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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 rainfail 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

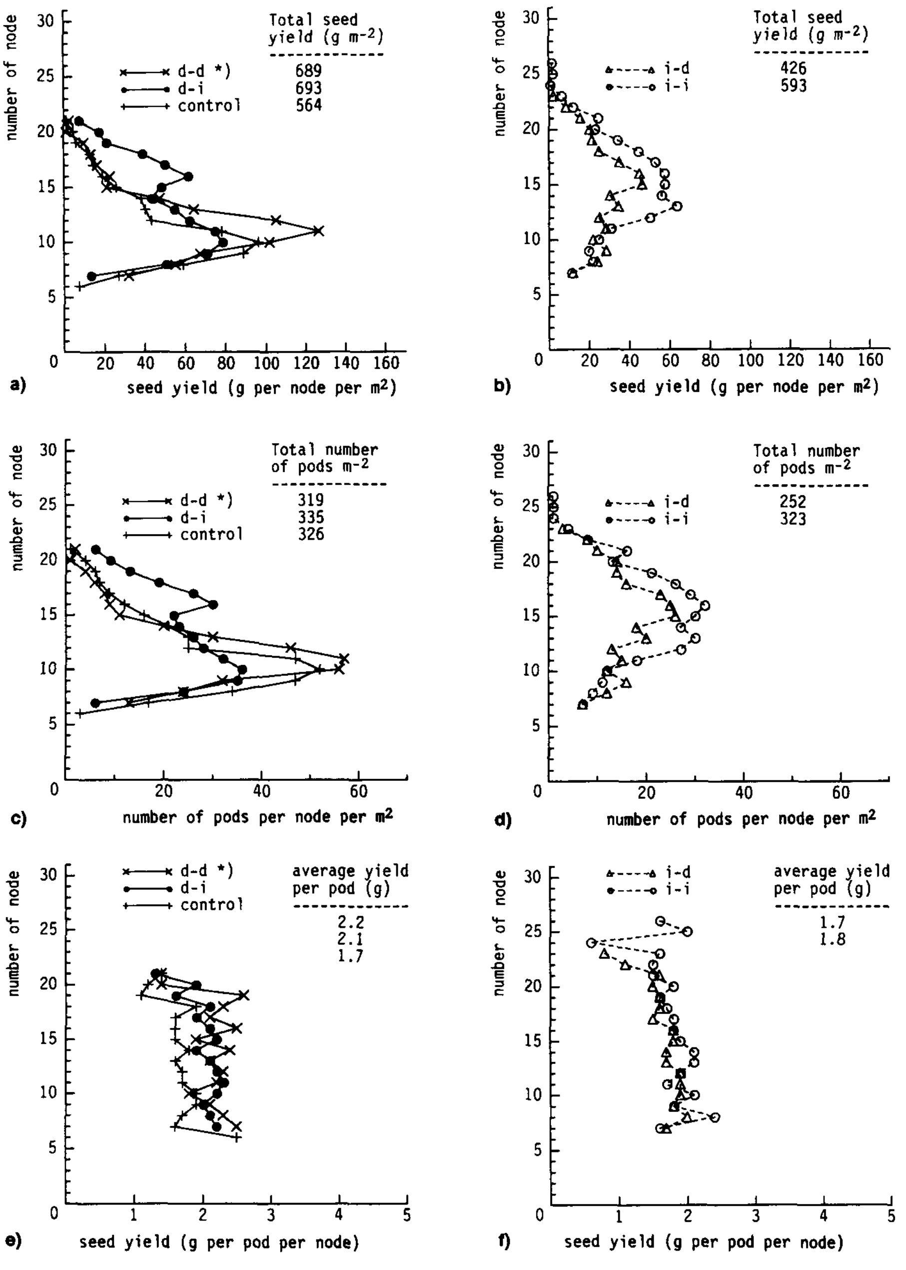


Fig. 1. Seed yield and seed yield components of successive plant nodes for cv. Alfred grown under five different patterns of water supply in 1982. (a and b) Seed yield per node. (c and d) Number of pods per node. (e and f) Average seed yield per pod, per node. (a, c, and e) Water supply patterns with 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.

