

**CARBON BALANCE OF GROWING FABA BEAN AND ITS EFFECT ON CROP GROWTH:  
EXPERIMENTAL AND MODELLING APPROACHES.**

**BALANÇO DE CARBONO E CRESCIMENTO DE LEGUMINOSAS: MODELOS E  
EXPERIMENTOS.**

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**SUMMARY**

Measurements of photosynthetic capacity, respiration rate and expansion of individual leaves of faba bean (*Vicia faba L. cv. Gobo*) were taken throughout the summer of 1992. Modelling techniques were used to scale up from from single leaves to canopy carbon balance. The model was developed to simulate canopy photosynthesis for different leaf layers (growing, recently fully expanded and mature). The results revealed that growing leaves were the major contributor to canopy photosynthesis at the beginning of the season. However, by the end of the season the contribution of recently expanded leaves was around 60% greater than the growing leaves. Mature leaves contributed with only 10% of the total canopy photosynthesis, although, by the end of the season, they comprised about 50% of the total canopy leaf area.

**Key words:** carbon balance, crop growth, modelling.

**RESUMO**

Medidas da capacidade fotossintética, taxa de respiração e expansão de folhas individuais de Faba bean (*Vicia faba L.*) foram tomadas durante o verão de 1992. A associação de técnicas de modelagem

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com a experimentação permitiu a simulação da taxa de assimilação do dossel através do conhecimento da taxa de assimilação de folhas individuais. Baseado em resultados do experimento o modelo foi desenvolvido considerando a divisão do dossel em três camadas de folhas (em crescimento, recentemente expandidas e maduras). Os resultados mostraram que no início da estação a assimilação do dossel era, em grande parte, devido a assimilação das folhas em crescimento. No entanto, tal situação se inverteu no final da estação, quando as folhas recentemente expandidas apresentaram uma taxa de assimilação cerca de 60% maior do que as folhas em crescimento. Apesar de serem responsáveis por cerca de 50% da área foliar da cultura no final da estação, as folhas maduras contribuíram somente com cerca de 10% da assimilação do dossel.

**Palavras-chave:** balanço de carbono, crescimento, modelos.

## INTRODUCTION

The increasing interception of solar radiation that accompanies canopy growth is a critical aspect of what has been termed resource capture by crops (MONTEITH *et al.*, 1994). As the canopy grows, however, not only do environmental conditions change but so do the physical structure of the canopy, the age of leaves and the relative distribution of material among plant compartments. In particular, as leaves unfold, expand and then senesce, their photosynthetic and respiratory characteristics change (LUDLOW & WILSON, 1971; CONSTABLE & RAWSON, 1980). These changes alter the efficiency with which light energy is captured and used by plants.

The relationships between canopy growth, light interception and crop growth have been studied extensively (MONTEITH, 1977). However, relatively little attention has been given to changes in canopy characteristics over time, and few crop models have considered the effects of leaf age-class dynamics on the crop carbon balance (WULLSCHLEGER & OOSTERHUIS, 1992).

In the understanding of a crop carbon balance, the use of a simple models, with only a few classes of leaves, instead of a complex canopy model have proved to be very useful tool (SINCLAIR *et al.*, 1976; SINCLAIR, 1991).

A very simple model is the one that uses a simple relationship between radiation intercepted and crop growth. Recently, there has been some controversy about the use of this model (DEMETRIADES-SHAH *et al.*, 1992; MONTEITH, 1994). Part of this uncertainty arises because few studies have considered the detailed dynamics of the changes in the efficiency of conversion of radiation to dry matter, (Radiation Use Efficiency, RUE; amount of dry matter produced per unit radiation intercepted) as crop grows.

It is well known that the canopy age-class dynamics and the partitioning of material between plants components affects the ratio photosynthesis: respiration. Therefore, it is very likely that these changes will induce changes in the RUE (SINCLAIR, 1991 WHEELER *et al.*, 1993).

The objective of this paper was to use a simple simulation model to explore changes in the ability of a growing canopy to capture and use light.

## MATERIAL AND METHODS

**Faba Bean Crops:** The experiment was carried out at Sonning Farm, University of Reading (51°27'N, 0°57'W), during the summer of 1992. The plot size was 8 x 6 m and the sowing date was 10 of April. The average crop density was 46 plants m<sup>-2</sup>. Rainfall was supplemented with irrigation throughout the season.

