Variability in yield of faba beans (*Vicia faba* L.)

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Variability in yield of faba beans (*Vicia faba* L.)

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Abstract

Yield variability is one of the major problems in growing faba beans. In this thesis, the effect of water supply pattern on yield variability of the crop is studied with experiments in the field and under controlled conditions, and with a simulation model. In a series of field experiments, water shortage during flowering, followed by plenty of water after flowering resulted in 30-200% higher pod retention at early formed nodes, a 7% higher Harvest Index, equal average seed yields (6 t ha^{-1}, 100% d.m.), but a 57% larger seed yield range, compared with plenty of water during and after flowering. In some experiments, mild water shortage during flowering resulted in final seed yields which were significantly higher (0.3-0.6 t ha^{-1}) than with plenty of water both during and after flowering. Water shortage after flowering resulted in yield limitations of more than 3 t ha^{-1} and a 200% larger seed yield range. Crop physiological measurements showed that faba beans have insufficient osmotic adjustment and/or adaptation of cell wall elasticity. Thus, the turgor of young stems and leaves, the expansive growth and the vegetative sink strength decrease already with mild water shortage. The stomatal conductance and photosynthesis decrease only at more severe water shortage. It is argued how this may explain the positive effect of mild water shortage on the dry matter partitioning to reproductive organs. The effects are compared with those found in cotton. In a simulation model the physiological knowledge is implemented and calibrated. The model outcomes correspond with the measured average seed yields and account for up to 80% of the measured yield variation of data sets of several locations in Western Europe. Applying plenty of water after flowering increases the average seed yields with 17%-42% and reduces the standard deviation of the seed yields, a measure for the variability, with 43%-73%. Plenty of water during and after flowering has almost no additional effects. It is shown that the positive effect of mild water shortage during flowering on seed yield has only limited value as a target for crop management. But, plenty of water after flowering is crucial for high and stable seed yields. Model explorations show that a doubling of the rooted depth reduces the seed yield variability with about 30%, but a doubling of the water extraction capacity of the crop does not reduce the yield variability at all. It is concluded that variations in water availability after flowering (i.e. during the grain filling period) are a major factor in yield variability of faba beans in Western Europe. However, when water shortage is eliminated as the *limiting* factor, yield *reducing* factors, especially diseases, may be more important than was expected before. It is shown how feasibility studies with the model can support management and breeding research by evaluating 'ideotypes' and conditions for optimum productivity in present and future climate. As an example, some effects of climate change on average yield and yield variability of rain-fed and irrigated crops are assessed.

Keywords: Vicia faba L., irrigation, drought, water shortage, dry matter partitioning, yield variability, pod retention, pod filling, plant water relations, expansive growth, stomatal conductance, simulation, modeling, feasibility studies, climate change, cotton

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Stellingen

1. Watertekort is één van de hoofdoorzaken van de grote opbrengstvariabiliteit van veldbonen in de gematigde klimaatzônes.

   Dit proefschrift

2. De hogere zaadopbrengst van veldbonen bij een mild watertekort tijdens de bloei is verklaarbaar uit een vermindering van de sinksterkte van jonge stengels en bladeren en een daaruit voortvloeiende toename van het verhoudingsgetal tussen reproduktieve en vegetatieve sinksterkten.

   Dit proefschrift

3. Mogelijke klimaatsverandering (stijging van CO_2-gehalte in de atmosfeer en temperatuursstijging) verandert niet de noodzaak van een ruime vochtvoorziening voor het verkrijgen van stabiele opbrengsten bij veldbonen.

   Dit proefschrift

4. Een betrouwbare simulatie van de opbrengst van veldbonen vergt geen expliciete simulatie van de stikstofhuishouding in de bodem en in het gewas.

   Dit proefschrift

5. Erwten zijn door een kortere groeiperiode minder gevoelig voor watertekort dan veldbonen, maar door legering gevoeliger voor schimmelziekten bij koud en nat weer. Bij de teelt van peulvruchten verdient het daarom voorkeur om erwten te telen in Noord- en Midden-Frankrijk en veldbonen te telen in de noordelijke EG-lidstaten.

6. De teelt van erwten en veldbonen in de EG als alternatief voor de import van eiwitrijke grondstoffen (onder meer sojaschroot) zal nauwelijks verbeteringen tot gevolg kunnen hebben voor de benarde positie van kleine boeren in Brazilië ten opzichte van de grootgrondbezitters-sojaproducenten.

   cf: 'Soja sonee', soja produktie op grote schaal: de gevolgen voor arme boeren in Brazilië en voor ons. Uitgave Solidaridad en Vereniging Milieudefensie (1981).

7. Door een 'braakregeling' neemt het mestoverschot in Nederland toe; in dit verband is het gunstiger om peulvruchten te telen als grondstof voor krachtvoer, in plaats van braaklegging.

8. Zetmeelwinning uit korrelmaïs zou in de veenkoloniën kunnen leiden tot een ruimere vruchtwisseling met aardappelen. Technologisch en kwalitatief is zetmeel uit korrelmaïs een redelijk alternatief voor de in deze regio gevestigde zetmeelindustrie.

9. Zowel een uitbreiding van de aktie 'rij alcoholvrij' tot Europese schaal, als een verplichting om de ingrediënten van pils op de etiketten te vermelden, zullen de teelt van brouwgerst stimuleren.

10. Hoe meer we te weten komen van een 'veelbelovend' nieuw gewas, hoe meer onderzoek vervolgens nodig blijkt te zijn om het gewas de beloften te laten vervullen.

11. De zogeheten 'B-status' binnen het Algemeen Burgerlijk Pensioenfonds (ABP) hoeft geen belemmering te zijn voor het adekwaat functioneren van een verzelfstandigde marktgerichte onderzoeksorganisatie.

12. De proefstations en de DLO-instituten van het Ministerie van LNV moeten beide tot een marktgerichte organisatie worden verzelfstandigd.

13. De huidige Gereformeerde Kerken in Nederland en die van zo'n 40 jaar geleden lijken vrijwel in niets meer op elkaar. Door het voortzetten van dit veranderingsproces kunnen deze kerken een functie blijven vervullen voor hen die willen leven en werken in het spanningsveld tussen de christelijke traditie en de huidige samenleving.

    G. Dekker, De stille revolutie. De ontwikkeling van de Gereformeerde Kerken in Nederland tussen 1950 en 1990. (1992) p. 15 en p. 226.

14. 'Deeltijdwerkers' kunnen minder worden aangesproken op het doen van overwerk dan traditionele 'voltijdswerkers'.

15. Het geluidssignaal waarmee de Nederlandse Spoorwegen op een aantal stations de reizigers attenderen op mededelingen over kleine en grote treinvertragingen, vertoont een verrassende overeenkomst met de koorinzet van J.S. Bach's cantate 106: 'Gottes Zeit ist die allerbeste Zeit'. Jammergenoeg is dit signaal op Utrecht CS verdwenen, terwijl de vertragingen bleven.

Stellingen behorend bij het proefschrift van C. Grashoff:
'Variability in yield of faba beans (*Vicia faba* L.)'.

Wageningen, 11 november 1992.

ter nagedachtenis aan
mijn vader Kees Grashoff
mijn leermeester dr. ir. G. Dantuma

Foto voorzijde:
van links naar rechts: veldboneplanten (ras Minica) opgegroeid onder: a) watertekort vanaf begin bloei tot einde groeiseizoen; b) natuurlijke regenval (1983); c) watertekort vanaf begin bloei, gevolgd door irrigatie vanaf einde bloei; d) irrigatie vanaf begin bloei, gevolgd door watertekort vanaf einde bloei; e) irrigatie vanaf begin bloei tot einde groeiseizoen. Watervoorziening c) en e) gaven een verdubbeling van de zaadopbrengst t.o.v. de watervoorzieningen a), b) en d).

Foto gemaakt in Engeland in een 'Joint trial' van de Universiteit van Nottingham (School of Agriculture) en het DLO-Centrum voor Agrobiologisch Onderzoek (CABO-DLO) te Wageningen (Foto: C.F. Green / C. Grashoff).

Photo cover:
from left to right: faba bean plants (cv Minica) grown under: a) water shortage from onset of flowering till the end of the growing season; b) natural rainfall (1983); c) water shortage from onset of flowering, followed by irrigation after the end of flowering; d) irrigation from onset of flowering, followed by water shortage after the end of flowering; e) irrigation from onset of flowering till the end of the growing season. The water supply treatments c) and e) resulted in a doubling of the seed yield, compared to the treatments a), b) and d).

Photo made in England in a 'Joint trial' of the University of Nottingham (School of Agriculture) and the DLO-Centre for Agrobiological Research (CABO-DLO) in Wageningen, Netherlands (Photo: C.F. Green / C. Grashoff).

Woord vooraf

Dit proefschrift beschrijft onderzoek dat is uitgevoerd op het DLO-Centrum voor Agrobiologisch Onderzoek (CABO-DLO) te Wageningen in de periode 1980-1990. Deze wat langere periode, die ik deels als student, deels als medewerker op dit instituut heb meegemaakt, heeft als bijkomend gevolg dat ik inmiddels bijna een heel instituut zou kunnen bedanken voor alle bijdragen aan de tot stand koming van dit eindresultaat in boekvorm. Dat is onmogelijk en ik zal me dus moeten beperken - iets waar ik vaker, maar in dit geval terecht, enige moeite mee heb.

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Next, I wish to thank all the colleagues of the EC-Joint Faba Bean Trials (JFBT), especially dr. D.A. Bond and dr. P.D. Hebblethwaite (United Kingdom), and dr. E. Ebmeyer and dr. E. von Kittlitz (Germany), for the co-operation and inspiring discussions concerning our joint faba bean experiments, during the international workshops and symposia of the last 10 years.

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Contents

Account

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

Chapter 1: Grashoff, C., 1990a. Effect of pattern of water supply on *Vicia faba* L.
1. Dry matter partitioning and yield variability.
Netherlands Journal of Agricultural Science 38: 21-44.

Chapter 2: Grashoff, C., 1990b. Effect of pattern of water supply on *Vicia faba* L.
2. Pod retention and filling, and dry matter partitioning, production and water use
Netherlands Journal of Agricultural Science 38: 131-143.

Chapter 3: Grashoff, C. & D.R. Verkerke, 1991. Effect of pattern of water supply on *Vicia faba* L.
3. Plant water relations, expansive growth and stomatal reactions.
Netherlands Journal of Agricultural Science 39: 247-262.

Chapter 4: Grashoff, C. & R. Stokkers, 1992. Effect of pattern of water supply on *Vicia faba* L.
4. Simulation studies on yield variability.
Netherlands Journal of Agricultural Science (accepted; in press).

General introduction

General introduction

Seed legumes in the European Community

In the European Community, the demand for protein-rich raw materials for the animal feed compounding industry increased from 2.5 million t in 1960 to about 43 million t in 1990. In the last decades, the degree of self-sufficiency of the EC for these raw materials was low, less than 35 %. After the soya bean crisis in 1973 the EC started with financial support measures for the production of protein crops in the Community itself. In this way the imports from third countries could be reduced. Besides this, the production of protein-rich crops was seen as an alternative for the overproduction of cereals.

Due to the support measures, the interest in growing seed legumes, an important group of protein-rich crops, increased in the period from 1978 to 1988. The Dutch Grain Centre (NGC, 1985) estimated an industrial demand for seed legumes of 8 million t in the EC, which requires an area under cultivation of almost 2 million ha. For The Netherlands, the NGC estimated that an area of 75 000 ha is possible without problems in crop rotation systems or market problems. The area of seed legumes under cultivation in The Netherlands increased from 8200 ha in 1981 to 48500 ha in 1987 (Landbouwcijfers, 1990). In the EC, the area increased from 515000 ha in 1981 to 988000 ha in 1986 (Anon., 1984-1988).

However, the increase in area, of which two third consists of green peas (Pisum sativum L.) and less than one third consists of faba beans (Vicia faba L.), stabilized after 1987. Especially the increase in faba beans was slow, or stopped completely and turned into a decrease in many EC-countries. For instance, in The Netherlands the area with faba beans reached a maximum of 13400 ha in 1988 and hence almost halved in each of the next years and at this moment an area of not more than 2500 ha is cultivated with faba beans.

Yield variability: a bottleneck for growing faba beans

There may be two reasons for this decrease. Firstly, although it is a recent development, the EC decreased the minimum farmer's price for faba beans and peas since 1989 with almost 20%. This reduced the interest of the farmers for growing legumes.

Secondly, *bottlenecks in crop growth* have been reported for many years and these are the general subject of this thesis. It has become very clear that not the *yield potential* of faba beans is a major bottleneck. The productivity of faba beans is comparable with that of other arable crops like winter wheat, sugar beet and maize. In the phase of linear growth, the growth rate of a healthy faba bean crop is 200-250 kg ha^{-1} d^{-1}. Sibma et al. (1989) showed that the crop can have a period of complete soil cover of about 75 days. With an average growth rate of 200 kg ha^{-1} d^{-1}, this results in a possible dry matter production of 15 t ha^{-1}. With a Harvest

Index of 0.60, this implies potential seed yields of more than 9 t ha^{-1}. The measured maximum seed yields of faba beans in long term trials are ca 8000 kg ha^{-1} (at 100% d.m.), with 30% of crude protein (Grashoff et al., 1987). At final harvest, the seeds contain 80-90% of the total amount of nitrogen accumulated by the crop.

Yield variability, defined as the variation in yield from year to year and from location to location, has been a major reason for decline in cultivated area in most European countries (Hawtin & Hebblethwaite, 1983). Figure 1 illustrates the variability of national average yields in the United Kingdom (UK) for faba beans and winter wheat from 1885 to 1980. The amplitude of fluctuation for faba beans is greater than that for wheat, and the increase in average yield is much less. This is illustrated with a 'variability index' (defined in Table 1), calculated from the UK average data from 1866 to 1968 and from 1866 to 1979. This index shows that yields of faba beans are far more unstable than those of wheat, oats, barley and potatoes (Table 1).

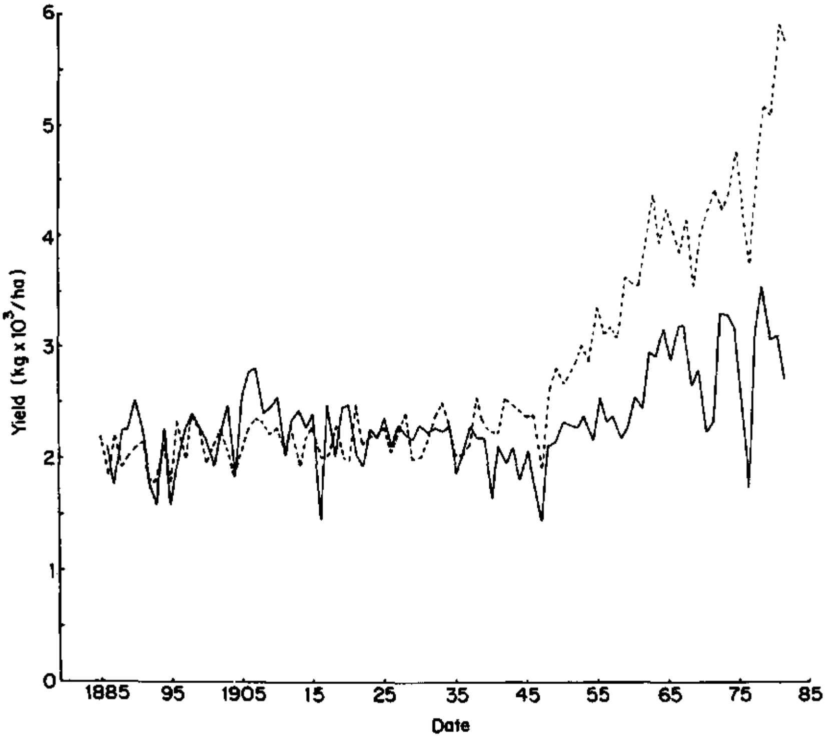

Figure 1. National average yields of faba beans (solid line) and wheat (dotted line) in the United Kingdom, 1885-1980 (MAFF statistics). From: Hawtin & Hebblethwaite, 1983.

Table 1. Yield variability index (%) of various crops, 1866-1968 and 1866-1979. From: Hawtin & Hebblethwaite (1983)

Crop	Variability index * 1866-1968	Variability index 1866-1979
Faba beans	113	137
Wheat	52	53
Barley	34	35
Oats	31	33
Potatoes	70	71

*This index is calculated by expressing the annual deviation from a five-year moving average as a percentage of this moving average. These percentages are then squared to remove negative signs

Differences in yield between 7-10 locations in Western Europe were analyzed in the EC-Joint Faba Bean Trials (JFBT) (Dantuma et al., 1983; Ebmeyer, 1984). The yield of, for instance, cv Wierboon, averaged over 3 years, varied from 2.4 t ha^{-1} at the location Fuchsenbigl (Austria) to 5.8 t ha^{-1} at the location Noordoostpolder (Netherlands). Analysis of variance showed, that the yield variability was due to variety, to environment and to environment x variety interaction (Bond, 1984). Even within one small geographic area, differences in seed yields between locations can be large: the yield of 8 farmers' fields in the province of Gelderland (Netherlands) varied between 1 and 4.5 t ha^{-1} in 1983 (Consulentschap Tiel, 1984). Differences in seed yields from year to year at one location can be more than 4 t ha^{-1}. For instance, on a heavy clay soil near Wageningen, the seed yield of cv. Minica varied between 2.5 and 6.7 t ha^{-1} over a period of 14 years (Grashoff et al., 1987).

Possible causes of yield variability

To find the major causes of this yield variability, several factors have been considered in the previous years. The effects of various *fertilizer nitrogen applications* (Roughly et al., 1983), various *planting densities* (Dantuma et al., 1983; Ebmeyer, 1984) and enhanced *self-fertility* (Bond & Poulsen, 1983) were investigated. Effective methods and materials were available for protection against *pests and diseases* (Dekker, 1985a, 1985b). None of these factors appeared to be major causes of yield variability. Since the leguminous crops are generally characterized as sensitive to *water shortage* (Brouwer, 1976), research was started to investigate the effects of various (natural or imposed) water supply patterns on yield variability.

Water shortage as affecting yield variability: the general topic of this thesis

Many authors observed large increases (50-100%) in seed yield and in total dry matter production in irrigation experiments, regardless of the developmental stage of the crop when irrigation was applied (Hebblethwaite et al., 1977; French & Legg, 1979; Farah, 1981). However, others (Brouwer, 1959) reported that especially irrigation during the flowering period provided high yield increments. In contrast, Stock & El-Naggar (1980) and Smith (1982) reported that lower seed yields were obtained with irrigation before and during flowering.

Even under the moderate climatic conditions of The Netherlands, contrasting results with respect to water supply were found. On the one hand, it was indicated that faba beans show larger yield reductions with water shortage than some other arable crops. In experiments in the dry year 1976, faba beans yielded 47% lower than the average yield of a group of reference years without water shortage. Winter wheat yielded in 1976 only 16% lower than its reference, and spring barley yielded in 1976 even 2% higher than its reference (Dekker, 1979). In trials near Wageningen on a heavy clay soil with a high water retention capacity, the yield of faba beans in 1976 was the lowest (2.5 t ha^{-1}) of a series of 14 years with an average of 5.4 t ha^{-1}. On a soil in the Noordoostpolder with a very adequate water supply due to capillary rise, the yield in 1976 was not lower than 5 t ha^{-1}. Dantuma & Klein Hulze (1979) indicated that, like in soya beans, water shortage might be one of the major reasons for yield limitation in faba beans. These indications were based partly on the above results, and partly on visual observations in the field trials of the low-productive locations of the Joint Faba Bean Trials (JFBT). On these locations, clear indications of water shortage (severe wilting, partly followed by enhanced leaf senescence) could be observed (Dantuma, pers. comm. 1982).

On the other hand, it was indicated that the *absence* of any water shortage can reduce the seed yields of faba beans. In very wet years, like in 1972, it was observed that very leafy and tall faba bean crops were found (2.1 m height for cv Wierboon, which has an average of about 1.5 m). The final total dry matter was 13.1 t ha^{-1}, but the seed yield was only 2 t ha^{-1}. This showed that not only *dry matter production*, but also *dry matter partitioning* between vegetative and reproductive plant organs was affected by water supply.

In the faba bean crop, such effects of water supply on dry matter partitioning are possible, as in this crop vegetative and reproductive growth occur simultaneously during an important part of the period of crop growth. This is illustrated in Figure 2. In cv. Minica for instance, the first flowers occur already shortly after the formation of the fifth node. The plant continues the formation of new stem parts with leaves and flowers during the next 20-25 days (Figure 2). During this period, the filling of the pods and seeds at the lower nodes has already started, while at the plant top the formation of new vegetative nodes is still continued. If water shortage in this period reduces the vegetative sink strength more than the reproductive sink strength, this may result in a shift in dry matter partitioning, and not only in dry matter production.

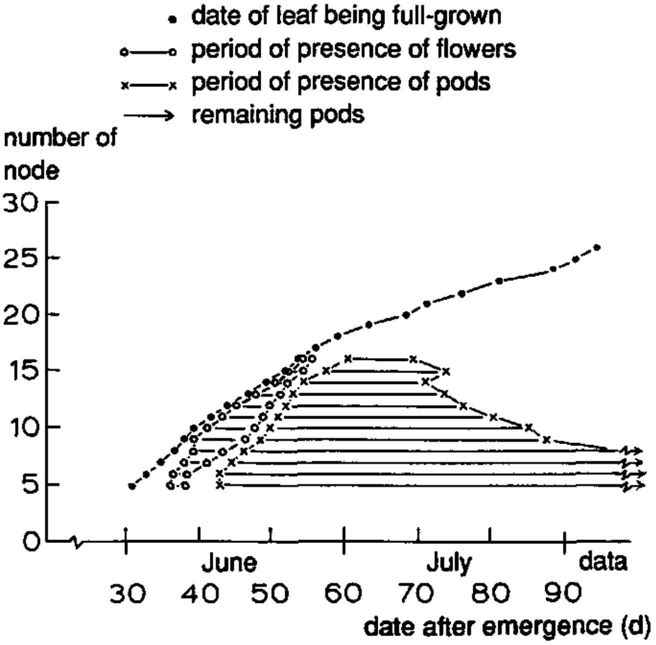

Figure 2. Calendar data and number of days after emergence at which, at subsequent stem nodes, the leaves finished growth, flowering started and ended and pods emerged and disappeared for cv Minica, 1979. From: Sibma et al. (1989).

Objectives and approach of the thesis

Obviously, more insight was needed in the productivity and yield variability of faba beans as affected by different water supply patterns, with special attention to timing, level and duration of the water shortage. The present study tries to answer the question: 'is water shortage a major factor in yield variability of faba beans, via effects on dry matter production, vegetative and reproductive sink strength, dry matter partitioning and yield formation?'

Field experiments are used to analyze the effect of different water supply treatments (during and after flowering) on final above ground yields, seed yields and yield components. Growth analyses are made to study the effect of water supply pattern on seasonal course of Leaf Area Index (LAI), plant length, dry matter production and dry matter partitioning over the plant organs (Chapter 1). The consequences for reproductive growth are studied with detailed measurements of pod retention and pod filling at successive nodes of the plants (Chapter 2).

This research is combined with crop physiological measurements, to gain a better understanding of the mechanisms behind the effects of water shortage on sink strength and dry matter partitioning. This study involves diurnal field measurements of the plant water relations (water potential, osmotic potential, turgor and relative water content) and leaf conductance. Under controlled conditions, the plant water relations are studied in combination with the expansive growth (Chapter 3).

The observed physiological mechanisms of water shortage of Chapter 3 are incorporated in a simulation model. This enables the study of the effects of water shortage, integrated in a general system in which radiation, temperature, rainfall, air humidity, windspeed, soil water balance and crop properties affect crop growth and production (Chapter 4). This may provide a better understanding of the complex and contrasting effects of various levels, timings and durations of water shortage on production, dry matter partitioning, yield formation and yield variability. The model is used to find out if water shortage is a major factor in yield variability of faba beans in Western Europe. Besides that, the model is used to explore the effects of suggested management activities and breeding objectives. This gives more insight in promising aims for further experimental crop management and breeding research to reduce the yield variability of the faba bean crop.

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Chapter 1

Effect of pattern of water supply on *Vicia faba* L.
1. Dry matter partitioning and yield variability

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Effect of pattern of water supply on *Vicia faba* L. 1. Dry matter partitioning and yield variability

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Abstract

The effects of various amounts and timings of water supply during and after the flowering period on growth, total dry matter production and partitioning of dry matter, and variability of yield were studied in faba beans. In field experiments in 1980 and 1981, plenty of water during and after flowering (i-i) resulted in stimulation of vegetative growth, but reduced initial reproductive growth as well as final seed yield, compared with a control with mild water shortage during flowering but plenty of water after flowering (d-i). In further field experiments in 1982-1984, d-i resulted in high average seed yield of 7.0 t ha^{-1} (cv. Minica), optimum harvest index (HI) (0.61 g g^{-1}) and relatively small seed yield range over the experiments (2.2 t ha^{-1}). In i-i, average seed yield (7.1 t ha^{-1}) did not differ significantly from d-i and HI was lower (0.57) but seed yield range was small with 1.4 t ha^{-1}. D-d, i-d and natural rainfall control provided much lower average seed yields and a larger seed yield range; i-d also provided the lowest HI (0.54 g g^{-1}). Data for cv. Alfred showed the same trend as for cv. Minica. It is concluded that differences in distribution pattern and amount of rainfall are a major reason for the variability in seed yield of faba beans. During flowering a mild water shortage might be preferable to plenty of water, to limit vegetative growth and stimulate early reproductive growth. After flowering, plenty of water is crucial for high and stable seed yield responses.

Keywords: faba beans, *Vicia faba* L., irrigation, dry matter partitioning, seed yield, yield variability

Introduction

The area with seed legumes under cultivation in the European Community has increased importantly. In total in ten member-states 515 000 ha were grown in 1981 and 988 000 ha in 1986 (Anon., 1984-1988). This was mainly a result of financial support measures for protein crops as part of the plant productivity programme of the European Community. About a third of this area is cultivated with faba beans. In the Netherlands the area with faba beans has increased from about 30 ha in 1977 to 13 400 ha in 1988 (Anon., 1977-1988). The present increase followed after a steady decrease from 30 000 ha in the period around 1930.

Like in most European countries, a major reason for the decrease in area with faba beans in the Netherlands between 1930 and 1975 has been the high yield variability. The crop is still considered to be highly unreliable in this respect (Hawtin & Hebblethwaite, 1983). Much research has been undertaken to identify key factors influencing yield, and causing yield variability.

As it is generally accepted that water shortage is a major yield-determining factor (Day & Legg, 1983), the effect of water availability has been the subject of several studies. Attention has been paid to the identification of growth stages especially sensitive to lack of water.

Many authors have reported that irrigation had a positive effect on seed yield, regardless of time of application (Hebblethwaite et al., 1977; French & Legg, 1979; Farah, 1981). Krogman et al. (1980) found linear correlations between total water applied (irrigation and rainfall) and seed yield and also between water applied and straw yield. Results of other authors confirm this correlation (Day & Legg, 1983). Husain et al. (1983) stated that special moisture-sensitive phases did not exist in faba beans grown in New Zealand.

However, this conclusion is not generally accepted. Brouwer (1959) reported that especially irrigation during flowering provided high yield increments.

In contrast, also negative effects of irrigation on seed yield were reported. Yield depressions seem to be linked to irrigation before and during flowering (Stock & El-Naggar, 1980; Smith, 1982) or are described as rare deviations from a general positive effect (McEwen et al., 1981).

Smith (1982) reported that under West European conditions, irrigation applied during flowering may favour vegetative growth at the expense of reproductive growth. This conclusion was mainly based on reduced pod retention caused by irrigation during flowering.

In recent studies on productivity and yield variability in countries of the European Community, it was postulated that in some environments insufficient water supply is the major yield-limiting factor. However, in more maritime regions growing conditions could also lead to excessive vegetative growth and low seed yields (Dantuma et al., 1983).

The present study was carried out to gain a better understanding of the effects of various levels of water availability during and after flowering on dry matter partitioning and production throughout the growing season and to draw conclusions about water availability as a major limiting factor for yield and yield stability. In this paper (Part 1) these effects are discussed and integrated in a functional but qualitative way. In three following publications (Grashoff, in prep.) crucial details of this mechanism will be presented and discussed: pod retention, pod fill and yield components (Part 2) and dry matter partitioning in relation to plant water status (Part 3); a quantitative integration of growth processes that are affected by water availability will be presented in the form of a simulation study, (Part 4), and a generalization to other locations, climates and soil types will be given.

Materials and methods

Water supply treatments

Two groups of field experiments were conducted (Table 1). In the first group (in 1980 and 1981), the effect of full irrigation during and after flowering (further called i-i) was compared with a non-irrigated control. In the second group (1982-1984), five different combinations of soil water conditions during flowering and after flowering were created:

- d-d: a period with limited water availability from onset of flowering to the end of the growing season.
- i-d: irrigated to keep soil close to field capacity during flowering, followed by a period with limited water availability to the end of the growing season.
- d-i: a period with limited water availability during flowering, and irrigated after flowering to bring and keep soil water content close to field capacity.
- i-i: irrigated to keep soil close to field capacity from onset of flowering to the end of the growing season.
- natural rainfall: control treatment only exposed to rainfall conditions of the various experimental seasons.

Technical realization of treatments

The irrigation system consisted of perforated polythene tubes laid on the soil, connected to a central water pump. In each irrigation a quantity of 20 mm (20 kg m^{-2}) water was applied within half an hour. The frequency of application was one to three times a week, depending on the course of soil water content and reference

Table 1. Short description of water supply treatments, crop data collection, years, sites, cultivars, trial designs and number of replicates of the experiments in 1980-1984 with faba beans.

Water supply treatments	Crop data collection at	Year	Sites	Cultivars	Trial designs	Number of replicates
Control	14-day	1980	clay(N)	Minica	split plot	12
i-i	intervals	1981	sand(N)	Minica, Kristall	split split plot	4
Control	Final	1982	clay(N)	12[a]	trial in one-fold	
d-d	harvest	1982	sand(N)	12[a]	trial in one-fold	
d-i	only	1983	sand(N)	Minica, Alfred,	strip plot[b]	5[c]
i-d		1983	sandy loam(GB)	Optica and	strip plot	3
i-i		1984	sand(N)	Kristall	strip plot	5

[a] Cultivars obtained from colleagues involved in the EC joint field bean test, and cultivars Minica, Optica, Cebeco number (Alfred), and Kristall.

[b] A split plot with cultivars in horizontal, and water supply treatments in vertical strips.

[c] Two replicate blocks excluded (water logging; see text).

values of evapotranspiration provided by the Royal Dutch Meteorological Institute (KNMI). In all experiments, early-flowering cultivars and late-flowering cultivars were irrigated separately, to allow adaptation to the dates of onset and end of flowering.

The drying-out periods were realized by covering the soil between the plant rows with white polythene sheets to drain off about 80-90 % of rainwater. The period of soil covering depended on treatments. Sheets were not placed in the field before flowering to avoid effects on germination and early growth.

Locations, trial designs, fertilizers and drilling

Locations and trial designs are presented in Table 1. 'Sand(N)' is referring to the experimental farm Droevendaal on a humic sandy soil near Wageningen, Netherlands. 'Clay(N)' is referring to the experimental farm De Bouwing at heavy river clay (about 60 % lutum) in Randwijk, Netherlands. The 'Sandy Loam(GB)' location was the experimental farm of the University of Nottingham, UK, at Sutton Bonington (results of a joint experiment of the School of Agriculture of the University of Nottingham and the Centre for Agrobiological Research, Wageningen).

P and K fertilizers were applied according to the current recommendations which are based on soil testing. Depending on analysis of P and K soil test values, P application varied from 95 to 184 kg P_2O_5 per ha for the location on clay soil and from 38 to 133 kg P_2O_5 per ha for the location on sandy soil; K application varied from 120 to 480 kg K_2O per ha for the clay soil and from 52 to 182 kg K_2O per ha for the sandy soil.

Gross plot sizes varied from 6 m^2 in the experiments of 1980 to 15 m^2 in 1982-1984.

In all experiments in the Netherlands a precision drill was used (Vicon mono-air); plant density was 20 plants m^{-2} with 50 cm row spacing, which is usually practised in this country. In the experiment in England, plant density was 28 plants m^{-2} with 44 cm row spacing.

