Konzept einer verbesserten Unkrautunterdrückung durch Erhöhung der Lichtabsorption des Pflanzenbestandes ein. Ferner werden methodische Aspekte der Anwendung von Modellen zur Untersuchung von Konkurrenzverhältnissen diskutiert und der kombinierte Einsatz von deskriptiven und mechanistischen Modellen wird kritisch beleuchtet. Zum Schluss werden Fragen zum langfristigen Vorgehen bei der Unkrautregulierung sowie weitere Vor- und Nachteile von Mischkulturen, wie sie bei der Praxiseinführung eines Mischkultursystems in eine hochmechanisierte Landwirtschaft relevant sind, erörtert.

Die erfolgreiche Verbesserung der Unkrautunterdrückung durch Entwicklung eines Mischkultursystems, bei dem die morphologischen und physiologischen Charakteristiken zweier Kulturarten kombiniert werden, zeigt, dass auch im Bereich der Unkrautregulierung eine Erhöhung der Biodiversität funktionell sein kann.

Résumé

Les légumes sensibles à la compétition due aux mauvaises herbes, comme le poireau, nécessitent une attention toute particulière en terme de gestion des adventices causant une augmentation des coûts de production. Si le concept de seuil critique d'intervention est appliqué, il est possible de limiter les opérations de désherbage à la période critique de désherbage. Toutefois ce concept ne prend généralement pas en compte les effets à long terme de la production de semences par les mauvaises herbes. Les adventices qui apparaissent tardivement ne sont pas contrôlées si ce concept est appliqué et elles contribuent à l'augmentation du réservoir de mauvaises herbes présentes dans le sol. Ceci peut causer des problèmes substantiels pour les cultures ultérieures. La culture du poireau, tout comme celle de l'oignon et du fenouil, conserve une structure de feuillage très ouverte permettant l'émergence tardive de mauvaises herbes et la production de graines. Aussi ces cultures, considérées comme salissantes, posent des problèmes potentiels au niveau du raisonnement à long terme de la lutte contre les mauvaises herbes.

Les stratégies de lutte contre les adventices et plus particulièrement celles de désherbage ont pour objectif de réduire le degré de compétition pour la lumière, l'eau et les nutriments. La capacité intrinsèque de la culture à lutter contre les adventices peut être utilisée comme un facteur important dans le raisonnement de ces stratégies de lutte. Il fut émis l'hypothèse selon laquelle l'association d'une culture sensible aux mauvaises herbes, comme le poireau, avec une culture plus compétitive pourrait ralentir le développement des adventices et réduire leur production de semence.

Le Chapitre 1 présente les divers avantages liés aux cultures associées, système nécessitant une main d'œuvre intensive et largement utilisé dans les zones tropicales. Les hypothèses relatives à un système de cultures associées réduisant la quantité de mauvaises herbes et incluant deux cultures commerciales ont été développées en se basant sur ces expériences. Les objectifs de recherche, la méthodologie et les lignes directrices de la thèse doctorale y sont également présentés. Le céleri fut introduit en tant que culture secondaire dans le but d'améliorer la capacité des plantes à lutter contre les mauvaises herbes (Chapitre 2). Afin d'étudier la compétition intra- et interspécifique en cultures associées de poireau/céleri, deux expérimentations en plein champ ont été conduites; une avec et une autre sans compétition due aux mauvaises herbes. Les mesures d'interception lumineuse effectuées pour le poireau et le céleri en culture monospécifique et en culture associée montrent que le céleri et le mélange poireau/céleri absorbent plus rapidement et en proportion plus importante les radiations disponibles. La forme de la courbe matérialisant l'interception

lumineuse dans le mélange poireau/céleri reflète que le développement foliaire fut plus rapide et que la croissance horizontale des céleris plus conséquente. L'effet de la compétition inter-plantes sur la croissance et la productivité de *Senecio vulgaris*, une mauvaise herbe importante en culture légumière, fut également étudiée en plein champ et en serre (Chapitre 3). Dû à un développement foliaire rapide et à la morphologie des plantes de céleri, la suppression de *Senecio vulgaris* se produisit significativement plus tôt pour les espèces en mélange que pour le poireau en monoculture. La période critique de désherbage se trouva ainsi raccourcie. L'augmentation de la compétition pour la lumière entraîna des modifications morphologiques, réduisit la biomasse et modifia le ratio capitule/tige des *Senecio vulgaris* émergeant tardivement. La production de semence fut particulièrement réduite tandis que la viabilité de ces dernières ne fut pas affectée.

Afin de quantifier la compétition intra- et interspécifique existante entre les poireaux et les céleri rave ou céleri en branche, trois essais de plein champ furent conduits. Les effets de la densité de plantation, la proportion relative de poireau et céleri en mélange, la disposition spatiale des plantes et la fertilisation azotée sur les rendements, la qualité des produits et l'utilisation de l'azote furent évalués grâce à une modélisation hyperbolique du rendement en fonction de la densité de plantation (Chapitre 4). L'analyse des données obtenues indique que des paramètres comme le développement foliaire en début de croissance et le coefficient d'extinction sont des facteurs déterminants qui définissent la compétitivité relative des plantes de poireau par rapport à celles de céleri. La compétitivité du céleri en branche (ou céleri rave) fut significativement supérieure à la compétitivité des plantes de poireau. Le "land equivalent ratio" (*LER*), supérieur à 1, témoigne d'une meilleure utilisation des ressources en cultures associées. Toutefois, le récolte totale relative ("relative yield total", *RYT*) et l'index de différencion de niche ("niche differenciation index", *NDI*) proche de l'unité montrent qu'un réel gain de productivité ne fut obtenu en cultures associées. Les effets de la compétition intra- et interspécifique eurent pour conséquences de réduire la qualité des deux légumes produits.