**Growth samples:** At 7-day intervals 10 plants 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 served as a buffer zone. After harvesting, the plants were separated into leaves, stems, roots and pods. To obtain the roots, trenches were cut with spades. The average area of the trenches was 0.5 m<sup>2</sup> and the depths varied from 15 to 80 cm. 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 h. The leaf area was measured using the Area Measurement System Mk2 (Delta-T Devices Ltd.). The expansion of individual leaves developed at different phenological phase, leaf 9 (vegetative phase), leaf 13 (flowering phase) and leaf 20 (podfilling phase) was also followed, from appearance to maturity, by sampling 10 leaves at an average 2-day intervals.

**Gas Exchange measurements:** Photosynthetic and respiratory CO<sub>2</sub> exchanges 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 by using a portable lamp unit, supplied with a quartz bulb (100 W, 12 v), 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.

Measurements were taken in three individual leaves (leaf 9, leaf 13 and leaf 20), at three times during their life span (young leaf, recently fully expanded leaf and mature leaf). The asymptotic exponential model (GOUDRIAAN, 1982) fitted to the data was used to describe the photosynthetic light-response curve of each leaf.

*Model development:* A simulation model was developed to describe the time course of dry matter production of faba bean based on the description of the photosynthesis and respiration characteristics of individual leaves. To scale from single leaves to canopy photosynthesis the canopy was assumed to be formed by three leaf layers: growing, recently fully expanded; and mature. Each leaf layer was assumed to have its own photosynthetic and respiration characteristics (Tables 1,2).

The extinction of radiation in the canopy was assumed to be exponential and the canopy was assumed to have a spherical leaf angle distribution.

The solar radiation was divided into direct and diffuse component (SPITTERS *et al.*, 1986). The amount of sunlit and shaded leaf area and the effect of multiple scattering and reflection were considered in the model (SPITTERS *et al.*, 1986, GOUDRIAAN, 1982) (Table 3).

**Table 1.** The maximum rate of photosynthesis (AMAX) and the light-use efficiency (PLE) used in the model for the different classes of leaves considered

Leaf/Class	AMAX (g CO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup> )	PLE [g CO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup> (J m <sup>-2</sup> s <sup>-1</sup> ) <sup>-1</sup> ]
Vegetative and Flowering phases		
Growing	1.2 x 10 <sup>-3</sup>	0.8 x 10 <sup>-5</sup>
Fully expanded	0.9 x 10 <sup>-3</sup>	0.8 x 10 <sup>-5</sup>
Mature	0.5 x 10 <sup>-3</sup>	0.4 x 10 <sup>-5</sup>
Podfilling phase		
Growing	1.4 x 10 <sup>-3</sup>	1.3 x 10 <sup>-5</sup>
Fully expanded	1.0 x 10 <sup>-3</sup>	0.8 x 10 <sup>-5</sup>
Mature	0.5 x 10 <sup>-3</sup>	0.4 x 10 <sup>-5</sup>

**Table 2.** Rates of maintenance respiration (RM) and the growth efficiency (GE) used in the model for the different plant parts.

Organ	RM [g CO <sub>2</sub> (g dwt) <sup>-1</sup> dal]	GE (%)
Leaf	16.0 x 10 <sup>-3</sup>	0.75
Stems	8.0 x 10 <sup>-3</sup>	0.80
Roots	5.3 x 10 <sup>-3</sup>	0.80
Pods	8.0 x 10 <sup>-3</sup>	0.75

Table 3. The Scattering (SCT) and the reflection (REF) coefficient for light. The light extinction coefficient for direct (KDIR) and for diffuse light (KDF) used in the model.

Condition	Coefficient
SCT (%)	0.20
REF (%)	0.05
KDIR	0.73
KDF	0.72

Each layer was assumed to have its own coefficient for maintenance respiration. Also, maintenance respiration was assumed to have priority over the growth process and its rate was considered to be dependent on temperature with  $Q_{10}= 1.5$  (COSTA, 1994).

Maintenance respiration and the growth efficiency (ratio of the increment in plant dry mass over the increment in plant dry mass plus the substrate respired) for the leaves, stem, roots and pods were based on a constituent composition typical of faba bean plants (PENNING DE VRIES *et al.*,1989).

