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**EFFECTS OF WATER STRESS ON PHOTOSYNTHESIS, RESPIRATION AND GROWTH OF
FABA BEAN (*VICIA FABA L.*) GROWING UNDER FIELD CONDITIONS.**

**EFEITOS DO ESTRESSE HÍDRICO NA CAPACIDADE FOTOSSINTÉTICA, RESPIRAÇÃO E
CRESCIMENTO DE FABA BEAN (*VICIA FABA L.*) SOB CONDIÇÕES DE CAMPO.**

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SUMMARY

The effects of soil water deficit on photosynthesis, respiration, radiation intercepted and growth of faba bean (*Vicia faba L.*) were studied in field grown plants. Measurements of photosynthesis and respiration of individual leaves were taken in irrigated and water stressed plants. The measurements were taken considering both leaf ontogeny and crop phenology. Water stress reduced leaf photosynthetic capacity, leaf area, leaf dry weight and leaf respiration rate. However, the effects were greater on leaf photosynthetic capacity, leaf area and leaf dry weight than on leaf respiration rate. Evidence was found that for plants growing under field conditions, the respiration rate was not directly related with leaf photosynthetic capacity, leaf carbohydrate content or leaf nitrogen content. The results also showed that soil water deficit reduced the crop maximum leaf area by around 67% whereas the seasonal amount of PAR absorbed was reduced by only 24%. The Biomass Radiation Coefficient was 2.48 and 1.94 g/MJ (PAR), respectively for the irrigated and for the dry crops.

Key words: Water stress, photosynthesis, respiration

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RESUMO

Os múltiplos efeitos da deficiência de água no solo na capacidade fotossintética, respiração, crescimento e radiação interceptada pela faba (*Vicia faba L.*) foram estudadas em plantas cultivadas sob condições de campo. Medidas de fotossíntese e respiração de folhas individuais foram tomadas em plantas irrigadas e em plantas sob estresse hídrico. As medidas foram tomadas considerando a idade das folhas e o estágio fenológico da cultura. A deficiência de água no solo reduziu a capacidade fotossintética, a área foliar, o peso e a taxa de respiração das folhas. Os efeitos foram mais evidentes na taxa fotossintética, área foliar e matéria seca do que na taxa de respiração. Evidências foram encontradas que para plantas em condições de campo, a taxa de respiração não está diretamente relacionada com a fotossíntese, nível de carboidrato, e nível de nitrogênio nas folhas. Os resultados mostraram ainda que o estresse hídrico reduziu a área foliar da cultura em cerca de 67%, enquanto a Radiação Fotossinteticamente Ativa (RAF) absorvida pela cultura foi reduzida em apenas 24%. O uso eficiente da radiação foi de 2,48 e 1,94 g/MJ(RFA) respectivamente para as culturas sob irrigação e sob estresse hídrico.

Palavras-chave: Estresse hídrico, fotossíntese, respiração

INTRODUCTION

Water stress reduces crop yield mainly by its effect on the crop ability to capture and to use light for its growth process. It is well known that the effects of water stress on the crop ability to capture light is via reduction of leaf area (HSIAO, 1973). However, the effects of water stress on the crop use of light is a more complex matter as it is given by a balance between photosynthesis and respiration. Therefore in a way to fully understand the effects of water stress on the plant ability to use light it is needed to study its effect on the plant carbon balance.

Several studies have shown that water stress can have different effects on photosynthesis and respiration. Whereas most of the studies have shown that water stress reduces photosynthesis (HSIAO, 1973; LEVITT, 1980; MULLER *et al.*, 1986; GRZESIAC *et al.*, 1989), respiration has been reported to increase (UPCHURCH *et al.*, 1955; SHEARMAN *et al.*, 1972; XIA, 1994), to decrease (BOYER, 1970; BELL *et al.*, 1971; BROW and THOMAS, 1980; McCREE *et al.*, 1984; RICHARDSON and McCREE, 1985) and even to be insensitive to water stress (CASTONGUAY and MARKHART III, 1992).

These differences can be seen as an indication that the control mechanisms of photosynthesis and respiration of higher plants do not respond in the same way to water stress, so there is not a direct link between photosynthesis and respiration of plants growing under different environmental conditions. If it is so,

the concept used in most crop growth modelling, that any factor reducing photosynthesis has the same effects in respiration, does not hold for all situations.

