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Physiological factors limiting growth and yield of faba beans

A.J. KARAMANOS*
C. GIMÉNEZ**
*AGRICULTURAL UNIVERSITY OF ATHENS
LABORATORY OF CROP PRODUCTION
75 IERA ODOS, 118 55 ATHENS, GREECE
**DEPARTAMENTO DE AGRONOMÍA
UNIVERSIDAD DE CÓRDOBA
APDO. 3048, 14080 CÓRDOBA, SPAIN

SUMMARY - The main physiological factors responsible for yield fluctuations of faba beans and their sensitivity to environmental stress usually encountered in the Mediterranean areas are examined. The magnitude of crop photosynthesis is primarily determined by the size and longevity of the foliage and, to a lesser extent, by the efficiency of CO_2-fixation. Water shortage and air temperature strongly affect leaf production, expansion and death. Flower and pod abortion result from a temporary shortage of assimilates produced by intense intra-plant competition between vegetative parts, especially the stem apex, and reproductive organs at the beginning of flowering and pod-setting. Water shortage and increased crop density enhance the drop of reproductive organs by reducing the availability of assimilates and distorting hormonal balance. The behaviour of genotypes with determinate growth habits and independent vascular supply to inflorescences, as well as the effects of plant growth substances on flower and pod retention are also discussed. The limited possibilities of faba beans for efficient production in dry periods in comparison to other crops are indicated after examining water ratios and mechanisms of drought resistance.

RESUME - "Facteurs physiologiques qui limitent la croissance et le rendement de la fève". Les facteurs physiologiques les plus importants, responsables des fluctuations du rendement des fèves et de leur susceptibilité au stress environnemental dans la région méditerranéenne, sont étudiés. L'importance de la photosynthèse de la culture est déterminée principalement par la taille et la longévité des feuilles et en moindre mesure, par l'efficacité de fixation de CO_2*. Le déficit hydrique et la température atmosphérique ont un effet important sur la production, le développement et la mort des feuilles. L'avortement des fleurs et des gousses se produit comme résultat d'un déficit temporel des assimilats à cause d'une forte concurrence intra-plante entre les organes végétatifs, en particulier l'apex de la tige, et les organes reproducteurs en début de floraison et pendant la formation des gousses. Le déficit hydrique et une forte densité de semis augmentent la chute des organes reproducteurs à cause d'une réduction de la disponibilité d'assimilats et de l'altération de l'équilibre hormonal. Cet article examine le comportement de certains génotypes à croissance déterminée et avec une vascularisation indépendante vers ces inflorescences, ainsi que les effets des substances de croissance végétale sur le maintien des fleurs et des gousses. Les contraintes des fèves pour produire de façon performante pendant les périodes sèches par rapport à d'autres cultures sont indiquées après l'étude des coefficients hydriques et des mécanismes de résistance à la sécheresse.*

Introduction

Faba bean (*Vicia faba* L.) is a valuable crop plant. It can be used as an effective break crop in cereal rotations substantially improving soil fertility. At the same time it produces seeds with high protein content frequently exceeding 30% (for a review, see Sjodin, 1982). However, the faba bean cultivation is declining in most countries (Hawtin and Hebblethwaite, 1983), mainly because of yield unreliability between years or sites. For a 113-year period, yield stability of faba beans in U.K. was several times inferior to that of cereal crops (*ibid.*). Yield instability results from the impact of the aerial and soil environment on plant growth and development. The faba bean plant-environment interactions are more complex than in other crop plants primarily because of its indeterminate growth habit and other anatomical and physiological peculiarities, usually expressed in terms of unpredictable flower and pod shedding. It is, therefore, important to identify and understand the physiological factors responsible for the observed yield fluctuations, as well as their sensitivity to environmental stress usually encountered under field conditions.

Overall plant growth is a process of biomass accumulation. Accordingly, in this study special attention is paid to carbon assimilation, partition and losses in faba bean

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as well as to the factors affecting all these processes. Mineral nutrition as a limiting factor to crop growth and yield is also examined. Finally, a separate section describes water ratios in faba beans and its responses to drought, since water shortage is a very common yield-limiting factor in Mediterranean agriculture.

The production of assimilates

For a given time interval, net crop photosynthesis is the product of the size of the photosynthetic system and the rate of photosynthesis per unit leaf area. The former refers almost exclusively to foliage, given that the photosynthetic contribution of both stems and pods is small, not exceeding 15 and 20%, respectively of total plant photosynthesis (Austin *et al.*, 1981). The latter refers to the efficiency of CO_2-fixation.

Leaf area development

Leaves intercept the available amounts of solar energy and assimilate CO_2, hence their significance to crop growth and yield. Field studies of crop photosynthesis have shown a continuous increase in rate of CO_2-uptake with increasing values of leaf area index (LAI), up to a maximum of 6.9, at a saturating light intensity of about 700 W/m^2 (Fig. 1).

Furthermore, highly significant correlations between the leaf area duration (LAD) and both biological and seed yields of faba bean have been observed (Fig. 2). It is, therefore, important to achieve high values of LAD by increasing the size and the longevity of the foliage in order to ensure satisfactory yields. Leaf production and unfolding, leaf expansion and leaf death, all affect LAD.

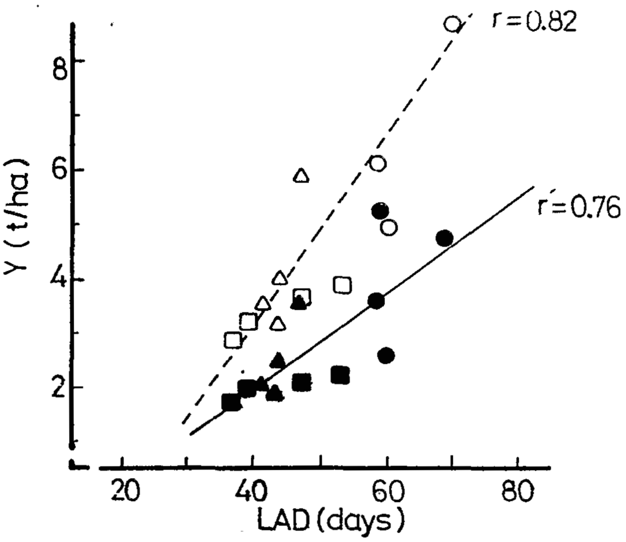

Fig. 2. The relationship between LAD and biological (open symbols, dashed line) and seed yields (filled symbols, continuous line) for faba beans grown in the field under polythene shelters. Results from frequently (circles), intermediate (triangles) and non-irrigated plots (squares). The fitted linear regression lines are also shown.