The partitioning of carbohydrate to different plant organs was based on experimental observations and took into consideration the phenological state of the crop (PENNING DE VRIES & VAN LAAR, 1982). The model also considered the amount of assimilated CO<sub>2</sub> that can be accumulated as a starch in a reserve pool.

To assess the general behaviour of the model, modelled values of LAI and plant dry weight were compared with an independent set of data obtained from *Vicia faba* (c.v. Gobo) grown during 1989 at Sonning Farm (COSTA, 1992). The crops were fully irrigated. The sowing date was 18 of April and the emergence has occurred at 20 DAS.

The model was written using the Continuous Simulation Modelling Program, CSMP (IBM, 1975).

## RESULTS

Leaf appearance (leaf number) was linearly related with Days After Emergence (DAE) and leaves appeared on average every 2.43 days. The rate of expansion of the individual considered in this work are presented in Figure 1. Analyses of the data showed that there were no statistical difference in the rates of expansion for the different leaves.

The linear rate of leaf expansion was estimated by fitting a regression to the points up to leaf age of 10 days. The final area was estimated by fitting a horizontal line to the points between 10 and 40 days

old leaves (DENNETT *et al.* 1978). By using this method the leaf growth rate and the maximum area were estimated to be respectively  $11.1 \text{ cm}^2 \cdot \text{d}^{-1}$  and  $131.1 \text{ cm}^2$ . Therefore the average time required for a leaf to fully expand was 11.8 days, and an average of 4.85 leaves could be expanding at the same time.

In the model the canopy was considered to be divided in three leaf layers: Growing Leaves,  $L_g$  (the top five leaves); recently fully expanded Leaves  $L_e$ ; (Fully expanded leaves with a maximum rate of photosynthesis reduced by at most 30%), mature leaves,  $L_m$ ; (leaves with a maximum rate of photosynthesis reduced by more than 30%).

Figure 2 presents the observed variation in  $L_g$ ,  $L_e$  and  $L_m$  as a fraction of the total crop LAI. The fraction of growing leaves ( $FL_g$ ) declined exponentially with increasing LAI. The fraction of recently fully expanded leaves ( $FL_e$ ) increased up to the LAI of 2.8 and then decreased. The fraction of mature leaves ( $FL_m$ ) only appeared for a LAI around 2.8 and then increased.

From these observations the fraction of each layer were expressed as a function of total LAI:

$$FL_g = \exp(-0.490 \text{ LAI}) \quad \mathbf{1}$$

$$FL_e = 0.574 \text{ LAI} - (0.106 \text{ LAI}^2) \quad \mathbf{2}$$

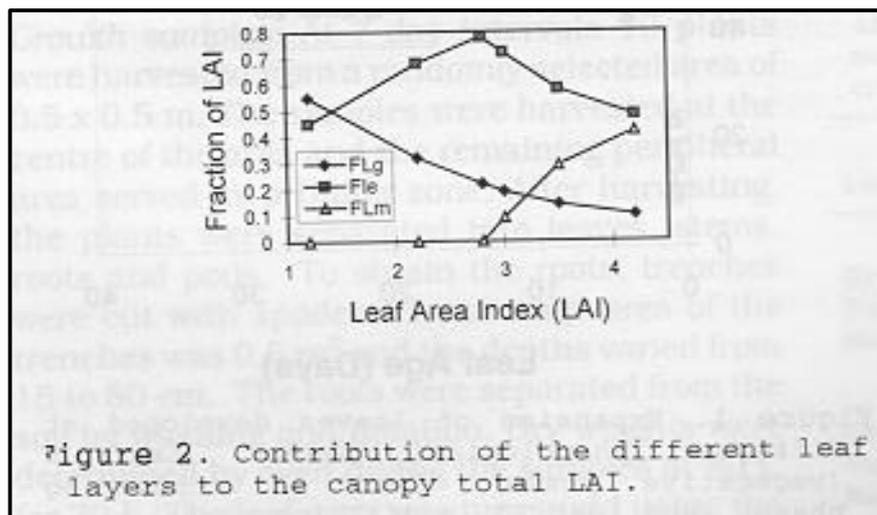
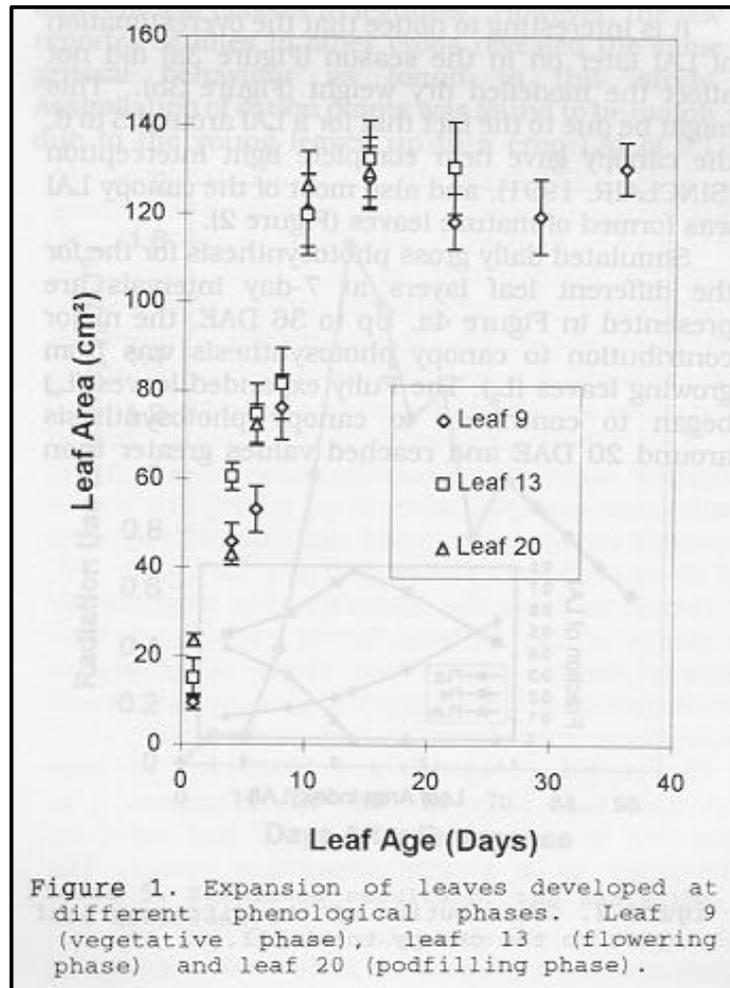
$$FL_m = 1 - (FL_g - FL_e) \quad \mathbf{3}$$

Two additional conditions were made: for values of  $\text{LAI} < 0.3$ ,  $FL_g$  was assumed to be 1; and for values of  $\text{LAI} > 5$ ,  $FL_e$  was:

$$FL_e = \exp(-0.320 \text{ LAI}) \quad \mathbf{4}$$

The simulated total LAI shows a good agreement with the measured LAI up to 90 Days After Emergence (DAE). Thereafter, simulated LAI continued to increase whereas measured LAI decreased (Figure 3a). This difference was due to leaf senescence which was not considered in the model.

Simulated crop total dry weight also agreed well with the measured weight (Figure 3b). It is interesting to notice that the overestimation of LAI later on in the season (Figure 3a) did not affect the modelled dry weight (Figure 3b). This might be due to the fact that for a LAI around 5 to 6, the canopy gave near complete light interception (SINCLAIR, 1991), and also most of the canopy LAI was formed of mature leaves (Figure 2).