Plant material

The used cultivars were not the same in all experiments (Table 1), but cv. Minica was used as a standard each time. The large-seeded varieties Minica and Optica were obtained from Nickerson-Zwaan BV (Stompwijk, Netherlands). The smaller-seeded varieties Alfred and Kristall were obtained from Cebeco-Handelsraad (Lelystad, Netherlands). All other varieties were obtained by exchange between participants of the 'joint field bean trials' (Dantuma et al., 1983).

Measurements and data collection

In all experiments, soil water content was determined gravimetrically at weekly intervals and before each irrigation, and rainfall was recorded daily.

In 1980 and 1981, net plot samples of 1 m^2 were harvested at about 14-day intervals from beginning of June to the end of the growing season. In 1980, samples were divided into leaves, stems, pod walls and seeds and fresh and dry weight were determined. LAI, leaf size and stem length were recorded at each harvest. In 1981, samples were divided in straw and seed. In 1982-1984, more experimental treatments were included (Table 1) and only final harvest data could be obtained.

In all experiments, plant length, harvest index (HI) and seed yield were recorded at final harvest in net plots of 3 m^2. Detailed data on individual plants were obtained from samples of 10 to 20 plants. Details about these samples will be presented in Part 2 (Grashoff, in prep.).

Trial performance, crop protection and important dates

In all experiments, the crop grew without hail or frost damage. In 1983 the experimental field in Wageningen was waterlogged in two of the five replicate blocks, due to excessive rainfall in March-May. This resulted in very poor crop growth and high heterogenity in those two blocks, which were excluded from analysis. In 1982, in contrast with the standard water supply treatment description, the d-d treatments were irrigated two times after mid July under the polythene sheets to prevent the d-d crop from total failure.

Preventive measures for weed, disease and pest control were taken as much as possible. Weed control started before emergence with spraying of a prometryn/simazin mixture; after emergence dinoseb-acetate was applied. Weevils (*Sitona lineatus* L.) were sprayed with parathion at first visible damage of leaf edges. Pirimicarb was sprayed against black aphids (*Aphis fabae* Scop.) as soon as the first aphids were observed. In case of wet and cold weather, vinchlozolin, zineb or benomyl were sprayed preventively against fungal attack (mostly *Botrytis* spec.). Important damage by one of these pests or diseases did not occur in any experiment.

Over all experiments, dates of sowing ranged from 14 March to 9 April, emergence from 16 April to 6 May, onset of flowering from 27 May to 9 June, cessation of flowering from 17 June to 6 July and final harvest from 10 August to 10 September.

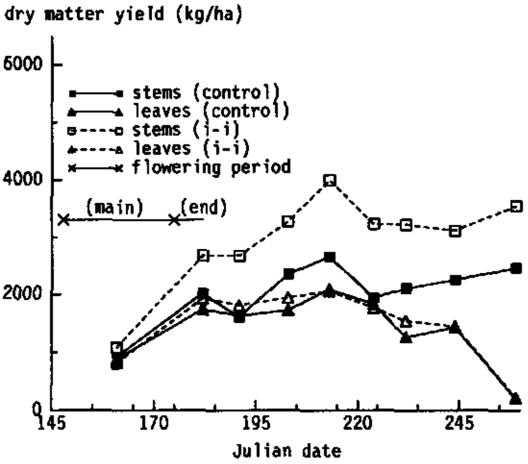
Results

Characterization of water supply in 1980 and 1981

In the months April to June total rainfall was 166 mm in 1980 and 123 in 1981, which is 10, respectively 53 mm lower than normal. Soil water content in the control steadily declined during the period of flowering and at the end of flowering (end of June) reached a minimum of 0.17 g g^{-1} in the clay (1980) and of 0.07 g g^{-1} in the sand (1981). Soil water contents in i-i treatments were kept at about 0.23 g g^{-1} (1980) and at 0.15 g g^{-1} (1981).

Due to heavy rains after the end of flowering, soil water content in the control treatment rose, reached the high values of i-i (in the first part of July) and did not decline again until mid July (in 1981) or August (in 1980). After this period, water

a) 1980 stems and leaves



b) 1980 pod walls and seeds

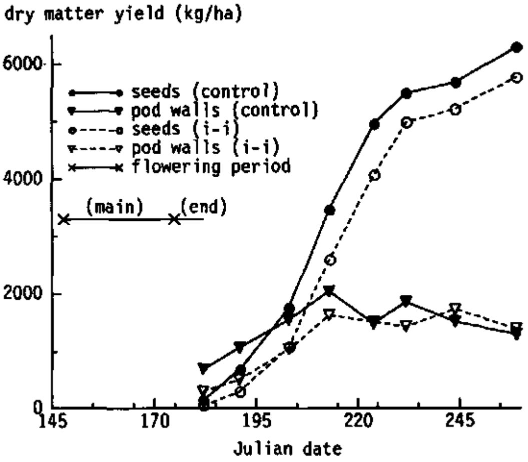


Fig. 1. Faba bean (cv. Minica) dry matter yields during the season 1980 in a field experiment with two water supply treatments. (a) stems and leaves; (b) pod wall and seed.

content in the control treatment remained only 0.02 g g^{-1} lower than in i-i in both years. The control treatments of 1980 and 1981 were characterized as a natural d-i situation.

Effects of irrigation on dry matter partitioning and on final yields

In the experiments of 1980 and 1981, irrigation did not affect the date of onset of flowering. The main flowering period was from day 150 (in 1980) or day 155 (in 1981) to day 175, but small numbers of open or rudimentary flowers were observed till about day 185, especially in i-i. Already during flowering, dry weight of stems in the i-i treatment of 1980 was larger than in the control treatment (Fig. 1a). Dry matter accumulation of stems was higher due to irrigation during flowering, and stems were longer from the first harvest onwards (Fig. 2a). Dry matter accumulation of leaves was little affected by irrigation (Fig. 1a), but leaf size and total leaf area were much larger (Figs. 2b, c), indicating a lower specific leaf weight.

In contrast, pod and seed weights in the i-i treatment were lower than in the control at the second harvest (which was the first possible weight analysis of those organs). Growth curves (Fig. 1b) indicate that irrigation during flowering resulted in a delay in pod and seed growth. In 1981 irrigation delayed and reduced early seed growth in the same way as in 1980 (Fig. 3b). In 1981 no significant variety × treatment interaction was found; therefore only results of Minica are presented.

In the phase of linear seed growth after flowering, both i-i and control resulted in high seed growth rates of 135 kg ha^{-1} d^{-1} (Figs. 1b, 3a). As the control was characterized earlier as a natural d-i treatment, the high rates of reproductive growth were the result of the high water availability after flowering in both treatments. Irrigation did not enhance further vegetative growth, as the plants terminated their elongation growth about two weeks after flowering (Fig. 2a).

However, seed growth in the i-i treatments was not continued long enough to catch up with the final seed production of the control treatments. Figures 3a and 3b show that in both years final seed yields of i-i were lower (significant at P = 0.01), but straw yields higher (P = 0.05) than in the controls. Final total yields of i-i treatments were slightly higher (only significant in 1980) than of the controls. Final harvest index (HI) of i-i was 0.53 in 1980 and 0.54 in 1981, which was significantly lower (at P = 0.005) than in the controls (0.62 in 1980 and 0.63 in 1981). High water availability during flowering not only reduced dry matter allocation to the seeds in a relative way (lower HI), by means of stimulation of vegetative growth and consequent delay of reproductive growth, but reduced seed yields in an absolute way as well.

Irrigation during flowering versus irrigation after flowering: experiments 1982-1984

In this series of experiments (with five different treatments) the effects of high water availability during flowering were separated from the effects of high water availability after flowering (after cessation of vegetative growth).

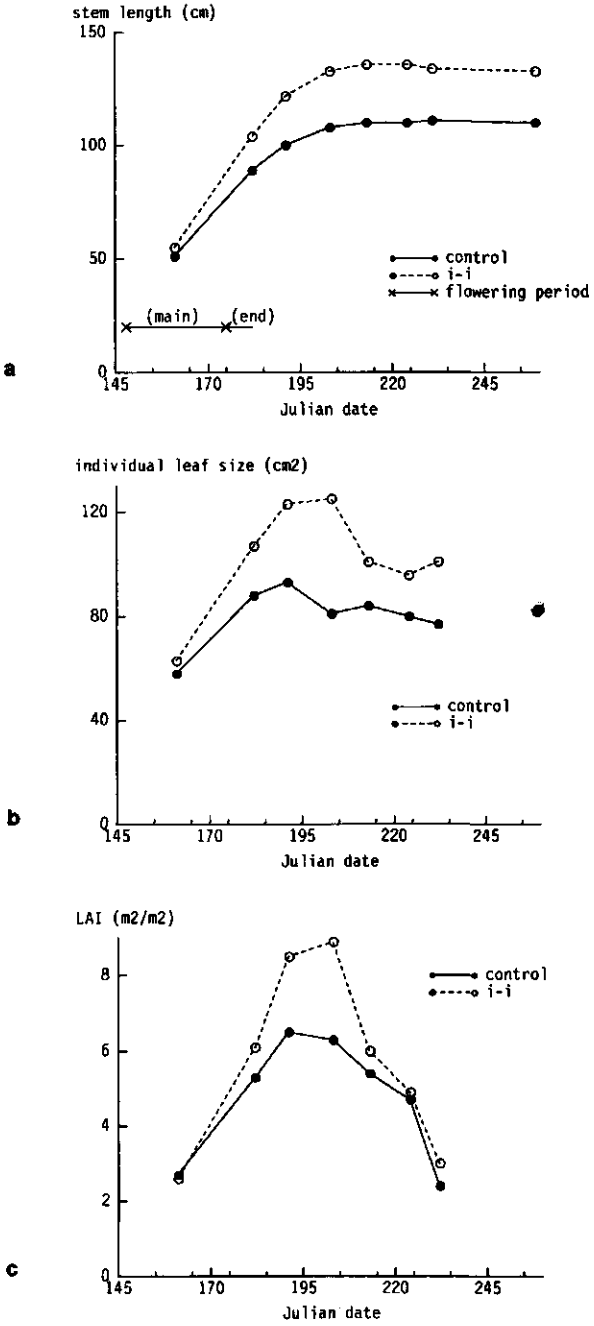
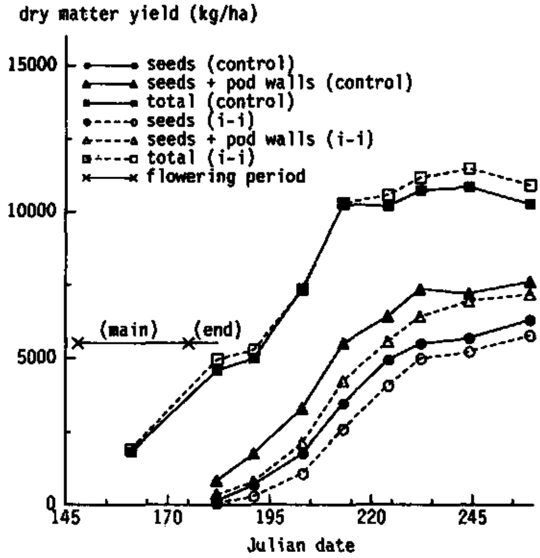


Fig. 2. Faba bean (cv. Minica) vegetative growth during the season 1980 in a field experiment with two water supply treatments. (a) stem length; (b) individual leaf size; (c) leaf area index.

a) 1980



b) 1981

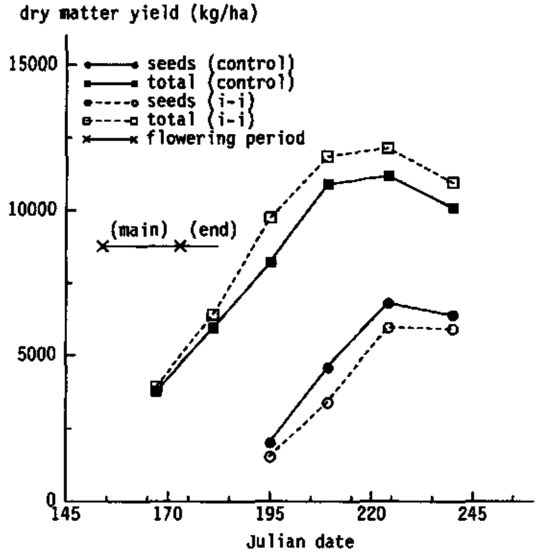


Fig. 3. Faba bean (cv. Minica) dry matter yields of seed, seed and pod wall, and total during the season in a field experiment with two water supply treatments. (a) season 1980 (clay); (b) season 1981 (sand).

Final stem length, harvest index and seed yield. Results of the five experiments are presented for cv. Minica (Fig. 4) as high-yielding standard cultivar and for Alfred (Fig. 5) as widely used cultivar in practice.

Averaged over the five experiments, final stem length in i-d and i-i treatments was 22 cm higher than in d-d and d-i treatments (Minica: Fig. 4b, and Alfred: Fig. 5b). In further comparison of d-d with d-i and of i-d with i-i, only a small additional effect of irrigation after flowering on average final stem length was observed: 4 cm for Minica (Fig. 4b) and 9 cm for Alfred (Fig. 5b). That confirms that vegetative growth is mainly enhanced by high water availability during flowering and is hardly affected by high water availability after flowering.

The d-i and i-i treatments both resulted in average seed yields which were 1.6 t ha^{-1} higher than in d-d and i-d (Minica: Fig. 4f, and Alfred: Fig. 5f). That confirms that seed production is mainly enhanced by high water availability after flowering. However, average total yield was higher in i-i than in d-i (Figs. 4h and 5h). So, total yield was enhanced by every irrigation during flowering and after flowering.

In d-i, reduced vegetative growth, due to reduced water availability during flowering, was followed by a high seed growth rate, due to high water availability after flowering. That resulted in a short-stem crop type (Figs. 4b and 5b), with most effi-

Table 2. Seed yields (t ha^{-1}, 86 % DM), plant length (cm) and harvest index (g g^{-1}) of an experiment with four faba bean cultivars grown under five different water supply treatments. Seed yields presented separately for each treatment and for each cultivar, and as average over cultivars (horizontally) or over treatments (vertically). Plant length and harvest index only presented as average over treatments or over cultivars. Results from sand(N) in the season 1984. Different letters (a, b, c, d) indicate significant differences at $P = 0.05$.

	Water supply treatments					Average seed yield	Average plant length	Average harvest index
	d-d	i-d	d-i	i-i	control			
Minica	6.4	6.6	8.2	7.8	7.0	7.2 (a)	151 (c)	0.53 (a)
Alfred	5.9	6.4	7.0	7.3	6.6	6.6 (b)	172 (b)	0.51 (b)
Optica	5.7	6.1	6.2	6.0	6.2	6.0 (c)	110 (d)	0.54 (a)
Kristall	5.8	5.9	6.1	6.0	6.3	6.0 (c)	192 (a)	0.47 (c)
Average seed yield	6.0 (c)	6.2 (bc)	6.9 (a)	6.8 (a)	6.5 (ab)			
Average plant length	149 (c)	161 (b)	154 (c)	169 (a)	149 (c)			
Average harvest index	0.51 (ab)	0.50 (b)	0.53 (a)	0.50 (b)	0.53 (a)			

Values of F-test on seed yield

Cultivar	32.7
Water treatment	11.9
Cultivar × treatment	4.5

cient dry matter partitioning (maximum harvest index, Figs. 4d and 5d) and average seed yield which was equally high as in i-i (Figs. 4f and 5f). In contrast, in i-d the stimulated vegetative growth followed by reduced seed growth resulted in a long-stem crop type, with the least efficient partitioning (minimum harvest index) and average seed yield which was equally low as in d-d. Both i-i and d-d showed sub-optimum dry matter partitioning (intermediate harvest indices; Figs. 4d and 5d). The two irrigations after flowering in the d-d treatments of 1982 had a strong positive effect on seed yield and harvest index for cv. Alfred (Figs. 5c and 5e).

Average seed yield of natural rainfall control (Figs. 4f and 5f) was only slightly higher than or equal to the d-d and i-d treatments. Irrigation after flowering resulted in yield enhancement of 1.5 t ha^{-1} (Minica) and of 1.7 t ha^{-1} (Alfred) compared with the control.

Effects of treatments on plant length, harvest index and yield were larger in experiments of 1982 and 1983 (England) than in 1983 (Netherlands) and 1984 (Figs. 4a, c, e and 5a, c, e).

However, the relatively small main effects of treatments in 1984 were significant (Table 2) and in agreement with the average effects presented above. Also, significant differences between cultivars were observed in 1984. For instance, Minica yielded higher than Alfred ($P = 0.05$) and Alfred higher than Optica and Kristall. Effects of treatment on growth and yield were larger in Minica and Alfred and smaller in Kristall and Optica. Those cultivar × treatment interaction effects were also significant, but, according to the F-values, main effects were stronger.

Variability of seed yield. Effects of water availability on variability of seed yield were studied within each experiment (over the five treatments) and within each treatment (over the five experiments).

Firstly, the yield variability expressed as the range of variation over the five treatments within one separate experiment was not equal for all experiments (Figs. 4e and 5e). But, within each experiment, highest yields were obtained in d-i or in i-i; lowest yields were always obtained in d-d, i-d or natural rainfall control (Figs. 4e and 5e). The yield responses to high water availability after flowering indicate that yield variability was related to variation in water supply, at least within each experiment.

Table 3. Total global radiation (kJ cm^{-2}), average daily temperature (°C) and rainfall (mm) in spring (April-June) and summer (July-September) for a normal 30-year standard and positive (+) or negative (−) deviations from that normal of the years 1982, 1983 and 1984. Standard (N-30) obtained from the Royal Dutch Meteorological Institute (KNMI) at De Bilt.

	Normal		1982		1983		1984	
	spring	summer	spring	summer	spring	summer	spring	summer
Radiation	147	128	+21	+ 13	− 15	+ 9	−17	−11
Temperature	11.8	15.7	+ 0.5	+ 1.5	norm.	+ 1.8	− 1.0	norm.
Rainfall	176	230	−41	−149	+123	−96	−39	−17

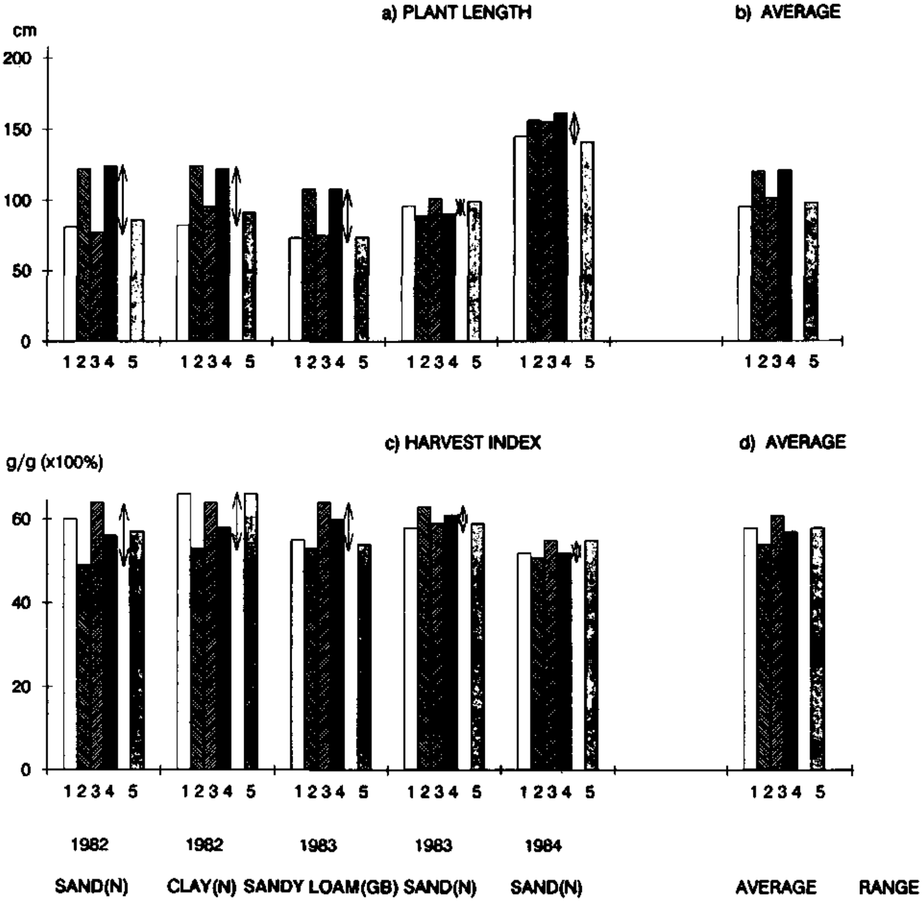


Fig. 4. Plant length (a,b), harvest index (c,d) seed yield (e,f) and total yield (g,h) of faba bean (cv. Minica) grown under five different soil water supply treatments in five experiments in 1982-1984. 1 = d-d; 2 = i-d; 3 = d-1; 4 = i-i; 5 = control. Arrows represent range over the five treatments of each experiment; 'Range' represents range for each treatment over the five experiments. Sand(N), clay(N) and sandy loam(GB) refer to the experimental sites (see Table 1 and text). In 1982 d-d got two irrigations after flowering.

Secondly, the relation between water supply and yield variability was confirmed by expressing the variability as the range from lowest to highest seed yield within one treatment over the five experiments. That range was largest in the control and small in both d-i and i-i treatments (Figs. 4f and 5f). High water availability after flowering not only increased average seed yield with 1.6 t ha^{-1}, but also reduced seed yield range over the five experiments with 2 t ha^{-1}, compared with the natural rainfall control. In contrast, total yield ranges were almost equal for all treatments (Figs. 4h and 5h).

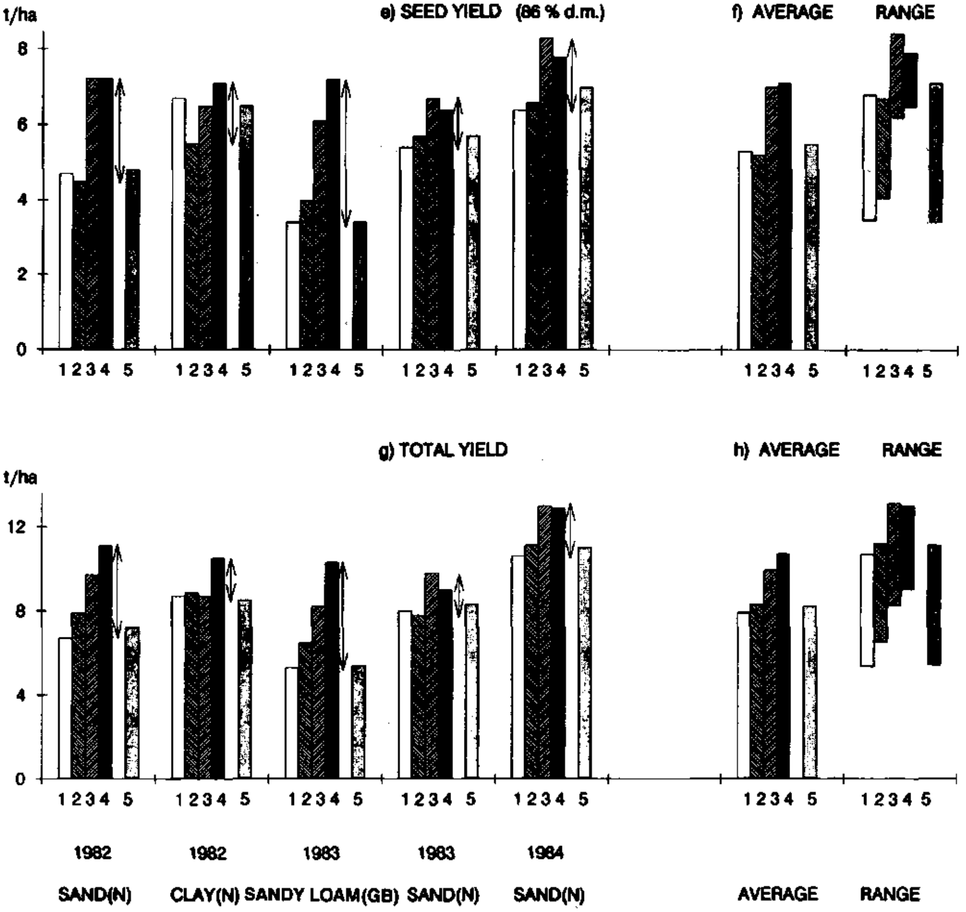


Fig. 4. Continued.

Growth and yield in relation with soil water content and weather. Both the unequal seed yield range for each separate experiment (Figs. 4e and 5e) and the large seed yield range in natural rainfall controls over all experiments (Figs. 4f and 5f) were related to differences in the course of soil water content and weather among the various experiments. In the sandy soils, detectable differences in plant water potential between irrigated and control field plots were only found below a soil water content of 0.10 g g^{-1} (Venekamp et al., 1987). This value, which corresponds to a pF of 3 for this soil type, was used for comparison of treatments in the experiments on

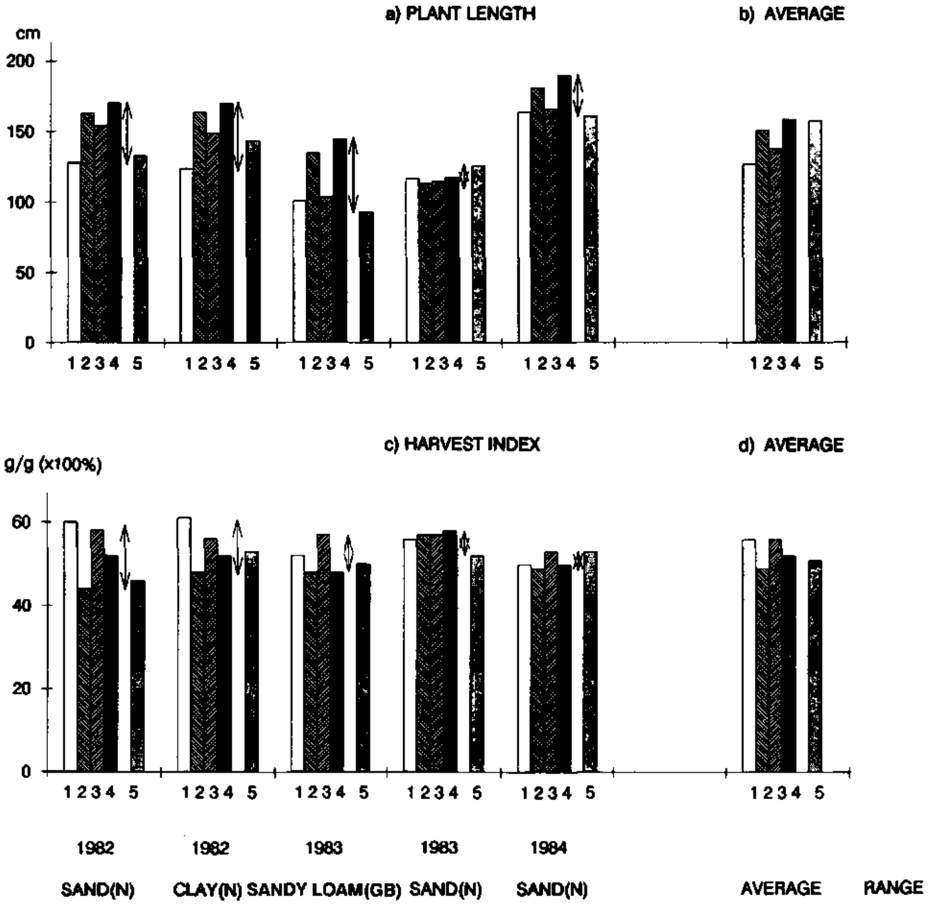


Fig. 5. As Fig. 4, for cv. Alfred.

sandy soils (1982-1984).

The growing season of 1982 as a whole was sunny, warm and dry (Table 3). In this season, soil water content of the natural rainfall control (Fig. 6a) underscored the value of 0.10 g g^{-1} much earlier than in 1983 (Fig. 6c), as the spring of 1983 was extremely wet (Table 3). In contrast, the summer of 1983 was very dry. In 1984 a second peak in control soil water content in July was recorded after a rainy period (Fig. 6e). The growing season of 1984 was dark, cold and slightly dry (Table 3). Seed yield of 1984 control was high, due to those moderate conditions; yield of the 1983 control was intermediate due to water shortage after flowering and yield of 1982 was low due to dry conditions during the whole growing season.

These weather conditions also interfered with the other treatments. Notwithstand-

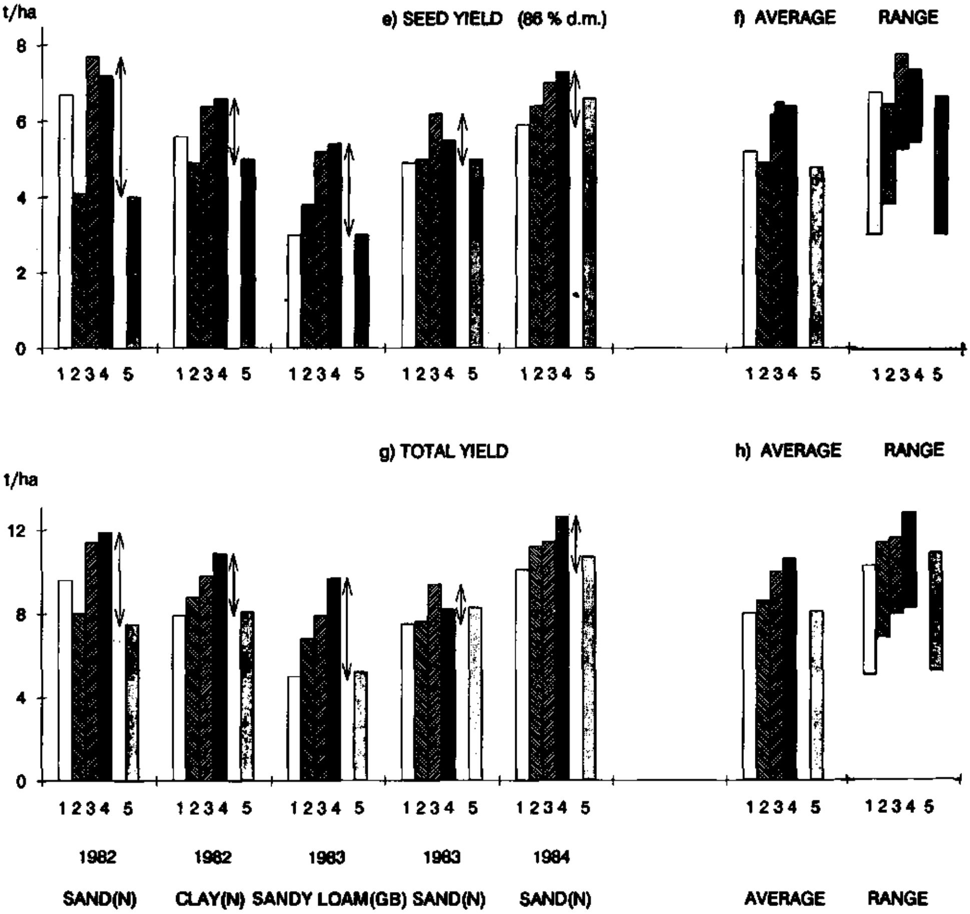


Fig. 5. Continued.

ing the polythene sheeting, water shortage (in d-i treatments, but also in d-d) during flowering was realized earlier in 1982 than in 1984 and was absent in 1983 (Fig. 6b, d, f). For that reason, differences in plant length and harvest index were expressed more clearly in the 1982 experiments.

In the treatments with planned water shortage after flowering (i-d), soil water content underscored the value of 0.10 g g^{-1} at about 18 days after the end of flowering (Fig. 6b, d, f). This explains why the treatment effect of water shortage after end of flowering on seed yield was clear in all experiments. However, this effect was smaller in 1984, as the cool and dark 1984 season moderated the water shortage, even in the d-d treatments.