Leaf production and unfolding are decisively affected by plant development and external factors. The rate of leaf production is relatively stable up to the middle of flowering, quickly declining thereafter (Fig. 3). The rate of unfolding follows a rising pattern reaching a maximum around mid-flowering and falling subsequently

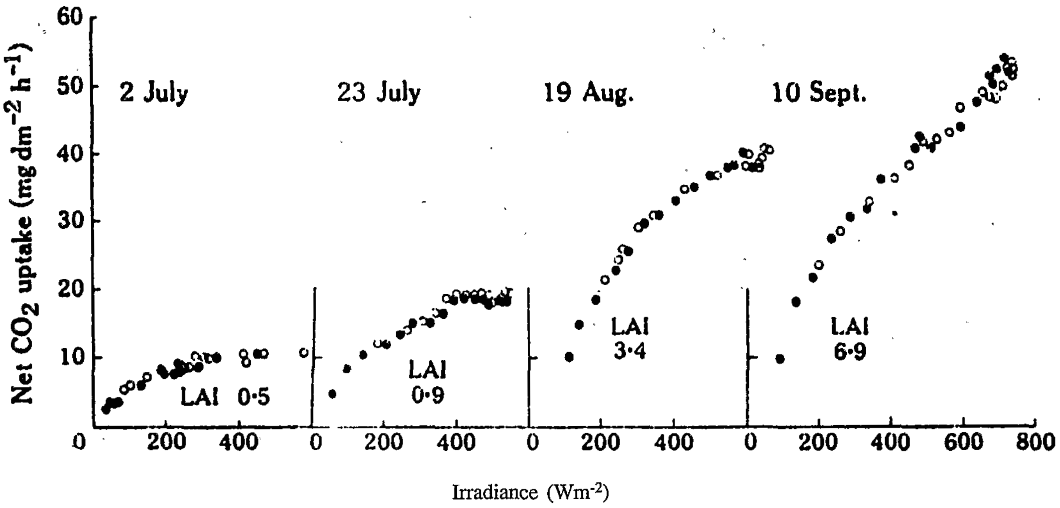

Fig. 1. Relationship between net CO_2-uptake and irradiance at different growth stages of a faba bean crop in Australia. Air temperature range from 5 (July 2) to 20 °C (September 10). Open and closed symbols refer to data taken before and after midday, respectively (Sale, 1977).

(Fig. 3). Both rates are adversely affected by water shortage as soon as the leaf water potential falls below -0.8 to -1.1 MPa (Karamanos, 1978a). On the other hand, air temperature exerts a positive influence on the rate of leaf production in the 12 to 26 °C range (Dennett *et al.*, 1979).

The expansion of the lamina of individual leaves follows a kind of sigmoid curve expressed by an initial (area at unfolding) and a final value, as well as by an average rate and duration. Under favourable growth conditions upper leaves (above nodes 8 to 9) show a greater area at unfolding, attain a greater final area and exhibit higher expansion rate than the lower leaves, whereas, variation in the duration of expansion is less systematic (Karamanos, 1976; Dennett *et al.*, 1979). Two to four leaves usually expand at any one time. Water shortage adversely affects the areas at unfolding and the average expansion rate, eventually leading to a drastic reduction in the final leaf area (Fig. 4). The negative effects of leaf water potential start at about -0.4 to -0.5 MPa, i.e. less negative than those affecting leaf production and unfolding. The duration of growth is not systematically affected by water shortage.

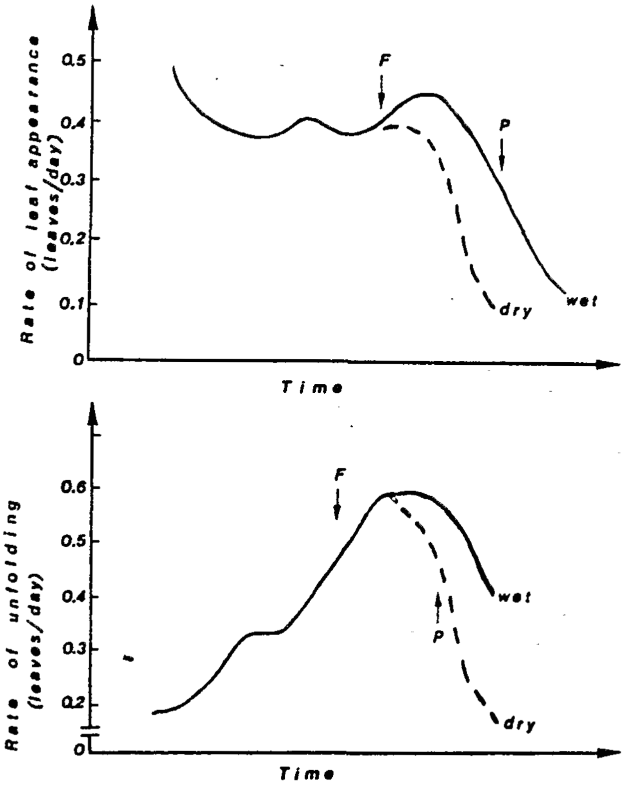

Fig. 3. Time courses of leaf production rates (upper) and unfolding (lower diagram) in frequently (wet) and non-irrigated (dry) faba beans. F and P denote the beginning of flowering and podding, respectively (Karamanos, 1986).