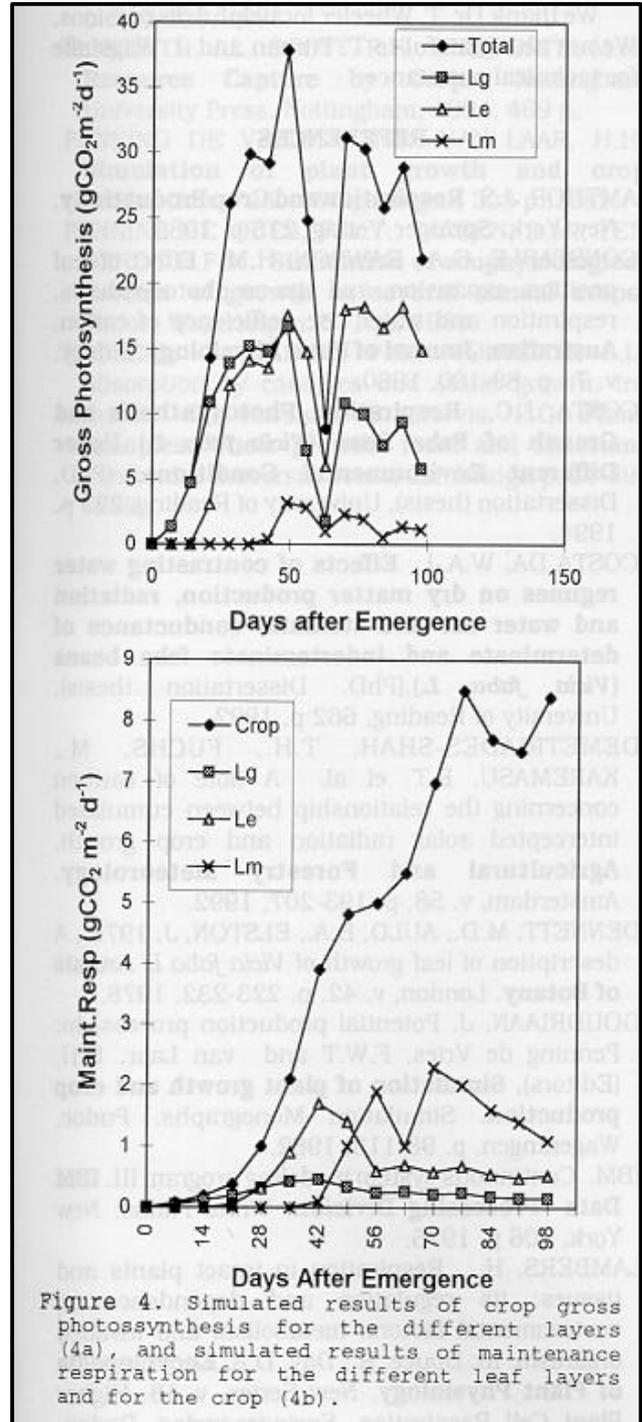
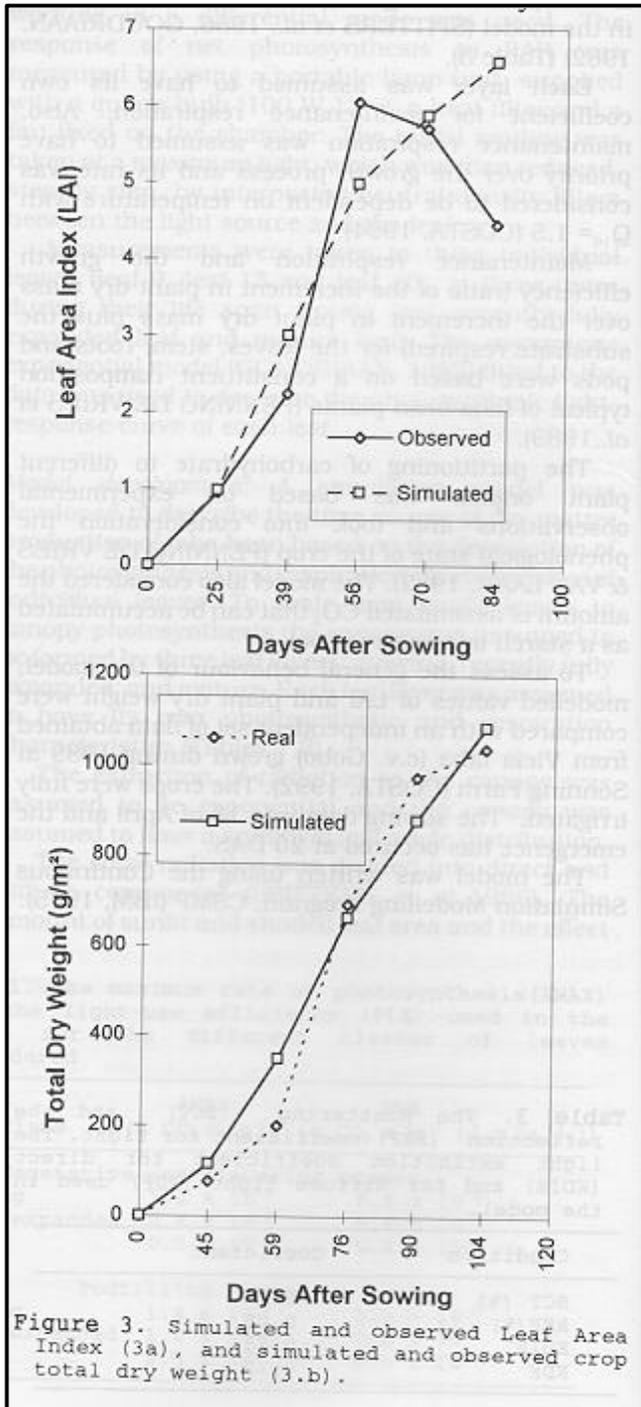