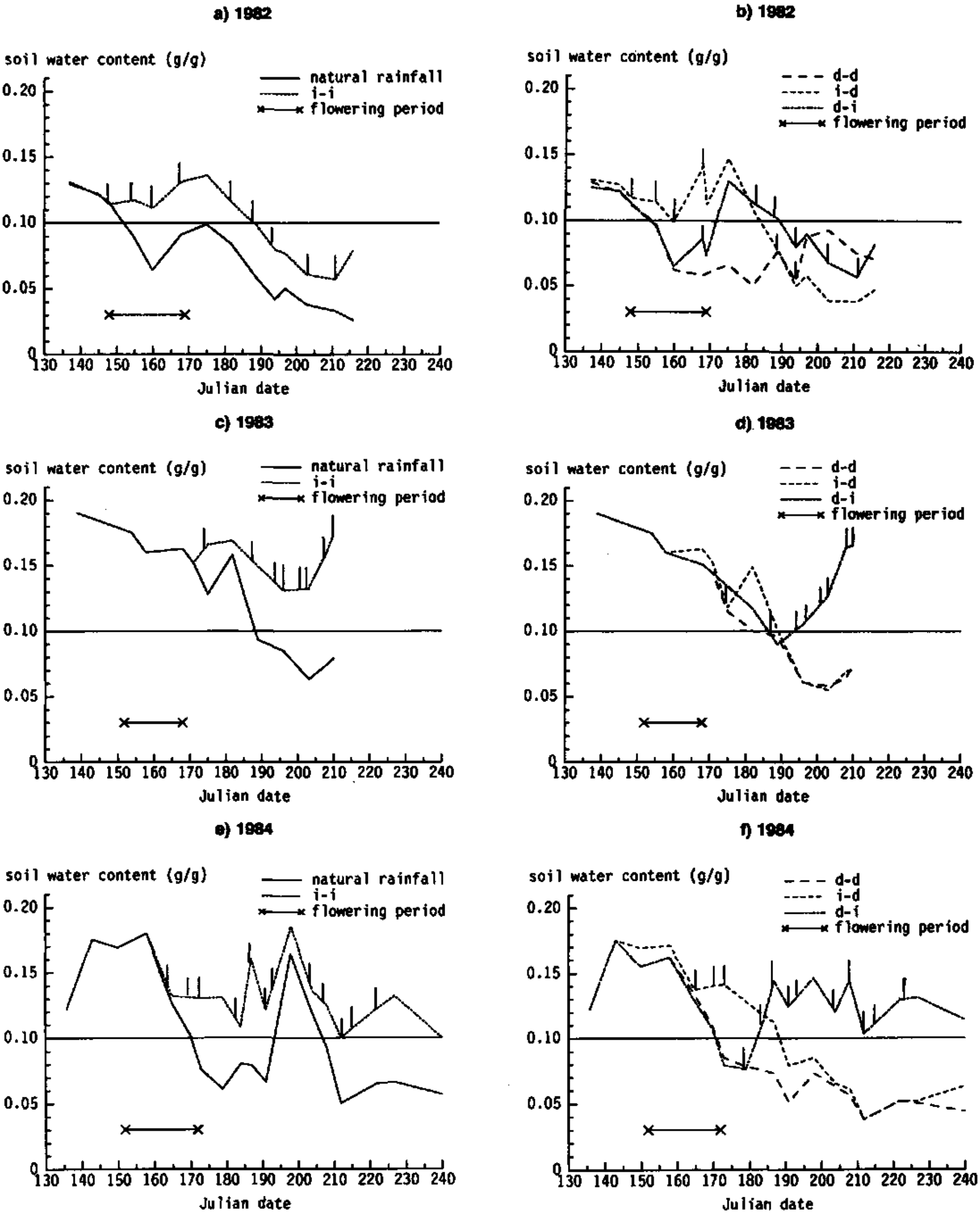


Fig. 6. Seasonal course of soil water content in faba bean experiments with different water supply treatments. Experiments on sand(N) 1982-1984; horizontal lines = soil water content at pF 3 (see text); vertical marks represent times of irrigation.

Discussion

The consequences of various amounts and timings of water supply on growth are arranged in a flow chart (Fig. 7). According to definitions of Hsiao et al. (1976a), in the chart two alternative situations for the crop during flowering are distinguished: absence of water shortage (the expansive growth is high) versus 'mild' water shortage (the expansive growth is reduced, but the rate of photosynthesis hardly).

Decrease of leaf expansion and reduction of stem extension due to water shortage were reported by Karamanos (1978), Elston et al. (1976) and Tamaki & Naka (1971). Extension rates of stems and leaves of faba beans were very sensitive to a small decline of leaf turgor caused by mild water shortage (Part 3; Grashoff, in prep.). Figure 2a (stem extension) and Figures 2b and 2c (leaf expansion) confirm that reduction of expansive growth is the earliest effect of water shortage on crop growth in the season, accompanied by reduced dry matter accumulation of stems (Fig. 1a), while total dry matter production is still nearly unaffected during flowering (1980: Fig. 3a; 1981: Fig. 3b). This is in agreement with Hsiao et al. (1976b) who concluded that a reduction in cell expansion is the first reaction to increasing water shortage. It confirms that water shortage in 1980 and 1981 was only 'mild'. In 1982-1984, soil water content during flowering in the sandy soil never reached importantly lower values than in 1981 (Fig. 6). For this reason, effects of water shortage during flowering were mainly caused by the 'mild' type of shortage, and effects of 'severe' water shortage during flowering (the rate of photosynthesis is reduced, Hsiao et al., 1976a) were not included in Figure 7. However, a more severe water shortage may have developed during flowering in clay(N) 1982, and in sandy loam(GB) 1983. This is discussed in Part 2 (Grashoff, in prep.).

Reduced expansive growth during flowering results in a smaller sink strength of the vegetative top (Hsiao & Acevedo, 1974). So, in situations with mild water shortage, more assimilates are available for organs at a lower plant position, as for instance young pods, which have a lower competitive strength (Jaquiéry & Keller, 1978; 1980). This was confirmed by the initial stimulation of dry matter increase of pods under mild water shortage (Figs. 1b, 3), which was accompanied by higher pod retention (and higher final seed yield) at early developed flowering nodes (Part 2; Grashoff, in prep.), and this supports the results of Smith (1982), who recorded higher pod retention in a natural d-i control than in treatments which were irrigated during and after flowering. Dependant on the water supply during flowering, a more vegetative crop type and a more reproductive type are distinguished at the end of flowering (Fig. 7), comparable with the situations in Figures 1, 2 and 3 at the end of flowering.

After flowering, expansive growth is terminated in both crop types (Fig. 2a), so the competition between vegetative top and reproductive organs is also terminated. In this period, the two extremes, water shortage versus absence of water shortage, are distinguished in the flow chart, for each of the two crop types. Water shortage now reduces rate and period of further reproductive growth, the extent depending on the severeness of the water shortage. That results in reduced number of later

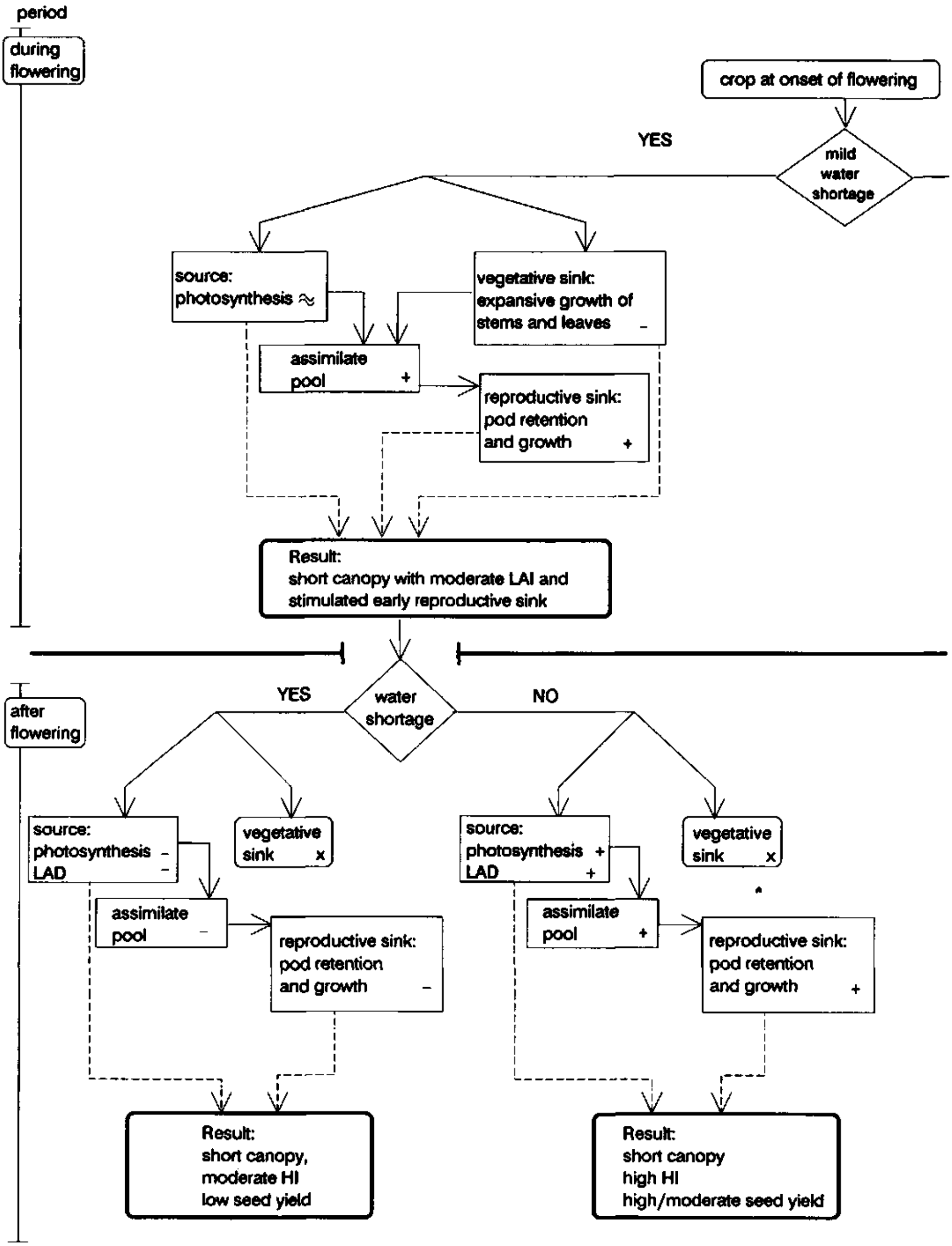
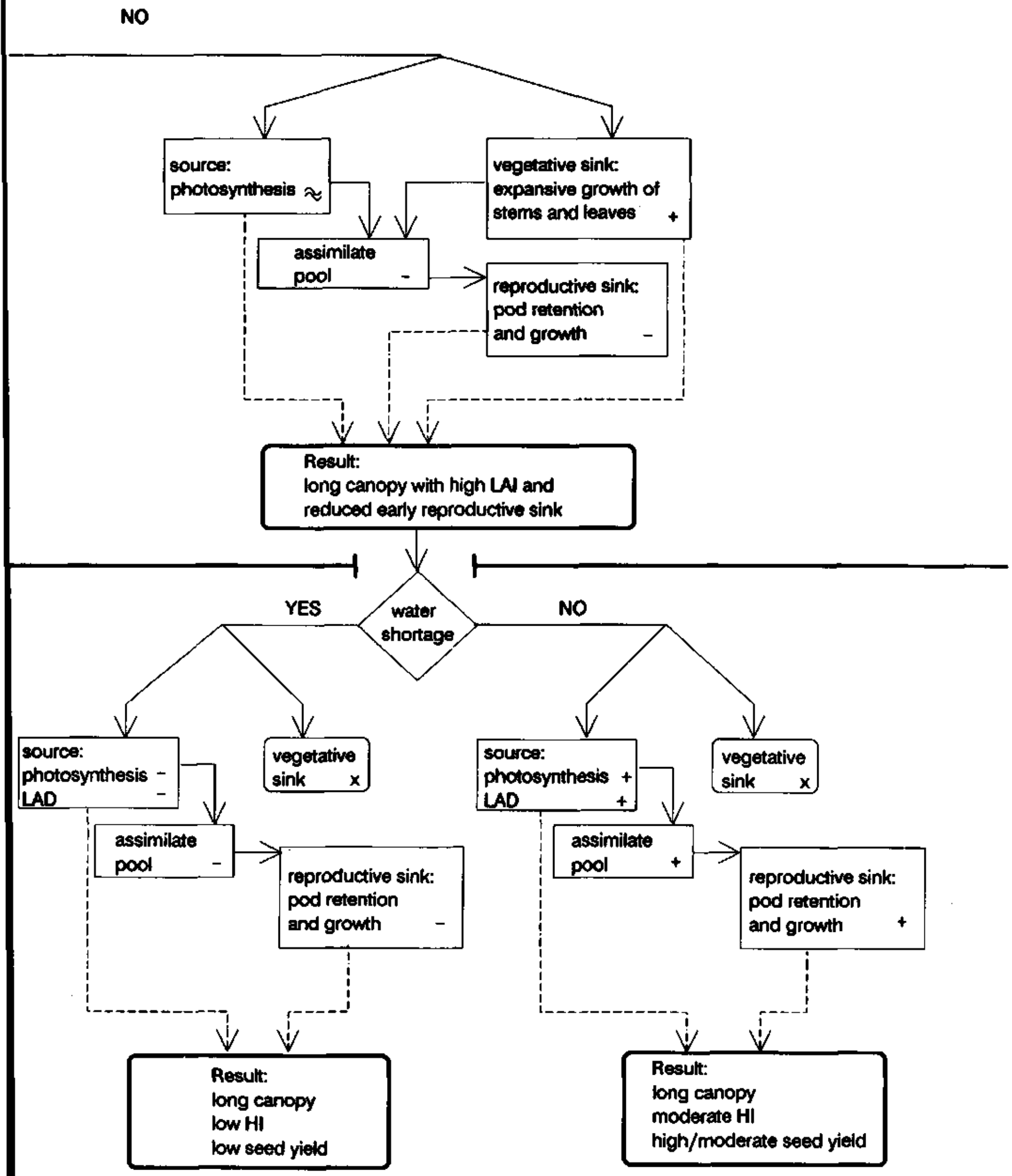


Fig. 7. Effects of different soil water contents on growth, dry matter partitioning and yield of faba beans summarized in a flow chart. Traced arrows = 'has influence on'; dotted arrows = 'has the following final result'; + = stimulated; – = reduced; × = terminated; ≈ = not changed.


NO
source:
photosynthesis ≈
vegetative sink:
expansive growth of
stems and leaves +
assimilate
pool -
reproductive sink:
pod retention
and growth -
Result:
long canopy with high LAI and
reduced early reproductive sink
water
shortage
YES
NO
source:
photosynthesis -
LAD -
vegetative
sink x
assimilate
pool -
reproductive sink:
pod retention
and growth -
Result:
long canopy
low HI
low seed yield
source:
photosynthesis +
LAD +
vegetative
sink x
assimilate
pool +
reproductive sink:
pod retention
and growth +
Result:
long canopy
moderate HI
high/moderate seed yield

formed pods and reduced pod fill (Part 2; Grashoff, in prep.). As a consequence, four extremes of final crop types are distinguished (Fig. 7), identical with the average results in Figures 4 and 5.

These results prove that differences in amounts and timings of water supply not only highly affect final seed yield but also initial dry matter partitioning, leading to differences in final harvest index. That contrasts with several reports which concluded that harvest index was not influenced (Krogman et al., 1980; Kogbe, 1972). However, other workers reported variable harvest indices as well. Our results confirm that the largest differences are most probably the result of natural i-d or d-i situations. Sprent et al. (1977) found a harvest index of only 0.24 g g^{-1} in 1974 and of 0.50 g g^{-1} in 1975 for the cultivar Maris Bead. Total rain, radiation and temperature were not much different for both years. However, in May and June 1975 (before and during flowering) there was much less rain than in those months in 1974. Thus, there is evidence to qualify these results of 1974 as i-d situations and 1975 as d-i situations.

Green et al. (1986) concluded from experiments in England with polythene sheeting and irrigation that dry matter partitioning and final harvest index were not systematically affected by different irrigation treatments. However, results of irrigation during flowering versus after flowering were not compared.

Figure 7 indicates why in some d-i situations higher seed yields than in i-i were found in combination with lower or equal average total dry matter production (Fig. 3; Fig. 4 1984 and Fig. 5 1982 sand). As total amount of applied water in i-i situations is higher than in d-i, it is assumed that the amount of consumed water in i-i is higher as well, which is confirmed by the higher total dry matter yield. This is in agreement with the conclusion of de Wit (1958), who found linear relationships between total dry matter yield and water use in many situations. However, in our experiments, mild water shortage during flowering is essential for high early pod retention (Fig. 7) which on its turn is a requirement for an early and strong reproductive sink. It results in the most efficient dry matter partitioning during the whole season and absolutely higher seed yields, even with slightly reduced total dry matter production.

It supports the statement of Smith (1982) and Dantuma et al. (1983) that irrigation during flowering favours vegetative growth at the expense of reproductive growth. So, correlation between seed yield and total water received may not be as close as between total yield and water.

These conclusions are in contrast with the conclusion of Day & Legg (1983) and Krogman et al. (1980). They found a linear relationship between seed yield and water use, and a near-constant value of harvest index of 0.45 g g^{-1} for crops, grown under a range of irrigation plus rain from 100-700 mm.

On the other hand, our conclusions are in agreement with the results of Stock & El-Naggar (1980) who concluded from regression analysis that the optimum soil water content during flowering was at 40-60 % of 'utilizable field capacity' (a concept, which is used by Stock & El-Naggar (1980) for the water content range between pF 2 and 4.2). Both higher or lower soil water contents resulted in sub-optimum seed yields. After the flowering period, a linear correlation between utilizable field capacity and seed yield was found. Stock & El-Naggar (1980) did not present data about straw yields, harvest index, or records on pod retention, but with our results and conclusions presented above, the graph made by Stock & El-Naggar (1980) can be hypothetically complemented with effects of water supply on total dry matter production and partitioning.

Based on total yields in Figures 4 and 5 and the conclusions of de Wit (1958), it is stated in Figure 8 that the relation between total dry matter production and utilizable field capacity is linear during flowering and after flowering (provided that water use is closely related with utilizable field capacity). Following the regression for seed yield and utilizable field capacity of Stock & El-Naggar (1980), Figure 8 shows that the correlation between seed yield and water use is also linear in the lower and middle range of amounts of used water during flowering. This represents situations with more or less severe water shortage and is in agreement with Krogman et al. (1980). In contrast with Krogman et al., the regression line for seed yield reaches an optimum at moderate levels of water used during flowering (that means with mild water shortage during flowering). The line then decreases at high amounts of used water (absence of any water shortage), due to vigorous vegetative growth and consequent processes described above (Fig. 7), while correlation between total dry matter production and water used remains positive. After flowering, linear relations are described in Figure 8 between water use and total yield and between water use and seed yield. The water supply patterns of Figures 3, 4 and 5 are placed in Figure 8, based on the description of the soil water content during and after flowering. Only a rough comparison can be made, but it is worth noting that the yield results of the i-i treatments can be compared with the left back corner of Figure 8 and those of the i-d treatments with the left front corner; d-i with the middle of the back side, and d-d with the middle of the front side of Figure 8.

Figure 8 has consequences for the analysis of maximum possible seed yield. If maximum total dry matter production (for Minica about 15 t ha^{-1}, obtained in 1984) could be combined with maximum harvest index (about 0.65 g g^{-1}) this should result in a potential seed yield of about 10 t ha^{-1}. However, Figure 8 indicates that it may not be possible to combine these two maxima in one crop.

The negative effects of irrigation during flowering are in contrast with the conclusion of Day & Legg (1983) that, in general, similar seed yield responses were observed to irrigation when water availability is limited in any time in the season. However, deviations from these general conclusions are only to be expected in the situation of absence of water limitation ('plenty of water') during flowering (Figs. 7 and 8). These conditions may occur more often in the temperate climate in Western Europe than in Egypt, Canada and the United States, on which the conclusions of Day & Legg were mainly based.

Although plenty of water during flowering has a negative effect on dry matter partitioning and seed yield, the most important negative effects on yield and yield stability were the result of water limitation after end of flowering (Figs. 4 and 5). The lower yield variability in combination with higher average yields in the d-i and i-i treatments (compared with the natural rainfall, i-d and d-d treatments) lead to the general conclusion that natural differences in distribution pattern and amount

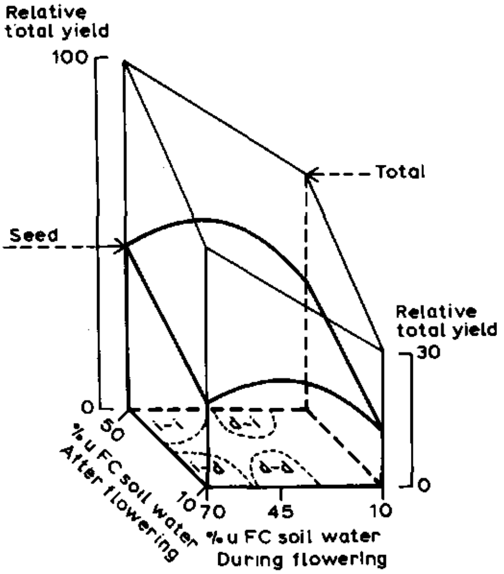


Fig. 8. Relation between relative yield of faba beans and water use, expressed as percentage of utilizable field capacity (% uFC) during and after flowering. Thick lines after Stock & El-Naggar (1980) for seed yield; thin lines as hypothetical complement for total dry matter production. Symbols i-i, d-i, etc., correspond to four different water supply patterns (see text).

of rainfall are an important cause of the high natural yield variability of faba beans. During flowering a mild water shortage might be preferable to plenty of water, but after flowering plenty of water is essential for a high seed yield and low yield variability of faba beans.

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Chapter 2

Effect of pattern of water supply on *Vicia faba* L. 2. Pod retention and filling, and dry matter partitioning, production and water use

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Effect of pattern of water supply on *Vicia faba* L. 2. Pod retention and filling, and dry matter partitioning, production and water use

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Abstract

Pod retention and pod filling of faba beans were studied under different patterns of water supply. Mild water shortage during flowering, followed by plenty of water after flowering (d-i), resulted in high seed yields at lower stem nodes (defined as the first podding node to node number 11) in cv. Alfred. The inverse treatment (i-d: plenty of water during flowering, followed by increasing water shortage after flowering), but also i-i (plenty of water during and after flowering), showed 20-60 % lower seed yields at those nodes. This effect was mainly due to a lower number of pods per node. In i-i, but not in i-d, the low pod retention at lower nodes was compensated at higher nodes (defined as node 12 to the last podding node). These results help to explain the mechanism of the interaction between water supply pattern and the development of reproductive sinks. The quantitative consequences of these effects on the relation between total water use and seed yield are discussed. Without taking into account different water supply patterns, a linear relation between total water use (represented by total dry matter production) and seed yield explains already 75-85 % of the variation in seed yield. If different water supply patterns are included in the regression analysis, more than 90 % of the variation in seed yield can be explained. The i-i patterns, compared to d-i, result in sub-optimum dry matter partitioning to reproductive organs, but show a smaller seed yield variability. This indicates that defining and maintaining the optimum level of (mild) water shortage under varying climatological conditions needs further attention.

Keywords: faba beans, *Vicia faba* L., water supply, pod retention, pod filling, yield variability

Introduction

Yield variability is a major problem in faba beans (*Vicia faba* L.). In a preceeding publication (Grashoff, 1990) evidence was presented that, besides variation in total water supply, differences in pattern of water supply are an important cause of yield variability.

Mild water shortage during flowering, followed by high water supply after flowering (d-i) were the optimum conditions for limited vegetative growth and enhanced reproductive growth. Crops grown under these conditions had lower total dry matter production than crops with high water supply during and after flowering (i-i), but harvest indices in d-i crops were always higher than in i-i crops. Averaged over five experiments, seed yields in d-i crops (7.0 t ha^{-1} for cv. Minica and 6.5 for cv. Alfred) were equal to seed yields in i-i (7.1 t ha^{-1} for Minica and 6.4 for Alfred). In contrast, seed yields were low in i-d crops (5.2 t ha^{-1} for Minica and 4.9 for Alfred) and also in d-d (5.3 t ha^{-1} for Minica and 5.2 for Alfred). The i-d crop showed the least efficient dry matter partitioning, with even lower harvest indices than d-d (Grashoff, 1990).

Apparently, a mild water shortage during flowering has a positive effect on the development of an early and strong reproductive sink. However, after flowering a high water supply is important to support the assimilate requirements of that reproductive sink. The present paper concerns the effect of different patterns of water supply on pod retention and pod filling in successive canopy layers, and forms a basis for the explanation of the effects on total seed yield shown before (Grashoff, 1990).

Materials and methods

Field experiments

Experiments with different water supply treatments during and/or after flowering were carried out in the years 1980-1984. In 1980 and 1981, crops irrigated during and after flowering (i-i) were compared with a natural rainfall control. In both years, these controls had a precipitation pattern which caused mild water shortage during flowering, followed by a high water supply after flowering (d-i; Grashoff, 1990). Also in 1988 a natural d-i pattern could be compared with an i-i pattern.

In 1982-1984, five experiments were laid out with five water supply treatments: limited water availability from onset of flowering to the end of the growing season (further called d-d); limited water availability during flowering, followed by irrigation after flowering to bring and keep soil water content close to field capacity (d-i); irrigation during flowering to keep the soil close to field capacity, followed by a period of limited water availability after flowering (i-d); irrigation to keep the soil close to field capacity from onset of flowering to the end of the growing season (i-i); and a natural rainfall control.

The irrigation system consisted of perforated polythene tubes. Limited water availability was realized by covering the soil between the plant rows with white polythene sheets to drain off 80-90 % of the rain water. Further details about technical realization of treatments, locations, fertilizers, drilling and plant material are as described before (Grashoff, 1990).

Harvest analysis

Detailed harvest analysis on plant basis was carried out in the experiments of 1981, 1982 and 1984 on sandy soil (experimental farm Droevendaal, Wageningen). In 1981, the trial was a split plot with 4 replicates and 2 cultivars (Minica and Kristall). In 1982 the trial was laid in onefold with 12 cultivars and in 1984 a 'strip' plot was used, which is a split plot with 4 cultivars (Optica, Minica, Alfred and Kristall) in horizontal, and 5 replicates in vertical 'strips'. In 1981 and 1982, 20 plants from each plot were sampled at final harvest, and in 1984 10 plants. In each sample, seed yield per node and number of pods per node were recorded. These records, on basis of plant nodes, were corrected to a standard unit of soil area by multiplication with plant density (number of plants per m^2). Average seed yield per pod at each node was calculated following the equation:

$$SYP = NSY/PPN$$

where:
SYP = seed yield per pod (g pod^{-1})
NSY = seed yield per node per unit soil area (g $node^{-1}$ m^{-2})
PPN = number of pods per node per unit soil area (pods $node^{-1}$ m^{-2})

Total seed yield and total number of pods per unit soil area, and average seed yield per pod were calculated using:

$$SY = \sum_{1}^{n} NSY \; ; \; NP = \sum_{1}^{n} PPN \; ; \; ASYP = SY/NP$$

where:
SY = seed yield, cumulated over all nodes, per unit soil area (g m^{-2})
NP = number of pods, cumulated over all nodes, per unit soil area (pods m^{-2})
ASYP = average seed yield per pod (g pod^{-1})

$\sum_{1}^{n}$ = sum over all nodes

The samples for detailed analyses were supplementary to the samples, which were used for bulk measurements of total dry matter yield and seed yield (Grashoff, 1990).

Results and discussion

Pod retention and pod filling at successive plant nodes

For the relatively dry year 1982 (Grashoff, 1990), the effects of water supply in cv. Alfred were representative for the other cultivars, although minor differences between cultivars occurred. However, as the trial in 1982 was laid in one-fold, a statistical analysis of the results was not possible. In the trial of 1984, statistical analysis was possible, but in this cooler and darker season (Grashoff, 1990), the differences between the water supply treatments were much smaller. Therefore, the results of Alfred are presented for both years. For 1981, only the results of Minica are presented, as these were essentially equal to those of Kristall.

Pod retention and pod growth take already place at lower plant nodes before vegetative growth and flowering of the whole plant is terminated (Sibma et al., 1989; Stülpnagel, 1984). Therefore, the number of pods per node and the seed yield per pod at lower nodes, recorded at final harvest, provide information about pod retention and pod growth during flowering. Recordings from higher nodes provide information about pod retention and growth after flowering. Recordings on basis of plant nodes were multiplied by plant density (20 plants m^{-2} in 1981 and 1982 and 24 in 1984). Recordings of successive plant nodes can then be interpreted as recordings of successive canopy layers.

In 1982, mild water shortage during flowering resulted in a cumulative seed yield at lower nodes (from node number 4, the lowest pod bearing node, to node number 11) of 343 g m^{-2} (Fig. 1a) and 172 pods m^{-2} (Fig. 1c). Irrigation during flowering resulted in a seed yield at the nodes 4-11 of only 112 g m^{-2} (Fig. 1b) and 60 pods m^{-2} (Fig. 1d).

These differences were also found in 1984: mild water shortage during flowering resulted in an average seed yield at the nodes 4-11 of 421 g m^{-2} (Fig. 2a) and 207 pods m^{-2} (Fig. 2c) and irrigation during flowering resulted in a significantly ($P<0.001$) lower seed yield at the nodes 4-11 of 347 g m^{-2} (Fig. 2b) and a significantly (at $P=0.013$) lower number of pods of 155 m^{-2} (Fig. 2d). A maximum number of pods per node of 45.4 m^{-2} was found at an averaged node number of 8.1 in treatments with mild water shortage during flowering (the 'peak' in Fig. 2c). With irrigation during flowering, the maximum number of pods per node (38.2 m^{-2}) was smaller (at $P<0.001$), and was found at a higher ($P=0.075$) node number 10.5 (Fig. 2d). Also the maximum seed yield per node (the 'peak' in Fig. 2b) was significantly ($P=0.025$) smaller with irrigation during flowering and was found at a higher ($P=0.003$) node number than with mild water shortage during flowering (Fig. 2a).

Seed yield per pod at lower nodes in treatments with mild water shortage (1982: Fig. 1e; 1984: Fig. 2e) hardly differed from that in treatments with irrigation during flowering (1982: Fig. 1f; 1984: Fig. 2f).

It is concluded that mild water shortage during flowering results in high seed yield at lower nodes, due to a higher pod retention at those nodes, compared to situations with high water supply during flowering. These results corroborate the existence of such a positive effect of mild water shortage during flowering on retention and growth of pods at lower nodes, as was put forward in the flow chart of Part 1 (Grashoff, 1990).