Un modèle de simulation éco-physiologique se basant sur des données physiologiques, morphologiques et phénologiques fut utilisé pour expliquer la compétition entre les plantes de poireau et céleri. Une description détaillée du modèle de simulation est fournie au Chapitre 5. Les performances agronomiques de la culture en mélange furent évaluées en utilisant les résultats expérimentaux de plusieurs saisons culturales pour calibrer le modèle de simulation et en se basant sur les caractéristiques des poireaux et céleris en monoculture. La validation du modèle montra que la croissance et les effets de la compétition entre les deux cultures furent

simulées de façon cohérente. Les adaptations portées au modèle de compétition éco-physiologique ont permis de réaliser une simulation précise de la production de biomasse, de la qualité des légumes et de la production de graines de _Senecio vulgaris_ pour une large gamme de densité de plantation et différentes périodes d'apparition de cette mauvaises herbes. Les résultats montrent clairement que la capacité de la culture de poireau à lutter contre les adventices est moindre que celle du céleri. Préalablement à la validation du modèle le degré d'interception lumineuse lorsque les cultures sont plantées en bandes intercalaires fut comparé à celui d'un système dans lequel les feuilles couvrent l'intégralité de la surface. Les différences entre ces deux simulation étant inférieures ou égale à 3,5% il a été conclu qu'il n'était pas nécessaire de prendre en compte la géométrie des cultures dans la simulation de l'interception lumineuse.

Dans le Chapitre 6 les approches descriptives et mécanistiques de la modélisation furent conjointement utilisées pour analyser et optimiser les rendements, la qualité des produits et la capacité globale de système poireau/céleri à lutter contre les mauvaises herbes. Une densité de 20 poireaux par mètre carré et un ratio poireau/céleri d'environ 2 se révéla être une combinaison très productive et rentable dans le contexte économique actuel. La capacité de cette association à lutter contre les mauvaises herbes se trouva nettement améliorée par rapport au système de poireau en monoculture.

Dans le Chapitre 7 le concept selon lequel la suppression des mauvaises herbes est améliorée par l'accroissement de l'interception lumineuse de la canopée est approfondi. Des aspects méthodologiques relatifs à la modélisation de la compétition et l'utilisation conjointe de l'approche mécanistique et descriptive de la simulation sont traités dans ce Chapitre. Les conséquences directes de la mise en œuvre de ce système de culture associée sur le raisonnement à long terme des stratégies de lutte contre les adventices, les avantages et limitations de ce système alternatif furent évaluées.

Combiner les caractéristiques morphologiques et physiologiques de deux espèces végétales pour augmenter la capacité du mélange à lutter contre les mauvaises herbes semble approprié. Ces résultats montrent qu'une augmentation, même sensible, de la biodiversité est utile pour améliorer la gestion à long terme des stratégies de lutte contre les mauvaises herbes. C'est une des fonctions de la biodiversité.

References

Abbott R.J., 1976a. Variation within common groundsel, *Senecio vulgaris* L. II. Local differences within cliff populations on Puffin Island. *New Phytologist* 76: 165-172.

Abbott R.J., 1976b. Variation within common groundsel, *Senecio vulgaris* L. I. Genetic response to spatial variation of the environment. *New Phytologist* 76: 153-164.

Abraham C.T. and Singh S.P., 1984. Weed management in sorghum - legume intercropping systems. *Journal of Agricultural Science* 103: 103-115.

Akobundu I.O., 1980. Live mulch: a new approach to weed control and crop production in the tropics. In: *Proceedings of British Crop Protection Conference - Weeds,* Brighton, 377-382, BCPC, Farnham, UK.

Aldrich R.J., 1984. *Weed-crop ecology. Principles in weed management.* Breton Publishers, North Scituate, MA (USA).

Altieri M.A., 1988. The dynamics of insect populations in crop systems subject to weed interference. In: *Plant stress-insect interactions.* Heinrichs E.A. (ed.), 433-451. Wiley, New York.

Altieri M.A., 1994. *Biodiversity and pest management in agroecosystems.* 185 pp. Food Products Press, New York.

Altieri M.A. and Liebman M., 1986. Insect, weed and plant disease management in multiple cropping. In: *Multiple cropping systems.* Francis C.A. (ed.), 183-218. Macmillan Publishing Company, New York.

Altieri M.A. and Gliessman S.R., 1983. Effects of plant diversity on the density and herbivory of the flea beetle *Phyllotreta cruciferae* Goeze, in Calefornia collard (*Brassica oleracea*) cropping systems. *Crop Protection* 2: 497-501.

Ammon H.U., Garibay S. and Bohren C., 1995. The use of dead or living mulch in maize and its suppression with herbicides. In: *Proceedings of 9th EWRS Symposium "Challenges for Weed Science in a Changing Europe",* Budapest, 527-534, EWRS, Wageningen, The Netherlands.

Ammon H.U. and Niggli U., 1990. Weed control in transition. *Landwirtschaft Schweiz* 3: 33-44.

Andrews D.J. and Kassam A.H., 1976. The importance of multiple cropping in increasing world food supplies. In: *Multiple cropping.* Papendick R.I., Sanchez P.A. and Triplett G.B. (eds.), Vol. 27, 1-10. American Society of Agronomy, Madison, Wisconsin.

Angus J.F., Cunningham R.B., Moncur M.W. and Mackenzie D.H., 1981. Phasic development in field crops. I. Thermal response in the seedling phase. *Field Crops Research* 3: 365-378.

Anonymous, 1973. Multiple cropping. In: *Annual Report of International Rice Research Institute (IRRI)*, 15-34. Los Banõs, Philippines.

Anonymous, 1995. *Anforderungskatalog für die integrierte Produktion im Gemüsebau*. Schweizerische Gemüse Union, Ins, Switzerland.

Amy A.C., Stoa T.E., McKee C. and Dillman A.C., 1929. Flax cropping in mixture with wheat, oats, and barley. *Technical Bulletin* 133, US Department of Agriculture, Washington DC.

Ayeni A.O., Duke W.B. and Akobundu I.O., 1984. Weed interference in maize, cowpea, and maize/cowpea intercrop in a sub humid tropical environment. I. Influence of cropping season. *Weed Research* 24: 269-279.

Bantilan R.T., Palada M. and Harwood R.R., 1974. Integrated weed management. I. Key factors affecting weed/crop balance. *Philippine Weed Science Bulletin* 1:14.

Bastiaans L., Kropff M.J., Kempuchetty N., Rajan A. and Migo T.R., 1997. Can simulation models help design rice cultivars that are more competitive against weeds? *Field Crops Research* 51: 101-111.