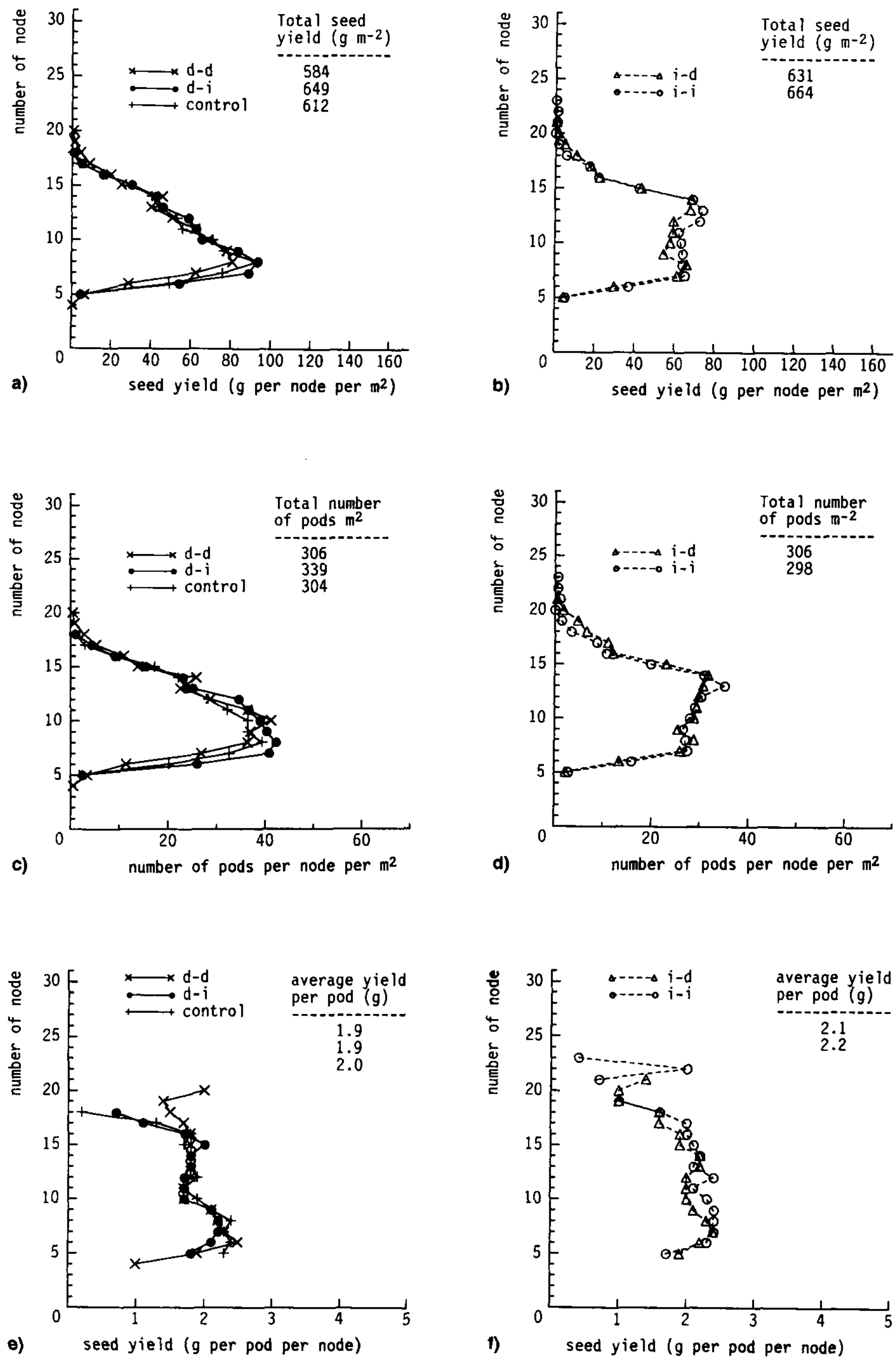


Fig. 2. As Fig. 1, for 1984.