At higher nodes (numbers 12-end), seed yield in d-i (405 g m^{-2}) was higher than in d-d (306 g m^{-2}) and than in the control (207 g m^{-2}) in 1982 (Fig. 1a), and seed yield in i-i (485 g m^{-2}) was higher than in i-d (310 g m^{-2}) in this year (Fig. 1b). The number of pods at nodes 12-end in d-i (202 m^{-2}) was higher than in d-d (137 m^{-2}) and than in the control (126 m^{-2}) (Fig. 1c), and the number of pods at these nodes in i-i (266 m^{-2}) was higher than in i-d (190 m^{-2}) (Fig. 1d). Differences in

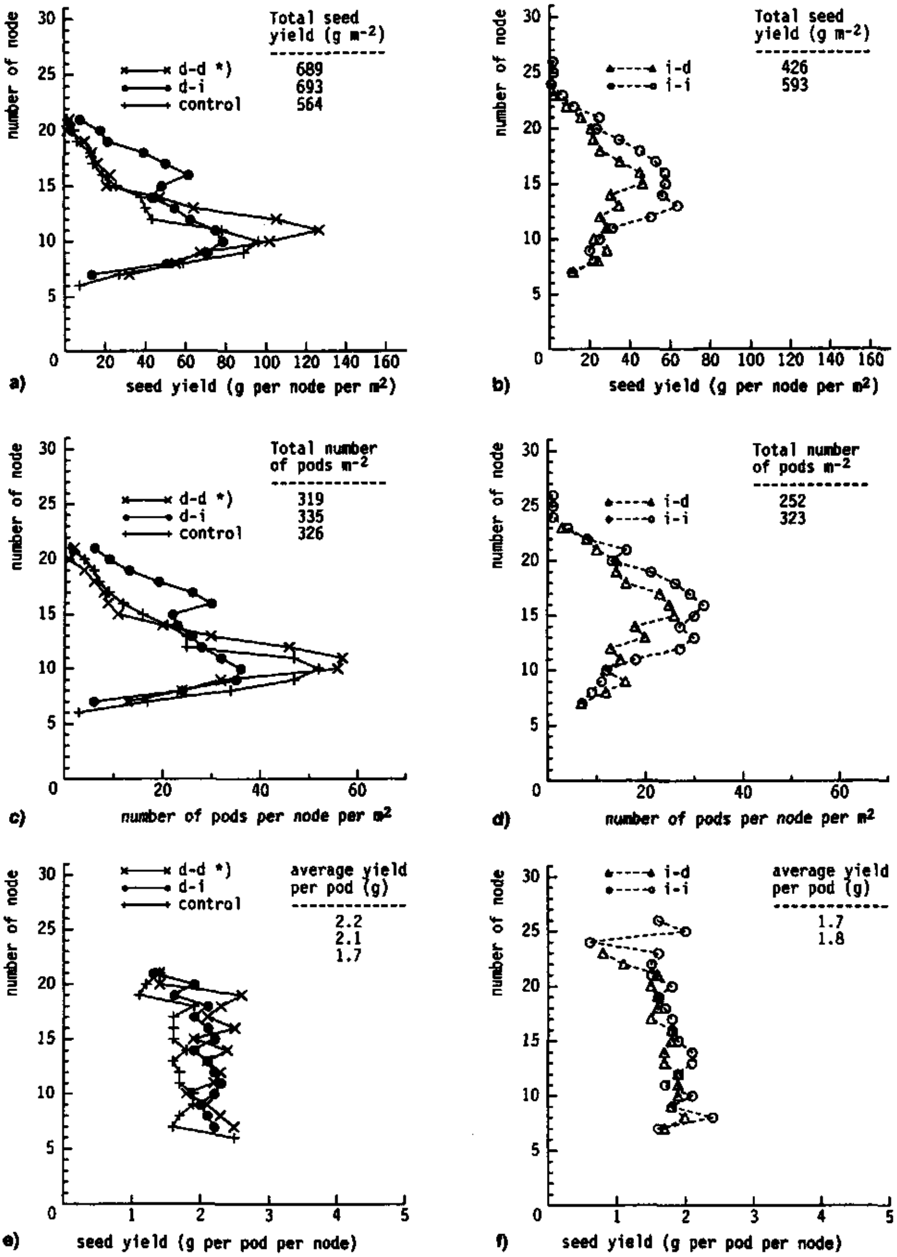

Fig. 1. Seed yield and seed yield components of successive plant nodes for cv. Alfred grown under five different patterns of water supply in 1982. (a and b) Seed yield per node. (c and d) Number of pods per node. (e and f) Average seed yield per pod, per node. (a, c, and e) Water supply patterns with mild water shortage during flowering. (b, d, f) Patterns with high water supply during flowering. * In 1982, d-d got two irrigations after flowering. Results from experimental farm Droevendaal.

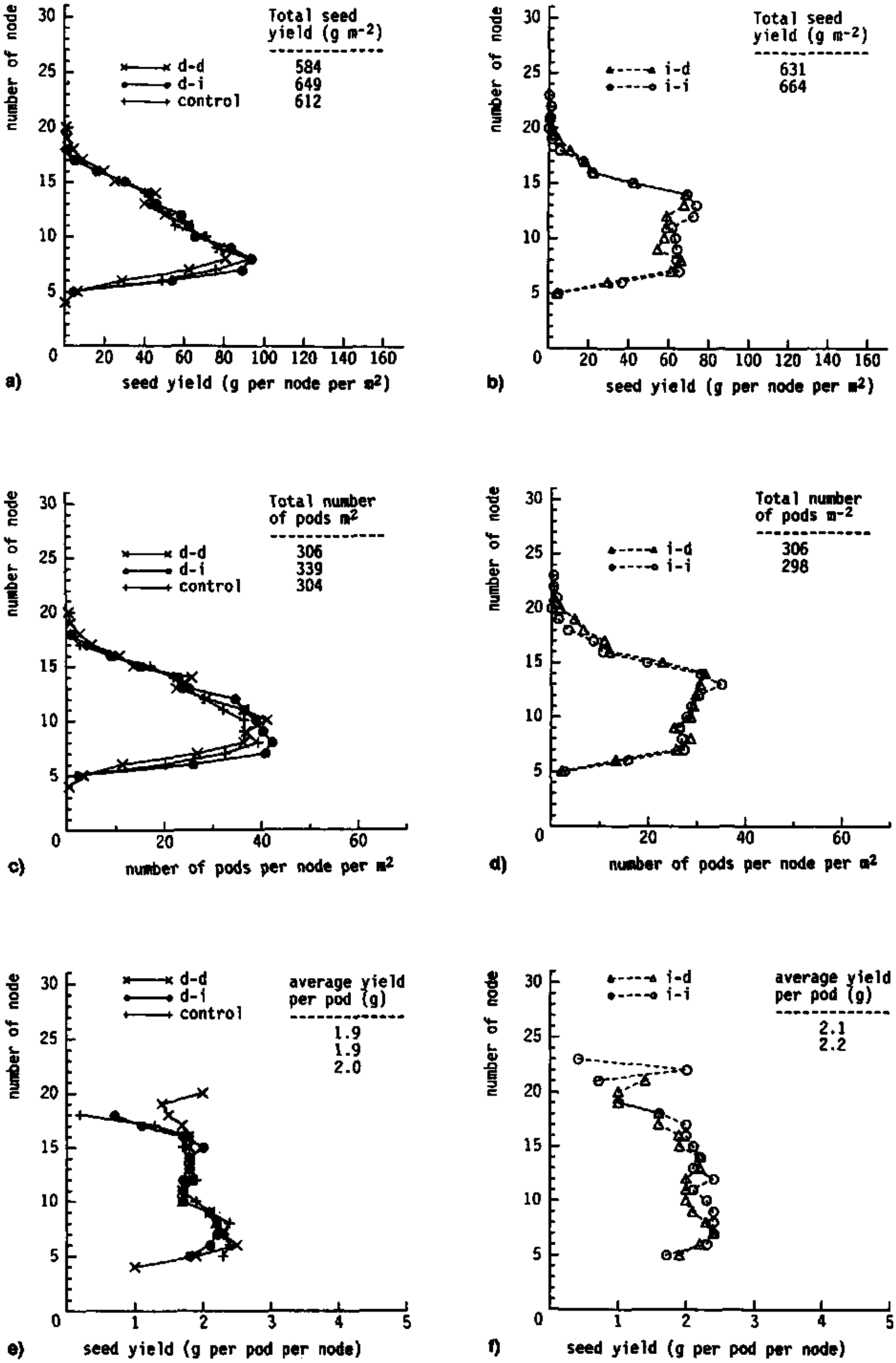

Fig. 2. As Fig. 1, for 1984.

seed yield of each individual pod among the treatments were small, but concerning the complete zone of pod-bearing nodes of the plants, some trends were visible. In d-i (but also in d-d!) this seed yield per pod was higher than in control (Fig. 1e), and i-i showed higher seed yields per pod at higher nodes than i-d (Fig. 1f). High water supply after flowering in 1982 resulted in higher pod retention at higher nodes, together with a higher filling of each individual pod. The high seed yields of individual pods in d-d do not contradict this conclusion. In 1982, d-d got two irrigations after end of flowering (Grashoff, 1990) which had a remarkable positive effect on the seed yield (cumulated over all nodes) compared with the control (Fig. 1a). In fact the high seed yield per pod in this treatment confirms the positive effect of water supply after flowering on the filling of individual pods.

In 1984 however, significant effects of high water supply after flowering on the yield components were not found, most probably because of the cool and dark season, which generally resulted in relative small differences between all water supply treatments (Grashoff, 1990). Based on the 10-plant samples presented in this paper, only weak indications were found that cumulative seed yield in d-i was higher than in d-d (Fig. 2a), and that i-i yielded higher than i-d (Fig. 2b). It is worth noting that these trends were in agreement with the significant differences, based on the yield results of the more accurate samples of 3 m^2: Alfred yielded 5.9 t ha^{-1} in d-d and 7.0 in d-i; 6.4 in i-d and 7.3 in i-i (Grashoff, 1990).

It is concluded that the results provide a basis for the explanation of a positive effect of high water supply after flowering on pod retention and pod growth later in the season, as was put forward in Part 1 (Grashoff, 1990).

Summarized over 1982 and 1984 the most consistent positive effect mentioned above is the early and high pod retention and pod growth due to the d-i pattern of water supply. This effect was not only observed in all experimental d-i situations, but also in all natural d-i rainfall patterns in 1980 and 1981. Figure 3 shows an example for cv. Minica in 1981. Seed yield at lower nodes (in this variety the numbers 2-9) in the natural d-i water supply pattern (645 g m^{-2}) was higher ($P = 0.075$) than in i-i (488 g m^{-2}) (Fig. 3a). The number of pods at these nodes in d-i (154 m^{-2}) was also higher ($P = 0.025$) than in i-i (114 m^{-2}) (Fig. 3b). The filling of each individual pod was not significantly different (Fig. 3c). The d-i pattern indicated also a slightly higher seed yield cumulated over all nodes (702 g m^{-2}) than in i-i (674 g m^{-2}). Based on the 20-plant samples, these differences were not significant, but were in agreement with the significant ($P = 0.01$) differences of the more accurate yield measurements on plot basis as presented in Grashoff (1990): 6.4 t ha^{-1} for d-i and 5.9 t ha^{-1} for i-i.

In Grashoff (1990) it was shown that limitation of the vegetative growth is the earliest effect of mild water shortage during flowering on crop growth. It was put forward then, that this might result in a higher availability of assimilates for the young pods which might provide an early and strong reproductive sink, which on its turn is crucial for an optimum dry matter partitioning to reproductive organs during the rest of the growing season (maximum harvest index). Provided that a high and early retention of pods is crucial for the development of a strong reproductive sink, the results of the present paper corroborate that mild water shortage dur-

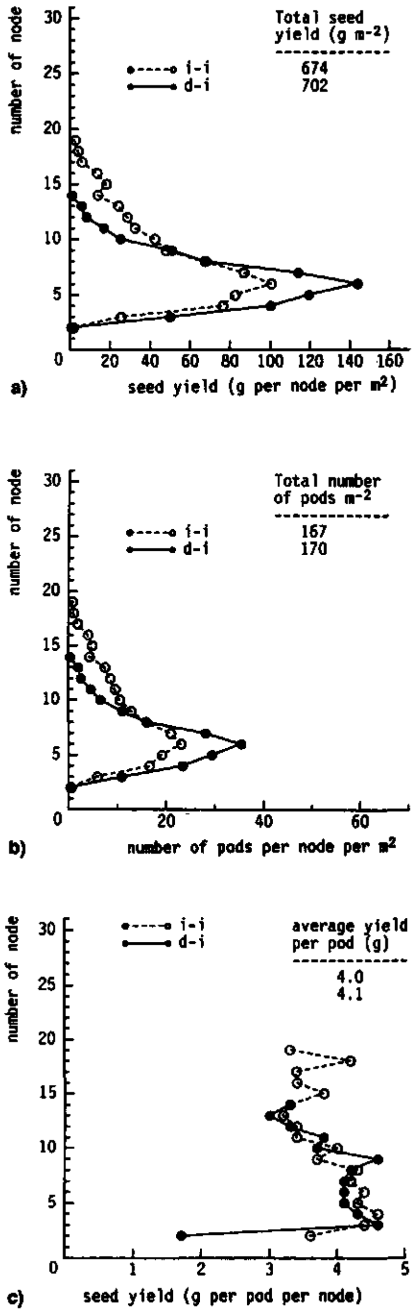

Fig. 3. Seed yield characteristics of successive nodes for cv. Minica grown under two different patterns of water supply in 1981. (a) Seed yield per node. (b) Number of pods per node. (c) Average seed yield per pod, per node. Results from experimental farm Droevendaal.

ing flowering results in a significantly higher sink at lower nodes, which is in agreement with the results of Smith (1982). The results of the present paper corroborate further that this high sink actually realizes significantly higher seed yields at lower nodes, compared with i-d and with i-i patterns. The detected shift in distribution of pods along the stem due to mild water shortage during flowering helps to explain the finding, that not only final harvest index but also final seed yields in the d-i patterns can be higher than in the i-i patterns, as was found in 1980 and 1981 (Grashoff, 1990).

Dry matter production and partitioning as affected by pattern of water supply

Effects of different patterns of water supply on dry matter partitioning interfere with effects on total water use and total dry matter production. An example of this interference is that, notwithstanding the maximum harvest index in d-i patterns of water supply, highest seed yields were not always obtained in d-i, but alternately in d-i or in i-i. The i-d patterns showed a minimum harvest index, but lowest seed yields were observed alternately in d-d or i-d (Grashoff, 1990).

The relation between seed yield and total dry matter production provides information about these interferences. Figure 4a presents this relation for a large data set of cv. Minica, including all yield data from Grashoff (1990), together with all data of Minica obtained at the Dutch locations of the EC-Joint Faba Bean Trials (Dantuma et al., 1983; Ebmeyer, 1984; Ebmeyer 1986). Results of 1988 were also included. Irrespective of water supply pattern, a linear regression between total dry matter production and seed yield explains already 86 % of the variation. In non-linear regression analyses, additional terms did not contribute significantly to a higher percentage of variance accounted for.

A linear relation between total water use and total dry matter production was put forward by de Wit (1958). The transpiration coefficient for total dry matter production is still considered to be fairly constant (Tanner & Sinclair, 1983). Therefore, Figure 4a can be taken to represent the relation between total water use and seed yield. That implies that the linear relationship between total dry matter production and seed yield is also valid for total water use and seed yield. This supports the conclusion of Day & Legg (1983) that, in general, a linear relationship exists between seed yield and total water use. They deduced from data of Krogman et al. (1980) a near-constant value of harvest index of 0.45 ± 0.02 for faba beans grown under a range of irrigation plus rain from 100-700 mm at the sites Brooks and Vauxhall, Canada. In the Brooks series, however, straw yields were higher than at the Vauxhall series for the same water use, and the regression lines for the Brooks series may even suggest a tendency to declining harvest index with higher water use (comparable with our i-i treatments).

In Figure 4b the same relation as in Figure 4a is plotted for all yield data with a known water supply pattern (experimental or natural), which were presented in Grashoff (1990). A linear regression for the whole data set of Figure 4b accounted for 78 % of the variation. Keeping the slope at a constant value, four intercepts were fitted for the 4 groups of different water supply patterns. These 4 fitted regres-

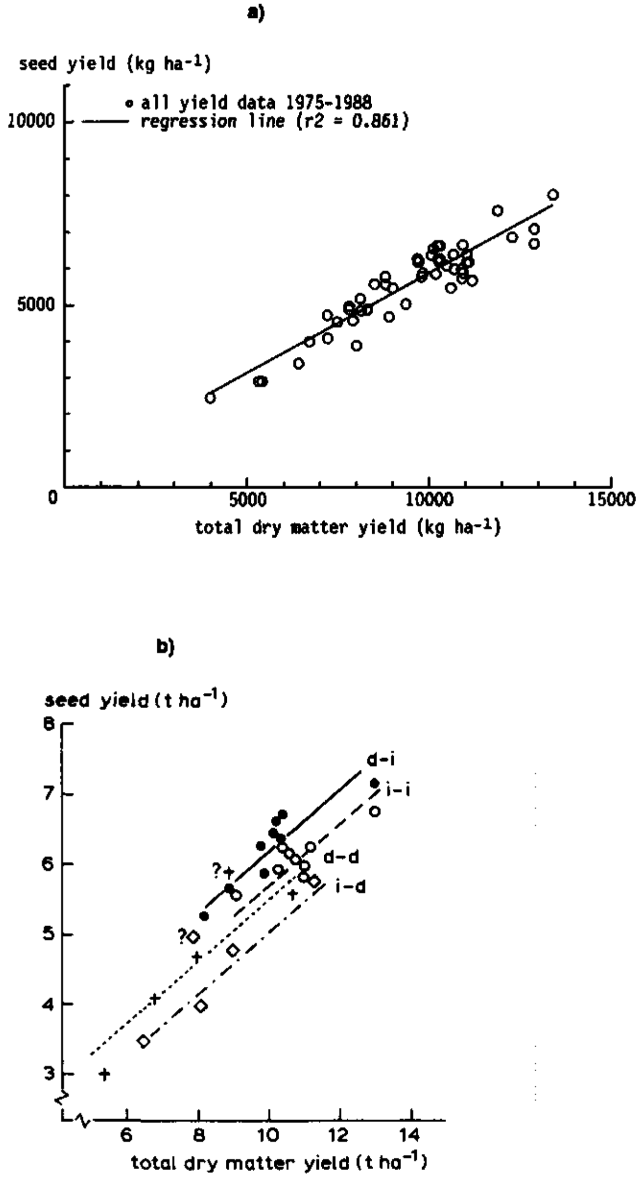

Fig. 4. Seed yield plotted versus total dry matter production for a yield data set of cv. Minica 1975-1988 (see text). (a) All available data plotted without classification of water supply pattern. (b) Only data plotted with classified water supply pattern. General form of the fitted lines: SY = 0.44 DMY + B. Intercept B = 1.75 (d-i); 1.26 (i-i); 1.06 (d-d); 0.59 (i-d). Percentage of accounted variation is 90.6. SY = seed yield; DMY = total dry matter. ?◇ = questionable point obtained from a partly waterlogged trial in 1983; ?+ = a d-d treatment which got two irrigations after end of flowering (and does fit very well to the curve for d-i!).

sion lines accounted for a significantly ($P<0.001$) higher percentage of variation (91 %). Figure 4b shows, that, at a chosen level of total dry matter production, the d-i pattern of water supply has the highest line and intercept, corresponding to the highest harvest index and the i-d pattern the lowest. These results support the conclusions of the previous sections and Grashoff (1990) that the positive effect of the d-i water supply pattern on early pod retention and pod growth can help to explain the maximum harvest indices. Moreover, the present paper shows that the relation between water use and seed yield (Fig. 4a), combined with the effect of a known pattern of water supply on dry matter partitioning (Fig. 4b) can explain most of the variation in seed yield in a healthy faba bean crop.

In Figure 5 the effect of the d-i pattern is compared with the effect of the i-i pattern, for a set of different growing seasons. In situations with relative low dry matter production in d-i patterns (1983e and 1982b in Fig. 5), the positive effect of irrigation during flowering on total dry matter production more than compensates the negative effect on dry matter partitioning, which result in higher seed yields in i-i in these growing seasons. In situations with a moderate level of total production in d-i, a small positive effect of irrigation during flowering on total dry matter production is still observed, but as this irrigation mainly stimulates vegetative growth and reduces early pod retention and growth, seed yield in d-i is now absolutely higher than in i-i. These effects were significant in 1980 (not included in Fig. 5) and 1981; also in 1988 the d-i pattern showed significantly higher seed yields than the i-i pattern. In situations with very high levels of dry matter production, irrigation during

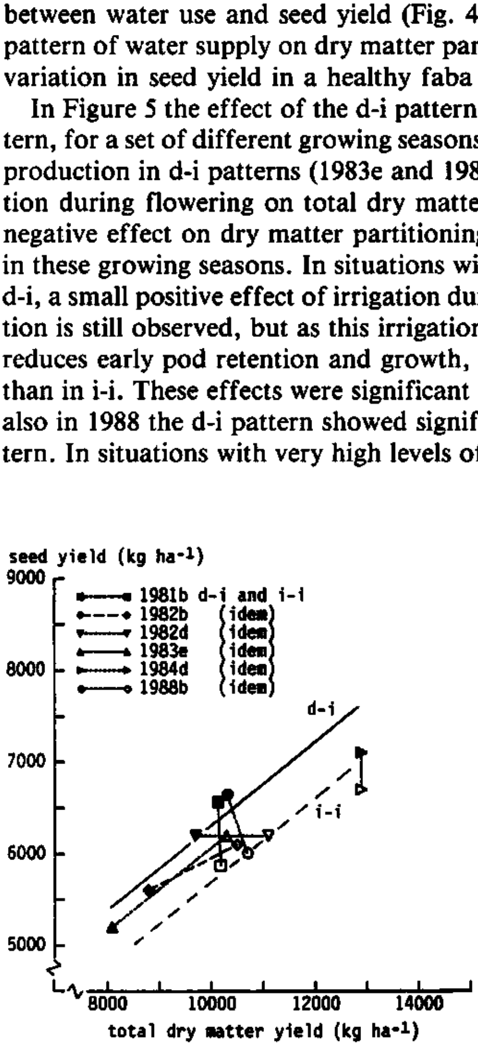

Fig. 5. Seed yield versus total dry matter production for d-i and i-i data pairs of several seasons. Regression lines are derived from Fig. 4b. Upper line for all d-i data; lower line for all i-i data. Each data pair is connected by a dotted line. Letters after the years indicate results from exprimental farms De Bouwing (b), Droevendaal (d) and Sutton Bonington (e), a joint trial of the Centre for Agrobiological Research and the University of Nottingham.

flowering has only a negative effect on dry matter partitioning to the seed and on final seed yield, without any effect on total dry matter production (1984d in Fig. 5).

Consequently, an absolute positive effect of water shortage during flowering on seed yield is only to be expected if this shortage hardly limits total dry matter production. That shows that this water shortage has to be 'mild' (Hsiao et al., 1976). This means that it limits expansive growth, but that an effect on the rate of photosynthesis is absent. The results of 1983e and 1982b in Figure 5 indicate that maintenance of such a mild water shortage in d-i patterns is not always possible and may turn into severe shortage.

The present analysis may contribute to a better understanding of the result presented in Grashoff (1990), that average seed yields of d-i patterns were equal to those of i-i situations, but that the seed yield range (a measure for yield variability) was larger in d-i patterns than in i-i patterns. That explains also why some investigators observed that irrigation during flowering resulted in the highest positive yield responses, due to strongly enhanced pod retention (Brouwer 1959; Mohamed, 1981). The yield levels which they obtained under natural conditions (dry matter productions of about 3 t ha^{-1}) are extremely low in comparison with the yield data in Figure 4, and pod retention was apparently also low. This indicates the occurrence of severe water shortage. According to Hsiao (1976), severe water shortage results in a shortage of assimilates in the whole plant. In this situation also the young pods suffer from lack of assimilates and abort. Under the conditions presented by Brouwer (1959) and Mohamed (1981), irrigation during flowering may have been crucial to avoid severe water shortage. Starting the irrigation after flowering had no positive effect, as there were apparently not sufficient pods left to be filled.

That emphasizes the need for an exact definition of the optimum soil water content during flowering. Such a criterion was presented by Stock & El-Naggar (1980). This value cannot easily be generalized. The question is whether the soil water content at which mild water shortage turns into severe, will be constant under different climatic conditions. Soil water content is only one of the (indirect) factors which affects transpiration and assimilation processes. It may be necessary to define separately the effect of water shortage on vegetative growth and on pod set and pod filling, in relation to assimilate availability and competition.

Moreover, simple classifications of water supply patterns as presented in the Figures 4b and 5 may not be found under the majority of climatological conditions. So, for a comprehensive analysis of the yield variation as explained by water use and water supply pattern on the yield of faba beans, interpolation and extrapolation of the observed relations by means of a simulation model is desirable. Simulation studies with varying soil moisture contents and water supply patterns in different seasons may help to define strategies for optimum water supply.

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Chapter 3

Effect of pattern of water supply on *Vicia faba* L. 3. Plant water relations, expansive growth and stomatal reactions

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Effect of pattern of water supply on *Vicia faba* L.
3. Plant water relations, expansive growth and stomatal reactions

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Abstract

Leaf water potential (ψ), osmotic potential (π), turgor (P) and relative water content (RWC) of six faba bean cultivars were studied in a treatment with limited water availability from onset of flowering to the end of the growing season (d-d), and in a treatment with full irrigation during the same period (i-i), in the field in 1982 and 1984. ψ, π and P were linearly related to leaf RWC, and there were no significant cultivar effects. The osmotic potential π at full turgor hardly differed between the water supply treatments (–0.7 MPa in d-d and –0.6 MPa in i-i) and the slopes of π versus RWC showed no significant difference ($P < 0.01$). This indicates the absence of osmotic adjustment. Significant effects of water supply treatment on the slope of P versus RWC (the bulk modulus of elasticity, BME) were absent. It is concluded that the six faba bean cultivars showed a general lack of mechanisms to keep P on a high level at increasing water shortage. Internode expansive growth rate during flowering was in i-i 2 to 3 times higher than in d-d. Under controlled conditions (22 or 28°C; 400 μE m^{-2} s^{-1}), expansive growth linearly declined with decreasing P. Maximum stomatal conductance in the field decreased with ψ from an estimated maximum level of 1.0 s cm^{-1} (at full turgidity and light intensity >800 μE m^{-2} s^{-1}), following a negative exponential curve. It is concluded that vegetative (expansive) growth decreases faster with decreasing P or ψ than the stomatal conductance (and most probably faster than the rate of photosynthesis). This result, combined with the inability to maintain P at increasing water shortage, helps to explain the positive effect of mild water shortage on reproductive growth of faba beans.

Keywords: faba beans, *Vicia faba* L., plant water relations, expansive growth, dry matter partitioning, stomatal conductance

Introduction

Growth of faba beans is very sensitive to level and pattern of water supply (Grashoff, 1990a). Turgor (P) is considered as an important driving force for expansive growth, although recent research underlines that more factors are involved (van Volkenburgh & Boyer, 1985; Nonami & Boyer, 1989). Mechanisms to maintain turgor at declining water supply have been discovered for several species. Such mechanisms are osmotic adjustment and adaptation of bulk modulus of elasticity

(*BME*). These mechanisms enable the plants to maintain a high level of expansive growth and a high rate of photosynthesis under water shortage and thus increase drought tolerance (Weatherley, 1970; Hellkvist et al., 1974; Jones & Turner, 1978; Sobrado & Turner, 1983).

In faba beans however, even a mild water shortage during flowering reduces the vegetative expansive growth (Grashoff, 1990a). In general, such a reduction of expansive growth is accompanied by a decrease of metabolic cell growth processes (Hsiao & Acevedo, 1974). Consequently the sink strength of the vegetative plant top will be reduced. If the plant is not able to restore expansive growth to the original level, but concomitantly maintains assimilation rate, increasing amounts of assimilates cannot be incorporated into vegetative top tissue. The assimilate surplus may flow down to organs at a lower plant position such as the developing pods or the roots. Actually, Grashoff (1990a, 1990b) established that mild water shortage during flowering reduces stem extension and leaf expansion, and stimulates retention and growth of the first developing pods. This stimulation of reproductive growth during water shortage may be related to the absence of osmotic adjustment or *BME* adaptation in the vegetative top of faba beans. In the present study, this hypothesis is tested.

Materials and methods

Field experiments

Plants were grown in the field on the experimental farm Droevendaal on a humic sandy soil under five different water supply conditions. Details about materials and methods were presented in an earlier publication (Grashoff, 1990a). This study concerns plants of the two extreme treatments 'd-d' (limited water availability from onset of flowering to the end of the growing season), and 'i-i' (irrigated to keep the soil close to field capacity, from onset of flowering onwards).

Procedure of measurements in the field

On 7 days in 1982 and 3 in 1984, 10 to 15 neighbouring plants per treatment and per cultivar were selected (Table 1). The third fully unfolded but still expanding leaf from the top of 2 to 3 plants of each treatment and of each cultivar were sampled at 10.00 h a.m. (1982) or at dawn (1984) and, with 2 to 3 h intervals, till 17.00 h (1982) or till the end of the light period (1984). ψ was measured within 2 minutes after excision of each leaf. Subsequently, this leaf was frozen in liquid nitrogen and stored in small polythene cups at −20°C for determination of π and calculation of *P*. Immediately thereafter, the leaf growing one node lower than the previous one, was excised for measurement of *RWC*, using a gravimetrical procedure.

At some data, additional measurements were carried out (Table 1). In 1982, after each pair of top leaves, also the oldest leaf which was still completely green was used (for ψ and π measurements) and the leaf growing one node higher than the oldest green leaf (for *RWC* measurements). Expansive growth in the field was mea-

Table 1. Years, treatments, cultivars used, measurements and calendar data (presented as day/month) of the water supply experiments with faba beans.

Year	Treatments	Varieties	Measurements	Calendar data
Field experiments				
1982	d-d, i-i	Minica, Wierboon, Kristall, Felix	1) ψ, π, P and RWC of upper and lower leaves	1) 9/6, 15/6, 17/6, 24/6, 1/7, 7/7, 8/7
			2) Field measurements of expansive growth.	2) 17/6-22/6, 22/6-29/6, 29/6-5/7, 5/7-9/7
1984	d-d, i-i	Minica, Optica, Alfred, Kristall	1) ψ, π, P, stomatal conductance	1) 20/6, 11/7, 25/7
			2) ψ (only), stomatal conductance	2) 7/6, 13/6, 27/6, 4/7, 18/7, 1/8
Controlled environment experiments				
1983	dark-light-dark	Minica	ψ, π, P, expansive growth	11/5
	light-dark-light	Minica	ψ, π, P, expansive growth	13/5
	dark-light-dark	Minica	ψ, π P, expansive growth	8/6

sured during and shortly after flowering.

In 1984, at five other days during June and July and one in August, only ψ of the top leaves was measured, without measurements of π and calculations of P, but following the same measuring scheme during a day as presented above. On all the measuring days and within half an hour after finishing the ψ measurements of each series, the stomatal conductance of the youngest fully expanded leaves was measured of 3 plants, neighbouring those used for the ψ measurements. Together with this measurement, radiation was measured. On all measuring days, water content of the top soil layer (0 to 40 cm) was measured gravimetrically, close to the selected plants for the ψ measurements.

Experiments under controlled conditions

Plants of cv. Minica were grown in the greenhouse in 1-l pots, filled with peaty soil. The pots were watered daily with Hoagland solution. As soon as the 8th leaf started unfolding, the plants were placed in a room with a constant temperature of 22°C. In two experiments (Table 1) ψ and π of the fifth leaf were measured and P was calculated, prior to the start of the light period, in the middle of the light period, and prior to the end of the light period ('dark-light-dark' experiment, D-L-D) or vice-versa in the L-D-L experiment. The light period in D-L-D was 5 h (with 10 h of darkness before and 9 h after the light period). The dark period in the L-D-L experiment was also 5 h (with 5 h of light before this dark period and 2 h of light afterwards, and 12 h of darkness to complete a 24-hours' day). Expansive growth was measured continuously, with an auxanometer clamped to the 7th leaf of undisturbed plants, neighbouring those used for measurements of water relations.

In the third experiment (D-L-D), plants were placed on aerated water culture (Hoagland solution) in a room at 28°C. Water relations and expansive growth were measured in the same way as in the pot experiments.

Light intensity in these experiments was 400 μE m^{-2} s^{-1} (Philips HPI-lamps) and relative air humidity (measured with the porometer) varied between 30 and 50 %.

Methods of measurement of ψ, π, stomatal conductance and expansive growth

Leaf water potential (ψ) was measured with a pressure chamber (Scholander et al., 1965). Before excision, the leaves were wrapped in small polythene bags. The chamber was pressurized at a rate of about 50 kPa s^{-1}. The applied pressure at which sap was expelled from the xylem vessels was taken as a measure of ψ, without correcting for the osmotic potential of the sap, which was not measured. This osmotic potential is near zero, typically >–0.1 MPa, and remains essentially constant with leaf water potentials decreasing to –1.5 MPa in many species (Boyer, 1967; Boyer, 1969; Day et al., 1981). The osmotic potential of the leaf tissue (π) was measured with a freezing point depression osmometer (Knauer) or with a dew-point osmometer (Wescor), after thawing of the frozen leaves and a centrifugation procedure to collect and purify the cell sap. Relative water content (*RWC*) of the leaves was measured according to the method of Stocker (1929), which includes determination of: (1) fresh weight direct after excision (w_f), (2) turgid weight after an overnight saturation in small polythene cups (w_t) and (3) weight after oven drying (w_d), with the equation:

$$RWC = \frac{w_f - w_d}{w_t - w_d}$$

Turgor (P) was calculated with the equation: $P = \psi - \pi$. The bulk modulus of elasticity (*BME*) was calculated with the equation:

$$BME = \frac{\Delta P}{\Delta RWC}$$

Some preliminary measurements showed that the water status of two succeeding leaves was almost the same. Therefore, we assumed that ψ, π, P and RWC, measured at two subsequent top leaves (or oldest green leaves) were applicable to one and the same top (or oldest green) leaf.

Stomatal conductance was measured on the lower leaf surface with a Li-cor porometer, and radiation, air humidity and cuvette temperature were recorded. Expansive growth in the field was measured every day, as the increment of the distance between two painted marks of the youngest expanding internode. Expansive growth in the controlled environment experiments was measured with an auxanometer described by Kleinendorst & Brouwer (1970). The auxanometer was clamped on the top of the youngest expanding leaf, in such a way that the total expansive growth of the young stem parts and the youngest leaf were recorded.