Baumann D.T. and Imhof T., 1996. Untersaaten in Gemüsekulturen. In: *Tagungs-unterlagen der 14. Tagung über Unkrautbekämpfung*, 2 pp., FAL, Zürich, Switzerland,

Baumann D.T., Potter C.A.P. and Müller-Schärer H., 1993. Zeitbezogene Schadens-schwelle bei der integrierten Unkrautbekämpfung im Freilandgemüsebau. In: *Proceedings of EWRS-Symposium "Quantitative approaches in weed and herbicide research and their practical application"*, Braunschweig, 807-813, EWRS, Wageningen, The Netherlands.

Baumann D.T., Bastiaans L. and Kropff M.J., 1999. Effect of light competition on seed production and viability of common groundsel (*Senecio vulgaris* L.). In: *Proceedings of 11th International Symposium of the European Weed Research Society (EWRS)*, Basel, Switzerland, 52, EWRS, Wageningen, The Netherlands.

Baumann D.T., Kropff M.J. and Bastiaans L., 2000. Intercropping leeks to suppress weeds. *Weed Research* 40: 359-374.

Baumann D.T., Bastiaans L. and Kropff M.J., 2001a. Effects of intercropping on growth and reproductive capacity of late emerging *Senecio vulgaris* L., with special reference to competition for light. *Annals of Botany* 87: 209-217.

Baumann D.T., Bastiaans L. and Kropff M.J., 2001b. Competition and crop performance in a leek-celery intercropping system. *Crop Science* 41. in press.

Benoit F. and Ceustermans N., 1994. Ecological growing of leeks with plastics. *Plasticulture* 101: 45-49.

Blais P.A. and Lechowicz M.J., 1989. Variation among populations of *Xanthium stumarium* (*Compositae*) from natural and ruderal habitats. *American Journal of Botany* 76: 901-908.

Booij R., Kreuzer A.D.H., Smit A.L. and Van der Werf A., 1996. Effect of nitrogen availability on dry matter production, nitrogen uptake and light interception of Brussels sprouts and leeks. *Netherlands Journal of Agricultural Science* 44: 3-19.

Brewster J.L., 1994. *Onions and other vegetable alliums*. 236 pp., CAB International, Wallingford.

Briggs D. and Block M., 1992. Genecological studies of groundsel (*Senecio vulgaris* L.) I. Maintenance of population variation in the Cambridge University Botanic Garden. *New Phytologist* 121: 257-266.

Brown R.F. and Mayer D.G., 1988. Representing cumulative germination. 2. The use of the Weibull function and other empirically derived functions. *Annals of Botany* 61: 127-138.

Bulson H.A.J., Snaydon R.W. and Stopes C.E., 1997. Effects of plant density on intercropped wheat and field beans in an organic farming system. *Journal of Agricultural Science* 128: 59-71.

Caporali F., Campiglia E., Paolini R. and Mancinelli R., 1998. The effect of crop species, nitrogen fertilization and weeds on winter cereal/pea intercropping. *Italian Journal of Agriculture* 2: 1-9.

Cavero J., Zaragoza C., Bastiaans L., Suso L.M. and Pardo A., 2000. The relevance of morphological plasticity in the simulation of competition between maize and *Datura stramonium*. *Weed Research* 40: 163-180.

Christensen S. and Rasmussen G., 1994. Differential weed suppression and weed control in winter wheat. *Aspects of Applied Biology* 40: 335-342.

Coaker T.H., 1987. Cultural methods: The crop. In: *Integrated Pest Management*. Brun A.J., Coaker T.H. and Jepson P.C. (eds.), 69-88. Academic Press, London.

Coaker T.H., 1988. Insect pest management by intercrop diversity: Potential and limitations. In: *Progress of pest management in field vegetables*. Cavallore R. and Pelerents C. (eds.), 281-288. Balkema, Rotterdam.

Connolly J., 1986. On difficulties with replacement-series methodology in mixture experiments. *Journal of Applied Ecology* 23: 125-137.

Cousens R., 1985. An empirical model relating crop yield to weed and crop density and a statistical comparison with other models. *Journal of Agricultural Science* 105: 513-521.

Cousens R., 1987. Theory and reality of weed control thresholds. *Plant Protection Quarterly* 2: 13-20.

Cousens R. and Mortimer M., 1995. *Dynamics of weed populations*. 332 pp., Cambridge University Press, Cambridge, UK.

Dalal R.C., 1974. Effects of intercropping maize with pigeonpeas on grain yield and nutrient uptake. *Experimental Agriculture* 10: 219-224.

Dawson J.H., 1986. The concept of perod thresholds, In: *Proceedings of the European Weed Research Society (EWRS) Symposium on Economic Weed. Control.* 327-331 EWRS, Stuttgart-Hohenheim, EWRS, Wageningen, The Netherlands.

De Wit C.T., 1960. On competition. *Verslagen Landbouwkundig Onderzoek* 66: 1-82. Pudoc, Wageningen, The Netherlands,

De Wit C.T., Van Laar H.H. and Van Keulen H., 1979. Physiological potential of crop production. In: *Plant breeding perspectives*. Sneep J. and Hendriksen A.J.T. (eds.), 47-82. Pudoc, Wageningen, The Netherlands.

De Wit C.T. and Penning de Vries F.W.T., 1982. L'analyse des système de production primaire. In: *La productivité des pâturages Sahéliens*. Penning de Vries F.W.T. and Djitèye M.A. (eds.), 20-27. Pudoc Wageningen, The Netherlands.

Den Belder E., Elderson J. and Vereijken P.F.G., 2000. Effects of undersown clover on host-plant selection by *Thrips tabaci* adults in leek. *Entomologia Experimentalis et Applicata* 94: 173-182.

Dobolyi S., Städler E. and Baumann D.T., 1996. Bekämpfung von *Thrips tabaci* im Lauchanbau. *Der Gemüsebau* 5: 9-10.

Dyke G.V. and Barnard A.J., 1976. Suppression of couchgrass by Italian ryegrass and broad red clover undersown in barley and field beans. *Journal of Agricultural Science*, Cambridge 87: 123-126.

Embrechts A. and Pijnenburg H., 1991. Papiervlekken hebben met stro geen kans. *Groenten en Fruit/Vollegrondsgroenten* 30: 7.