Whereas the main control mechanism for photosynthesis are well known: CO₂ level, stomatal aperture and level of protein in the leaves, there is a lot of controversy about the control mechanism of respiration. The control of respiration rate in higher plants has been linked with leaf nitrogen and carbohydrate content, leaf photosynthetic rate and plant activity. FARRAR (1980,1985) has pointed out that the control mechanism of respiration can be divided in two groups: source, meaning carbohydrate availability and sink, meaning plant demand for growth. Therefore, studies are still needed to test the control mechanism of photosynthesis and respiration for plants growing under field condition.

Water stress is considered one of the main factors in limiting yields of faba bean (HUSSAIN *et al.*, 1988). However, very little information is available about the effects of water stress on crop growth, considering its differential effects on the capture and use of light by the crop.

The purpose of this paper is to examine the effects of water stress on the ability of Faba bean to capture and to use light. To do so measurements of leaf area, leaf photosynthesis, leaf respiration rate and intercepted radiation were taken and related to growth.

MATERIAL AND METHODS

The experiment was carried out at the experimental fields of Reading University, during the summer of 1992. The soil was a sandy loam overlying gravel. Seeds of field beans (*Vicia faba L. cv. Gobo*) were sown on April 10. The plot size was 8 X 6 m. The average crop density, measured at 48 days after sowing (DAS) was 46 plants m⁻². The plants were grown under natural field conditions until 42 DAS, when two treatments were imposed:

Irrigated: Crops received all the rainfall available throughout the season and irrigation was applied in order to avoid any limitation of water supply. The irrigation was applied using a trickle irrigation system. Fifteen tubes, linked to the main supply line, were laid in each plot between every pair of crop rows. Irrigation was applied four times during the season, 150 mm at 47 DAS, 40 mm at 54 DAS, 25 mm at 63 DAS and 90 mm at 75 DAS. The total rainfall during the growth season was 213 mm.

Dry: crops were covered by a polythene rainshelters throughout the season to avoid direct rainfall, and therefore had available during the season only the soil water reserves stored before the imposition of the treatments.

Volumetric soil moisture content was monitored at 7 day intervals and also 24 hours before and after any irrigation using a Neutron Moisture Meter (Didcot Instruments Co. Ltd.). The calibration curve for sand soils given in the instruction manual was used for the calculation of the volumetric soil water content. Ten

measurements were taken, in each plot, at 10 cm depth intervals down to a depth of 1 m. The access tube was installed in the middle of each plot.

Measurements of the fractional transmission of solar radiation through the crops were taken by placing a tube solarimeters, 80 cm long and 3 cm wide, beneath the crop. A solarimeter was also placed, outside at the height of the crops, to provide a continuous reference for the incoming radiation. The output of the solarimeters readings were integrated daily throughout the growing season by using a logger (Delta-T Devices) The solarimeters were individually calibrated against a pyranometer Kipp and Zonen.

Measurements of Photosynthetically Active Radiation (PAR) were made by using a Sunfleck Ceptometer (Delta-T Devices). Ten measurements of incident and transmitted radiation were taken weekly by placing the ceptometer at four different levels in the canopy: top, bottom, and at two intermediate levels. Measurements of PAR reflected by the canopy and by the soil were taken by directing the instrument sensor either towards the crop or to the soil.

At 7 day intervals ten plants in each plot were harvested from a randomly selected area of 0.5 x 0.5 m. The samples were harvested at the centre of the area and the remaining peripheral area worked as a buffer zone. After harvesting the plants were separated in leaves, stems, roots and pods (when applicable). To obtain plants with roots, trenches were cut with spades. The average area of the trenches were 0.5 m² and the depths varied from 15 to 80 cm, according to the plant size. The roots were separated from the soil by washing and flotation. Dry weights were determined by oven drying the samples at 80°C for 72 hours. The leaf area was determined using the Area Measurement System Mk2 (Delta-T Devices Ltd.).

The total available non-structural leaf carbohydrate content was determined using the method suggested by SMITH *et al.*, (1964). The leaf nitrogen content was determined by using an FP228 Organic Nitrogen-Protein Analyser (Leco Instruments Ltd.). For each phenological phase considered (vegetative, and flowering) five leaves from each treatment, were sampled at three times during their life span (young leaf, fully expanded leaf and mature leaf) and the carbohydrate and nitrogen content were determined.