Results

Development of water shortage during the season

The growing season of 1982 was relatively dry and warm. Clear differences in soil water content between the treatments d-d and i-i were found from 28 May onwards (Grashoff, 1990a). On 9 June, ψ at mid-day was –1.12 MPa in d-d and –0.74 MPa

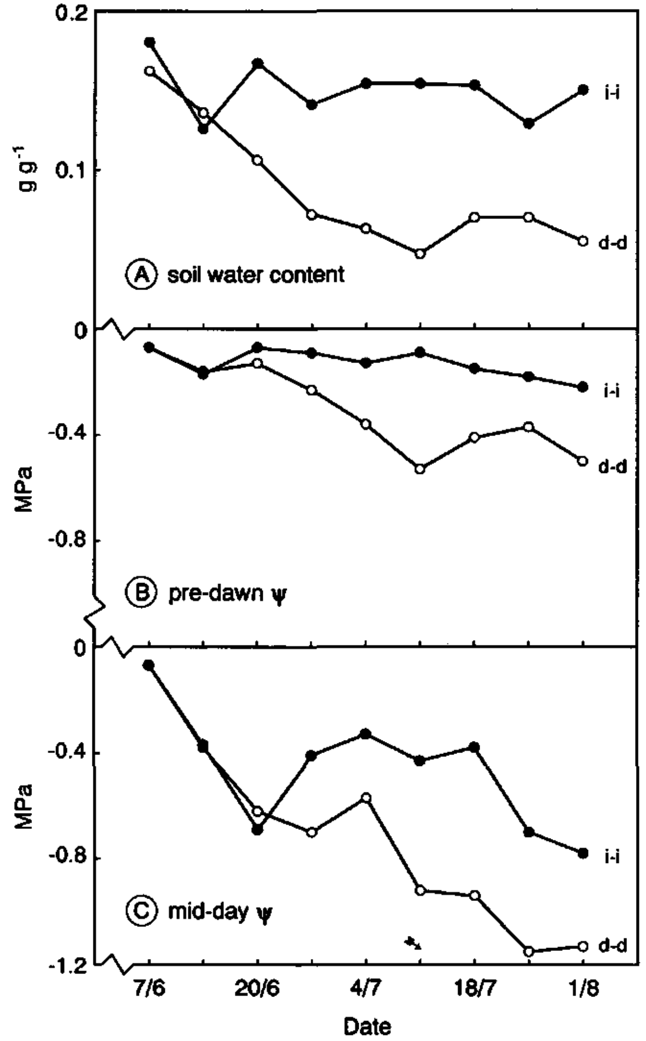

Fig. 1. Seasonal course of (A) soil water content, (B) pre-dawn ψ and (C) mid-day ψ in two water supply treatments in 1984. A heavy thunderstorm on 11 July (11/7) is indicated by ↘. Calendar data presented as day/month.

in i-i, at soil water contents of respectively 0.06 g g^{-1} (in d-d) and 0.11 g g^{-1} (in i-i). Differences in ψ between d-d and i-i were present at almost all the following measuring days; on the last measuring day, 8 July, the mid-day ψ was −1.63 MPa (in d-d) and −1.09 MPa (in i-i) at soil water contents of 0.04 g g^{-1} (d-d) and 0.10 g g^{-1} (i-i).

In 1984, differences in soil water content between the treatments occurred after 13 June (Figure 1a). After the soil water content in d-d fell below 0.10 g g^{-1} (on 20 June), pre-dawn ψ followed the further decline of soil water content in d-d (Figure 1b). From that point onwards, pre-dawn and mid-day ψ values (Figure 1c) were lower in d-d than in i-i. Apparently, a soil water content of 0.10 g g^{-1}, corresponding to a pF 3 (0.1 MPa) in this sandy soil type, was a critical value for the development of water shortage in the plants.

Water relation characteristics

Figure 2 shows the relation between ψ, π, *P* versus *RWC*, plotted for the upper leaves of cv. Minica. This Figure represents a graphical view of the regressions needed for the analysis of plant water relations (a general analysis will be presented in the next paragraph). The linear regression analyses on d-d and i-i data together in

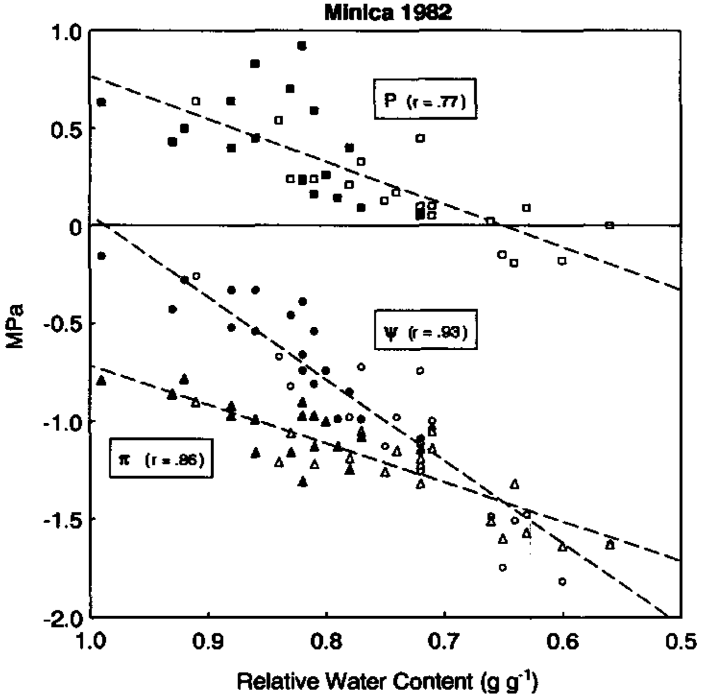

Fig. 2. Diagram of water relation characteristics for upper leaves of cv. Minica. Data obtained from 9 June to 8 July, 1982, on 7 days. Open symbols: data from d-d; closed symbols: data from i-i.

Figure 2 show high correlation coefficients, already indicating the absence of strong effects of water supply treatment on the water relation characteristics. A majority of data points of d-d were found at the right-hand side of the diagram, while i-i points were located more at the left hand side. This difference in location illustrates the general difference in level of water availability between the two treatments. This is demonstrated in detail in Figure 3, where P is plotted directly versus ψ. On 1 July 1982, P in the top leaves of d-d was 0.5 MPa lower than in i-i, averaged over the day. This Figure also shows, that even the smallest decline in ψ results in a proportional decline in P.

Table 2 shows the regression analyses of the water relation characteristics for all data obtained in 1982. Linear regressions of ψ, respectively π and P versus RWC accounted for 80 %, respectively 60 % and 45 % of the variation. Significant main effects of cultivar and of cultivar × RWC interactions were not found. A significant

Table 2. Results of regression analysis of water potential (ψ), osmotic potential (π) and turgor (P) versus relative water content (RCW): percentage of accounted variation, coefficients a and b. Fitted lines have the following form: $y = a \times RWC + b$, where y is ψ, π or P; cv = cultivar; water = water supply treatment; leaf = leaf position; cv, water, leaf and interaction effects were subsequently included in the analysis. *** = significant effect (at $P < 0.01$); n.s. = not significant. Data obtained from measurements on 7 data between 9 June and 8 July, 1982, on experimental farm Droevendaal.

y	% of accounted variation (and coefficients a and b)						
	RWC	(*RWC*+ cv)	(*RWC*+ cv)+ (*RWC* × cv) interaction	(*RWC*+ water)	(*RWC*+ water)+ (*RWC* × water) interaction	(*RWC*+ leaf)	(*RWC*+ leaf)+ (*RWC* × leaf) interaction
ψ	81.1*** (a= 3.78) (b=−3.84)	81.0 n.s.	80.8 n.s.	85.3*** (a = 3.19) (b1=−3.47; d-d) (b2=−3.25; i-i)	85.5 n.s.	81.1 n.s.	81.0 n.s.
π	60.5*** (a= 2.10) (b=−2.72)	60.1 n.s.	59.7 n.s.	61.9*** (a = 1.87) (b1=−2.57; d-d) (b2=−2.48; i-i)	61.9 n.s.	77.6*** (a = 1.87) (b1=−2.41; lower leaf) (b2=−2.64; upper leaf)	77.6 n.s.
P	43.5*** (a= 1.68) (b=−1.13)	42.7 n.s.	42.4 n.s.	47.5*** (a = 1.32) (b1=−0.90; d-d) (b2=−0.77; i-i)	47.3 n.s.	65.9*** (a= 1.93) (b=−1.46; lower leaf) (b2=−1.21; upper leaf)	65.9 n.s.

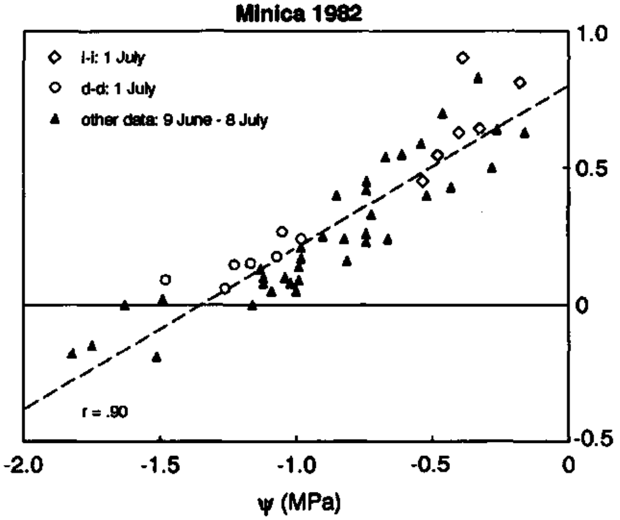

Fig. 3. Turgor (P) versus water potential (ψ) for upper leaves of cv. Minica. Open circles: data from d-d at 1 July; open diamonds: data from i-i at 1 July. Closed triangles: all other data obtained between 9 June and 8 July, 1982.

main effect of water supply treatment was found, but this increased the percentage of accounted variation with only 1.5 to 4 % and the differences in intercepts were very small. For instance, the intercept of the regression of π versus RWC+water was −2.48 MPa in i-i and only 0.09 MPa lower in d-d (Table 2). This shows that osmotic adjustment due to water supply treatment was negligible. Significant $RWC \times$ water supply treatment interactions were absent, which implies that the slopes of the regression lines were the same for both treatments. It is concluded that the bulk modulus of elasticity (BME), defined as the slope of the regression of P versus RWC, showed no adaptation due to water supply treatment. Only a clear main effect of leaf position was present. When upper leaves and lower leaves were separated in the analysis, the percentage of variation accounted for increased with 15 % and 20 % for π, respectively P versus RWC (Table 2). From the data in this Table it was calculated that π at full turgidity was −0.54 MPa for the lower leaves and −0.77 MPa for the upper leaves which implies that the lower leaves contained 30 % less osmotically active solutes. As no differences in BME were found, lower leaves lost their turgor at an RWC of 0.75, but upper leaves not until 0.65. Important cultivar × treatment interactions were not found in any of the relations showed before.

Table 3 shows the regression analysis for P versus ψ of 1982 and 1984, combined for all cultivars. The regression accounted for 60 % of the variation in both years. Significant effects of cultivar, water supply treatment and interactions were not found and differences between the years were small. P-value at $\psi = 0$ (which means full turgidity), was 0.8 MPa in 1982 and 0.9 MPa in 1984 and the ψ-value at zero P was −1.5 MPa in both years. These data show that osmotic adjustment and adapta-

Table 3. Results of regression analysis of turgor (P) versus water potential (ψ): percentage of accounted variation, coefficients a and b. Fitted lines have the following form: $P = a \times \psi + b$; cv = cultivar; water = water supply treatment; leaf = leaf position; cv, water, leaf and interaction effects were subsequently included in the analysis. *** = significant effect (at $P < 0.01$); n.s. = not significant. Data obtained from measurements in 1982 and in 1984 on experimental farm Droevendaal.

P fitted for year	% of accounted variation (and coefficients a and b)						
	ψ	(ψ+cv)	(ψ+cv) +($\psi \times$ cv) interaction	(ψ+water)	(ψ+water) +($\psi \times$ water) interaction	(ψ+leaf)	(ψ+leaf) +($\psi \times$ leaf) interaction
1982	61.8^{***} (a=0.48) (b=0.61)	61.3 n.s.	60.8 n.s.	61.6 n.s.	61.5 n.s.	83.4^{***} (a =0.52) (b1=0.52 lower leaf) b2=0.76 upper leaf)	83.8 n.s.
1984	59.4^{***} (a=0.61) (b=0.91)	59.2 n.s.	58.8 n.s.	59.0 n.s.	58.9 n.s.	(lower leaves not measured)	

tion of *BME* due to cultivar, water supply treatment or season were absent or negligible. Again, only a significant effect of leaf position was present. After split-up of the regression analysis in lower and upper leaves (1982-data) the variation accounted for increased up to 80 % ($P < 0.001$). In the lower leaves, complete wilting (P=0) was reached already at a ψ of –1.0 MPa but in upper leaves this happened not before a ψ of –1.5 MPa.

Water shortage and expansive growth

During and shortly after flowering, the average rate of internode expansive growth in the field in i-i was, dependent on the cultivar, 2.5 to 5 times higher than in d-d treatments (Table 4). In the controlled environment, the rate of expansive growth (of the young stem parts and the youngest leaf together) followed the changes in P. At the start of the light period transpiration increased, and resulted in a sharp decline in ψ and P of the top leaves and a concomitant cessation of expansive growth. During the light period the expansive growth slightly recovered but remained very low. After the end of the light period, ψ and P raised importantly, and the expansive growth immediately recovered. The relation between P and the rate of expansive growth is plotted in Figure 4. Although there is some scatter, the data indicate that expansive growth is linearly related to P. Linear regression (which accounted for 70 % of the variation) showed the absence of a minimum turgor for expansive growth (turgor threshold).

Table 4. Internode expansive growth rate (mm d^{-1}) of four faba bean cultivars at two water supply treatments (d-d and i-i), averaged over four periods of measurements in the field in 1982 (Experimental farm Droevendaal).

Cultivar	Internode expansive growth rate (mm d^{-1})	
	d-d	i-i
Minica	1.0	3.0
Felix	0.5	2.0
Kristall	2.0	5.0
Wierboon	1.5	5.0

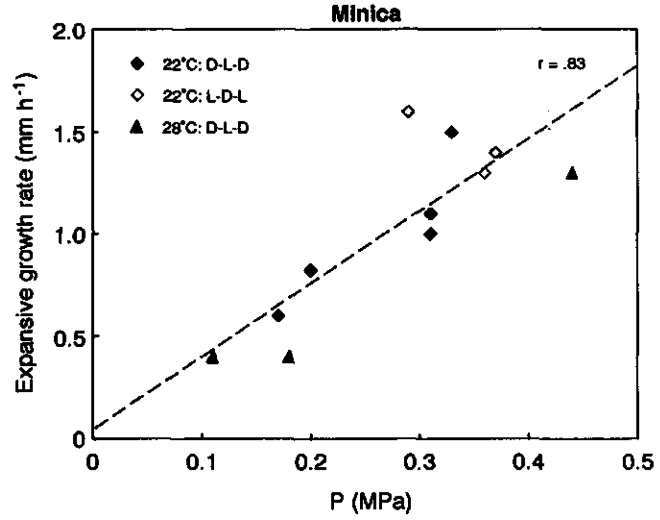

Fig. 4. Expansive growth versus turgor (*P*) for cv. Minica. All data from experiments under controlled conditions, 1983.

Stomatal conductance

In Figure 5a the water potential (ψ) of top leaves was plotted against the stomatal conductance. Data pairs of ψ-conductance measurements were collected diurnally under strongly varying environmental conditions, which resulted in a large scatter pattern. According to Jarvis (1976), a curvilinear border line can be estimated, indicating the maximum stomatal conductance at a given ψ-value. This border line decreased with ψ from a level at about 1.0 cm s^{-1} at full turgidity, following a negative exponential curve to zero at a ψ of about –1.6 MPa. Clear differences between cultivars were not found.

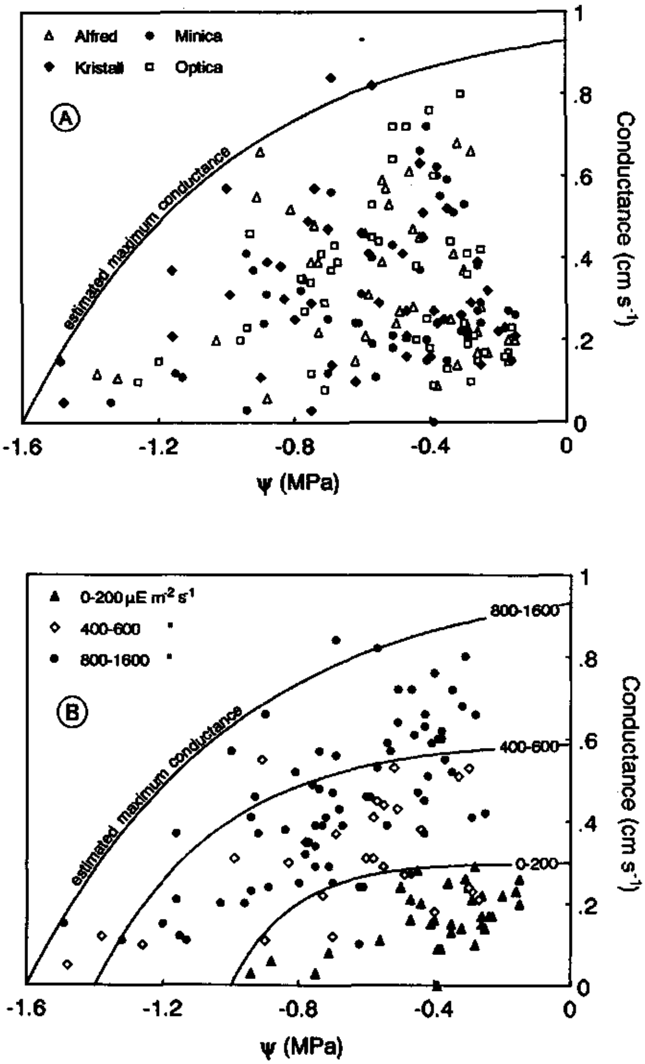

Fig. 5. Stomatal conductance, as influenced by environment, for the top leaves of the four varieties tested in 1984. (A) all data versus water potential (ψ) and (B) all data versus ψ, classified in different radiation levels. Curves are fitted using the equation: $c = c_{max}(1\text{-}\exp(-((\psi\text{-}\psi_{c0})/(a \times c_{max}))))$; c_{max} = maximum stomatal conductance; $\psi_{c0} = \psi$ at stomatal conductance = 0; a = initial slope at ψ_{c0}.

From Figure 5b it can be seen that the scatter in Figure 5a is strongly determined by the level of light intensity. At each light intensity, maximum stomatal conductance can be plotted versus ψ, following the same kind of negative exponential curve.

Discussion

The water relation characteristics of the top leaves of faba beans (Figure 2) showed much resemblance to those found by Turner et al. (1978) in soya beans. In agreement with Turner et al. (1978) we found linear relations. However, curves are theoretically more correct (Weatherley, 1970), but the scatter in field data was too large to find significant effects of non-linear regression.

Lower leaves always contained a lower solute content (a higher π) than upper leaves. This may explain why lower leaves in the field wilt earlier than upper leaves during the development of water shortage. The observed differences between upper and lower leaves cannot be explained in terms of adaptation to water shortage, since differences between water supply treatments were absent (Table 2). The lower solute content of lower (oldest green) leaves might be related with a lower light exposure and attraction of osmotically active solutes by the developing pods.

The results presented in this paper do not show any adaptation of the bulk modulus of elasticity (*BME*) due to water supply treatment. Also in faba beans, Elston et al. (1976) found an adaptation of *BME* in a dry relative to an irrigated treatment. This adaptation, however, was not sufficient for compensating the general fall of *P* during water shortage.

Similar to soya beans (Turner et al., 1978), faba bean cultivars did not show any important osmotic adjustment or adaptation of *BME* due to water supply or season (Tables 2 and 3; Figures 2 and 3). It implies, that each decline in leaf-*RWC* is followed by a proportional decline in ψ and in *P*. So the six faba bean cultivars which we tested, showed a general lack of mechanisms to maintain *P*-level during water shortage.

In our experiments indoors, expansive growth declined proportional with declining *P* (Figure 4). This kind of relation is in agreement with results of Bunce (1977). Hsiao et al. (1976a) found in sorghum even a sharper decline of expansive growth with *P*, namely an exponential relation, with a turgor threshold of 0.05 to 0.1 MPa. However, Bunce (1977) showed that turgor threshold values may depend on growing conditions.

Anyhow, applying the relationship between expansive growth and *P* (Figure 4) to the field situation, it may be expected that expansive growth falls sharply when ψ and *P* decline due to an increasing water shortage (Figure 1). This prospect was confirmed by our field data, showing a strong reduction of internode expansion rate (Table 4), plant length and leaf area index (Grashoff, 1990a) in d-d treatments, relative to i-i. Full recovery of expansive growth during the night is not likely in d-d, since even predrawn ψ remains lower than in i-i, below a critical soil water content (Figure 1). Moreover, Karamanos et al. (1982) established a close correlation between *P* at noon and final leaf size in field grown *Vicia faba.*

Consequently, as a decline in ψ and *P* results in a decline in all metabolic processes (Hsiao & Acevedo, 1974), less photosynthate will be incorporated into structural material of young stem parts and young leaves. Grashoff (1990a) showed that the reduction of stem elongation rate during water shortage was immediately followed by a reduction of stem dry matter accumulation rate. Water shortage might result in a higher specific leaf weight (Grashof, 1990a), probably by starch accumulation. Recently, however, Bunce (1990) showed an increased export of photosynthate from young leaves under mild water shortage. Spraying of abscisic acid (ABA) mimicked this effect and Bunce (1990) concluded that ABA, perhaps even more than just turgor decline, might mediate the effects of mild water shortage, due to an inhibition of cell wall elongation. So, the reduction in expansive growth of the vegetative top by water shortage might bring about a shift in assimilate distribution in favour of other sink organs.

This reasoning, however, only holds true when the assimilate source, photosynthesis, is not or less reduced. Our evidence on photosynthesis is derived from data on maximal stomatal conductance (Figure 5). The estimated borderlines suggest that maximum stomatal conductance is negative exponentially related to ψ over a wide range. As in general leaf mesophyll conductance and ψ decline concomitantly (Hsiao, 1973), it seems that in faba beans a negative exponential relation exists between rate of photosynthesis and ψ (Figure 5). This agrees with the results of Kassam (1973). He provided evidence for the faba bean cultivar Maris Bead, that stomatal conductance was hardly reduced at small declines of ψ and P, until a threshold value at low ψ, where the leaves were almost flaccid. Boyer (1970) and Hsiao et al. (1976b) also found this kind of non-linear relations for other crops. Turner et al. (1978) showed with soya beans, that a decrease of photosynthesis commenced at a ψ below 1.5 to 1.7 MPa. Grashoff (1990a) showed in field experiments in 1980 and 1981, that stem elongation was already markedly reduced in the d-i treatment, while total dry matter accumulation rate was still the same in i-i and d-i.

According to Shimshi (1963) and Slatyer & Bierhuizen (1964), a decrease of stomatal conductance reduces transpiration rate more than rate of photosynthesis. Vos & Groenwold (1989) reported increasing water use efficiency at water shortage in potatoes. Passioura (1977) found important cultivar differences in water use efficiency in wheat. Verkerke (pers. comm.) found increased water use efficiency in faba beans when water shortage was created in water cultures with polyethylene glycol. This shows that photosynthesis might be even less sensitive to increasing water shortage than could be derived from the response of stomatal conductance.

The combination of the relations of photosynthesis and expansive growth with P or ψ (Figure 6) clearly indicate the development during water shortage of an assimilate surplus. Since also no osmotic adjustment was observed, these assimilates become available for investment elsewhere in the plant. According to the theory of the functional equilibrium (Brouwer, 1983), the roots might benefit from these assimilates. However, when mild water shortage occurs in reproductive plants during flowering, young developing pods on the stem basis might compete successfully for assimilates. Actually, Grashoff (1990b) established an increased retention of the first pods under mild water shortage during flowering, thus providing the basis for an early and strong reproductive sink and a high final seed yield. It has to be emphasized that mild water shortage should be released after cessation of vegetative growth. The strongest positive effects on dry matter partition and seed yield were found in treatments with mild water shortage during flowering and plenty of water afterwards (Grashoff, 1990a). It seems remarkable that young pods were able to

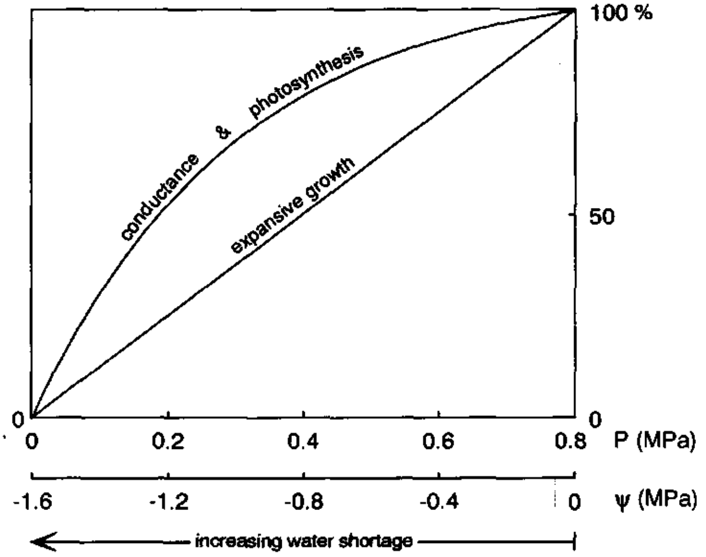

Fig. 6. Hypothetical relations between rate of expansive growth, conductance and photosynthesis versus water potential (ψ) and turgor (P), for faba beans according to the results of this paper and for various crop types, according to Hsiao et al. (1976b) and others (see text); NB: shapes of curves are a qualitative representation!

grow better under conditions with mild water shortage than the vegetative top. Additional research on the nature of this mechanism is interesting, as it might be a key factor in the distribution of assimilates in the plant.

The results presented in this paper provide no evidence for important cultivar differences in water relation characteristics. This agrees with the results of Vos & Groenwold (1988) for potato cultivars. Since some cultivars did differ significantly in the response on pattern of water supply (Grashoff, 1990a), it is questionable whether measurement of the water relation characteristics is an effective way to identify genotypic tolerance or resistance to water shortage.

Varietal differences in properties that enable the plant to avoid water shortage (e.g. rooting depth) or to escape from it (e.g. timing of flowering period, rate of development) and differences in water use efficiency may be more relevant characteristics. However, the improvement of tolerance or resistance to water shortage may not be considered apart from dry matter partitioning characteristics.

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Chapter 4

Effect of pattern of water supply on *Vicia faba* L.
4. Simulation studies on yield variability

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Effect of pattern of water supply on *Vicia faba* L.
4. Simulation studies on yield variability

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Abstract

The effects of water supply patterns on yield variability of Vicia faba L. were studied by means of a crop growth model. The model simulates crop dry matter production and soil water availability in dependence on plant characteristics and weather and soil data. Consequences of various weather conditions on growth were evaluated, using 4 data sets from various soils and sites in Western Europe. In set 1 (14 years; heavy clay soil; Netherlands) and set 3 (2 years; 9 locations in Western Europe), linear regressions of measured versus simulated seed yields, fitted through the origin, had slopes of almost 1 and accounted for 68% (set 1) and 12% (set 3) of the yield variation. In both sets, these regressions accounted for about 80% of the variation, if deviations, due to damage effects of hail, lodging, and diseases were excluded (these damage effects are not calculated in the model). In set 1, the average seed yield was 5.3 t ha^{-1} (measured and simulated) and the standard deviation (s.d.) was 1.3 (measured) and 1.5 t ha^{-1} (simulated). Simulated irrigation after the end of flowering (i.e. from grain filling onwards) stabilized yield (s.d.=0.4 t ha^{-1}) on a high level (6.2 t ha^{-1}). Simulated irrigation during the whole season had almost no additional effect. The results for set 3 were similar to set 1. Simulations for set 1 showed that the 'target' soil water contents during flowering for optimum final seed yields varied from 0.27-0.32 cm^3 cm^{-3} for this soil type (pF-values of respectively 3 and 2.3), depending on temperature and air humidity. After flowering a water content higher than 0.32 cm^3 cm^{-3} was required. Two strategies for breeding ideotypes were evaluated; doubling the rooted depth and root growth rate stabilized seed yields (the s.d. was reduced by 30% in set 1), but doubling the water extraction capacity of the crop had almost no effect. The model accounted for less than 1% of the variation in set 2 (14 years; light silty loam; Netherlands) and 4 (3 years; 5 regional experimental farms; Netherlands). This was different from set 1 and 3 and probably due to effects of capillary rise (in set 2) and diseases (in set 4), which are not included in the model. In set 4, the yield gap between simulated and measured yields increased with observed disease attack in the field, from less than 1 t ha^{-1} with 'absent or low' attack to more than 3.5 with 'severe' attack. The simulation studies show how control of water availability stabilizes faba bean yields in many environments. They also indicate the importance of disease control and of breeding ideotypes with deeper rooting capacity.

Keywords: faba beans, *Vicia faba* L., simulation, modeling, water supply, yield variability

Introduction

Faba bean (*Vicia faba* L.) is a protein-rich seed crop and can be an alternative for imported soya bean residues as a raw material for the animal-feed compounding industry. Variability in yield is a major problem with this crop. In field experiments yield and dry matter partitioning were strongly affected by the amount and temporal distribution of water supply (Grashoff, 1990a, 1990b). Grashoff & Verkerke (1991) showed that faba beans are inefficient in adapting to conditions of water shortage.

The objective of this paper is to investigate whether variation in natural water supply is a major cause of the yield variability of faba beans in Western Europe. A general crop growth simulation model was adapted for faba beans and used to analyse results of field experiments under various weather conditions, soil types and sites in Western Europe. Next the model was used to explore the possibilities for improvement of yield stability with crop management and breeding.

Model description

Figure 1 shows the simplified structure of the model. The calculation of crop growth under adequate soil water conditions is based on general crop growth simulators (Spitters et al., 1989; Penning de Vries et al., 1990). The development stage of the crop is simulated through integration of the rate of development, which is influenced by temperature (letter A in Figure 1). Assimilation rate is calculated from the incident amount of photosynthetically active radiation (PAR) (letter B in Figure 1), the fraction of PAR intercepted by the canopy (letter C in Figure 1), and the photosynthesis/light response curve of individual leaves. The total amount of carbohydrates available for growth is calculated from the assimilation rate, the reallocation and redistribution of dry matter on the one hand, and losses due to respiration of the plant organs ('maintenance respiration' in Figure 1) on the other. Dry matter growth of the plant organs is determined by the total net carbohydrate production, the fraction of carbohydrates allocated to the plant organs and the values for conversion of carbohydrates into dry matter ('growth respiration' in Figure 1). The fraction of carbohydrates allocated to the organs is affected by the development stage of the crop (cf. Van Heemst, 1986) (letter D in Figure 1). Leaf area growth is calculated from the dry matter allocated to the leaves and the specific leaf weight, which is also influenced by the development stage of the crop.

The parameters and functions specific for faba beans were mainly derived from experiments presented in Table 1a. The parameters for growth respiration were calculated from the chemical composition of plant organs, using equations of Vertregt & Penning de Vries (1987). Table 2 presents some of the essential parameters and functions for faba beans*).

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*) A complete, documented listing of the simulation model and a quantification of all the parameters and functions can be requested at the author's address.