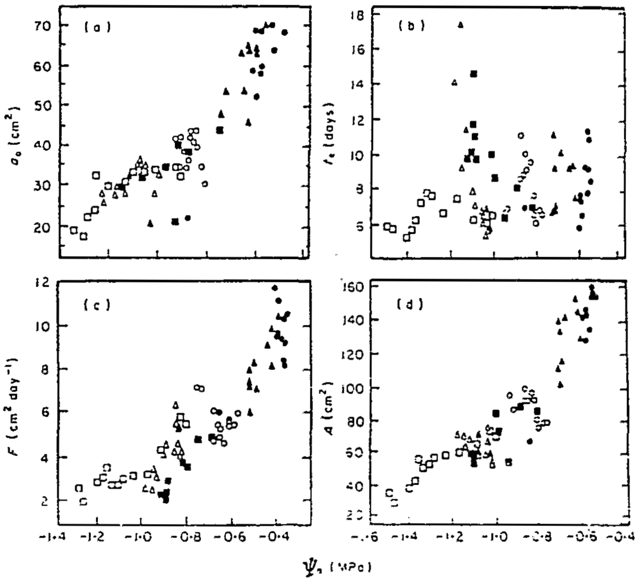

Fig. 4. Relationship between leaf water potential in the afternoon (ûa) and the parameters of laminar growth. (a) Area at unfolding (ao). (b) Duration of growth (te). (c) Mean growth rate (F). (d) Final leaf area (A). Results from two years (open and closed symbols) and three irrigation treatments, wet (circles), medium (triangles) and dry (squares) (Karamanos *et al.*, 1982).

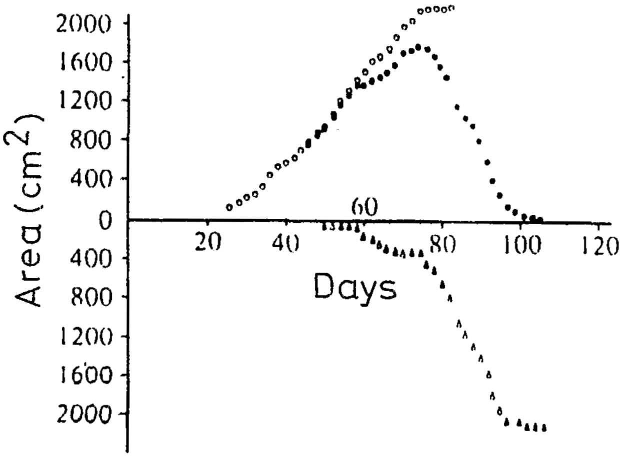

Fig. 5. Time course of the mean leaf area per plant shown as the amount of leaf area produced (open circles), the amount of senescing and dead leaf area (triangles) and the actual leaf area present (filled circles) for field-grown faba beans (Finch-Savage and Elston, 1982).

Increasing air temperatures in the range of 14 to 23 °C positively affect final leaf size by increasing the average expansion rate (Auld *et al.*, 1978; Dennett *et al.*, 1978). However, at levels of solar irradiance above 20

MJ/m^2/day the positive effects of temperature are masked by the negative effects of high insolation on leaf growth.

Leaf senescence and death become important determinants of the total leaf area as plants grow older (Fig. 5). In faba bean, leaf death initially occurs slowly until pods are physiologically mature, followed by an accelerated rate thereafter (Finch-Savage and Elston, 1982).

There is evidence that leaf senescence is more marked as the number of pods per plant increases (Hill-Cottingham and Turner, 1976), implying a kind of dependence of fruit growth on the nutrients released from senescing leaves. Thus, the observed increase in the rate of leaf death after the physiological maturity of the pods may indicate that leaves have yielded up most of their nutrients to the pods and are of no use to the plant any more. Apart from plant development, leaf death is enhanced to a considerable extent by high temperatures and water shortage (*ibid.*; Karamanos, 1978a).

On the basis of the evidence presented above it follows that total plant leaf area is decisively affected by both air temperature and water stress. Bull (1968) and Dennett *et al.* (1978) found significant positive correlations between maximum daily air temperatures and relative leaf growth rates of faba beans between 9 and 25 °C, giving a Q_{10} of about 2.0 for the increase of leaf area per plant. Other environmental factors such as solar irradiance and vapour pressure deficit produced very low or no correlations. Significant positive correlations were also found between average leaf pressure potential and the relative leaf growth rate, indicating that the rate becomes zero when pressure potential drops to about 0.08 MPa (Karamanos, 1986). The high sensitivity of leaf area growth to water shortage is also obvious in Fig. 6. The data show a continuous decrease in leaf area for values of leaf water potential below -0.5 MPa at an average rate of 20 dm^2 per MPa. This sensitivity can be attributed mainly to leaf expansion which already started decreasing at -0.5 MPa. Leaf death appears to follow in sensitivity, whereas leaf appearance is the least sensitive to water shortage (Karamanos, 1986).

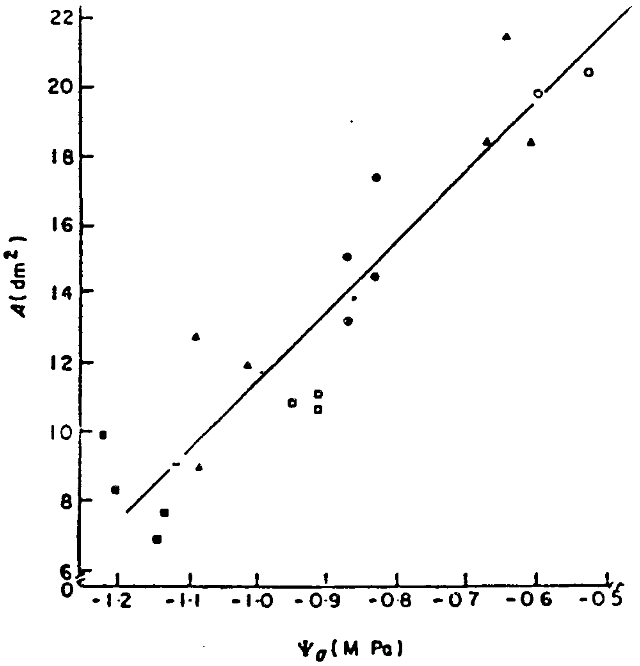

Fig. 6. The relationship between the total active leaf area of the main stem of faba bean plants and the average values of leaf water potential (ûa) over two growth periods (open and closed symbols). Results from a wet (circles), medium (triangles) and dry (squares) treatment. The fitted linear regression is also shown (Y=32.0+20.0X, r=0.92; Karamanos, 1978a).