The photosynthetic and respiratory CO₂ exchange of leaves in this study were determined by infra-red gas analysis techniques. A battery operated, portable, integrated, open system (LCA-3, ADC Ltd.) working in a differential mode was used. The response of net photosynthesis to PAR was measured using a portable lamp unit, supplied with a quartz bulb (100W, 12v), a heat filter and a fan, fixed on the chamber. The initial reading was taken at a maximum light, which was then reduced, step by step, by interposing neutral density filters between the light source and the leaf. Dark respiration was measured, using the same equipment without the light unit, by excluding light from the chamber before the measurements. The measurements started 5 minutes after excluding light from the chamber.

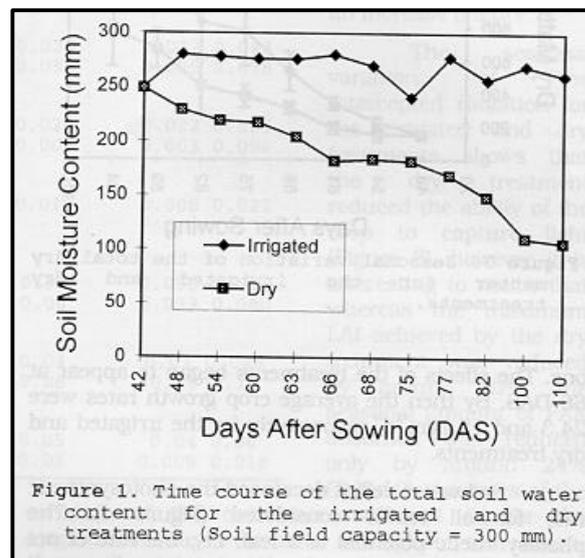
The photosynthesis light response curve was taken in three individual leaves, from each treatment, at three times during their life span (young leaf, fully expanded leaf and mature leaf). Measurements of dark

respiration were taken following individual leaves from unfolding to maturity. Ten measurements were taken in each treatment, up to the time of leaf fully expansion, at two day intervals and from then on at weekly intervals.

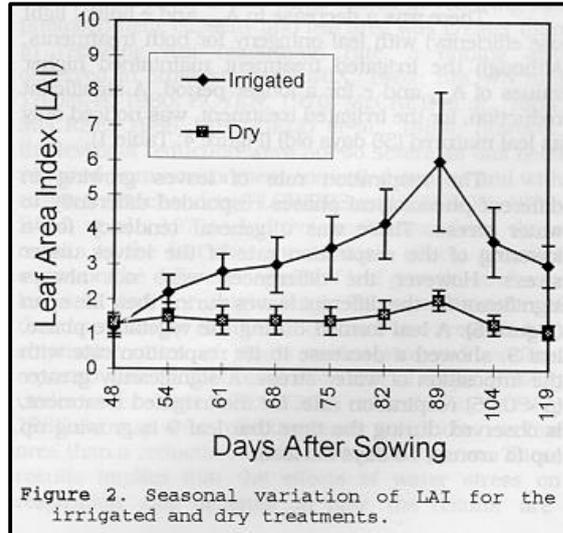
The measurements of photosynthesis and respiration were taken on leaves developed during different phenological phases: leaf 9 (vegetative phase), leaf 13 (flowering phase) and leaf 20 (podfilling phase). The leaf temperature was taken using a thermistors and all the results were corrected to 20° C using a Q_{10} of 1.5 (COSTA *et al.*, 1996). The response of leaf net photosynthetic rate to incident light was fitted by using the asymptotic exponential (GOUDRIAAN,1982).