Enyi B.A.C., 1973. Effects of intercropping of maize or sorghum with cowpeas, pigeonpeas or beans. *Experimental Agriculture* 9: 83-90.

Erbach D.C. and Lovely W.G., 1976. Machinery adaptations for multiple cropping, In: *Multiple cropping*. Pappendick R.I., Sanchez P.A. and Triplett G.B. (eds.), 337-346, American Society of Agronomy, Knoxville, Tennessee.

Firbank L.G. and Watkinson A.R., 1985. On the analysis of competition. *Journal of Applied Ecology* 22: 503-517.

Fleck N.G., Machado D.M.N. and De Souza R.S., 1984. Efficiencia da consorciacao de culturas no controls de plantas daninhas. *Pesquisa Agropecuaria Brasileira* 19: 591.

Francis C.A., 1986. *Multiple cropping systems*. 383 pp., Macmillan Publishing Company, New York.

Garnier E., 1992. Growth analysis of congeneric annual and perennial grass species. *Journal of Ecology* 80: 665-675.

Garrett K.A. and Mundt D.D., 1999. Epidemiology in mixed host populations. *Phytopathology* 89: 984-990.

Gijzen H. and Goudriaan J., 1989. A flexible and explanatory model of light distribution and photosynthesis in row crops. *Agricultural and Forest Meteorology* 48: 1-20.

Goudriaan J., 1977. *Crop micrometeorology: A simulation study*. Simulation Monographs, 257 pp. Pudoc, Wageningen, The Netherlands.

Goudriaan J. and Monteith J.L., 1990. A mathematical function for crop growth based on light interception and leaf area expansion. *Annals of Botany* 66: 695-701.

Goudriaan J. and Van Laar H.H., 1994. *Modelling potential crop growth processes*. 238 pp. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Graf B., Gutierrez A.P., Rakotobe O., Zahner P. and Delucchi V., 1990. A simulation model for the dynamics of rice growth and development. Part II - The competition with weeds for nitrogen and light. *Agricultural Systems* 32: 367-392.

Grime J.P., 1979. *Plant strategies and vegetation processes*. 222 pp. John Wiley & Sons, New York.

Grundy A.C., Bond W., Burston S. and Jackson L., 1999. Weed suppression by crops, In: *Proceedings of 1999 Brighton Conference - Weeds*, 957-962, British Crop Protection Council, Brighton, UK.

Hall R.L., 1974. Analysis of the nature of interference between plants of different species II. Nutrient relations in Nandi *Setaria* und Greenleaf *Desmodium* association with particular reference to potassium. *Australian Journal of Agricultural Research* 25: 749-756.

Harper J.L., 1977. *Populations biology of plants*. 892 pp. Academic Press, London, UK.

Harper J.L. and Ogden J., 1970. The reproductive strategy of higher plants. Part 1: The concept of strategy with special reference to _Senecio vulgaris_ L. _Journal of Ecology_ 58: 681-698.

Hartwig N.L., 1983. _Crownvetch and no-tillage crop production for soil erosion control._ 4 pp. Cooperative Extension Service, Pennsylvania State University.

Hermanutz L.A. and Weaver S.E., 1996. Agroecotypes or phenotypic plasticity? Comparison of agrestal and ruderal populations of _Solanum ptycanthum_. _Oecologia_ 105: 271-280.

Hill D.S., 1987. _Agricultural insect pests of temperate regions and their control._ 659 pp. Cambridge University Press, Cambridge, UK.

Holliday R., 1960. Plant population and crop yield. Part I. _Field Crop Abstracts_ 13: 159-167.

Holm L., Doll J., Holm E., Pancho J. and Herberger J., 1997. _World weeds._ 750 pp. John Wiley & Sons, New York.

Horie T., De Wit C.T., Goudriaan J. and Bensink J., 1979. A formal template for the development of cumcumber and its vegetative stage, In: _Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen_, Series C, Vol. 82 (4): 433-479.

Horwith B., 1985. A role of intercropping in modern agriculture. _Bioscience_ 35: 286-291.

Hull P., 1974. Self-fertilisation and the distribution of the radiate form of _Senecio vulgaris_ L. in Central Scotland. _Watsonia_ 10: 69-75.

Huxley P.A. and Maingu Z., 1978. Use of a systematic spacing design as an aid to the study of intercropping: some general considerations. _Experimental Agriculture_ 14: 49-56.

ICRISAT, 1983. _Research highlights 1983._ ICRISAT, Patencheru, India.

Imhof T., Baumann D.T., Städler E. and Wyser-Hammel I., 1996. Untersaat in Herbstlauch reduziert die Thripspopulation. _Agrarforschung_ 3: 337-340.

Itulya F.M. and Aguyoh J.N., 1998. The effects of intercropping kale with beans on yield and suppression of redroot pigweed under high altitude conditions in Kenya. _Experimental Agriculture_ 34: 171-176.

Jolliffe P.A., Minjas A.N. and Runeckles V.C., 1984. A reinterpretation of yield relationships in replacement series experiments. _Journal of Applied Ecolology_ 21: 227-243.

Keen A. and Engel B., 1988. _CBW Genstat Procedure (Library Manual Release 4.1 No. 78)._ CPRO-DLO, Wageningen, The Netherlands.

Kira T., Ogawa H. and Sakazaki N., 1953. Intraspecific competition among higher plants. I. Competition-yield-density interrelationships in regularly dispersed populations. *Journal of Institute for Polytechniques* D4: 1-16.

Kropff M.J. and Spitters, C.J.T., 1991. A simple model of crop loss by weed competition form early observations on relative leaf area of the weeds. *Weed Research* 31: 97-105.

Kropff M.J. and Lotz L.A.P., 1992. System approaches to quantify crop-weed interaction and their application in weed management. *Agricultural Systems* 40: 265-282.

Kropff M.J. and Spitters C.J.T., 1992. An eco-physiological model for interspecific competition, applied to the influence of *Chenopodium album* L. on sugar beet. I. Model description and parameterization. Weed Research 32: 437-450.

Kropff M.J., Vossen F.J.H., Spitters C.J.T. and De Groot W., 1984. Competition between a maize crop and a natural population of *Echinochloa crus-galli* (L.). *Netherlands Journal of Agricultural Science* 32: 324-327.