The rate of photosynthesis

Faba bean is a typical C_3-plant. On a leaf basis, the normal photosynthetic rate at light saturation is about 20-25 mg CO_2/dm^2/h (Breeze and Elston, 1978; Kogure *et al.*, 1986). On a crop basis, however, these figures are much higher (Fig. 1). Air temperature does not seem to decisively affect the CO_2-fixation rate in the wide range of 5 to 30 °C (Sale, 1977; Kogure *et al.*, 1986). There are no detailed studies on the influence of water shortage on the rate of photosynthesis. Judging from the sensitivity of stomatal response to water shortage (Fig. 12), a drastic stomatal control of photosynthesis is also expected. Nevertheless, mesophyll resistance appears to be at least equally important to stomatal response under conditions of high atmospheric vapour pressure deficits (Leach, 1977). Accordingly, an effective control of photosynthesis by water stress has to be expected. On a crop basis, however, the net assimilation rate was not significantly correlated with plant water status (Karamanos, 1984a).

The respiratory losses

About 20 to 30% of the carbon fixed at saturating light intensity is lost by photorespiration (Voskresenskaya *et al.*, 1974), while dark respiration appears to proceed at lower rates (15 to 20% of the maximum daily rate of photosynthesis; Sale, 1977). Similar figures have been reported by Pearson (1974), who found that of the total carbon fixed during 24 h, about 50% was lost during the current photoperiod, 14% during the dark period and 5% during the following photoperiod. The temperature sensitivity of dark respiration varies with the available substrate, reaching values of Q_{10} of about 1.8 at high and of 2.1 at low substrate contents (Breeze and Elston, 1978).

The allocation of assimilates

The products of the current photosynthesis are rapidly translocated via the phloem sieve tubes (Fritz and Eschrich, 1970; Pearson, 1974) away from the source leaves towards the nearest sinks. The evidence concerning the translocation of assimilates before flowering is contradictory. Pearson (1974) found that the youngest photosynthesizing leaves fed mainly the stem apex and the newly expanding leaves, while most of the assimilates from the basal leaves went to the roots and the stem. In other experiments, however, basal leaves were found to export mainly upwards while the apical leaves exported mainly downwards (Crompton *et al.*, 1981; Ismail, 1984). These results show that there is a bidirectional transport along the stem towards the stronger sinks, namely growing leaves and roots. In addition, a considerable amount, between 10 and 50% of the plant's photosynthates (Crompton and Lloyd-Jones, 1980) is temporarily stored in the stems (Tamaki and Naka, 1958, 1959; Ismail and Sagar, 1981). The presence of additional sinks (flowers and growing pods) considerably increases intra-plant competition for assimilates after flowering. At the initial stages, the photosynthates are allocated mainly to leaves, stems and roots, whereas flowers receive a smaller proportion up to the end of flowering (Kogure *et al.*, 1978; Jacquiery and Keller, 1980; Haisch *et al.*, 1988). From then on, increasing amounts of assimilates move from the leaves towards the growing pods. There is no preferential translocation between the leaf on a fruiting node and the pods on the same node. Thus, leaves contribute photosynthates to fruits above and below their node (Crompton *et al.*, 1981). A considerable mobilization from the stem and root reserves also takes place (Ismail and Sagar, 1981; Crompton *et al.*, 1984). The importance of the stem as a temporary storage organ of assimilates has already been emphasized in crop growth studies (Ishag, 1973) and appears to be more marked under drought, when the overall crop photosynthetic activity is lower (Karamanos, 1984a). It is worth mentioning that roots continue to behave as sinks for a considerable period after flowering, since energy- consuming nitrogen fixation is also maintained at high levels during fruit growth (Cooper *et al.*, 1976; Kogure *et al.*, 1978). Translocation of assimilates from root nodules is not observed earlier than seed ripening (Haisch *et al.*, 1988). The overall pattern of the allocation of assimilates after flowering is summarized in Fig. 7.

In conclusion, young flowers and young pods are weaker sinks for assimilates in comparison to other plant organs in indeterminate plant types. Accordingly, the consequences of a possible shortage of assimilates at the initial stages of flowering and podding will be more severe on the reproductive organs. This is examined in more detail below.

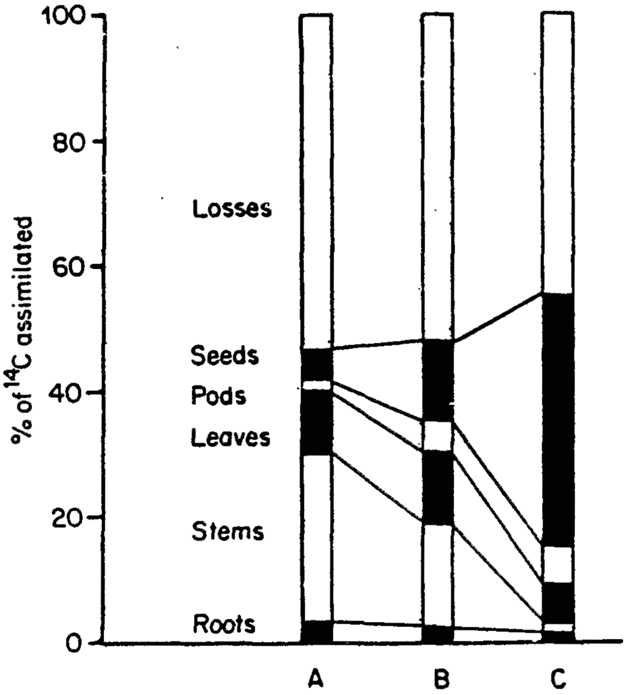

Fig. 7. The distribution at maturity of labelled assimilates incorporated at different times during development. (A) At the beginning of flowering. (B) At the end of flowering (25 to 30 days after (A)). (C) At green pod maturity (60 days after (A)). Measurements were taken 70 to 80 days after (A) (Peat, 1983, based on data from Kogure *et al.*, 1978).