RESULTS

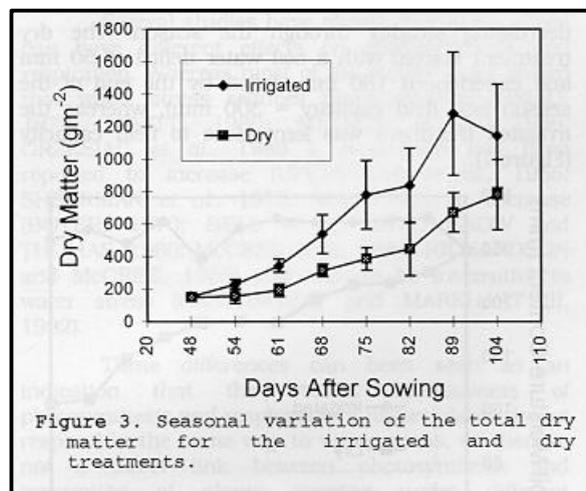
The time course for the total soil water content for the irrigated and dry treatments shows that the plants growing under dry treatment experienced a large soil water deficit with the water in the soil decreasing steadily through the season. The dry treatment started with a soil water deficit of 50 mm and experienced 180 mm deficit by the end of the season (soil field capacity = 300 mm), whereas the irrigated treatment was kept close to field capacity (Figure 1).

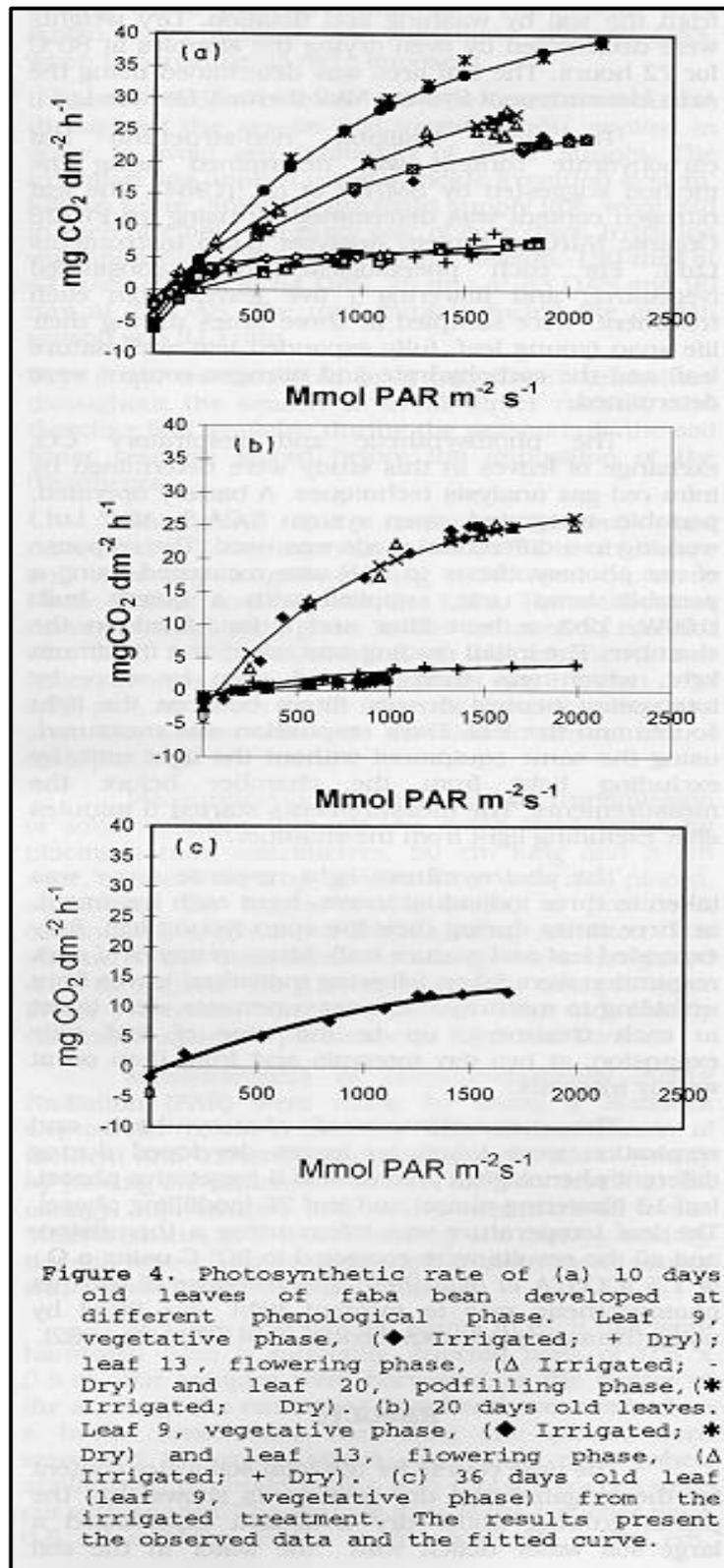


The crop growing under dry treatment had a significantly lower LAI throughout the season than the irrigated one (Figure 2). The irrigated treatment reached its maximum LAI on 89 DAS (LAI=6), whereas the dry treatment only kept the level of LAI that it had before the treatments were imposed (LAI between 1.5 and 2).