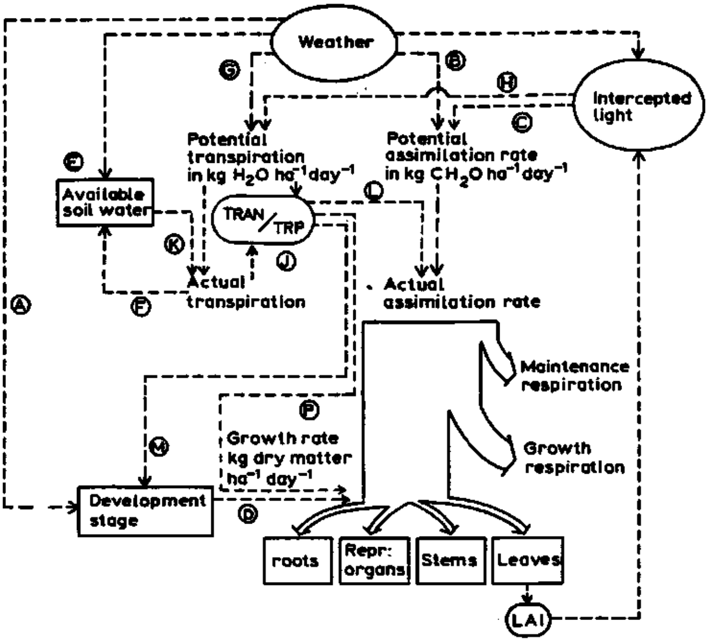

Figure 1. Schematic representation of faba bean growth. NB: the scheme provides an overview, not a relation diagram. All the letters (A,B,C... to P) at the dotted arrows correspond with explanations of the relations in the text. The arrows have to be interpreted as '...has effect on....' (in the direction of the arrow). For instance: TRAN/TRP has effect on photosynthesis (letter L), on development (letter M), and on dry matter partitioning (letter P).

Table 1. Experiments used for a) calibration and b) simulation studies

Objective	Set	Sites	Years	Description	Reference
a)Calibration	silt	De Eest	1977	local growing conditions	Gr1
	heavy clay	De Bouwing	1980	2 irrigation treatments	Gr2
		"	1981	" " "	"
		"	1988	" " "	"
	sand	Droevendaal	1981	2 irrigation treatments	"
		"	1982	5 " "	"
		"	1984	5 " "	"
b)Simulation studies	1	De Bouwing	1975-1988	local growing conditions	Gr1
	2	De Eest	1976-1989	" " "	Gr1
	3 (JFBT) a)	9 locations, W-Europe	1985-1986	" " "	Ebm
	4 (MCB) b)	5 Dutch locations	1987-1989	sowings, irrigations, disease control	VdS

a) JFBT-locations in Cambridge (UK), Dijon (F), Gottingen (G), Hohenheim (G), Dundee (UK), Roskilde (D), Nottingham (UK) and Vienna (A). b) MCB-locations Ebelsheerd, Lelystad, Valthermond, Vredepeel, Wijnandsrade. References: Ebm: Ebmeyer (1984); Gr1: Grashoff et al., 1986; Gr2: Grashoff 1990a 1990b; VdS: Van der Schans & Van den Berg, 1991.

Table 2. Essential crop parameters and functions, specific for faba beans. Description in CSMP-format.

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* Developmental rate in the vegetative and in the reproductive phase, respectively (d-1).
PARAM  DVRV=0.0268, DVRG=0.0172
* Effect of average daily temperature (deg. C) on developmental rate in the vegetative and reproductive
* phase, respectively.
FUNCTION DVRVTT = -10.,0.01, 0.,0.01, 20.,1., 30.,0.8
FUNCTION DVRGTT =   0.,0.01, 4.,0.01, 20.,1., 30.,1.2
* Potential growth rate of roots into depth (m d-1), Potential dying rate of roots into depth (m * d-1),
* Maximum rooted depth (m), Minimum rooted depth (m).
PARAM  PGRRT=0.006, PDRRT=-0.006, RTDMAX=0.7, RTDMIN=0.5
* Specific leaf weight (kg ha-1) in dependence on development stage.
FUNCTION SLWT = 0.,360., 0.6,320., 0.8,240., 1.,200., 1.2,320., 2.1,320.
* Maximum photosynthetic rate of single leaves (kg CO2 ha-1 d-1) and initial photosynthetic efficiency
* (kg CO2 ha-1 h-1 (J m-2 s-1)-1 at reference temperatures of 15 and 10 deg C, respectively.
PARAM  PMAXP = 35., PEI = 0.48
* Extinction coefficient of the crop for diffuse radiation, scattering coefficient, and reflection  coefficient
* of the leaves for total radiation.
PARAM  KDIF=0.7155, SCV=0.2, RCLV=0.1
* Fraction of the crop growth rate allocated to the roots, shoots, leaves, stems, pod walls, seeds and
* reserves, in dependence on developmental stage.
FUNCTION CARTT  =  0.,0.5,    1.,0.2,    1.2,0.,    2.1,0.
FUNCTION CASHT  =  0.,0.5,    1.,0.8,    1.2,1.,    2.1,1.
FUNCTION CALVT  =  0.,0.70,   0.8,0.40,  1.,0.30,   1.2,0.10,  1.3,0.,    1.6,0.,    2.1,0.
FUNCTION CASTT  =  0.,0.25,   0.8,0.50,  1.,0.45,   1.2,0.35,  1.3,0.30,  1.6,0.,    2.1,0.
FUNCTION CAPWT  =  0.,0.,     0.8,0.,    1.,0.10,   1.2,0.30,  1.3,0.30,  1.6,0.,    2.1,0.
FUNCTION CASET  =  0.,0.,     0.8,0.,    1.,0.,     1.2,0.25,  1.3,0.40,  1.6,1.,    2.1,1.
FUNCTION CARET  =  0.,0.05,   0.8,0.10,  1.,0.15,   1.2,0.00,  1.3,0.,    1.6,0.,    2.1,0.
* Conversion factor for CH2O to dry matter for roots, leaves, stems, podwalls, seeds and * reserves
PARAM CFRT=0.652, CFLV=0.534, CFST=0.693, CFPW=0.687, CFSE=0.608, CFRE=0.790
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Detailed measurements of maintenance respiration were not available, so commonly used coefficients for the different plant organs were used (Spitters et al., 1989; Penning de Vries et al., 1990). For leaves and stems, the decrease of these coefficients with plant development was accounted for, using an approach described by Kropff (1989).

Soil water balance

A water balance model for a free draining soil profile is included, according to van Keulen (1975; 1986) and Jansen & Gosseye (1986). In this concept, the soil is divided in 10 layers of 10 cm. The daily change in soil water content is calculated from rainfall (and irrigation) (letter E in Figure 1), crop transpiration (letter F in Figure 1), soil evaporation and percolation. Percolation is calculated as the amount of water in excess of field capacity, which drains to the next soil layer. Potential transpiration and evaporation are calculated with the combination equation of Penman. In this equation are included: the incoming radiation, air humidity and wind speed (all included in letter G in Figure 1), LAI and properties of the transpiring cq. evaporating surfaces (e.g. roughness, emissivity, reflectance, resistance for vapour transport) (generally represented by letter H in Figure 1). Soil evaporation is reduced when the upper layer of the soil dries out. The model does not calculate capillary rise, however the relative contribution of each soil layer to the total soil evaporation is calculated following a mimic procedure (van Keulen, 1975). In this concept, the relative contribution of each soil layer to the total evaporation decreases exponentially with the depth of the layer. The relative contribution of each soil layer to the total transpiration is based on the rooted length in each layer and the maximum water uptake per rooted length.

Crop-water relations

When the soil dries out, stomata close and transpiration falls below its potential value. The ratio between actual and potential transpiration (TRAN/TRP) (see at letter J in Figure 1), is supposed to decrease linearly with soil water content from unity at a critical water content, to zero at wilting point (Feddes et al., 1978) (letter K in Figure 1). The critical water content at which water uptake is reduced (which is somewhere below the field capacity of the soil) is not only dependent on the soil type. According to Doorenbos & Kassam (1979) and Driessen (1986), the critical soil water content is also affected by the water extraction capacity of the crop and this differs between species. Based on the sensitivity of faba beans to water shortage, this crop belongs to the group with a rather 'weak' extracting capacity, like clover and carrots (Driessen, 1986). The critical soil water content is also affected (from day to day!) by TRP and the leaf area index (LAI) (Jansen & Gosseye, 1986). The ratio TRAN/TRP linearly affects the actual assimilation rate (letter L in Figure 1), thus assuming a constant water use efficiency. The ratio TRAN/TRP indicates the level of the water availability to the crop.

Two other crop-water relations were included in the simulation model. Firstly, water shortage accelerates the development of the faba bean crop. With water shortage, pod development begins earlier in the season and maturity is reached earlier (Grashoff, 1990a; Table 3). In the model this process is accounted for by dividing the development rate (and the relative death rate) by the ratio TRAN/TRP, which represents the level of water availability to the crop. This relation is represented by letter M in Figure 1. Our way of simulation implicitly assumes the following underlying mechanism: water shortage causes stomatal closure, lower transpiration rates, decreased 'cooling' of leaves, higher leaf temperatures and a higher development rate of the canopy (cf Van Keulen & Seligman, 1987). These arguments can only give a qualitative explanation. The quantification of our way of simulation was done by calibration based on experiments. This is shown in the section on model calibration of this article.

Table 3. Measured and simulated dates of onset of flowering (Julian date), seed yields (t ha-1 100% dry matter), harvest indices (g g-1) and dates of crop maturity (Julian date) for different water supply treatments during and after flowering in 1980 and 1988 (clay soil) and 1982 (sandy soil). d=dry; i=irrigated; nr =natural rainfall.

Year	Treatment	Onset of Flowering		Seed yield		Harvest Index		Date of crop maturity	
		Meas	Simu	Meas	Simu	Meas	Simu	Meas	Simu
1980									
	d-i	152	152	6.3	6.3	0.62	0.52	259	251
	i-i	152	154	5.8	5.9	0.53	0.46	259	254
1982									
	d-d *)	150	151	4.0	4.0	0.60	0.51	231	218
	i-d	150	151	3.9	3.6	0.49	0.38	222	220
	d-i	150	151	6.2	6.4	0.64	0.54	237	238
	i-i	150	151	6.2	6.0	0.56	0.49	237	241
	nr.	150	151	4.1	4.6	0.57	0.48	222	224
1988									
	d-i	155	151	6.7	6.4	0.65	0.57	259	246
	i-i	155	151	6.0	6.2	0.56	0.51	266	249

*) in 1982, d-d got two irrigations after flowering (also included in the simulation).

Secondly, faba beans show little osmotic adjustment under water shortage and, most probably by this reason, the expansive growth decreases linearly with decreasing leaf water potential (Grashoff & Verkerke, 1991). The relative stomatal conductance, relative transpiration (TRAN/TRP) and relative assimilation decrease slower, following a negative exponential curve (Figure 2a). Grashoff & Verkerke (1991) stated that, with decreasing leaf water potential, these relations might result in a shift in competition for assimilates in favour of developing reproductive organs. In our simulation model however, calculation of leaf water potential is not included. When the leaf water potential in Figure 2a is omitted, this results in an exponential curve for the relative expansive growth versus TRAN/TRP, and in a linear relation of relative assimilation versus TRAN/TRP (as shown in Figure 2b). It is assumed that the expansive growth determines the sink strength of the vegetative shoot and consequently determines the fraction of assimilates flowing to the growing stems and leaves (Hsiao, 1976; Grashoff & Verkerke, 1991). So, with decreasing TRAN/TRP, the fraction of assimilates flowing to the stems and leaves (COMPET) decreases much faster than the assimilation rate (Figure 2b). The surplus assimilate is used for the developing pods and seeds. This effect is present from about onset of flowering till the end of allocation of assimilates to stems and leaves (about 6 weeks after end of flowering!). This relation is represented by letter P in Figure 1. The root growth is not affected by TRAN/TRP as we could not measure a clear effect of water shortage on root growth.

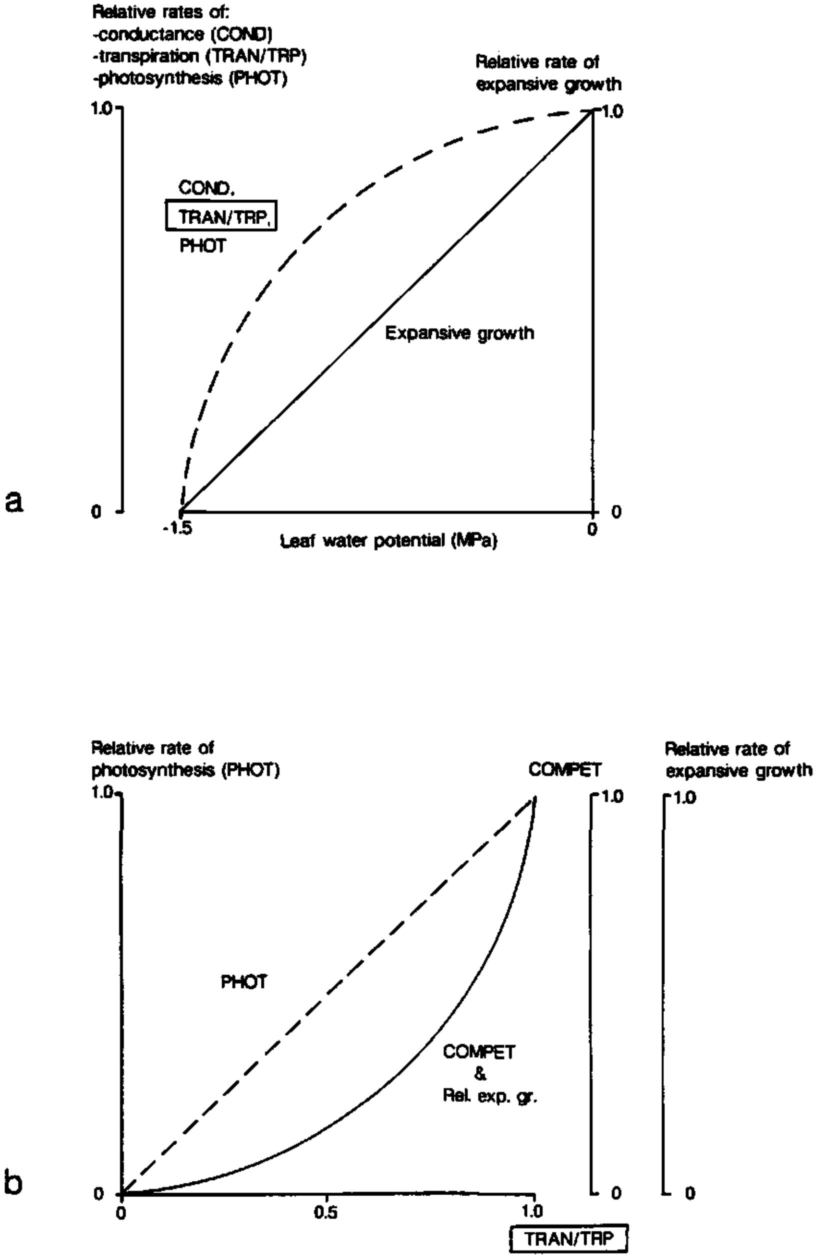

Figure 2. a: the relations of relative conductance, transpiration (TRAN/TRP), photosynthesis and expansive growth rate versus leaf water potential (from Grashoff & Verkerke 1991); b: The derived relations of vegetative growth, vegetative competition strength (COMPET) and photosynthesis versus TRAN/TRP. Rel. exp. gr. = relative rate of expansive growth.

Input data

The input variables for the model are standard data of daily solar radiation, temperature, rainfall, air humidity and wind speed; date of crop emergence and values of crop dry matter and leaf area index at emergence; rootable depth; some characteristics of soil water retention, such as total pore space, volumetric soil water content at field capacity, at wilting point and at air-dry soil; reflection coefficient for total radiation of the soil, average clod height and extinction coefficient for soil evaporation.

Model calibration

Simulation of crop growth was calibrated on the basis of 7 field experiments with varying water supply patterns (Table 1a). This calibration is illustrated in Figure 3. Figure 3a shows the measured dry matter production of cv. Minica grown on a heavy clay near Wageningen in 1988. Two irrigation treatments were included: 1) irrigated during and after flowering (henceforward referred to as i-i) and 2) the natural rainfall. This rainfall pattern resulted in mild water shortage during flowering, followed by plenty of water afterwards (d-i). The d-i treatment showed the typical advanced start of seed growth, earlier maturity and higher final seed yields compared to i-i, as described earlier by Grashoff (1990a) for similar experiments in 1980 and 1981.

A simulation, including the relation of TRAN/TRP versus assimilation rate, but omitting the relations of TRAN/TRP versus development rate, and of TRAN/TRP versus dry matter partitioning, showed essential deviations from the experimental results: the advanced start of seed growth in d-i was not found in the simulation, and the simulated final seed yield of i-i was higher than in d-i (Fig. 3b). Figure 3c shows the simulation result including the relations of TRAN/TRP versus (1) assimilation rate and (2) development rate. The simulated advanced start of seed growth in d-i agreed with the measured effect in Figure 3a. Also the earlier maturity in d-i than in i-i is simulated more correctly. However, the simulated seed growth in i-i caught up with d-i and final seed yield in the i-i simulation was higher than in d-i (Fig. 3c). This essential contrast with the measurements remained in the simulation, even when (by means of 'trial and error') stronger accelerating effects of TRAN/TRP were explored with the model.

Figure 3d shows the simulation result including the relations of TRAN/TRP versus (1) assimilation rate, (2) development rate and (3) assimilate partitioning, calibrated by means of 'trial and error'. This simulation shows the most correct agreement with the experimental results in Figure 3a.

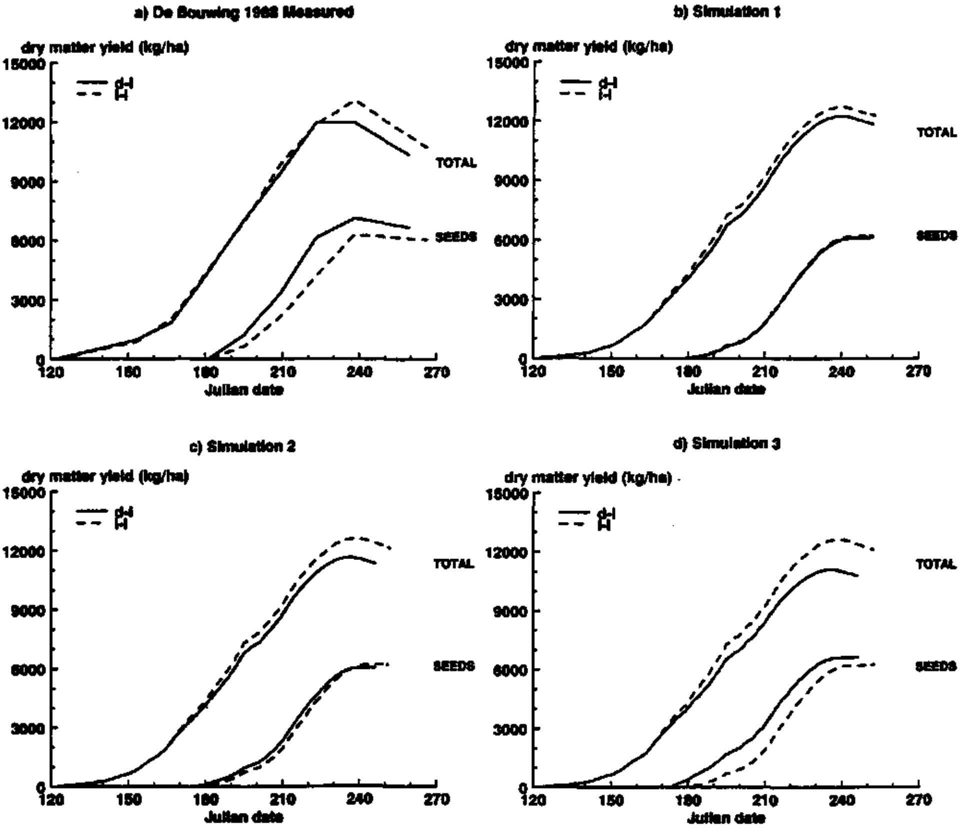

Figure 3. Calibration of the simulation model. a: measured dry matter yields of two irrigation treatments d-i and i-i, Wageningen, 1988; b: simulation with water shortage only affecting assimilation rate ; c: as b but with added effect of water shortage on development rate (and relative death rates) of plant organs; d: as c but with added effect of water shortage on assimilate partitioning.

This calibration gave also good results for the other experiments of Table 1a. Some examples are shown in Table 3. The model showed not only a good calculation of the positive effect of mild water shortage during flowering on seed yield and Harvest Index in 1980 and 1988, but also the growth and yield limitation due to water shortage after flowering in the experiments of 1982 was simulated correctly. However, the model showed some systematical over-estimation of the final Harvest Index, due to an over-estimation of straw weight in the last weeks before maturity. No attempt was made to simulate this feature correctly, because detailed measurements on respiration losses during maturation were not available.

Data collection for studies on yield variability

As input for the following simulation studies, data sets of crop performance, weather and soils were collected from four groups of locations in The Netherlands and Western Europe. Set 1: 14 years of experimental results on heavy clay in The Netherlands; set 2: results of 14 years on a silty loam soil with high capillary rise in The Netherlands; set 3: results of 2 years at 9 locations in Western Europe (subsequently called 'JFBT-trials'); set 4: results of 3 years on 5 regional experimental farms in The Netherlands ('MCB-trials'). An overview of the characteristics of all data sets is given in Table 1b.

To compare the simulations with experimental results, above-ground dry matter yield and seed yield at final harvest were used. In the MCB-trials, 3 different sowing times were used, classified as 'early' (beginning of April), 'middle' (end of April) and 'late' (end of May). Disease attack was classified as 'absent or mild', 'moderate' or 'severe', based on observations in the canopy. 'Absent or mild' was defined as: no occurrence of disease symptoms, or only late in senescence; 'moderate' was: clear occurrence of leaf damage during pod filling; 'severe' was: damage of canopy early in the season, and damage of pods and seed loss at final stages (Van der Schans & Van den Berg, 1991). The observed diseases were mainly leaf-spot diseases (Botrytis,Uromyces) and virus diseases (especially the Bean Leaf Roll Virus, BLRV). The above classifications were used for further analysis of residual deviations between simulated and measured yields.

Results of the studies on yield variability

Yield variability on De Bouwing 1975-1988 (data set 1)

The data set of the De Bouwing Experimental Farm (set 1 in Table 1b) shows a good agreement between measured and simulated average seed yields (measured 5.3 and simulated 5.3 ton ha^{-1}) (Fig. 4a). The yield variability, expressed as the standard deviation, was 1.3 t ha^{-1} for the measured data set and 1.5 t ha^{-1} for the simulated set. This set is subsequently referred to as the 'control' simulation. For 1979, the model showed a large over-estimation of the seed yield. A possible explanation is the fact that the 1979 crop was severely damaged by frost in spring and by hail. These effects are not included in the model, as quantified relations between hail or frost and crop damage are not available for faba beans. A linear regression of simulated versus measured yields, fitted through the origin, had a slope of 0.99 and accounted for 68% of the variation. When the data pair of 1979 was excluded from analysis, this percentage increased to 77%.

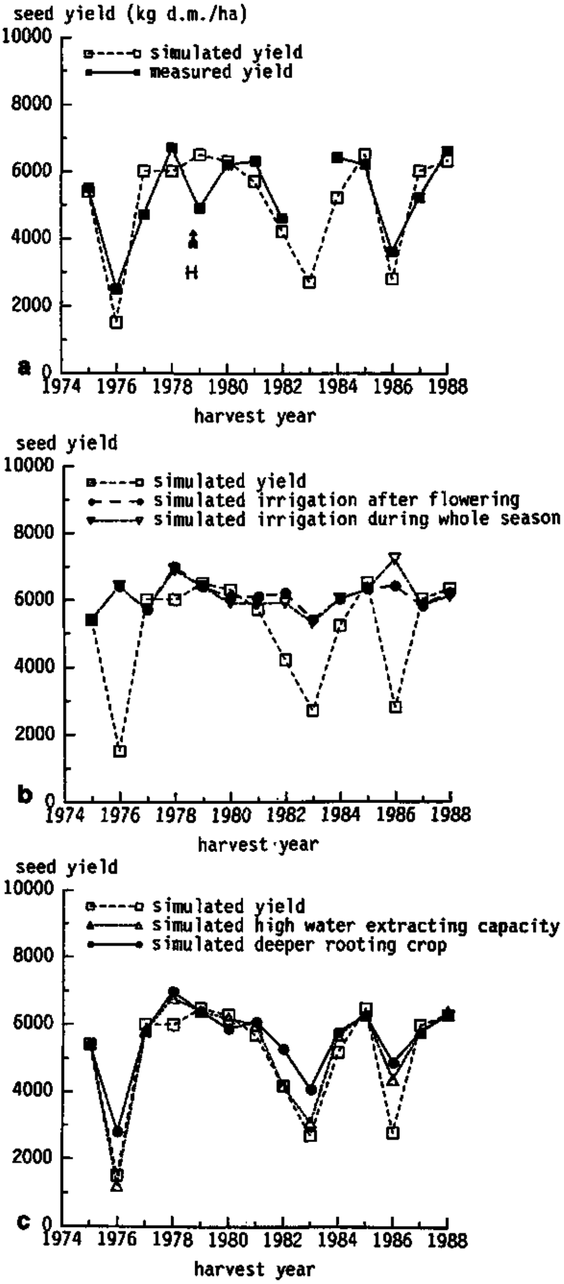

Figure 4. Simulation studies with the data set of De Bouwing 1975-1989 (data set 1). a: comparison between measured and simulated yields; b: model explorations with irrigation; c: model explorations with breeding strategies. H= hail and frost damage in 1979.

Simulation of a situation with plenty of water after the end of flowering resulted in stabilization of yield (standard deviation was 0.4 ton ha^{-1} compared with 1.5 ton ha^{-1} for the 'control' simulation) on a high level of seed production (average of 6.2 ton ha^{-1}) (Fig. 4b). Plenty of water during whole season was slightly less advantageous, with an average seed yield of 6.1 t ha^{-1} and a standard deviation of 0.5 t ha^{-1}. Only in 1986, plenty of water during the whole season gave a higher seed yield than plenty of water after flowering. This exception will be discussed later. In the model, plenty of water was realized by surplus irrigations of 20 mm d^{-1}. This results simply in a soil at field capacity. Surplus water drains off (in the model) and has no negative effect on growth.

In a second simulation study the effect of a deeper rooting crop was explored. The standard values for root growth rate (0.006 m d^{-1}) and maximum rooted depth (0.7 m) were doubled to 0.012 m d^{-1} and 1.4 m respectively. This corresponds to a larger available and exploitable water buffer. Compared to the 'control' simulation, this resulted in an increase of average seed yield to 5.7 ton ha^{-1} and a reduction of variability (standard deviation = 1.0 ton ha^{-1})(Fig. 4c). Increasing only the root growth rate or only the maximum rooted depth showed almost no effect compared to the 'control' simulation.

In a third study, the root growth rate and the rooting depth were kept at their original values, but now it was assumed that a faba bean crop could be 'breeded' with a soil water extraction capacity comparable to sorghum and sugar cane (Driessen, 1986). In the model, this is expressed as a change of the water uptake characteristics of the crop. It means a doubling of the average soil water content range between field capacity and the critical soil water content below which actual crop transpiration is reduced. Compared to the 'control' simulation, the average seed yield increased only to 5.4 ton ha^{-1} and the standard deviation remained 1.5 ton ha^{-1} (Figure 4c).

Yield variability on De Eest 1976-1989 (data set 2)

In contrast with the results for De Bouwing, the data set of De Eest (set 2 in Table 1b) showed little agreement between measured and simulated seed yields (Fig. 5). The measured average seed yield (6.4 t ha^{-1}) was underestimated by the simulation (5.6 t ha^{-1}) and the measured variability (standard deviation 1.0 t ha^{-1}) was overestimated (1.4 t ha^{-1}). Moreover, a linear regression fitted through the origin accounted for less than 1% of the variation. A regression not fitted through the origin accounted for only 10% of the variation. No data pair could be excluded from analysis for specific reasons.

The soil of De Eest can provide the crop with important amounts of capillary rising ground water. A capillary supply of 2 mm d^{-1} is possible at a distance of 1.3 m between the ground water level and the bottom of the rooted zone (this is called the 'Z-value'). The ground water level at De Eest is about -1.2 m from the soil surface in normal years and never falls below -2 m, not even in extremely dry years (J.Sinke, pers. comm.).

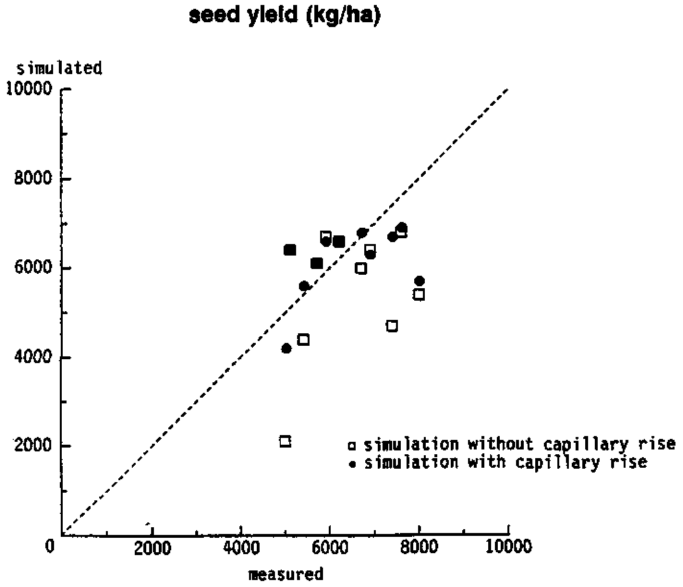

Figure 5. Measured versus simulated seed yields of the data set of De Eest 1976-1989 (data set 2). Open squares: standard simulation; closed circles: explorative simulation with 'capillary rise' with a maximum of 5 mm d^{-1}.

The process of capillary rise is not included in the model, but the effect of capillary rise was explored in a rough and simple way. It was assumed that a negative linear relation exists between the averaged soil water content of the upper 70 cm of the soil profile and the additional water supply by capillary rise from deeper soil layers. The maximum capillary water supply was assumed to be reached at the permanent wilting point. To avoid complex adaptations of the model, the additional water was supplied at the top layer of the soil. For each year at De Eest, five simulation runs were carried out with amounts of maximum 'capillary water supply' of respectively 0, 5, 7.5, 10 and 15 mm d^{-1}. The largest improvement of correlation between measured and simulated seed yields was reached with a maximum capillary rise of 5 mm d^{-1}, and these results were included in Figure 5. The simulated average seed yield increased from 5.6 t ha^{-1} to 6.2 t ha^{-1} (measured: 6.4 t ha^{-1}) and the standard deviation decreased from 1.4 t ha^{-1} to 0.8 t ha^{-1} (measured 1.0 t ha^{-1}). The percentage of variation accounted for increased from 10% to 21%.

Yield variability in JFBT-trials 1985 and 1986 (data set 3)

Analysis of the data from the 9 West-European JFBT-locations (set 3 in Table 1b) showed that a linear regression of simulated versus measured seed yields, fitted through the origin, accounted for only 12 % of the variation. Figure 6 shows that for 6 out of 8 locations, simulated values showed almost a one-to-one relation with the measured values of 1985 and 1986. Yields were strongly overestimated for the locations at Dundee and Roskilde. It is not likely that these deviations are due to effects of low temperatures at these northern locations. The effects of temperature (on development rate, photosynthesis and respiration) are included in the model. Dundee 1985 and 1986 and Roskilde 1985 showed high average values for lodging (5 on a scale of 1 =no lodging, to 9 =severe) and damage by Botrytis fabae was observed. These effects are not included in the model, as quantified relations between lodging or diseases and crop damage are not available for faba beans. When these locations were excluded from analysis, a linear regression fitted through the origin showed a slope of 1.0 and accounted for 81% of the variation. The average of the simulated seed yields over all locations and both years (4.5 t ha^{-1}) was higher than the measured value (3.9 t ha^{-1}). The simulated variability was only slightly overestimated, with a standard deviation of 1.4 t ha^{-1} for the simulated yields and a standard deviation of 1.2 for the measured yields. The relative standard deviation for simulated and measured yields was equal (30 %).

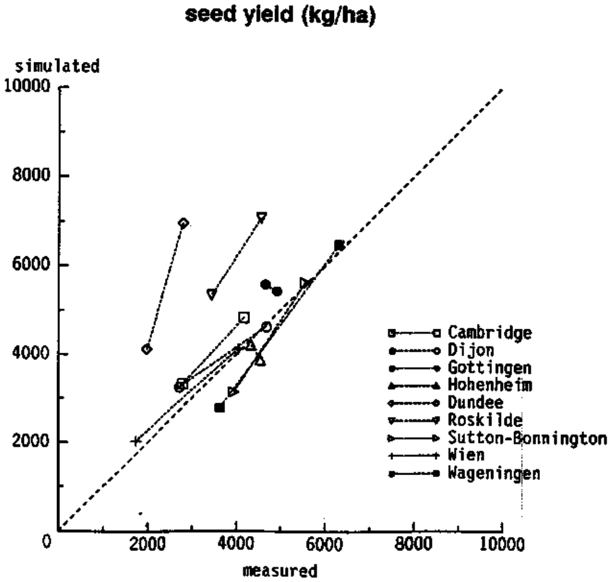

Figure 6. Measured versus simulated seed yields of the data set of 9 locations in Western Europe 1985 and 1986 (data set 3).