The loss of reproductive organs

The number of pods per plant is one of the least stable, yet one of the most important seed–yield components (Peat, 1982). All known reports have shown that the total number of flowers initiated is always substantially greater than the eventual number of pods reaching maturity. It is, therefore, important to understand the nature of the mechanisms involved in flower and pod abortion and the factors affecting them.

Flower tripping and fertilization do not seem to be the major factors involved in flower drop (Kambal, 1969; Chapman *et al.*, 1979; Smith, 1982; Stoddard, 1986). The availability of assimilates, anatomical features of the vascular system and hormonal factors are very likely to interact and play the major role in the abscission of reproductive organs. In general, the earliest formed flowers, both within and between inflorescences, are most likely to survive. Accordingly, there is a priority for flower retention and pod formation in the lower fruiting-nodes as well as in the basal flowers of each inflorescence (Fig. 8). This means that flowers at higher nodes and more distal positions on the racemes are weak sinks for assimilates at the time of the more intense intra-plant competition. Indeed, the removal of stronger sinks, such as the stem apex and the basal racemes, dramatically increases pod-setting at higher nodes (Chapman *et al.*, 1978; Crompton *et al.*, 1981). Experiments using $^{14}CO_2$ have shown that shed pods and flowers contain the smallest amounts of ^{14}C (Jacquiery and Keller, 1980). Furthermore, exposure of faba beans to CO_2-enriched air strongly inhibited early pod fall (Freye and Schilling, 1983). We conclude, therefore, that shortage of assimilates is the main cause of poor fruit-setting.

This shortage becomes more acute for the distal flowers because of the definite priority for anthesis of the basal flowers within a raceme. Considerable attention has been paid to the architecture of the vascular bundles in the inflorescence. Smith (1982) and Gates *et al.* (1983) found in commercial cultivars the basal flower of a raceme to have a separate vascular supply, while the flower above it was linked to successive apical flowers by a dichotomously branched vascular system. Apparently, such a vascular system would minimize the already restricted supply of assimilates to the more distal flowers. Other researchers, however, consider the number of vascular bundles as unlikely to be a yield-limiting factor in faba bean (Hoppe and Pommer, 1986).

The role of plant growth regulators may well be of great importance in the loss of reproductive organs. A localized change in the hormonal balance of the plants, probably caused by the intense intra-plant competition for assimilates, may act as a signal to induce the abscission process in flowers and pods. Indeed, a decrease in the concentration of auxins, gibberellins, and cytokinins was observed in the period of more intense shedding (El-Antably, 1976a,b) accompanied by an increase in ABA (Sivakumaran and Hall, 1978; Diethelm *et al.*, 1986) and ethylene concentrations (El-Beltagy and Hall, 1975). Extensive experimental work has been done in order to examine the effects of exogenously applied plant growth regulators on the intensity of flower and pod shedding (for reviews see El Fouly, 1982; Keller and Bellucci, 1983). The contradictory results obtained, due to the different combinations of substances and the timing of application, are indicative of the complexity of the problem.

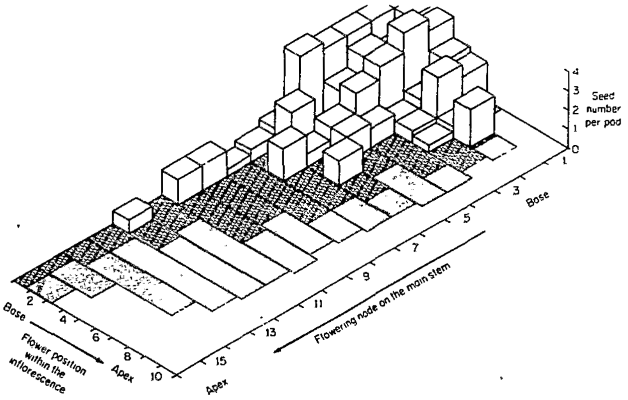

Fig. 8. Performance of individual flowers and fruit according to their position on the plant. The vertical blocks show the numbers of seeds produced by successfully matured pods. The shaded area represents pods that set but failed to complete development. The stippled area represents flowers that failed to produce pods (Peat, 1983, based on data of Sadjadi).

The loss of reproductive organs is decisively affected by environmental factors which alter the competitive balance between vegetative and reproductive organs. Water shortage increases flower and pod abortion (El Nadi, 1969; Meriaux, 1972), especially in the upper nodes and the more distal positions of the racemes, and this is not related to a lack of fertilization (Kogbe, 1972). Excessive water during flowering exerts a similar effect (Smith, 1982; El Rahman *et al.*, 1980). In both cases, an increase in the endogenous ethylene concentration is observed (El Beltagy and Hall, 1975), while ABA-concentration is raised in the water-stressed plants. On the other hand, high levels of water availability at the beginning of flowering can induce vegetative growth and increase the shading of the lower nodes, thus inducing an extensive flower abscission (Smith, 1982). Bud, flower, and pod abortion are also enhanced as crop density increases (Hodgeson and Blackman, 1956; Ishag, 1973), because of the increased mutual shading of foliage and the strong inter-plant competition for nutrients. Temperatures also appear to play a role: plants grown at a regime of 26 °C day/16 °C night aborted newly formed flowers and pods more easily than plants grown at a 16°/16 °C regime (Dekhuijzen *et al.*, 1981). The acceleration of leaf senescence caused by the higher temperatures might be responsible for this phenomenon.

Mineral nutrition

Faba beans are more or less self-sufficient for their nitrogen nutrition. Plants not receiving fertilizer-N fix from 80 to 90% of their N-requirements (Richards and Soper, 1979; Huber *et al.*, 1987). The fact that strains of *Rhizobium leguminosarum* are widespread in temperate agricultural soils practically minimizes the necessity for cultural interventions. Indeed, numerous experimental works have shown little or no response of faba beans to N-fertilizer applications (for a review, see Roughley *et al.*, 1983). More important is the examination of the effects of other external factors on nodule formation and function. Water shortage exerts a definite negative effect on nitrogen fixation by reducing the number of developing nodules per plant (Sprent, 1972). In fact, the maximum activity is observed on soil field capacity and remarkably falling with the onset of visible wilting in the lower leaves (Fig. 9).