The results of crop total dry matter (Figure 3) shows that throughout the season the irrigated treatment had a higher total dry matter than the dry one. The effects of the treatments began to appear at 68 DAS. By then the average crop growth rates were 24.3 and 15.1 gm⁻²d⁻¹ respectively for the irrigated and dry treatments.





Soil water deficit decreased the photosynthetic rate for all leaves considered (Figure 4). The photosynthetic potential of a leaf, i.e., the rate of net photosynthesis at saturating level (A_{max}) decreased with increasing soil water deficit (Table 1).

For a young fully expanded leaf (10 days old) developed during the vegetative phase (leaf 9) the decrease in A_{max} was 62% for a soil water deficit of 27%. For a 10 day old leaf developed during the flowering phase (leaf 13), the A_{max} decreased 73% and the soil water deficit was 40%. A ten day old leaf developed during the podfilling phase (leaf 20) had the A_{max} reduced by 78%, and the soil water deficit was 53%.

Table 1. Rate of net photosynthesis at saturated light intensity, A_{max} ($\text{mgCO}_2\text{dm}^{-2}\text{h}^{-1}$), and the initial light use efficiency, e ($\text{mgCO}_2\text{dm}^{-2}\text{h}^{-1}$) ($\text{mmol PAR m}^{-2}\text{s}^{-1}$) for the irrigated and dry treatments, obtained from the fitted light response curve for leaves 9, 13 and 20, at different ages. The 95% confidence interval (C.I.) is also given.

	A_{max}	95% C.I.	e	95% C.I.
Leaf 9 - 10 days old				
Irrigated	32.6	30.1 35.0	0.038	0.033 0.043
Dry	12.2	11.0 13.4	0.052	0.025 0.078
Leaf 9 - 24 days old				
Irrigated	43.7	26.1 45.3	0.029	0.022 0.035
Dry	3.6	1.7 5.5	0.005	0.003 0.006
Leaf 9 - 36 days old				
Irrigated	19.2	11.0 27.2	0.016	0.008 0.022
Dry	-	-	-	-
Leaf 13 - 10 days old				
Irrigated	34.8	30.3 39.2	0.04	0.032 0.046
Dry	9.35	7.9 10.8	0.06	0.033 0.080
Leaf 13 - 24 days old				
Irrigated	36.4	31.7 26.8	0.04	0.03 0.048
Dry	5.2	4.3 6.3	0.08	0.06 0.10
Leaf 20 - 10 days old				
Irrigated	49.7	40.9 58.4	0.05	0.04 0.06
Dry	11.1	8.2 13.9	0.01	0.008 0.016

There was a decrease in A_{max} and e (initial light use efficiency) with leaf ontogeny for both treatments. Although the irrigated treatment maintained higher values of A_{max} and e for a longer period. A significant reduction, for the irrigated treatment, was noticed only as leaf matured (36 days old) (Figure 4; Table.1).

The respiration rate of leaves growing in different phenological phases responded differently to water stress. There was a general tendency for a lowering of the respiration rate of the leaves under stress. However the differences were not always significant for the different leaves during their life span (Figure 5). A leaf formed during the vegetative phase, leaf 9, showed a decrease in its respiration rate with the imposition of water stress. A significantly greater ($p < 0.05$) respiration rate, for the irrigated treatment, is observed during the time that leaf 9 is growing up (up to around 10 days old leaf).

As the leaf ages thereafter the differences become smaller and the differences hardly significant (Figure 5).

Although the effects of water stress is also seen on the respiration rate of a leaf developed during the flowering phase (leaf 13) the results are less evident than the effect on a leaf formed during the vegetative phase (leaf 9). The respiration rate of the leaves in the irrigated plot were not significantly greater than the dry ones during most of their life span, except for a 15 and a 22 days old leaves (Figure 5).