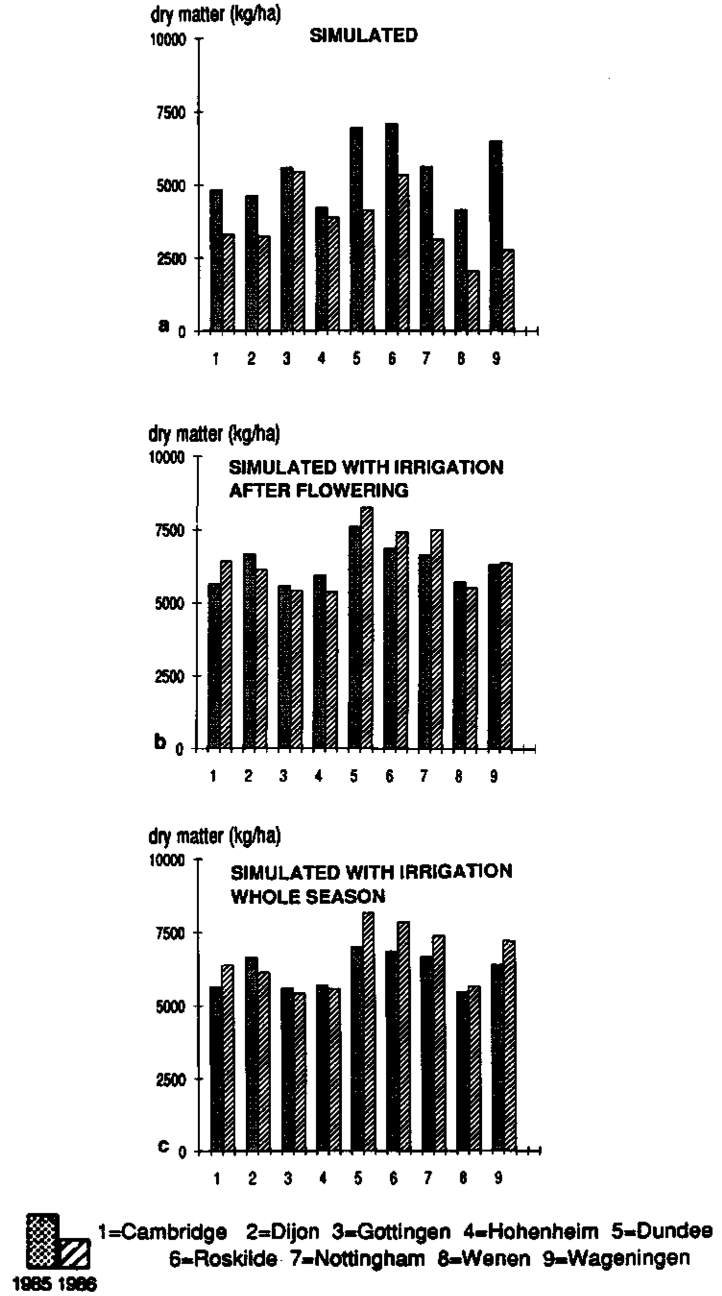

Figure 7. Simulation studies with the JFBT data set of 9 locations in Western Europe, 1985 and 1986 (data set 3). a: simulated yields; b and c: model explorations with irrigation.

In an exploration with plenty of water after the end of flowering, the model simulated a large reduction in variability of seed yield (standard deviation = 0.8 ton ha^{-1}) and a higher average seed yield (6.4 ton ha^{-1}). This was mainly due to the fact that the irrigations enhanced the low yields of 1986 (compare the 1986 data in the Figures 7a and 7b). Actually, the growing season of 1986 had less rainfall and higher temperatures than 1985 at most locations. Averaged over the locations, the precipitation rate of June and July was 150 mm in 1985 and 90 mm in 1986. An exploration with plenty of water during the whole season resulted also in an average seed yield of 6.4 t ha^{-1} and a standard deviation of 0.8 t ha^{-1} (Fig. 7c). At some locations, seed yields with plenty of water after flowering were slightly higher than with plenty of water during the whole growing season (compare Figures 7b and 7c: especially Dundee 1985, but also Hohenheim 1985 and Wien 1985). But, for some other locations the reverse effect was simulated (Figures 7b and 7c: Roskilde 1986, Wageningen 1986). It is concluded that plenty of water after flowering is almost as effective for yield stabilization as plenty of water during the whole season, but does not always give the optimum seed yields.

Exploration of optimum soil water content for seed production of faba beans

Next, the required soil water contents in different development stages for optimum seed yield were explored. Fixed values for soil water content were used as input 'forcing functions' for the model and simulation runs were made, varying these values in the development periods 'during flowering' and 'after flowering'. The soil water content 'before flowering' was kept at field capacity in all runs and was allowed to change immediately after the start of the next development period. The first results showed that the best stages for changing soil water contents for optimum seed production, were not exactly the beginning and end of flowering, but the start of the first pod development (about one week after onset of flowering) and the point at which the assimilate partitioning to reproductive organs exceeds the flow to stems and leaves (about two weeks after end of flowering). In subsequent runs, these stages were used.

Figure 8 shows the results for the clay soil of experimental farm De Bouwing, with a volumetric soil water content of 0.40 cm^3 cm^{-3} at field capacity and of 0.22 at permanent wilting point. In this example, the climatic data of 1976 were used. The total dry matter yield increased with increasing soil water content until a level at 0.32 cm^3 cm^{-3} either during or after flowering. However, the curve of simulated final seed yields showed an optimum at an average soil water content during flowering of 0.30 cm^3 cm^{-3}. The simulated seed yields increased with increasing average soil water content after flowering.

When other years were simulated, the general shape of the resulting curves was the same as in Figure 8. However, the optimum soil water content during flowering was different for each of the years (1976-1988) and varied between 0.27 and 0.32 cm^3 cm^{-3} for this soil type (Fig. 9). Seed yield reductions up to 500 kg ha^{-1} were found with super-optimum water contents during flowering. Sub-optimum water contents during flowering resulted in larger yield reductions.

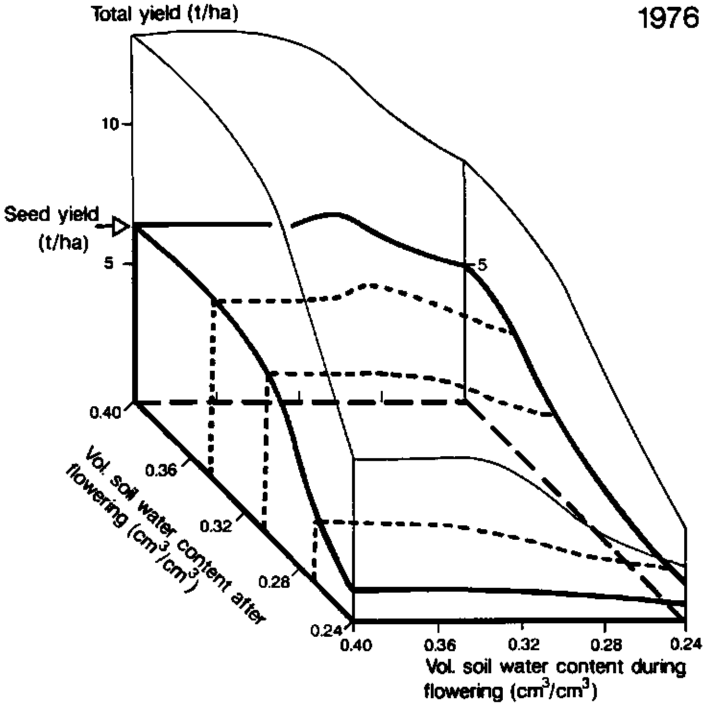

Figure 8. Simulation studies with various 'fixed' soil water contents during flowering and after flowering. Climatic and soil data for De Bouwing, 1976. Vol. = volumetric.

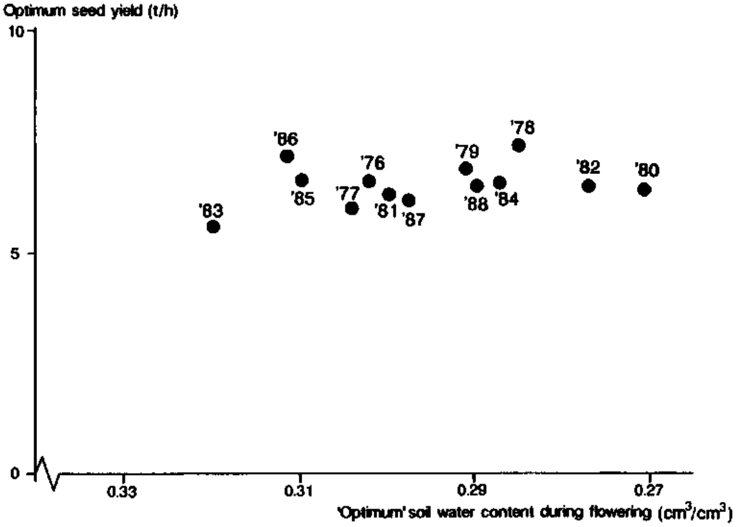

Figure 9. Simulated soil water contents during flowering, required for optimum final seed yields for De Bouwing 1976-1988 (data set 1). The water content after flowering was kept at field capacity in all years.

In all the years, final seed yields increased with increasing average soil water contents after flowering, but showed no further increase with soil water contents higher than 0.32 $cm^3\ cm^{-3}$. Simulation results with other locations and soil types were comparable with those presented in the Figures 8 and 9.

Yield variability in the MCB-trials 1987-1989 (data set 4)

Finally, the data from the 5 regional farms in the Netherlands (set 4 in Table 1b) were analysed with the model. In contrast with the other trials, which were kept as healthy as possible, these 'MCB-trials' were practice-oriented (including treatments with different sowing times), with disease protection as commonly advised for practice. The growing seasons of 1987 and 1988 were 'wet', with more precipitation than normal in June and July (1987) or July and August (1988). The season of 1989 was warmer than normal, but periods of extreme water shortage did not occur (Van der Schans & Van den Berg, 1991). When all the results of the MCB-experiments were plotted as one group, a linear regression between measured and simulated results could not be fitted through the origin. Even a regression line not fitted through the origin accounted for only 19% of the variation and showed a large deviation from a one-to-one relation. From field observations it appeared that diseases might have had important effects in these trials. Disease damage is not included in the model, as relations between diseases and crop damage are not yet quantified for faba beans.

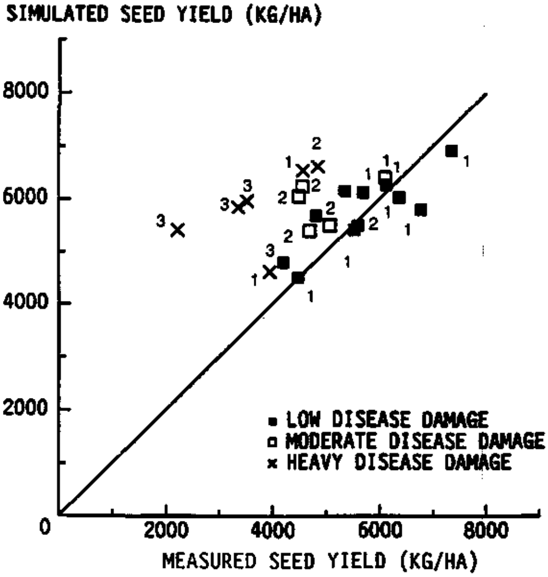

Figure 10. Simulation studies with the MCB data set of five regional experimental farms in 1987-1989 (data set 4). The data are classified in three groups of disease attack. The small numbers refer to the different sowing times (1='early'; 2='middle'; 3='late').

However, the measured yields (with possible disease damage) could be compared with simulated yields (without the effect of diseases). For this comparison, the results were classified according to the field observations about disease attack of the foliage. Now it appeared that measured and simulated yields in the group with 'absent or mild' disease attack agreed well, with only small deviations from the diagonal, up to about 1 t ha^{-1} (Fig. 10). In this group, a linear regression accounted for 32% of the variation (when it was fitted through the origin) or for 67% (when it was not fitted through the origin). In the group with 'moderate' disease attack, the deviations increased to 2 t ha^{-1} and with 'heavy' disease attack even to 3.5 t ha^{-1}. Figure 10 shows also, that the group with 'absent or mild' disease attack consisted mostly of data from crops which were sown 'early', at the beginning of April. The largest deviations in the group with 'heavy' disease attack were data from crops which were sown 'late', at the end of May. However, also some crops sown at the beginning or at the end of April belonged to the group with 'heavy' disease attack (Fig. 10).

Discussion

The regressions of simulated versus measured seed yields (excluding some disturbances due to hail or lodging) accounted for almost 80% of the variation of the data sets of De Bouwing (data set 1) and the West-European JFBT-locations (data set 3). This means that a large part of the observed yield variability is caused by variability of the input values in the model: radiation, temperature, air humidity, wind speed, rainfall and soil characteristics. Our results show that a large yield variation range is caused by the variation of these input data: for the West-European JFBT locations, the yield variation range due to the factors included in the model was 4.5 t ha^{-1}. (This is calculated from the difference between the lowest and the highest yield data on, or close to the diagonal in Figure 6.) These results were based on data sets of 9 locations, but only for 2 contrasting years, as weather data sets of many years were not available. The weather data set of 14 years for De Bouwing can be seen as an example for the variability in longer term data, but only for one location. Anyhow, as the yield variation range of the JFBT-locations was almost as large as that of De Bouwing (Fig. 4), this indicates that those two data sets covered at least an important part of possible variation in weather and yields in Western Europe.

In the simulation studies, irrigation increased the average yield by 15% for De Bouwing and 40% for the West-European JFBT locations and reduced the yield variability by 75% and 60%, respectively. That means that water supply is the major factor affecting yield variability. Irrigation stabilized the seed yields at an average level of about 6 t ha^{-1}, due to yield increments in dry years, not only for one location (Figure 4, De Bouwing), but for many locations in Western Europe (Figure 7). The simulation studies support that variability in rate and distribution of water supply between years is a major cause of variability in yield of faba beans grown in Western Europe.

The model does not account for effects of capillary rising ground water. The simulations accounted for less than 10% of the variation and underestimated the average seed yield with 0.8 t ha^{-1} for the location De Eest (data set 3; Figure 5), where capillary rise is likely to be important, due to soil type and ground water table. Our model was able to support the importance of capillary rise, using explorations with additional 'capillary water supply'. These showed an improved agreement between measured and simulated values of average seed yields and yield variability (Fig. 5). The percentage of accounted variation increased to 20%. However, this value is still very low and a regression fitted through the origin was not possible. This low value was mainly due to a measured top seed yield of 8 t ha^{-1} in 1982, which was not reached in any of the simulations for 1982. If this value was excluded, the percentage of accounted variation increased to 61% (regression not fitted through the origin) or 24% (fitted through the origin). Our method simulating 'capillary rise' was rough, as it was not based on independently quantified processes. Moreover, it was not realistic, as we added the additional water to the top layer of the soil, to avoid complex adaptations of the model. Models which simulate capillary rise in a physical proper way are available (Penning de Vries et al., 1990). However, the calibration of such models can be a bottle-neck, although improvements have been made (Woodhead et al., 1991).

At the other hand, it can be questioned if a model including capillary rise is needed for simulations in Western Europe. De Eest has a 'Z-value' (see before) for 2 mm capillary water supply per day of 1.3 m, with a ground water table of -1.2 m. Locations, with such a high capillary rise, combined with an almost optimum and constant ground water table, are scarce in Western Europe. For instance, the Z-value for De Bouwing is only 40 cm.

The presented results show that crop management methods and breeding strategies which reduce or avoid water shortage are very important. The simplest solution would be to grow faba beans on soils with high capillary rise, such as De Eest. In fact, this location was the highest-yielding location in almost all the JFBT trials from 1977 onwards (cf. Dantuma et al., 1983; Ebmeyer, 1984). However, as these soils are scarce, this solution is not very realistic.

Optimization of irrigation strategy is a second possibility. As simulation studies for De Bouwing did not differ essentially from our studies with other soil types without capillary rise, the results of De Bouwing will be discussed as an example. Figure 8 shows that, after flowering, the soil water content in the clay at De Bouwing has to be higher than 0.32 cm^3 cm^{-3} for both maximum seed yield and maximum total yield. Seed yield decreases linearly with lower soil water contents after flowering. During flowering, however, the required soil water content for optimum final seed yield is lower than for maximum total yield. For De Bouwing 1976, the simulated optimum value during flowering was 0.30 cm^3 cm^{-3}. Comparable simulations for 1975-1988 showed, that super-optimum water contents during flowering can reduce final seed yields with up to 500 kg ha^{-1}.

However, sub-optimum water contents during flowering can result in larger seed yield reductions than super-optimum contents (Figure 8). In fact, this Figure shows that, when the soil water content during flowering becomes much lower than the required optimum, onset of irrigation after flowering is too late. This might explain why in some exceptions, such as Wageningen 1986 (Figure 4) and Roskilde 1986 (Figure 7), the seed yields with plenty of water during the whole season were higher than with plenty of water after flowering. The spring of 1986 was in fact very dry. So, although postponement of irrigation till after flowering has a positive effect on dry matter distribution to the seeds (Figure 2, Table 3), it does not always give higher final seed yields than irrigation during the whole growing season.

From the previous sections it is concluded that, in general, the explorative simulation studies (Figures 4, 6, 7 and 8) support the conclusions from experimental work (Grashoff, 1990a and 1990b), that irrigation, applied mainly after flowering, can be as effective for yield stabilization as irrigation during the whole season. Defining and maintaining the 'optimum level of mild water shortage during flowering' needs further attention. The simulations indicate that these conclusions can be generalized to other weather conditions, soils and sites.

Grashoff (1990b) stated that simulation studies might help to define the critical soil water values for optimizing water supply. Figure 8 shows that the model can quantify the soil water content representing an 'optimum level of mild water shortage during flowering' (Grashoff, 1990a) . Figure 8, however, holds only for a single year. Figure 9 shows that this optimum itself is not constant. For the location De Bouwing, it varies between 0.27 and 0.32 cm^3 cm^{-3} for different years, corresponding to pF-values of 3 and 2.3, respectively. This is caused by the fact that daily temperature, air humidity and windspeed, which differ for the flowering period in each year, affect the daily potential transpiration TRP. In our model concept, this modifies the critical soil water content at which TRAN/TRP starts to decrease. Consequently, also the soil water content for optimum dry matter partitioning during flowering differs for each day and year and a 'general' optimum value cannot be defined. Nevertheless, the Figures 8 and 9 indicate, that a 'preferred' range of soil water contents during flowering can be defined which do not always give optimum yields, but stabilize yields on an acceptable level. For the soil of De Bouwing, the soil water content during flowering should be kept up or above the average value for optimum seed yields (0.30 cm^3 cm^{-3}). After flowering, water content should not be lower than is required for maximum total yields (for De Bouwing 0.32 cm^3 cm^{-3} in all years). It appears that the simulated 'target' soil water content during flowering is only slightly lower than the simulated 'target' water content after flowering. Obviously, under very dry weather conditions irrigation is not only needed after flowering, but even during flowering.

A third possibility to optimize faba bean yields was shown in the evaluation of some breeding strategies for ideotypes. A doubling of the rooted soil depth, combined with a doubling of the root growth rate, decreased the variability by 35%. That indicates that this breeding strategy is less effective for yield stabilization than irrigation activities are. Nevertheless, from an economical or practical point of view, breeding for deeper rooting varieties has some advantages, as irrigations are expensive or even simply not possible in some situations. Breeding for deeper rooting varieties may be more effective than breeding for a faba bean with 'sorghum-like' water extraction capability, which had no effect on yield variability at all (Fig. 4c). With a higher extraction capacity, the model calculates a higher growth rate in the early growing season of a dry year. But, at continuing water shortage, the soil water buffer is exhausted by the crop before the seed production is completed. That explains why the final seed yield can be even lower with higher extraction capacity (Figure 4c, 1976). In our simulations was not accounted for extra carbohydrate investments in a higher rooting density to obtain a higher water extraction capacity. Van Keulen et al. (1975) showed that rooting density is not likely to be the major limiting factor for the water extraction capacity.

The previously discussed management activities and breeding strategies dealt with water shortage. In our model, the nitrogen balance of the crop and processes concerning nitrogen fixation are not included. Nevertheless, the simulated yields agreed well with the measured yields, for many years and weather conditions (Figure 4) and at many locations (Figure 6). This indicates, that in a simulation model for a leguminous crop, the inclusion of, for instance, effects of water shortage on nitrogen fixation (Roughly et al., 1983; Shamsun Noor et al., 1989) are not needed, at least not explicitly.

However, other important factors were found. In the regressions shown before, some data pairs were excluded from analysis (Fig.4a, 1979; Fig. 6, Roskilde, Dundee). These data pairs deviated due to effects not accounted for in the model, like hail damage, lodging and diseases. These were interpreted as accidental disturbances and therefore excluded. The analysis of the MCB-data (set 4) clearly shows that this is an oversimplification of the situation in practice. The simulation model did not account for any substantial part of the variation in the total MCB-data set of five experimental farms in The Netherlands.

Nevertheless, Figure 10 shows that the deviation of measured and simulated yield pairs from the diagonal increased from 1 t ha^{-1} for the group of 'absent or low' disease attack to 3.5 t ha^{-1} in the 'severe' group. This shows that the model also helps to discover or estimate yield reductions due to factors not accounted for in the model. Apparently, in the MCB-data set, diseases were more important for yield variability than water shortage. An important question is why diseases were more important than in the previous data sets. A tendency was found that disease damage increased with later sowing times in the MCB-trials (Fig. 10). Fungi disease pressure usually increases with humid conditions in the season and these conditions occurred especially during July in both 1987 and 1988. At a certain calendar date the late sown crops are usually in an earlier development stage as the early sown crops. In this way, diseases may be more harmful in the late sown crops, as they may cause damage during a longer development period. However, there was disease protection in the MCB-trials, but this was obviously not effective enough. This is somewhat in contrast with opinions in the Netherlands Extension Service some years ago, that it was possible to control the most common diseases and pests in faba beans (chocolate-spot, rust, aphids) in an effective way. A first reason for this contrast might be, that the attack of the Bean Leaf Roll Virus (BLRV) during 1987-1989 was more important than in previous years, due to warm winters and early increase of aphid populations. Secondly, crop protection might have been more intense and preventive in trials at De Bouwing and in the JFBT, than in the practice oriented MCB-trials.

The general conclusion is that water shortage is in many cases the major limiting factor for yield in Western Europe and causes considerable yield variation. However, crop growth reducing factors such as diseases may sometimes overrule these effects (Fig. 10). The present simulation study has shown how control of water availability could stabilize faba bean yields within an acceptable range in many environments. In addition, the simulations indicate that disease control is then becoming even more essential.

Acknowledgements

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General discussion

General discussion

In the Dutch List of Varieties (RIVRO, 1990), starting at the issue of 1990, the following sentence was included in the chapter about faba bean management: 'A period of mild water shortage during flowering, followed by plenty of water after flowering provides a good ratio between reproductive and vegetative plant parts for a high seed yield'. This statement was based on the results of our study (pers. comm. I. Ouwerkerk, CPRO). Although it is a good 'message in a nutshell', it also provides many questions: Is water shortage the only major factor which affects yield variability? What are the further impacts of our study on applied and fundamental research? What is the value of our study for the agricultural practice? In the following sections these questions will be discussed.

Is water shortage the only major factor which affects yield variability?

Two types of factors are distinguished. Factors that *limit* crop yields (like water shortage), and factors that *reduce* crop yields due to damage (like diseases). It is already discussed in Chapter 4 that water shortage is the major yield *limiting* factor. However, the absence of water limitation is not a simple guarantee for high actual yields. Diseases (especially foliar and soil-borne fungal diseases) may sometimes *reduce* the actual yields under optimum water supply (Chapter 4). An interesting question for further research is why these yield reducing factors are a larger problem than was expected before (Dekker, 1985a, 1985b). This may be caused by the following reasons.

Firstly, faba beans were hardly grown in the years around 1973, so it was almost a 'new' crop. Since then, the knowledge has increased about the high crop potential and the importance to avoid water shortage as the major yield *limiting* factor. After removing this bottleneck, the problems with a next bottleneck, like the yield *shortening* factors, become more visible. This is generalizable to other 'new' crops, like hemp. When hemp was mentioned some years ago as an interesting alternative, Boeringa & Höbaus (1984) reported that hemp did not have problems with pests and diseases at that time and had average yields of 10 t ha^{-1}. However, recent research (Meijer & de Meijer, 1990) showed that hemp can have stem yields of 11-12 t ha^{-1}, but they found yield reductions of more than 5 t ha^{-1} due to high disease pressure (!) in combination with cool weather.

Secondly, when wheat is replaced by faba beans or peas in crop rotation, this is an increase of the frequency of dicotyledons in the crop rotation. This can increase problems with the group of soil-borne diseases specific for dicotyledons (Mulder, 1987). Indications have been found for increasing problems with *Verticillium dahliae* in crop rotations including pea or faba bean. This might decrease the yield of potatoes (Hoekstra et al., 1987).

What are the further impacts of this study on applied and fundamental research?

The agricultural question 'is water supply a major factor in yield variability of faba beans?' is answered in our study by integrating fundamental knowledge (plant/water relations) in a mechanistic model, and using this model for interpretation of field data. This methodology has impact for both the 'fundamental' and the 'applied' research. In the following sections this is discussed.

Amount of water supply or water supply pattern?

Amount of water supply and water supply pattern, both affect the yield variability, but they differ in importance. In a statistical analysis, the *amount* of water supply accounts for the largest part (about 80%) of seed yield variation (Chapter 2). The model calculations support this large importance of the amount of water supply for yield variability (Chapter 4). Differences in water supply *pattern* account for only about 10% of the seed yield variation (Chapter 2). This is also supported by the model, as it calculates that the positive effect of mild water shortage during flowering on seed yield will not be more than about 500 kg ha^{-1} (Chapter 4).

Although the quantitative effect may be small, this conclusion illustrates the fundamental observation that a physiological 'stress' is not always disadvantageous. With some restrictions (in this example: only mild stress, and only during flowering) stress can improve the reproductive productivity of a crop. This positive effect of 'stress' is not only found in faba beans; in one of the next sections our results will be compared to those in other crops.

The mechanisms behind this positive effect of stress are largely unknown. This problem was formulated in a humoristic but clear way: *can we give a better explanation than that it is a 'Calvinistic' behaviour of a crop: 'a little stress is good for you' ?* (D. Mackerron, SCRI, pers. comm.).

Our study provides a more 'physiological' answer to this question. For faba beans, this answer consists of two parts. Firstly, water shortage during flowering enhances the start of pod and seed growth and the senescence of the crop; secondly, water shortage reduces the daily dry matter partitioning to the stems and leaves and consequently enhances the growth of the young pods and seeds (Chapter 1 to 4). The first part of this answer is a specific form of the general observation that several environmental factors (temperature, daylength, water shortage) can speed up or reduce the rate of phenological development. However, phenological development is still not understood enough to provide an explanatory model of this process; hence, in many models a 'descriptive' way of modeling is used (Penning de Vries et al., 1989). We used such a descriptive way, by including a positive effect of decreasing relative transpiration on development rate (Chapter 4), *in addition* to the effect of *air temperature* on development rate. This way of modeling implicitly assumes the physiological mechanism that water shortage causes stomatal closure and a consequent increase of canopy temperature. In wheat it was found that water shortage increased the *canopy temperature* (Blum et al., 1982), which in its turn enhances the development rate. In explorative simulation studies for wheat this could account for the complete positive effect of water shortage on development rate (Van Keulen & Seligman, 1987; Van Keulen, pers. comm.). Our 'descriptive' way to model the effect of water shortage during flowering on development rate could account for the enhanced start of pod and seed growth. It could *not* account for the higher final seed yield (Chapter 4), as it also enhances the senescence of the crop. Thus, the period of pod filling is equal or even reduced. It is only a *part* of the answer to the above question.

The second part of the answer is a *possible physiological mechanism* how mild water shortage during flowering has a positive effect on *daily* dry matter partitioning towards reproductive organs and on final seed yield. In Chapter 3 and Chapter 4 it is discussed how mild water shortage reduces the growth of new stem parts and leaves; consequently, the assimilates which cannot be incorporated in new vegetative organs flow down towards the developing young pods and seeds. In this way, our study highlights some fundamental aspects of the mechanisms behind dry matter production and dry matter partitioning. In an overview, Marcelis (1992) describes 6 main groups of theories about dry matter partitioning. The mechanism presented in our study (Chapter 3) fits well with the theory that assimilate partitioning is regulated by the *proportion* of the potential growth rates of the various sinks (leaves, stems, pods and roots). Wolswinkel (1985) used the term sink strength to describe the competitive ability of a sink to attract assimilates. This is quantified by the potential growth rate of a sink, i.e. the growth rate under conditions of non-limiting assimilate supply. *In our mechanism, mild water shortage reduces turgor and the expansion of stems and leaves and, consequently, the potential growth rate of stems and leaves and thus their sink strength.* If the potential growth rate of pods and seeds is not or less affected by water shortage, this results in a higher ratio between the 'reproductive' sink strength and the sink strength of stems and leaves and thus in a stimulated reproductive growth. The way in which we modeled this effect (Chapter 4) is a simplified form of this mechanism: a decreasing relative transpiration results in a sharp (exponential) decrease of the amount of assimilates flowing to the stems and leaves. The surplus of assimilates flows to the pods and seeds. This effect accounted for a higher final seed yield with mild water shortage during flowering.

A question for further research is if and why the sink strength of the pods and seeds is not or less affected by water shortage in the (rest of the) plant. Grashoff (1981) found that the water potential of leaves at the canopy level where the pods develop is less negative than that of the top leaves. This indicates that under mild water shortage, the turgor and thus the expansive growth of young pods can be less reduced than that of the vegetative top. However, the water relations of the pods and the seeds itself are still obscure (D.R. Verkerke, CABO-DLO, pers. comm.). The xylem pathway between sink regions and transpiring leaves is much less developed than the phloem pathway, or even discontinuous in many species (Wolswinkel, 1990). In developing grains of wheat, grain water status is practically independent of whole-plant water status (Barlow et al., 1980). Probably, this explains why water shortage in the rest of the plant may not affect the potential seed growth. The accumulation of assimilates in the seeds is a complex process which involves 'unloading' of the phloem vessels, an apoplastic assimilate transport from the seed coat towards the seeds itself and an 'import' into these seeds (Wolswinkel, 1985). Probably, these processes more or less autonomously determine the sink strength of the seeds, without a reducing effect of water shortage (P. Wolswinkel, University of Utrecht, pers. comm.). The value of these research topics is not limited to a crop with a small economic importance like faba beans. In fact it can provide information about the effects of external factors on the mechanism of dry matter partitioning of all those crops of which the specialized storage organs are used for food, feed or other purposes.

Comparison with effects of water supply pattern in other crops

Examples of positive effects of stress on dry matter partitioning to storage organs are found in many 'indeterminate' or 'semi-determinate crops', which have a substantial period where growing stems and leaves compete for assimilates with the storage organs (like tubers in potato, lint bolls in cotton, seeds in sunflower and faba beans). Not only relative partitioning to these organs can be stimulated by water shortage, but, like in faba beans, there are examples that mild water shortage results in absolutely higher yields of storage organs.

In potato, Krug & Wiese (1972) showed that water shortage at a level of 20-30% of the water holding capacity (WHC) of the soil during 12-36 days after emergence followed by wet conditions (80-100% WHC) resulted in higher tuber yields and in higher above-ground yields. This was partly due to a longer period of high growth rate and partly to an increased net assimilation rate of 'drought hardened' plants compared to plants from the 'wet' treatment. The mechanism of this drought hardening effect probably could be a slower stomatal response to decreasing water potential (Van Loon, 1981). Obviously, this differs from our measurements in faba beans, where mild water shortage enhanced final seed yield, but always had negative effects on total dry matter yield. Struik & van Voorst (1986) found that water shortage in the stolon environment during tuberization enhanced the initiation of stolons and tubers. This treatment resulted in more large tubers per plant because there were more large tubers on the early-initiated stolons. However, this treatment caused a minor reduction in total tuber yield.