Waterlogging creates milder problems (Gallacher and Sprent, 1978); the same also applying to temperature: there is a broad optimum of 10 to 15 °C (20 to 30 °C or 15 to 25 °C) although marginal fixation still proceeds at 2 or 40 °C (Dart and Day, 1971; Fyson, 1981). Finally, a decrease in the overall photosynthetic activity (by shading, loss of foliage, etc.) results in a restricted amount of assimilates available to nodules with a concomitant decrease in nodule activity.

Field studies using ^{15}N have revealed the pattern of N-distribution within plants at different developmental stages (Dekhuizen and Verkerke, 1984). During flowering, leaves and the plant apex act as strong N-sinks and receive more N than the rest of the plant. During pod-filling, however, pods attract the greater portion of N. Considerable amounts of N are redistributed from vegetative organs to pods: about 85% in the period from flowering to maturity or about 50% from pod-filling to maturity. Nevertheless, the amounts of N redistributed from the vegetative organs to the fruits also depend to a large extent on the prevailing temperatures which decisively determine the longevity of the foliage (Dekhuizen *et al.*, 1981). At low temperatures leaves senesce slowly, remobilization of nutrients is restricted, and plants absorb more N from the soil.

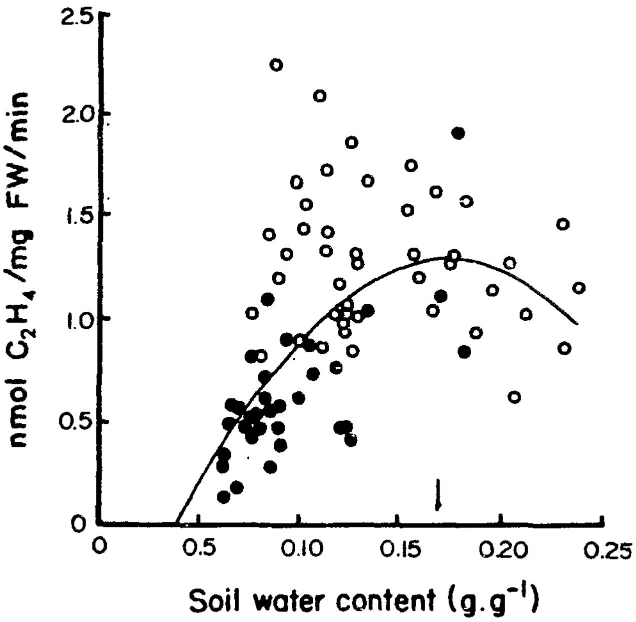

Fig. 9. The relationship between the N-fixing activity (expressed as acetylene reduction) and the gravimetric soil water content for field-grown faba beans. The arrow indicates the soil water content at field capacity for the given soil (Sprent, 1972).

The role of phosphorus is equally important. CO_2-fixation is affected by P-concentration, especially in the older leaves (Avdeeva and Andreeva, 1974). Furthermore, phosphorus is vital for normal vegetative growth and seed development (Kogure *et al.*, 1977), root growth and nodulation (Wilkinson, 1956; Tamaki and Naka, 1971), and synthesis of high molecular compounds (*ibid.).* It shows close resemblance to nitrogen as regards the patterns of accumulation and remobilization to the different organs (Biddulph, 1941; Kogure *et al.*, 1977).

Potassium affects CO_2-fixation positively by increasing the activities and efficiencies of various enzymatic systems involved in photosynthesis (Pfluger and Cassier, 1978). It is also associated with higher rates of N-fixation by increasing the carbohydrate, ATP and reduced electron supply to roots (Mengel *et al.*, 1974). It is accumulated primarily in the vegetative organs, especially in the stems, and does not appear to be remobilized to the seeds to the extent observed for N and P (Kogure *et al.*, 1977).

Plant water relations

As has been emphasized, the influence of water shortage on the growth of faba bean is quite decisive. In this section, special attention is paid to the water ratios of the plants, in order to detect some adaptive mechanisms to drought and understand the responses of the plants when grown under dry conditions.

Faba bean is a typical mesophyte with thin cell walls and fully vacuolated mesophyll cells. Therefore, the tissues behave like osmometers, their water potential (û) being determined only by the solute (ϕs) and pressure (ϕp) components (Karamanos, 1978b). A more elaborate approach towards the understanding of the water ratios of faba bean by including some tissue parameters (Elston *et al.*, 1976; Kassam and Elston, 1976; Karamanos, 1978b, 1981) has revealed the following: First, there is a systematic fall of the solute potential at zero turgor (ϕso) in plants growing under dry conditions. This is indicative of a mechanism of osmotic adjustment which enables plants to absorb water at more negative values of soil water potential. Secondly, the elasticity of the cell walls increases in water-stressed plants thus maintaining cell turgor (ϕp) as high as possible for a given water loss. This modification of cell wall elasticity is unlike that observed in more drought resistant plant species (e.g., sorghum, cotton, olive-tree) when grown under dry conditions (for a review, see Karamanos, 1984b). In contrast with ϕso, the changes in cell wall elasticity respond more readily to the daily fluctuations of evaporative demand and are easily reversible on the removal of water stress. We conclude, therefore, that faba bean plants adapt to prolonged drought mainly by means of a mechanism of osmotic adjustment. This can also be seen from