The leaf developed during the time of podfilling (leaf 20) produced a significant greater ($p > 0.05$) respiration rate for the plants growing under irrigation than the dry one up to the time of leaf fully expansion (around 10 days old leaf) (Figure 5)

For all leaves and treatments considered, respiration rate, per unit of area decreased with leaf age. The results also showed that for a given treatment and a given leaf age, a leaf developed during the vegetative phase (leaf 9), had a higher respiration rate than leaves 13 and 20 (Figure 5).

The carbohydrate contents of leaves 9 and 13 measured at three occasions during their life span, show that the plants under irrigated treatment had a tendency for higher, carbohydrate content (% by dry weight) than the dry treatment. As leaves aged there was a significant decrease in their level of carbohydrate content (Figure 6).

The nitrogen concentration of leaves 9 and 13 showed no significant differences between the irrigated and dry treatment. Also there was no clear behaviour with leaf ontogeny. Whereas leaf 9 showed a decrease as leaf aged, leaf 13 showed an increase (Figure 7).

The seasonal variation of the intercepted radiation for the irrigated and dry treatments shows that the dry treatment reduced the ability of the crop to capture light (Figure 8), however it is interesting to notice that whereas the maximum LAI achieved by the dry treatment was reduced by around 67% the seasonal amount of PAR absorbed was reduced only by around 24% (Table 2). Analyses of the variation of the extinction coefficient (k) for the irrigated and dry treatments throughout the season, shows that whereas the k values of the irrigated treatment decreased with DAS, the k values from the dry treatment increased (Table 3).

The effects of the soil water deficit in the use of light by the crop is reflected on the lower values of Biomass Radiation Coefficient (\hat{I}) for the dry treatments (Table 3).