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-

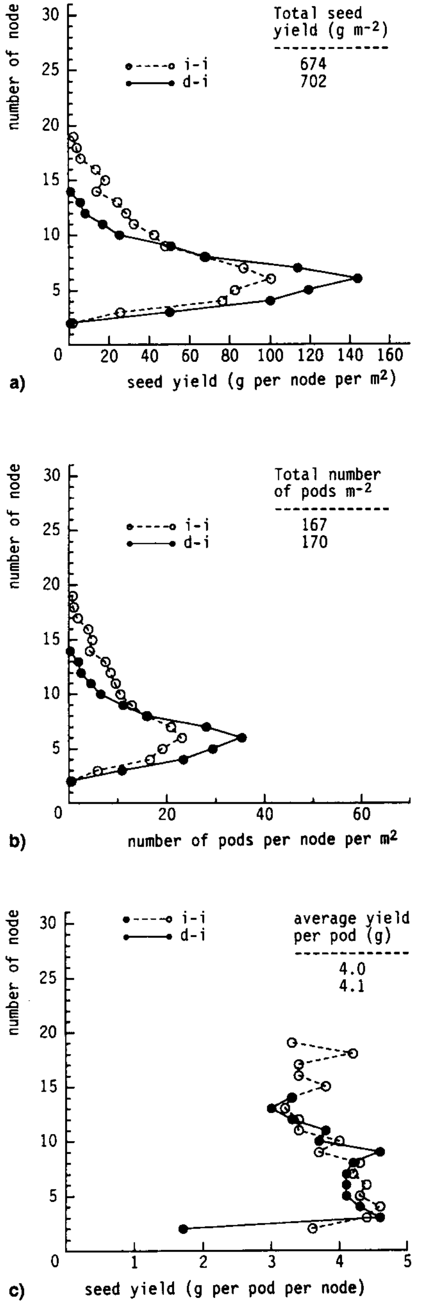


Fig. 3. Seed yield characteristics of successive nodes for cv. Minica grown under two different patterns of water supply in 1981. (a) Seed yield per node. (b) Number of pods per node. (c) Average seed yield per pod, per node. Results from experimental farm Droevendaal.

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).

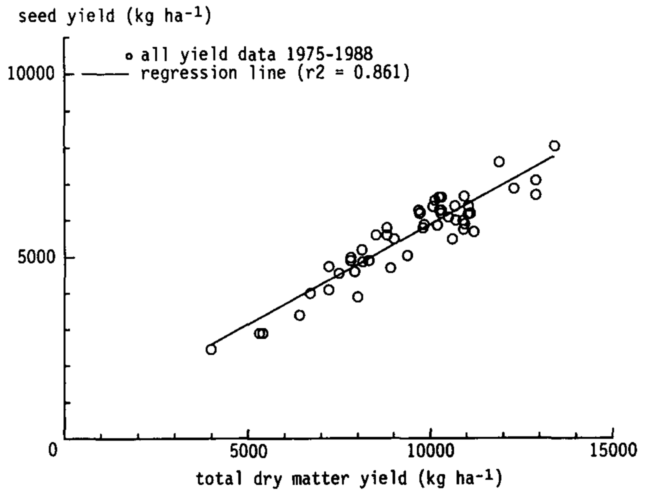
Dry matter production and partitioning as affected by pattern of water supply

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 regresa)



b)

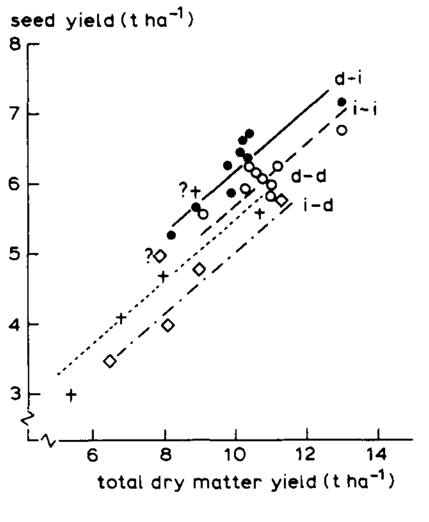


Fig. 4. Seed yield plotted versus total dry matter production for a yield data set of cv. Minica 1975-1988 (see text). (a) All available data plotted without classification of water supply pattern. (b) Only data plotted with classified water supply pattern. General form of the fitted lines: SY = 0.44 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

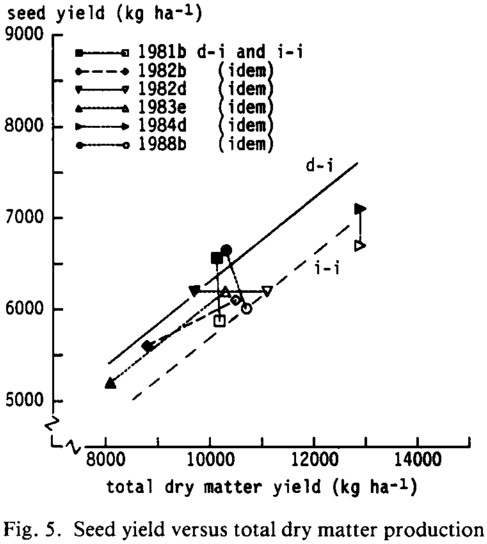


Fig. 5. Seed yield versus total dry matter production for d-i and i-i data pairs of several seasons. Regression lines are derived from Fig. 4b. Upper line for all d-i data; lower line for all i-i data. Each data pair is connected by a dotted line. Letters after the years indicate results from exprimental 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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