In sunflower, Sobrado & Turner (1986) found that during mild water shortage, assimilate partitioning to the stems decreased but partitioning to reproductive organs increased.

It is interesting to compare our results with those for cotton. For this crop, it was found that high availability of water and/or nitrogen resulted in excessive vegetative development, with associated reduction in lint yield. Plant height as measure of cotton vegetative growth, was linearly related to amount of applied water, but lint yield showed an optimum curve, with a maximum yield at intermediate levels of water supply (Grimes et al., 1969a, 1969b). Highest lint yields are obtained when the first postplanting irrigation is withheld until leaf water potential reaches -1.9 MPa. This supplies the optimum mild level of water shortage (for cotton!), sufficient to reduce plant height and the rate of leaf expansion (Grimes & Yamada, 1982; Grimes et al., 1978). Irrigation scheduling based on these results, is used in California nowadays to control vegetative growth and optimize lint yields (Kerby et al., 1990). It is concluded that our mechanism about the effects of water shortage on dry matter partitioning via turgor decrease and reduction of vegetative sink strength, agrees well with these results for cotton. It has to be added that in cotton other effects of water shortage may interfere with the effects described above. Thomas et al. (1976) showed that stomatal response of cotton plants to decreasing soil water potential was also altered by previous water shortage. Stomata on the lower leaf surface of preconditioned field grown plants remained open to lower leaf water potentials (-2.8 to -3.0 MPa) during final water shortage, than did equivalent stomata of plants which were not preconditioned (-2.2 MPa).

Feasibility studies

Our study has also impacts on more applied research. The developed model for faba beans provides a valuable instrument for 'feasibility studies'. In general, models which are based on physiological processes can be used for these studies. In such studies, the input values to the model and/or rate coefficients or other system parts of the model are changed and the effects are explored by simulations. Examples are explorations of yield level and yield variability under various climate conditions and/or with suggested crop management activities and new breeding strategies. In the following sections, some of these aspects are discussed in more detail.

1-exploration of yield level and yield variability in different climate regions. Simulation models are suited to assess the potential and actual yield level and yield variability in different geographic regions. For such studies, the model input has to consist of long term historical weather and soil data of those different regions. Our model is suited for such studies, or at least the parameter set which we developed for faba beans can be used in a model like WOFOST (Van Diepen et al., 1989). The simulation model WOFOST, linked with a Geographical Information System, has been used already in this way to assess potential and water-limited production of several crops in different regions of the EC. This study included faba beans, but our parameter set was not yet used. Faba bean yields were derived from the simulated wheat dry matter production. It was assumed that in the potential production situation, faba bean yields were 10% lower than wheat yields and in the water limited situation, linearly related to the precipitation deficit, 15-80% lower. This assumption was based on our regression analysis on measured seed yields in Chapter 2 (De Koning et al., 1992). The studies for wheat showed, that, without increasing the area under cultivation in the EC, the production volume of this crop can still increase with 65% under water-limited and with 120% under potential production conditions (Van Lanen et al., 1992). These feasibility studies provide the basic information for further agro-economic evaluation of land use and farming systems. This will be discussed later, in the section on impacts for agricultural practice.

2-feasibility studies for breeding strategies. For these studies, not the model input is changed, but 'gene analogs' are built into the model. These gene analogs take the form of rate coefficients or other system constants. Whisler et al. (1986) state that models with complete arrays of gene analogs in system constants have yet to be assembled. Nevertheless, some major physiological processes are represented by model characters, which may be 'inheritable'. In our study, some examples have been shown (Chapter 4) of the use of the model in evaluating particular plant characters like root growth rate, rootable depth and water extraction capacity. In this way, the model approach might help breeders in a fast exploration of the potential effectiveness of particular breeding strategies. With reference to the examples of Chapter 4, in this section two general remarks are made.

Firstly, it has to be realized that the reliability of model evaluations of physiological plant characteristics depends partly on the implicit presuppositions that were made. For instance, in the explorations with a deeper rooting crop it was presupposed that deeper roots are possible without an increased investment of assimilates into the root system. In general, this shows that the practical impact of the explorations is of no value for breeders without a detailed analysis of all those presuppositions. This might be one of the reasons that examples of models which helped to anticipate yield increases from particular breeding programmes are still scarce. Nevertheless, Whisler et al., (1986) identified two instances where physiological process models have helped to anticipate yield increases from particular breeding programmes. The model GOSSYM (Baker et al., 1983) correctly predicted increased cotton yields with increased stomatal sensitivity under dryland conditions. In the context of our study, it is interesting that GOSSYM also correctly suggested a yield advantage in irrigated conditions to cotton types with strongly reduced vigour of leaf growth ('okra-types') and a consequent more efficient dry matter partitioning towards the fruits. In normal rain-fed conditions, a cotton type with *intermediate* vigour of leaf growth showed higher lint yields per ha, compared both to a normal type with *high* vigour of leaf growth, and to the 'okra-types' with *strongly reduced* leaf growth (Landivar et al., 1983a, 1983b).

Secondly, it can be questioned if breeders have an urgent need for physiological models. Breeders are generally pragmatic in their approach and seem ahead of physiologists, concerning the aspect of crop improvement. For instance, indications were presented (Metz et al., 1991) that the faba bean yield can be improved with 25-50%, by breeding for hybrids or 'synthetic varieties' (i.e. 'varieties' which consist of the progeny after intercrossing of a group of pure lines). Those breeding programmes use the effects of heterosis and heterogeneity and those phenomena are by far not understood in a physiological way. It is clear that breeders do not need physiologists to gain results, from this point of view. Nevertheless, some breeders indicate that it is easy to *create* heterosis, but that it is difficult to *manipulate* it into the wanted way. In this aspect, the need for physiological knowledge and modeling work to evaluate the effectiveness of physiological plant characteristics comes back into the picture. For instance, it is suggested that these promising physiological characteristics (such as deeper rooting plants etc.) can be bred into the pure lines which form the basis for a new synthetic variety (D. Stelling, University of Göttingen, pers. comm.).

3-explorations of yield level and yield variability in future climate. At present, increasing research effort is paid to assessments of the effects of future climate on crop growth. The increasing presence of CO_2 in the atmosphere may influence the earth's climate by transmitting incoming solar radiation, while partly blocking outgoing terrestrial black body radiation. This 'greenhouse' effect may cause temperature rise. Different crop physiological processes are influenced by these aspects of climate change. CO_2-increase itself affects the stomatal conductance and increases photosynthesis rate of C3 plants (Lemon, 1983; Cure & Acock, 1986) and water use efficiency (Gifford, 1979; Sionit et al., 1980). Temperature rise may increase developmental rate of the crop, which may result in an adverse effect on crop production.

Evaluation of these effects which work in contrary directions with direct qualitative or quantitative methods is difficult. Physiological crop growth simulation models may be used for such a combined evaluation, as they include many of the effects of CO_2 increase and temperature rise on the growth processes of the crop. For instance, our model for faba beans includes the quantified effects of temperature on crop development rate, leaf photosynthesis, maintenance respiration, dry matter partitioning to organs and death rate of plant organs. The effects of CO_2 concentration on the initial light use efficiency (EFF) and on the maximum photosynthesis rate of individual leaves (AMAX) are included, based on quantifications of Goudriaan & Unsworth (1990) for C3 plants. At an average temperature of 20 ^{o}C, a doubling of the CO_2 concentration results in an increase of EFF by 15% and a doubling of AMAX. A higher CO_2 concentration also affects the stomatal resistance and consequently the transpiration. Typically in C3 plants, a doubling of CO_2 reduces transpiration with 10-20% and increases assimilation with 40%. By consequence, the water use efficiency is considerably increased (Goudriaan & Unsworth, 1990).

For this kind of feasibility study, sets of historical weather data are used as a basis. Values for temperature rise and CO_2 increase are based on assessments of the Intergovernmental Panel on Climate Change (IPCC) (Houghton et al., 1990). The average temperature rise is added to the daily historical temperatures and allowance can be made to keep the relative humidity of the air unchanged. The CO_2 increase is included by simply changing the input value to the model. Hence, the effects are studied separately and combined by model simulations.

Such studies into the combined effect of these processes are already carried out for rice (Jansen, 1990) and for winter wheat (Nonhebel, 1992). As we showed that the faba bean crop is very sensitive to water shortage and has a high yield variability at the present climate, it is important to assess what may happen with these aspects in future climate. For this reason, we used the faba bean model for a feasibility study of the effects of climate change on growth and production of this crop (Grashoff et al., 1992). As a basis for the study, historical weather data of three contrasting locations (Tel Hadya in Syria, Migda in Israel and Wageningen in the Netherlands) were used. The rest of the procedure was as described above. As an example of this approach, some results are presented in the following section.

The study showed that temperature rise causes a decrease in seed yield of rain-fed crops in Wageningen and Migda (Table 1), due to a shortening of the growing season. At Tel Hadya, seed yield of rain-fed crops increases, due to an accelerated start of the reproductive phase and consequently an 'escape' from water shortage later in the season. For fully irrigated crops, temperature rise causes at all locations a decrease in seed yield, most in Migda, and smallest in Tel Hadya. CO_2-enrichment causes in all situations an increase in growth and production of faba beans, which compensates the decrease due to temperature rise. The effects are not completely additive at all locations. Yield increases due to CO_2-enrichment are much higher than the yield decrease due to temperature rise (Table 1). In Wageningen, Tel Hadya and Migda the positive net effect of the two considered effects is respectively 12%, 68%, 28% for rain-fed crops and 5%, 16%, 13% for fully irrigated crops, assuming an increase of CO_2 concentration to 460 ppm and a temperature increase of 1.7°C. Fully irrigated crops show a remarkably smaller yield variability than rain-fed crops in all the assessments on climate change (Table 1). In rain-fed crops, the variation in yield over the years stays the same as in the present climate, or it is somewhat reduced due to the reduced sensitivity to water shortage. Thus the net effects on productivity and stability due to the scenarios used for global climate change are at all locations positive. But, to obtain the optimum yield stability of the faba bean crop in future, crop management activities to optimize water supply will stay essential, like they are in the present climate. Other effects, such as for example morphological effects may overrule these physiological effects. Such effects are not taken into account in this feasibility study.

Table 1. Average seed yields (y) in t ha^{-1}, absolute standard deviation (s) in t ha^{-1} and relative standard deviation s(%) in %, for standard simulations, simulations with temperature rise (T+1.7 and T+3.0), simulations with increased CO2 concentration (C460 and C700) and simulations with temperature rise and CO2 increase combined in two scenario's for 2030 and 2080 (SC 2030 and SC 2080). All simulations are presented for rain-fed and fully irrigated crops

Locations and runs	rain-fed			fully irrigated		
	y	s	s(%)	y	s	s(%)
Wageningen						
'standard sim'	5.1	1.6	32	6.1	0.5	9
T +1.7	4.4	1.4	32	5.2	0.3	7
T +3.0	3.8	1.2	32	4.7	0.3	5
C 460	6.4	1.8	28	7.4	0.7	9
C 700	8.2	2.0	24	9.0	0.8	9
SC 2030	5.7	1.7	29	6.4	0.4	7
SC 2080	6.7	1.5	22	7.2	0.4	6
Tel Hadya						
'standard sim'	2.8	1.1	41	6.9	0.8	11
T +1.7	3.5	1.3	37	6.4	0.4	7
T +3.0	3.6	1.2	32	5.7	0.3	6
C 460	3.6	1.5	43	8.5	1.1	12
C 700	6.2	2.5	40	10.6	1.5	14
SC 2030	4.7	1.7	35	8.0	0.6	8
SC 2080	7.4	1.6	22	9.5	0.6	6
Migda						
'standard sim'	3.9	1.5	39	6.4	0.6	9
T +1.7	3.5	1.5	42	5.2	0.6	12
T +3.0	3.1	1.3	41	4.3	0.6	14
C 460	5.4	2.1	40	8.4	0.6	7
C 700	7.9	2.8	36	11.0	0.7	7
SC 2030	5.0	2.0	41	7.2	0.7	10
SC 2080	6.7	2.4	35	8.5	0.9	11

The validity of feasibility studies - a critical remark

One general critical remark has to be made. In all the examples of feasibility studies mentioned above, extrapolation was used. As our faba bean model is a 'mechanistic' one, such extrapolations are allowed in principle. However, the validity of it is not unlimited. For instance, in our explorations with various soil water contents during flowering in Chapter 4, the model calculated seed yields of about 5 t ha^{-1} at soil water contents during flowering not much higher than the wilting point, followed by plenty of water after flowering. This is most probably not realistic. The reason is that in the model the crop growth simply stops during flowering and recovers afterwards, when water becomes available again. This might be true (if the plants do not simply die), but in that case the flower abortion will be so intense, that no pods can develop at all. This shows a possible fundamental shortcoming of our present simulation model: it includes many kinds of source limitation and effects of water shortage on (vegetative) sink *strength*, but effects of severe water shortage on pod abortion (reproductive sink *size)* are not included. Till now, in the model studies for Western Europe, differences between measured and simulated yields which could be due to pod abortion were not found. It has to be realized however, that extrapolation to other climatic conditions is worth doing as a first step, but has to be followed by further validation (comparison of model results with new experiments).

The same holds for other studies, like the one on climate change. In this feasibility study, the used effects of CO_2-increase on photosynthesis were maximum possible effects and effects on increase of Specific Leaf Weight (SLW) were not taken into account. As soon as validation is possible (for instance by semi-field experiments with CO_2-enrichment), these may indicate the need for further adaptations of the model. This is not a shortcoming of the model approach. On the contrary, it provides a much more exact view about which aspects of crop growth should be tested in those experiments (for instance: pod abortion, reactions of SLW etc). That may allow new explorations with the model and in this way, experimental and model approach will be 'discussion partners' in further research.

Are there impacts for agricultural practice?

Yield forecastings

Increasing research effort is paid to make real yield *forecastings* with the aid of simulation models. For instance, in a new study for the EC-Joint Research Centre (JRC), a simulation model is linked with a Geographic Information System (GIS). The first aim is to test the reliability of this approach for prognoses of crop yields at, or even before the date of harvesting, in different regions in the EC. This study includes the most common arable crops of the EC: wheat, barley, maize, sugar beet, pea, faba bean etc. The parameters and functions for faba beans which were collected in our study, will be included in this system (G.H.J. de Koning, CABO, pers. comm.).

Planning of irrigation

It is discussed already in Chapter 4 that our model allows a definition of a more or less 'safe range' of water contents during and after flowering (although the values depend on soil type and to some extend on weather conditions). This opens possibilities for an interactive crop management system, at least for irrigation practice, adapting a suggestion of Spitters et al. (1990). During the growing season, yields are simulated on the basis of the actual weather data up to the present date. Predictions about the yield increase during the rest of the season are made in two ways: one based on data of average weather for the location or region considered without irrigation, and one using these average weather data, but keeping the optimum soil water content and calculating the irrigation required for that. Based on a comparison between the final seed yield of these two forecastings, decisions about the effectivity of irrigation can be made from day to day. To include this in the management practice, it should be tested if, based on this approach, a simplified model could be developed. Such a model can be used for 'on line' simulation in a central management advice system. An other possibility is to make comprehensive model studies with weather data of many years, for many soils and various amounts and timings of irrigation. Based on the results, it may be possible to derive specific guidelines for management activities for various weather conditions and soils.

Integration in economic studies

Agricultural research as presented in our study, might help with *yield improvement on hectare basis* (through the discussed examples of explorations of improved crop management or breeding strategies). However, *improvement of the area under cultivation* depends not only on high yield levels, but may be affected also by political or economic measures. For instance, management activities for yield stabilization (irrigation!) of faba beans will give extra costs, and in contrast, the price for faba beans is at the moment much lower than for potato and sugar beet. In this way, decisions about possibilities for growing a crop like faba beans with or without extra management (irrigation, disease protection) and with or without breeding improvement are complex. Such decisions can only be made in an analysis of the whole farming system. The results of our study (simulated crop response to management or breeding efforts), can be used in such a further economic farming systems analysis.

As a first step, the simulated yields and soil and climatic data have to be used to calculate the required inputs and outputs for various crop rotation systems and various agricultural production techniques. De Koning et al. (1992) used the earlier described WOFOST-feasibility study, including faba beans, on potential and water-limited crop production as a basis. They calculated inputs (pesticides, irrigation water, nitrogen, labour and machinery) and outputs (crop yields and emissions of nitrogen and pesticides to the environment) for a yield-oriented agriculture and an environment-oriented agriculture. The results describe the input and output of these various cropping systems in technical coefficients.

In the next step, these technical coefficients have to be included in multiple goal linear programming activities. The results of the study of De Koning et al. (1992) are used in the GOAL (General Optimal Allocation of Land use) model of the Netherlands Scientific Council for Government Policy. With models like GOAL it is possible to evaluate the future land use and/or farming systems (c.f. Fresco et al., 1990). With such systems it can be calculated at which price levels it may become more interesting to grow faba beans. In the coming years, the protection of the environment may request more equilibrium in the nutrient balance of the soils. In this framework, a reduction of feed-stuffs imported from third countries and a stimulation of the production of those feed-stuffs in the EC itself is a possible measure. This might give new possibilities for leguminous crops.

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Summary

The interest in growing faba beans in the European Community increased during the last decade, but not as much as was expected, and then started to decrease again. In the General Introduction, it is stated that the potential seed yield of faba beans (estimated at about 8-9 t ha^{-1} at 100% dry matter) is not the bottle-neck. The large *yield variability,* the variation in yield from year to year and from location to location, is one of the important problems. The causes of this variability were not clear. From other studies, it appeared, that improvement of the *nitrogen supply, planting density* and *degree of self-fertility* had not much effect on yield variability. It was indicated that faba beans were sensitive to *water shortage*. In the present thesis, the effects of *water shortage* during various periods of development of the crop are studied with field trials, crop physiological measurements and a modeling approach. The central question of this study is: 'is water shortage a major factor in yield variability of faba beans, via effects on dry matter production, vegetative and reproductive sink strength, dry matter partitioning and yield formation?'

In field experiments, the presence or absence of water shortage in various developmental periods turned out to be an important factor determining growth and yield. During flowering of the crop, a mild water shortage might be preferable to plenty of water. In this stage, mild water shortage limits the vegetative growth and stimulates early reproductive growth (Chapter 1). Averaged over a group of field experiments, mild water shortage during flowering, followed by plenty of water after flowering resulted in a high Harvest Index of 0.60 g g^{-1}. This was higher than with plenty of water both during and after flowering (0.55 g g^{-1}), at equal average seed yields of 6 t ha^{-1} (at 100% dry matter). In some experiments with mild water shortage during flowering, even the final seed yields itself were significantly higher (0.3-0.6 t ha^{-1}) than with plenty of water both during and after flowering. The stimulation of reproductive growth due to mild water shortage was mainly expressed in a 30-200 % higher number of filled pods at early formed podding nodes (Chapter 2). After flowering, plenty of water was crucial for a high final seed yield (Chapter 1). This increased the retention of pods at later formed nodes and enabled the continuation of pod filling till the end of the growing season (Chapter 2). Water shortage in this stage resulted in yield limitations of more than 3 t ha^{-1}

In Chapter 3, some of the physiological backgrounds of the complex reaction of the crop to water shortage are highlighted. In the experiments, faba beans showed insufficient physiological adaptation to water shortage. Clear indications of osmotic adjustment and/or adaptation of cell wall elasticity due to water shortage were not found. By these reasons, the turgor of young stems and leaves and thus the expansive growth decrease already with mild water shortage. The stomatal conductance and photosynthesis decrease only at more severe water shortage. In Chapter 3 it is argued how this might explain not only the positive effect of mild water shortage during flowering on the dry matter partitioning to reproductive organs and on final seed yield, but also the negative effect of water shortage after flowering on seed yield.

In Chapter 4, the knowledge obtained in the Chapters 1-3 is integrated in a quantitative way, using a simulation model. The model outcomes correspond with the measured average seed yields and account for up to 80% of the measured yield variation of data sets of several locations in Western Europe. Explorative studies with the simulation model show that plenty of water after flowering increases the average seed yields with 17% - 42%. It reduces the standard deviation, a measure for the variability, with 43% - 73%. The model shows that plenty of water after flowering is a major factor for yield stabilization of faba beans in Western Europe. Plenty of water both during and after flowering has almost no additional effects. A positive effect of water shortage during flowering on seed yield can be simulated, at mild levels of shortage where the rate of photosynthesis is hardly reduced. At severe levels of water shortage, a negative effect on yield is calculated. For a heavy clay soil near Wageningen, it is simulated that the 'target' soil water contents during flowering for optimum final seed yields vary from 0.27-0.32 cm^3 cm^{-3} for this soil type (pF-values of respectively 3 and 2.3), depending on temperature and air humidity. After flowering a water content higher than 0.32 cm^3 cm^{-3} is required. The effect of some suggested breeding strategies for the aim of a faba bean 'ideotype' are explored. Doubling of rooted depth reduces yield variability with about 30%, but doubling the water extraction capacity of the crop does not reduce the yield variability at all.

In the General Discussion it is concluded that water shortage is the major yield *limiting* factor in faba beans. Yield *reducing* factors (especially diseases) may become more important than was expected before, when water limitation is eliminated. In healthy crops, differences in *amount* of water supply may account for about 80 % of the measured yield variation in faba beans. Differences in water supply *pattern* may account for about 10%. Model explorations indicate that the positive effect of mild water shortage during flowering on seed yield will not be more than about 500 kg ha^{-1}. Some consequences of these results for the underlying mechanism of dry matter partitioning in faba beans are highlighted and compared to effects in cotton, potato and sunflower. Next, it is discussed how feasibility studies with the developed simulation model can help in further management and breeding research, by evaluating faba bean 'ideotypes' and conditions for optimum productivity. It is also shown how feasibility studies can help in assessing effects of climate change (temperature rise and increase of CO_2 concentration) on average yield and yield variability. For three locations (Wageningen, Netherlands; Migda, Israel; Tel Hadya, Syria), simulations show increases of average seed yield of respectively 12%, 28%, 68% for rain-fed crops and 5%, 13%, 16% for fully irrigated crops, assuming an increase of CO_2 concentration to 460 ppm and a temperature increase of 1.7°C. Under these possible future climate conditions, the yield variability in rain-fed crops stays the same as in the present climate, or it is somewhat reduced, due to the reduced sensitivity of the crops to water shortage. In future climate, the yield variability in irrigated crops is much smaller than in rain-fed crops, like it is under the present climate conditions. Finally, it is shown how the simulation results can provide basic data for agro-economic evaluation of farming systems and land use.

Samenvatting

De interesse in de teelt van veldbonen in de EG nam toe gedurende de laatste 10 jaar, maar minder dan verwacht, en daalde uiteindelijk weer. In de algemene inleiding van dit proefschrift wordt gesteld dat de potentiële zaadopbrengst van veldbonen (geschat op 8-9 t ha^{-1} bij 100% d.s.) geen knelpunt is. De grote *opbrengstvariabiliteit*, de variatie in opbrengst van jaar tot jaar en van plaats tot plaats) is een van de belangrijkste problemen. De oorzaken hiervan waren niet goed bekend. Uit andere studies was gebleken, dat verhoging van de stikstofbemesting, plantgetal, en mate van zelffertiliteit weinig effect hadden op de opbrengstvariabiliteit. Er werden echter aanwijzingen gevonden dat veldbonen gevoelig waren voor *watertekort*. In dit proefschrift worden de effecten van *watertekort* gedurende verschillende ontwikkelingsstadia van het gewas bestudeerd aan de hand van veldproeven, gewasfysiologische metingen en simulatieonderzoek. De centrale vraagstelling van deze studie is: 'is watertekort een hoofdoorzaak van opbrengstvariabiliteit bij veldbonen, via effecten op drogestofproduktie, vegetatieve en generatieve sinksterkte, drogestofverdeling en opbrengstvorming?'

In veldexperimenten bleek de aan- of afwezigheid van watertekort in verscheidene ontwikkelingsstadia een belangrijke groei- en opbrengstbepalende factor te zijn. Gedurende de bloei van het gewas is een mild watertekort wellicht beter dan ruime watervoorziening. In dit stadium remt een mild watertekort de vegetatieve groei en stimuleert het een vroege generatieve groei (hoofdstuk 1). Gemiddeld over een groep van veldexperimenten leidde een licht watertekort gedurende de bloei, gevolgd door een ruime watervoorziening na de bloei tot een hoge Harvest Index van 0.60 g g^{-1}. Deze was hoger dan bij een ruime vochtvoorziening tijdens en na de bloei (0.55 g g^{-1}) bij gelijke gemiddelde zaadopbrengsten van 6 t ha^{-1} (bij 100% d.s.). In enkele experimenten met mild watertekort gedurende de bloei waren de uiteindelijke zaadopbrengsten zelfs significant hoger (0.3-0.6 t ha^{-1}) dan bij een ruime vochtvoorziening tijdens en na de bloei. De gestimuleerde generatieve groei als gevolg van mild watertekort kwam hoofdzakelijk tot uiting in een 30-200% hoger aantal gevulde peulen aan de vroegst gevormde peuletages (hoofdstuk 2). Na de bloei bleek een ruime vochtvoorziening essentieel voor een hoge uiteindelijke zaadopbrengst. Dit verhoogde het aantal blijvende peulen aan later gevormde etages en leidde tot een voortzetting van de peulvulling tot het einde van het groeiseizoen (hoofdstuk 2). Watertekort in dit stadium leidde tot opbrengstdervingen van meer dan 3 t ha^{-1}.

In hoofdstuk 3 worden enkele fysiologische achtergronden belicht van de complexe reactie van het gewas op watertekort. In de experimenten vertoonden veldbonen onvoldoende fysiologische aanpassing aan watertekort. Er werden geen duidelijke aanwijzingen gevonden voor osmotische aanpassing en/of aanpassing van de elasticiteit van de celwanden als gevolg van watertekort. Hierdoor daalt de turgor van jonge bladeren en stengels en daarmee de strekkingsgroei al bij een mild watertekort. De openingstoestand van de huidmondjes en daarmee de fotosynthese dalen pas bij een groter watertekort. In hoofdstuk 3 wordt beargumenteerd hoe dit niet alleen het positieve effect van mild watertekort tijdens de bloei op de drogestofverdeling naar generatieve organen en dus op eindopbrengst kan verklaren, maar ook het negatieve effect van watertekort na de bloei op de zaadopbrengst.

In hoofdstuk 4 wordt deze kennis op kwantitatieve wijze geïmplementeerd in een simulatiemodel. Het model geeft uitkomsten die goed overeenkomen met gemeten zaadopbrengsten, en verklaart tot 80% van de gemeten opbrengstvariabiliteit in proefveldresultaten van verschillende locaties in West-Europa. Verkennende studies met het model tonen aan, dat ruime vochtvoorziening na de bloei de gemiddelde opbrengsten doet toenemen met 17-42%. Het verkleint de standaardafwijking, een maat voor de variabiliteit, met 43-73%. Het model toont aan dat ruime vochtvoorziening na de bloei een hoofdvoorwaarde is voor opbrengststabilisatie van veldbonen in West-Europa. Ruime vochtvoorziening zowel tijdens als na de bloei heeft weinig additioneel effect. Een positief effect van watertekort gedurende de bloei op de uiteindelijke zaadopbrengst kan worden gesimuleerd, bij een mild watertekort waarbij de assimilatiesnelheid nog weinig geremd is. Bij een groot watertekort wordt een negatief effect gesimuleerd. Voor een zware kleigrond in de omgeving van Wageningen is een richtgetal gesimuleerd voor het bodemwatergehalte tijdens de bloei dat benodigd is voor optimale zaadopbrengsten. Dit getal varieert echter van 0.27-0.32 cm^3 cm^{-3} (pF-waarden van respectievelijk 3 en 2.3), afhankelijk van onder meer temperatuur en luchtvochtigheid. Na de bloei is een watergehalte van minimaal 0.32 cm^3 cm^{-3} vereist voor dit bodemtype. Het effect van een aantal gesuggereerde veredelingsstrategiën voor het verkrijgen van een 'ideotype'-veldboon is met het model verkend. Verdubbeling van de worteldiepte verkleint de variabiliteit in zaadopbrengsten met ongeveer 30%, terwijl verdubbeling van de wateronttrekkende kracht van het gewas geen enkele invloed heeft op de opbrengstvariabiliteit.

In de algemene discussie wordt geconcludeerd dat watertekort de belangrijkste *opbrengstlimiterende factor* is. *Opbrengstkortende factoren* (met name ziekten) worden wellicht belangrijker dan aanvankelijk verwacht, wanneer watertekort wordt geëlimineerd. In gezonde gewassen kunnen verschillen in *hoeveelheid* watervoorziening ongeveer 80% van de gemeten opbrengstvariabiliteit verklaren. Verschillen in het *patroon* van watervoorziening verklaren ongeveer 10%. Modelverkenningen geven aanwijzingen dat het positieve effect van mild watertekort tijdens de bloei op de zaadopbrengst niet meer dan ongeveer 500 kg ha^{-1} zal bedragen. Enkele gevolgen van deze resultaten voor het onderliggende mechanisme van drogestofverdeling in veldbonen worden belicht en vergeleken met effecten in de gewassen katoen, aardappel en zonnebloem. Vervolgens wordt besproken, op welke wijze verkennende studies met het simulatiemodel verder veredelings- en teeltonderzoek kunnen steunen, door het evalueren van 'ideotypen' en omstandigheden voor optimale groei. Ook wordt getoond hoe verkennende simulatiestudies kunnen helpen bij het schatten van de effecten van klimaatveranderingen (temperatuurstijging en verhoging van het CO_2 gehalte) op gemiddelde opbrengst en opbrengstvariabiliteit. Voor drie locaties (Wageningen, Nederland; Migda, Israël; Tel Hadya, Syrië), vertonen de simulaties stijgingen van de gemiddelde zaadopbrengsten met respectievelijk 12%, 28%, 68% voor niet-geïrrigeerde gewassen en 5%, 13%, 16% voor volledig geïrrigeerde gewassen, bij een veronderstelde toename van de CO_2-concentratie tot 460 ppm en een temperatuurverhoging van 1.7 °C. Onder deze mogelijke toekomstige klimaatsomstandigheden blijft de opbrengstvariabiliteit van niet-geïrrigeerde gewassen ongeveer gelijk aan die in het huidige klimaat, of wordt deze variabiliteit iets verkleind als gevolg van een gereduceerde gevoeligheid van de gewassen voor watertekort. In het toekomstige klimaat blijft de opbrengstvariabiliteit in geïrrigeerde gewassen aanzienlijk kleiner dan in de niet-geïrrigeerde gewassen, zoals ook het geval is onder de huidige klimaatomstandigheden. Tenslotte wordt besproken hoe de simulatieresultaten basisgegevens kunnen leveren voor een agro-economische evaluatie van bedrijfssystemen en landgebruik.

Curriculum vitae

Kees Grashoff werd op 22 januari 1957 geboren te Rotterdam. In juni 1975 behaalde hij het diploma Atheneum-B, waarna hij in september aanving met de studie biologie aan de Rijksuniversiteit te Utrecht. In 1984 slaagde hij *cum laude* voor het doctoraal examen biologie met als hoofdvakken oecofysiologie, en als bijvakken theoretische teeltkunde, didaktiek van de biologie en gewasoecologie. Het hoofdvak oecofysiologie, bewerkt onder leiding van prof. dr. R. Brouwer, had hem inmiddels in kontakt gebracht met het onderzoek aan peulvruchten dat werd verricht op het DLO-Centrum voor Agrobiologisch Onderzoek (CABO) te Wageningen, onder leiding van wijlen dr. ir. G. Dantuma. Daar werd zijn belangstelling gewekt voor het leggen van verbindingen tussen het fundamentele oecofysiologische onderzoek en het meer toepassingsgerichte onderzoek aan landbouwgewassen. Een gedeelte van het onderzoek voor de afstudeervakken werd uitgevoerd op het CABO en bij de vakgroep theoretische produktie-ecologie van de Landbouwuniversiteit te Wageningen. In juli 1984 werd hij aangesteld als wetenschappelijk onderzoeker op het CABO, vanaf 1985 in vaste dienst. Zijn hoofdtaak is het verrichten van experimenteel en modelmatig onderzoek naar de effecten van omgevingsfactoren op de produktiviteit, opbrengststabiliteit en kwaliteit van granen en peulvruchten.