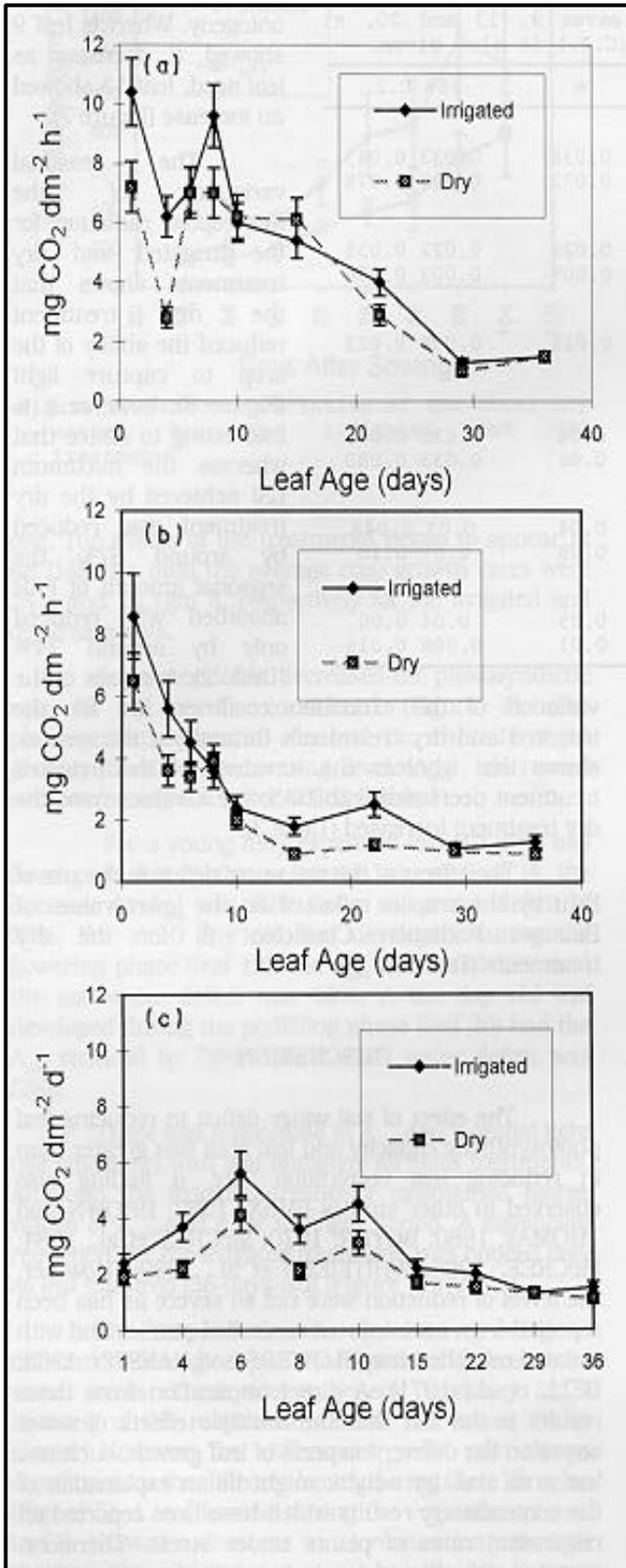


Figure 5. Respiration rate, per unit of area, of a leaf developed (a) at vegetative phase (leaf 9), (b) at flowering phase (leaf 13) and (c) at podfilling phase (leaf 20) from the irrigated and dry treatments.

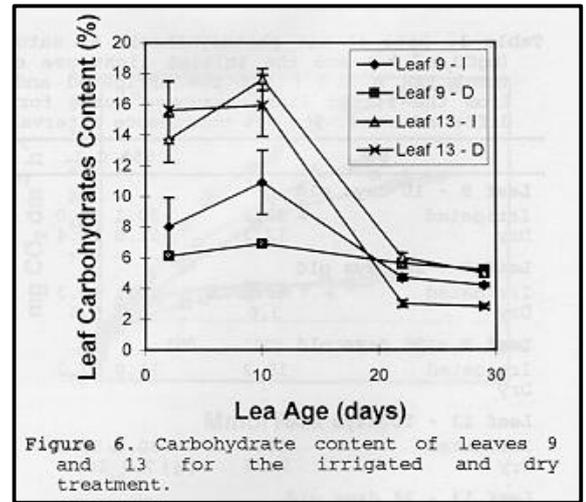


Figure 6. Carbohydrate content of leaves 9 and 13 for the irrigated and dry treatment.

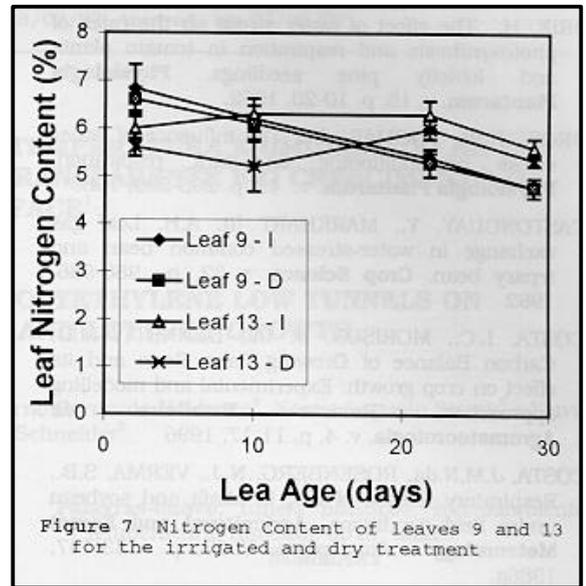


Figure 7. Nitrogen Content of leaves 9 and 13 for the irrigated and dry treatment

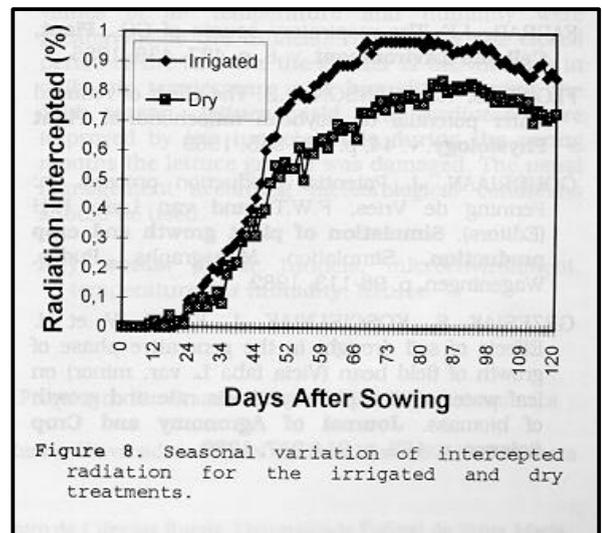


Figure 8. Seasonal variation of intercepted radiation for the irrigated and dry treatments.

Table 2. Seasonal amount of PAR absorbed (A_p), maximum LAI achieved and the Biomass Radiation Coefficient (\hat{I}) for the irrigated and dry treatment.