Kropff M.J., Spitters C.J.T., Schnieders B.J., Joenje W. and De Groot W., 1992. An eco-physiological model for interspecific competition, applied to the influence of *Chenopodium album* L. on sugarbeet. II. Model evaluation. *Weed Research* 32: 451-463.

Kropff M.J. and Van Laar H.H. (eds.), 1993. *Modelling crop-weed interactions*. 274 pp. CAB International, Wallingford, Oxon, UK.

Kropff M.J., Wallinga J. and Lotz L.A.P., 1996. Weed population dynamics. In: *Proceedings of Second International Weed Control Congress*, 3-14, DIAS, Slagelse, Denmark.

Kropff M.J. and Walter H., 2000. EWRS and challanges for weed research in the start of a new millennium. *Weed Research* 40: 7-10.

Lambers H., Cambridge M.L., Konings H. and Pons T.L., 1989. *Causes and consequences of variation in growth rate and productivity of higher plants*. 363 pp. SPB Academic Publishing, Den Haag, The Netherlands.

Lamberts M.L., 1980. *Intercropping with potatoes*, Cornell University, Ithaca, NY.

Latheef M.A. and Ortiz J.H., 1983. The influence of companion herbs on egg distribution of the imported cabbageworm *Pieris rapae* (*Lepidoptera:Pieridae*) on collard plants. *Canadian Entomologist* 115:1031-1038.

Leake A.R., 1999. Weed control and crop quality; the conflicting demands in organic and conventional farming systems. *Proceedings of the 1999 Brighton Conference - Weeds*, 889-896. British Crop Protection Council, Brighton, UK.

Leiss K.A., 2000. *Phenotypic plasticity and genetic differentiation in ruderal and agricultural populations of the weed* Senecio vulgaris *L.: implications for its biological control.* PhD-Thesis No. 1304, Université de Fribourg, Suisse, Fribourg.

Liboon S.P. and Harwood R.R., 1975. Nitrogen response in corn/soybean intercropping. In: *Proceedings of 6th Annual Science Meeting*, Philippines Crop Science Society, Bacolod City, Philippines.

Liebman M., 1986. *Ecological suppression of weeds in intercropping systems: Experiments with barley, pea, and mustard.* PhD-Thesis, University of California, Berkeley, CA.

Liebman M., 1988. Ecological suppression of weeds in intercropping systems: A review, In: *Weed management in agroecosystems: Ecological approaches.* Altieri M.A. and Liebman M. (eds.), 197-212, CRC Press, Boca Raton, FL.

Liebman M. and Dyck E., 1993. Crop rotation and intercropping strategies for weed management. *Ecological Applications* 3: 92-122.

Liebman M. and Ohno T., 1998. Crop rotation and legume residue effects on weed emergence and growth: Implications for weed management. In: *Integrated weed and soil management.* Hatfield J. L., Buhler D.D. and Steward B.A., (eds.), 181-221. Ann Arbor Press, Chelsea, MI.

Liebman M. and Davis A.S., 2000. Integration of soil, crop and weed management in low-external-input farming systems. *Weed Research* 40: 27-47.

Lotz L.A.P., 1989. *Variation in life-history characteristics between and within populations of* Plantago major *L.* PhD-Thesis, University of Nijmegen, Nijmegen, The Netherlands.

Lotz L.A.P., Groeneveld R.M.W. and Schnieders B.J., 1993. Evaluation of the population dynamics of annual weeds to test integrated weed management at a farming system level. *Landscape and Urban Planning* 27: 185-189.

Lotz L.A.P., Van Veen J.A. and Kropff M.J., 1997. Gewasbescherming. In: *Ontwerpen voor een schone landbouw.* Ketelaars J.J.M.H. and De Ruijter F.J. (eds.), Rapport 97/5. 35-58, Nation Council for Agricultural Research, The Hague, The Netherlands.

Martinez J. and Guiraud G., 1990. A lysimeter study of the effects of a ryegrass catch crop, during a winter wheat/maize rotation, on nitrate leaching and the following crop. *Journal of Soil Science* 41: 5-16.

Matteson P.C., 1995. The "50% pesticide cuts" in Europe: A glimpse of our future? *American Entomologist* 41: 210-220.

McNeal B.L. and Pratt P.F., 1978. Leaching of nitrate from soils. In: *Management of nitrogen in irrigated crops*. Pratt P.F. (ed.), 195-230, University of California, Riverside, CA.

Mead R. and Willey R.W., 1980. The concept of "Land Equivalent Ratio" and advantages in yields from intercropping. *Experimental Agriculture* 16: 217-228.

Mead R. and Riley J., 1981. A review of statistical ideas relevant to intercropping research. *Journal of the Royal Statistical Society* (Series A) 144: 462-509.

Meyer W. and Kessler H., 1990. Examples of integrated pest management in leek. *Gesunde Pflanzen* 42: 295-300.

Mineau P. and McLaughlin A., 1996. Conservation of biodiversity within Canadian agricultural landscapes: Integrating habitat for wildlife. *Journal of Agricultural and Environmental Ethics* 9: 93-113.

Monteith J.L., 1969. Light interception and radiative exchange in crop stands. In: *Physiological aspects of crop yield*. Eastin J.D., Haskins F.A., Sullivan C.Y. and Van Bavel C.H.M. (eds.), 89-111. Crop Science Society of America, Madison, WI.

Moody K. and Shetty S.V.R., 1979. Weed management in intercropping systems. In: *Proceedings of International Workshop on Intercropping*. 229-237. International Crop Research Institute for the Semi-Arid Tropics (ICRISAT), Hyderabad, India.

Mortensen D.A., Bastiaans L. and Sattin M., 2000. The role of ecology in the development of weed management systems: An outlook. *Weed Research* 40: 49-62.

Muller J.C., Morlet D.G. and Mariotti A., 1987. Influence of catch crops on mineral nitrogen leaching and its subsequent plant use. In: *Nitrogen efficiency in agricultural soils*. Jenkinson D.S. and Smith K.A. (eds.), Vol. 2, Elsevier, New York.