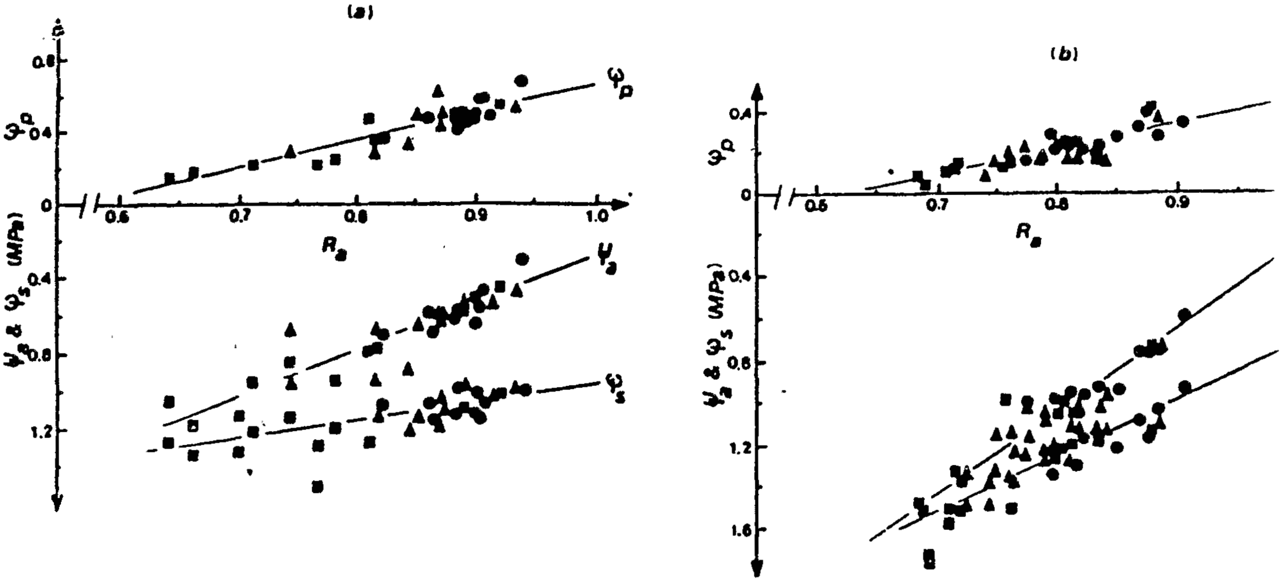

Fig. 10. The relationship between relative water content (R) and water (û), pressure (ϕp), and solute (ϕs) potentials in one wet (a) and one dry (b) season. Results from three irrigation treatments, wet (circles), medium (triangles) and dry (squares). The lines show the fitted linear regressions (Karamanos, 1978b).

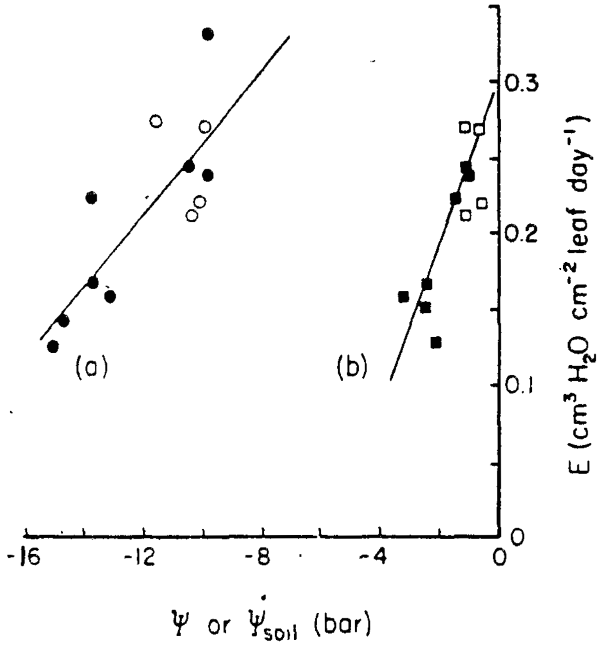

Fig. 11. The relationship between crop transpiration rate (E) and leaf (û) and soil ($\hat{u}_{soil}$) water potentials. (a) E vs. û. (b) E vs. $\hat{u}_{soil}$. Results from a wet (open symbols) and a dry treatment (filled symbols). The fitted linear regressions are also shown (Karamanos, 1980).

the relationship between û and relative water content (R) of faba bean crops in one wet and one dry season (Fig. 10). The more marked relationship between û and R in the dry year indicates that plants lower their water potential in order to sustain the driving force necessary for water uptake. However, this is achieved by means of a more intense lowering in ϕs caused by osmotic adjustment. On the other hand, the slopes of the ratio between ϕp and R remained virtually the same both years, indicating that cell turgor was maintained at values high enough for the continuation of most physiological processes. Nevertheless, despite the obvious tendency for osmotic adjustment, we must keep in mind that the lowest value of ϕso in the two seasons never fell below -2.0 MPa, a value substantially higher than those found in wheat, sorghum, and cotton (less than -2.3 MPa, for a review see Karamanos, 1984b), meaning that the possibilities for osmotic adjustments in faba bean are restricted in comparison to these crop plants.

Transpirational water loss is effectively controlled by either soil or plant water status (Fig. 11). The stomatal control of transpiration is very drastic at values of û more below -1.2 MPa (Fig. 12; cf. also Kassam, 1973). As for ϕso, this threshold value of û for stomatal closure is considerably higher than those encountered in other crop plants (e.g. -2.5 MPa in wheat, -1.7 MPa in maize, -2.2 MPa in sorghum, -2.5 MPa in cotton; for a review, see Turner, 1979; Karamanos, 1984b). Accordingly, faba bean plants can escape drought by controlling transpiration more easily than other crop plants, but at the expense of a concomitant reduction in their rate of photosynthesis. Apart from transpiration, considerable amounts of water are lost from the lower leaves via a direct transport to the younger leaves during periods of water stress (Kassam, 1975).

Faba bean plants absorb water from depths not exceeding 80-90 cm (Kutschera, 1960; French *et al.*, 1973; Hebblethwaite, 1982). Although high soil water contents are extremely favourable for optimum root development (Jones, 1963), increasing dryness of the surface soil layers promotes deeper root growth (El Nadi *et al.*, 1969; Karamanos, 1981). It should be stressed, however, that resistance to water uptake at a given value of soil water potential is much greater in deeper soil layers (Karamanos, 1980; Reid and Hutchinson, 1986). This might be due to changes in root ultrastructure brought about by increasing soil compaction and mechanical impedance to root extension in these layers, as well as to possible effects of anaerobiosis. Hence, it follows that it is important to avoid extreme desiccation of the surface soil layers in order to ensure an easier water supply to plants.