	Irrigated	Dry
A_p (MJ/m ²)	651	495
Maximum LAI	6.0	2.0
\hat{I} (g/MJ(PAR))	2.48	1.94

Table 3. Seasonal variation of the extinction coefficient (k) for the irrigated and dry treatment.

Days After Sowing (DAS)	Irrigated	Dry
48	0.85	0.60
54	0.73	0.63
61	0.73	0.75
68	1.00	0.93
75	1.00	0.99
82	0.77	1.00
89	0.50	0.86
104	0.60	1.00

DISCUSSION

The effect of soil water deficit in reducing leaf photosynthetic capacity and leaf area was greater than in reducing leaf respiration rate, a finding also observed in other studies (BRIX, 1962; BROWN and THOMAS, 1980; BOYER, 1970; McCREE et al., 1984; McCREE, 1986, WHITFIELD et al., 1989). However, the levels of reduction were not so severe as has been reported from environment controlled studies and with isolated mitochondria (FLOWERS and HANSON, 1969; BELL et al., 1971). A direct implication from these results is the fact that the multiple effects of water stress on the different aspects of leaf growth, such as , leaf area and dry weight, might be an explanation of the contradictory results which have been reported on respiration rates of plants under stress. Therefore, reported reduction of respiration rate of crops growing under water stress (UPCHURCH et al., 1955; COSTA, 1986a,b) may were reflecting more a

reduction in leaf area than a reduction in respiration rate *per se*. These results implies that the effects of water stress on respiration rate depends on how the results are expressed. Therefore care must be taken when comparing the results presented per unit of leaf area, per unit of dry mass and as CO₂ released per leaf. Another important point to be stressed from the results is the fact that there is a differential quantitative response between leaf photosynthetic capacity and leaf respiration rate to water stress, so a simple relationship between photosynthesis and respiration does not hold for faba bean plants growing under field conditions.

The variation of leaf carbohydrate content and leaf nitrogen content as leaves aged did not have the same intensity, or even the same pattern as leaf respiration rate. Therefore the respiration rate of individual leaves, and more important the differences in respiration rate of leaves developed at different phenological phases, can not be explained by leaf carbohydrate and nitrogen content

The multiple effects of soil water deficit on the different aspects of crop growth were stressed by the decreasing of the Biomass Radiation Coefficient (\hat{I}) for the dry treatment, a fact which is consistent with a decrease in the ratio photosynthesis: respiration, and also by the increasing in the values of k for the dry treatment. Similar changes in \hat{I} and k have been reported for *Vicia faba* (COSTA, 1992). These results seems to imply that there was a change in the plant architecture in order to increase its ability to capture light.

The results found in this study indicated that whereas the relationship which is normally assumed in crop modelling between leaf photosynthesis and leaf respiration rate has been proved very useful to predict crop growth, it maybe affecting a better understanding of the control of respiration rate and therefore of crop growth (FARRAR, 1980; 1985). The different respiration rate observed from leaves developed during different phenological phases are na indication that

the use of a mean for one leaf to indicate the behaviour of others and hence the whole canopy may lead to a misleading results. This fact was pointed out in a earlier paper by RICHARDS (1934) and stressed by AMTHOR (1989). These difference may be linked with the different light and temperature experienced by leaves developed at different phenological phases environments and also with the different plant demand for growth (sink theory) in each phase. However, more specific experiments are still need in order to fully understand the complex interaction between radiation , plants and photosynthesis in a natural environment. Indeed much of our present understanding of leaf photosynthesis stems from studies developed in completely artificial conditions and do not consider the substantial differences of light, temperature, water status that may be found trough the depth of the canopy.

Results from this study consistently lead to a conclusion that for plants growing under field condition photosynthesis and respiration can behave in a different manner under water stress, and therefore others factors, as for example crop growth and activity, or the sink and source theory (FARRAR, 1985), should be considering in explaining the variation of leaf respiration rate under such condition. However, further studies,

mainly considering whole plant respiration over a continuous period of time and different rates of growth, are clearly needed before an explicit explanation is available for the differential response of photosynthesis and respiration rate of plants under water stress. The small reduction in respiration rate, compared with photosynthesis and leaf area, stressed the indispensable character of respiration for crop growth (AMTHOR, 1989).

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