Müller-Schärer H. and Potter C.A.P., 1991. Cover plants in field grown vegetables: Prospects and limitations. In: *Proceedings of Brighton Crop Protection Conference - Weeds 1991*, 599-604. Brighton, BCPC, Brighton, UK.

Müller-Schärer H. and Baumann D.T., 1993. Unkrautregulierung im Gemüsebau: Konzepte zur Reduktion des Herbizideinsatzes. *Landwirtschaft Schweiz* 6: 401-412.

Müller-Schärer H., Potter C.A.P. and Grab F., 1992a. Zeitbezogene Schadensschwelle im Lauch. *Der Gemüsebau* 6: 7-9.

Müller-Schärer H., Potter C.A.P. and Hurni B., 1992b. Cover plants in field planted leek: Impact on yield, insect pests and nitrogen availability in the soil. In:

Proceedings of the 1st International Weed Control Congress, 353-355. Melbourne, Australia.

Nieto H.J., Brondo M.A. and Gonzales J.T., 1968. Critical periods of the crop growth cycle for competition of weeds. *Pest Articles and News Summaries (C)* 14: 159-166.

Niggli U. and Potter C.A.P., 1988. Die zeitbezogene Schadschwelle in konkurrenz-schwachen Kulturen. *Mitteilungen für die Schweizerische Landwirtschaft* 36: 44-50.

Osiru D.S.O. and Willey R.W., 1976. Studies on mixtures of maize and beams with particular emphasis on the time of planting beans. In: *Proceedings of the Symposium on Intercropping in Semi-Arid Tropics.* (ICRISAT), Morogoro, Tanzania.

Oyejola B.A. and Mead R., 1982. Statistical assessment of different ways of calculating land equivalent ratios (LER). *Experimental Agriculture* 18: 125-138.

Paolini R., Principi M., Froud-Williams R.J., Del Puglia S., Barcellona O. and Biancardi E., 1999. Competition between sugerbeet and *Sinapis arvensis* and *Chenopodium album,* as affected by timing of nitrogen fertilization. *Weed Research* 39: 425-440.

Papendick R.I., Sanchez P.A. and Triplett G.B., 1975. *Multiple cropping: Proceedings of a symposium.* 378 pp. American Society of Agronomy, Knoxville, Tennessee.

Paul N.D. and Ayres P.G., 1987. Survival, growth and reproduction of groundsel (*Senecio vulgaris*) infected by rust (*Puccinia lagenophorae*) in the field during summer. *Journal of Ecology* 75: 61-71.

Payne R.W., Lane P.W., Ainsley A.E., Bicknell K.E., Digby P.G.N., Gower J.C., Harding S.A., Leech P.K., Simpson H.R., Todd A.D., Verrier P.J. and White R.P., 1987. *GENSTAT 5 Reference Manual.* Oxford University Press, Oxford, UK.

Phatak S.C., 1992. An integrated sustainable vegetable production system. *Horticultural Science* 27: 738-741.

Pinchinat A.M., Soria J. and Bazan R., 1975. Multiple cropping in tropical America. In: *Multiple cropping.* Papendick R.I., Sanchez P.A. and Triplett G.B. (eds.), 24-29. Special Publications. American Society of Agronomy, Knoxville, Tennessee.

Poorter H. and Remkes C., 1990. Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. *Oecologia* 83: 553-559.

Poorter H., Remkes C. and Lambers H., 1990. Carbon and nitrogen economy of 24 wild species differing in relative growth rate. *Plant Physiology* 94: 621-627.

Potter C.A.P., 1991. Integrierte Unkrautbekämpfung. *Der Gemüsebau* 10: 12.

Potter C.A.P. and Niggli U., 1989. Unkrautbekämpfung, Bodenpflege und Untersaaten im Zuckermais. *Der Gemüsebau* 9: 26-27.

Putnam A.R., 1986. Allelopathy: can it be managed to benefit horticulture? *HortScience* 21: 411-413.

Radosevich S.R. and Holt J.S., 1984. *Weed ecology*. 265 pp. John Wiley & Sons, New York.

Rana K.S. and Pal M., 1999. Effect of intercropping systems and weed control on crop-weed competition and grain yield of pigeonpea. *Crop Research* (Hisar) 17: 179-182.

Roberts H.A., 1976. Weed competition in vegetable crops. *Annals of Applied Biology* 83: 321-324.

Rooney J.M., 1991. Influence of growth from on *Avena fatua* L. on the growth and yield of *Triticum aestivum* L. *Annals of Applied Biology* 118: 411-416.

Rubatzky V.E., Quiros C.F. and Simon P.W., 1999. *Carrots and related vegetable Umbelliferae*. 294 pp. CABI International, Wallingford, Oxon, UK.

Ryan J., Ryan M.F. and McNaeidhe F., 1980. The effect of interrow plant cover on populations of the cabbage root fly, *Delia brassicae* (Wiedemann). *Journal of Applied Ecology* 17: 31-40.

Sackville Hamilton N.R., 1994. Replacement and additive designs for plant competition studies. *Journal of Applied Ecology* 31: 599-603.

Samson D.A. and Werk K.S., 1986. Size-dependent effects in the analysis of reproductive effort in plants. *The American Naturalist* 127: 667-680.

Schnieders B.J., 1999. *A quantitative analysis of inter-specific competition in crops with a row structure*. PhD-Thesis, 165 pp. Agricultural University Wageningen, Wageningen, The Netherlands.

Schnieders B.J. and Lotz L.A.P., 1993. The relevance of row structures in crop-weed competition, analysed with a simulation model. In: *Proceedings of the 8th EWRS symposium "Quantitative approaches in weed and herbicide research and their practical application"*, Braunschweig, 33-40. EWRS, Wageningen, The Netherlands.

Schoofs A. and Entz M.H., 2000. Influence of annual forages on weed dynamics in a cropping system. *Canadian Journal of Plant Science* 80: 187-198.

Shennan C., 1992. Cover crops, nitrogen cycling, and soil properties in semi-irrigated vegetable production systems. *Horticultural Science* 27: 749-754.

Shetty S.V.R. and Rao A.N., 1981. Weed-management studies in sorghum/pigeopea and pearl millet/groundnut intercrop systems - some observations. In: *Proceedings of International Workshop on Intercropping*, Hyderabad, India.