Synopsis and suggestions

Among the environmental stress limiting the efficiency of faba bean production, drought is very usual in Mediterranean agriculture where beans are mainly cultivated as a winter dryland crop. The range of air temperatures usually encountered in the cultivation period seldom exceeds the optimal limits for the growth of faba bean. From the above survey, it follows that:

- The size of the foliage is very closely related to the overall production of assimilates, crop growth and yield. The extreme sensitivity of foliage growth to drought stress is basically responsible for the lower values of the efficiency of conversion of solar energy to biomass (Monteith, 1977) in water-stressed plants (Fig. 13).
- The partition of dry matter to the reproductive organs is restricted by an intense intra-plant competition between them and the vegetative organs, this resulting in flower and pod abortion. The balance of assimilate supply among the various organs is very sensitive to environmental stress, especially to water availability. During flowering, therefore, soil water has to be maintained at levels neither promoting extensive vegetative growth nor inducing ABA-accumulation. The production of cultivars able to bear more fruits per plant under drought conditions would be a possible way of tackling this problem. The effort to relieve the internal competition by introducing determinate plant types (Sjodin, 1971) has not be proved to be very successful, so far. Determinate genotypes exhibit lower yields than the commercial indeterminate cultivars because of their smaller photosyn-

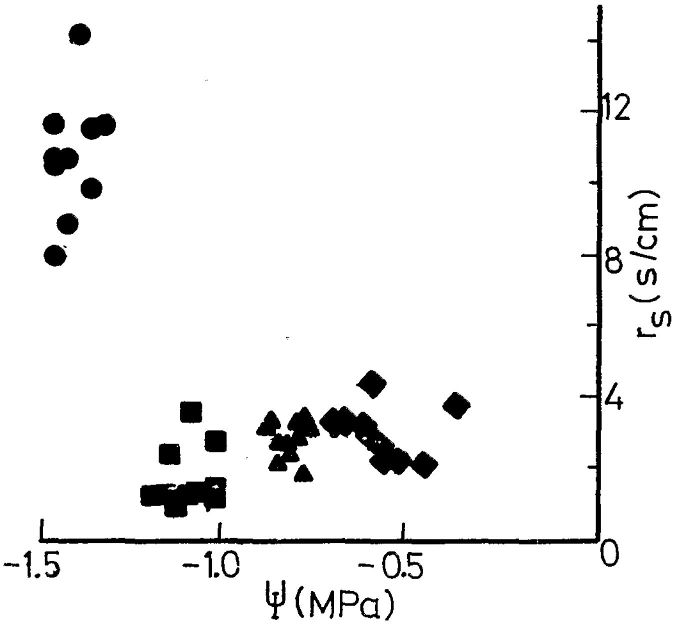

Fig. 12. The relationship between leaf water potential (sc212) and stomatal resistance (rs) for field-grown faba beans (Podimatas and Karamanos, unpublished data).

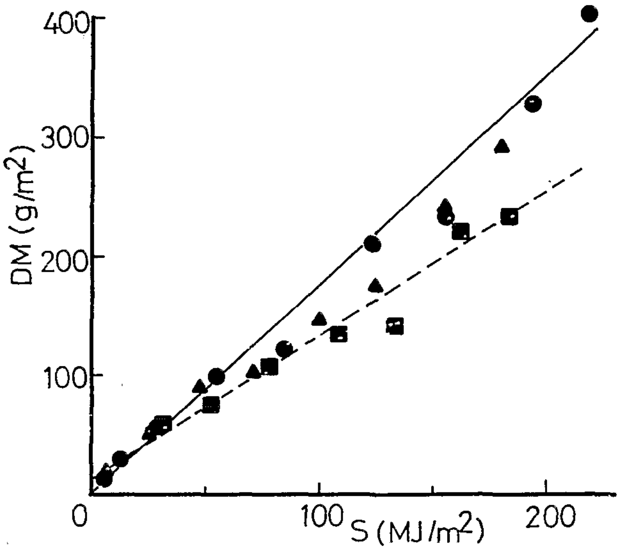

Fig. 13. The relationship between the above-ground dry matter of faba bean crops with the cumulative intercepted photosynthetically active radiation during crop development. Results from a wet (circles), medium (triangles) and dry treatment (squares). The slopes of the fitted linear regressions are 1.70 for the wet and the medium, and 1.20 for the dry treatment, indicating a lower efficiency of solar utilization in the latter case.

thetic area, fewer fruiting nodes per plant and their increased number of infertile axillary branches which act as alternative sinks for assimilates (Austin *et al.,* 1981; Baker *et al.,* 1984; Saxena *et al.,* 1986). Similarly the field behaviour of genotypes with independent vascular supply to each flower, a characteristic believed to alleviate the competition among flowers within a raceme (Gates *et al.,* 1983), is not very encouraging (Saxena *et al.,* 1986). It should be emphasized, however, that considerable breeding work is in progress in order to eliminate the undesirable characteristics of these new plant types. In addition, the effort to alter the hormonal balance of the plants in favour of the reproductive organs still continues, despite the observed difficulties and the complexity of the problem.

- A high proportion of assimilates is lost through darkness and photorespiration, especially when temperatures are higher than 10 to 15 °C. These losses may well become a real problem at the beginning of flowering when intra-plant competition is at its maximum. Thus, high day or night temperatures at this stage may be responsible for an enhanced flower and young pod abortion. Nevertheless, high temperatures are rather seldom during this period for winter crops.
- The available mechanisms of drought resistance are less effective in comparison to other crop plants, especially winter cereals. This problem could be faced by using drought-resistant genotypes, and, where possible, by irrigation. Faba bean responds readily to irrigation by increasing biological and economic yields considerably (Day and Legg, 1983). Adequate levels of water are indispensable for the production of assimilates and their allocation to the various organs, unimpeded growth and development, nitrogen fixation and other processes necessary for normal plant growth and high yields. Irrigation timing has been the subject of many experimental works, and different views have been expressed (for a review, see Green *et al.,* 1986). It appears that the maintenance of satisfactory hydration levels throughout plant life is necessary for high yields. Water is essential in the vegetative phase to ensure normal plant growth and differentiation of flower buds; it is equally essential after flowering in order to ensure a satisfactory supply of assimilates to the fruits via an extensive and long- lived foliage (Karamanos, 1984a).

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