238-248. International Crop Research Institute for the Semi-Arid Tropics (ICRISAT), Patencheru, India.

Shinozaki K. and Kira T., 1956. Intraspecific competition among higher plants. VII. Logistic theory of the C-D effect. *Journal of Institute for Polytechiques* D7: 35-72.

Sibma L., 1968. Growth of closed green crop surfaces in The Netherlands. *Netherlands Journal of Agricultural Science* 16: 211-216.

Smit A.L., Booij R. and Van der Werf A., 1996. The spatial and temporal rooting pattern of Brussels sprouts and leeks. *Netherlands Journal of Agricultural Science* 44: 57-72.

Snaydon R.W., 1991. Replacement or additive design for competition studies. *Journal of Applied Ecology* 28: 930-946.

Sobey D., 1987. Differences in seed production between *Stellaria media* populations from different habitat types. *Annals of Botany* 59: 543-549.

Solaimalai A. and Selvam S.P., 1998. Integrated weed management for sorghum based intercropping systems-a review. *Agricultural Reviews* (Karnal) 19: 205-208.

Soria J., Bazan R., Pinchinat A.M., Paez G., Mateo N., Moreno R., Fargas J. and Forsythe W., 1975. Investigacion sobre sistemas des produccion agricola para el pequeno agricultor del tropico. *Turrialba* 25: 283.

Spigt R.M., and Janssen T.L.J. (eds.), 1997. *Kwantitatieve Informatie Akkerbouw en Vollegrondsgroenteteelt* (PAV), Lelystad, The Netherlands.

Spitters C.J.T., 1983a. An alternative approach to the analysis of mixed cropping experiments. 1. Estimation of competition effects. *Netherlands Journal of Agricultural Science* 31: 1-11.

Spitters C.J.T., 1983b. An alternative approach to the analysis of mixed cropping experiments. 2. Marketable yield. *Netherlands Journal of Agricultural Science* 31: 143-155.

Spitters C.J.T., 1989. Weeds: Population dynamics, germination and competition. In: *Simulation and systems management in crop protection*. Rabbinge R., Ward S.A. and Van Laar H.H. (eds.), 182-216. Pudoc, Wageningen, The Netherlands.

Spitters C.J.T. and Aerts R., 1983. Simulation of competition for light and water in crop-weed associations. *Aspects of Applied Biology* 4: 467-483.

Spitters C.J.T., 1990. On the descriptive and mechanistic models for inter-plant competition, with particular reference to crop-weed interaction. In: *Theoretical Production Ecology: Reflections and prospects*. Rabbinge R., Goudriaan J., Van Keulen H., Penning de Vries F.W.T. and Van Laar, H.H. (eds.), 217-236. Simulation Monographs, Pudoc, Wageningen, The Netherlands.

Stark J.C., Jarrell W.M. and Letey J., 1982. Relationship between growth and nitrogen fertilization of celery. *HortScience* 17: 754-755.

Stribley D.P., 1990. Mycorrhizal associations and their significance. In: *Onions and allied crops*. Rabinowich H.D. and Brewster J.L. (eds.), 85-101. CRC Press, Boca Raton. FL.

Teasdale J.R., 1998. Cover plants, smother plants, and weed management. In: *Integrated Weed and Soil Management*. Hatfield J. L., Buhler D.D. and Steward B.A. (eds.), 247-270. Ann Arbor Press, Chelsea, MI.

Tetio-Kagho F. and Gardner F.P., 1988. Responses of maize to plant population density. I. Canopy development, light relationships, and vegetative growth. *Agronomy Journal* 80: 930-935.

Theaker A.J. and Briggs D., 1993. Genecological studies of groundsel (*Senecio vulgaris* L.), IV. Rate of development in plants from different habitat types. *New Phytologist* 123: 185-194.

Theunissen J., 1994. Intercropping in field vegetable crops. Pest management by agrosystem diversification: An overview. *Pesticide Science* 42: 65-68.

Theunissen J. and Schelling G., 1996. Pest and disease management by intercropping: Suppression of thrips and rust in leek. *International Journal of Pest Management* 42: 227-234.

Thompson B.K., Weiner J. and Warwick S.I., 1991. Size-dependent reproductive output in agricultural weeds. *Canadian Journal of Botany* 69: 442-446.

Tipton J.L., 1984. Evaluation of three growth curve models for germination data analysis. *Journal of the American Society of Horticultural Science* 109: 451-454.

Trenbath B.R., 1974. Biomass productivity of mixtures. *Advances in Agronomy* 26: 177-210.

Uvah I.I.I. and Coaker T.H., 1984. Effect of mixed cropping on some insect pests of carrots and onions. *Entomologia Experimentalis et Applicata* 36: 159-167.

Van der Werf, A., 1996. Growth analysis and photoassimilate partitioning. In: *Photoassimilate distribution in plants and crops: Source-sink relationships*. Zamski E. and Schaffer A.A. (eds.), 1-20. Marcel Dekker, New York.

Van der Werf A., Van Nuenen M., Visser A.J. and Lambers H., 1993. Effects of N-supply on the rates of photosynthesis and shoot and root respiration of inherently fast- and slow-growing monocotyledonous species. *Physiologia Plantarum* 89: 563-569.

Van der Werf A., Enserink C.T., Smit A.L. and Booij R., 1996. Components of relative growth rate and nitrogen productivity of Brussels sprouts and leeks grown at

two widely differing light intensities. *Netherlands Journal of Agricultural Science* 44: 21-29.

Van Keulen H., Goudriaan J. and Seligman N.G., 1989. Modelling the effects of nitrogen on canopy development and crop growth. In: *Plant canopies: Their growth, form and function*. Russell G., Marshall B. and Jarvis, P.G. (eds.), 84-104. Cambridge University Press, Cambridge, UK.

Vandermeer J., 1989. *The ecology of intercropping*. 237 pp. Cambridge University Press, Cambridge, UK.

Vereijken P. and Kropff M.J., 1996. Prototyping ecological farming systems. In: *Annual Report 1995*. DLO Research Institute for Agrobiology and Soil Fertility, Wageningen, The Netherlands.

Vleeshouwers L.M. and Streibig J.C., 1988. How often must we theoretically control weeds? In: *Weed control in vegetable production*. Cavalloro R. and El Titi A. (eds.), 85-98. Balkema, Rotterdam, The Netherlands.

Wallace R.W. and Bellinder R.R., 1992. Alternative tillage and herbicide options for successful weed control in vegetables. *Horticultural Science* 27: 745-749.

Wallinga J. and Van Oijen M., 1997. Level of threshold weed density does not affect the long-term frequency of weed control. *Crop Protection* 16: 273-278.

Walters R.F., 1971. *Shifting cultivation in Latin America*. Rep. No. 17. Food and Agricultural Organisation (FAO), Rome, Italy.

Watkinson A.R., 1981. Interference on pure and mixed populations of *Agrostemma githago*. *Journal of Applied Ecology* 18: 967-976.

Watkinson A.R., 1985. Plant responses to crowding. In: *Studies on plant demography*. White J. (ed.), 275-289. Academic Press, London, UK.

Weiner J., 1988. The influence of competition on plant reproduction. In: *Plant reproductive ecology: Patterns and strategies*. Lovett Doust J. and Lovett Doust L. (eds.), 228-245. Oxford University Press, New York.

Weis I.M., 1982. The effects of propagule size on germination and seedling growth in *Mirabilis hirsuta*. *Canadian Journal of Botany* 60: 1868-1874.

Wiles L.J., William R.D., Crabtree G.D. and Radosevich S.R., 1989. Analyzing competition between a living mulch and vegetable crop in an intercropping system. *Journal of American Society for Horticultural Science* 114: 1029-1034.

Willey R.W., 1979a. Intercropping: Its importance and research needs. Part 1. Competition and yield advantages. *Field Crop Abstracts* 32: 1-10.

Willey R.W. 1979b. Intercropping: Its importance and research needs. Part 2. Agronomy and research approaches. *Field Crop Abstracts* 32: 73-85.

Willey R.W. and Roberts E.H., 1976. Mixed cropping. In: *Solar energy in agriculture. Proceedings of Joint International Solar Energy Society Conference.* University of Reading, Reading, UK.

Williams W.A., Loomis R.S. and Lepley C.R., 1965. Vegetative growth of corn as affected by population density. I. Productivity in relation to interception of solar radiation. *Crop Science* 5: 211-215.

Wilson B.J., Peters N.C.B., Wright K.J. and Atkins H.A., 1988. The influence of crop competition on the seed production of *Lamium purpureum, Viola arvensis* and *Papaver rhoeas* in winter wheat. *Aspects of Applied Biology* 18: 71-80.

Wolfe M.S., 1985. The current status of and prospects of multiline cultivars and variety mixtures for disease resistance. *Annual Review of Phytopathology* 23: 251-273.

Wright A.J., 1981. The analysis of yield-density relationships in binary mixtures using inverse polynomials. *Journal of Agricultural Science* 96: 561-567.

Wright K.J., 1993. Weed seed production as affected by crop density and nitrogen application. In: *Proceedings of the Brighton Crop Protection Conference - Weeds,* Brighton, 275-280. BCPC, Brighton, UK.

Wulff R.D., 1986a. Seed size variation in *Desmodium paniculum*. II. Effects on seedling growth and physiological performance. *Journal of Ecology* 74: 99-114.

Wulff R.D., 1986b. Seed size variation in *Desmodium paniculum*. III. Effects on reproductive yield and competitive ability. *Journal of Ecology* 74: 115-121.

Wyss G.S., 1997. *Quantitative resistance in the weed-pathosystem* Senecio vulgaris *L.-Puccinia lagenophorae* Cooke. PhD-Thesis ETH Zürich, Switzerland.

Wyss G.S. and Müller-Schärer H., 1999. Infection process and resistance in the weed pathosystem *Senecio vulgaris - Puccinia lagenophorae* and implications for biological control. *Canadian Journal of Botany* 77: 361-369.

Yih W.K., 1982. *Weeds, intercropping, and mulch in temperate zones and the tropics - some ecological implications for low-technology agriculture.* PhD-Thesis, University of Michigan, Ann Arbor, MI.

Zhu Y., Chen H., Fan J., Wang Y., Li Y., Chen J., Fan J., Yang S., Hu L., Leung H., Mew T.W., Teng P.S., Wang Z. and Mundt C.C., 2000. Genetic diversity and disease control in rice. *Nature* 406: 718-722.

Zimdahl R.L., 1980. *Weed crop competition: A review.* International Plant Protection Centre, University of Oregon, Corvallis, OR.

Zink F.W., 1963. Rate of growth and nutrient absorption by celery. In: *Proceedings of the American Society of Horticultural Science* 82: 351-357.

Zollinger R.K. and Kells J.J., 1991. Effect of soil pH, soil water, light intensity, and temperature on perennial sowthistle (*Sonchus arvensis* L.). *Weed Science* 39: 376-384.

Curriculum vitae

Daniel Thomas Baumann was born in Zürich, Switzerland on March 12th, 1958. After completing basic education, he finished his first professional training as laboratory assistant in agrobiology in 1978. Practical work periods on different farms in Switzerland were followed by an agricultural education at the Agricultural College of the Kanton of Zürich "Strickhof", Lindau and the Schweizerischen Ingenieurschule für Landwirtschaft, Zollikofen, where he graduated in 1986. He started his professional career at the Research Station for Arable Farming and Field-Production of Vegetables (PAGV) in Lelystad, The Netherlands, where he worked on a project to optimise the use and application technique of organic manure in arable, vegetable and ornamental crops. In 1989, he changed to weed science and co-ordinated the research programme on weed control at PAGV. His interests developed mainly towards non-chemical and particularly mechanical weed control. Together with a Danish colleague, he established in 1994 a European working group on physical and cultural weed control, which he still chairs under the umbrella of the European Weed Research Society (EWRS). Since returning to Switzerland in 1992, he has been working at the Swiss Federal Research Station for Fruit-Growing, Viticulture and Horticulture (FAW) in Wädenswil, Switzerland as a weed scientist. After different research projects on weed control in vegetable crops, he started his PhD research at the former department of Theoretical Production Ecology of Wageningen University in 1996, maintaining his regular work at FAW in Switzerland, which he will continue after finishing his PhD.