Figure 3. Simulated and observed Leaf Area Index (3a), and simulated and observed crop total dry weight (3.b).

Figure 4. Simulated results of crop gross photosynthesis for the different leaf layers (4a), and simulated results of maintenance respiration for the different leaf layers and for the crop (4b).

Simulated daily gross photosynthesis for the for the different leaf layers at 7-day intervals are presented in Figure 4a. Up to 36 DAE, the major contribution to canopy photosynthesis was from growing leaves (L<sub>g</sub>). The Fully expanded leaves (L<sub>e</sub>) began to contribute to canopy photosynthesis around 20 DAE and reached values greater than growing m leaves at around 50 DAE. By the end of the season, fully expanded leaves accounted for two thirds of the crop photosynthesis.

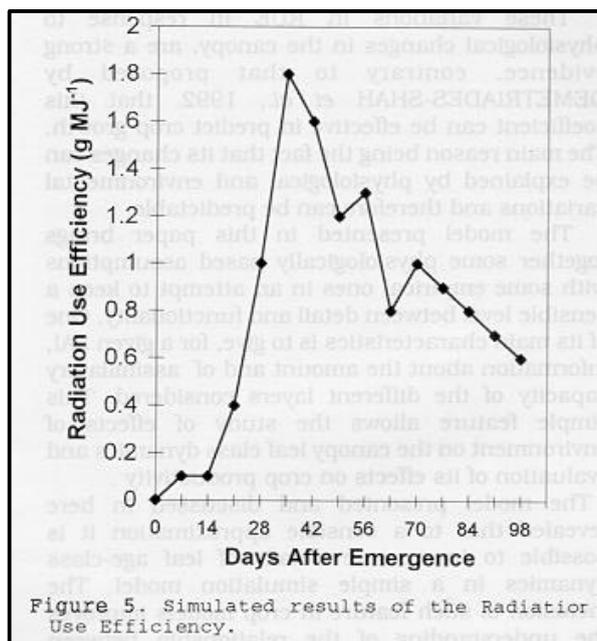
However, It is important to notice that the area of the fully expanded leaves was almost four times greater than the growing leaves at 50 DAE and around three and a half times greater by the end of the season. The mature leaf layer ( $L_m$ ) began to contribute to canopy gross photosynthesis at around 40 DAE, reaching a maximum photosynthetic rate at around 50 DAE, and from then on it had an almost constant, but small, contribution of only 10% of total.

As gross photosynthesis is affected by radiation level, the small rate observed at 62 DAE occurred on a very cloudy day (incident radiation level of  $6.24 \text{ MJ m}^{-2}.\text{d}^{-1}$ ). In this situation of low radiation, the photosynthetic rate of growing leaves was more affected than the others (Figure 4a). Under cloudy conditions most of the light was diffuse and then it could be more uniformly distributed among the layers than direct light. Therefore, in this situation, the top layer (growing leaves), loses some of its advantage in the capture of light over the lower ones (fully expanded and mature leaves).

The results of maintenance respiration for the different leaf layers are presented in Figure 4b. It can be seen that, from 50 DAE onwards, mature leaves ( $L_m$ ) had higher maintenance respiration than growing ( $L_g$ ) or fully expanded ( $L_e$ ) leaves. The mature leaves reached the end of the season with values around two times greater than fully expanded leaves and seven times greater than growing ones.

The maintenance respiration of leaves were a greater proportion of total plant maintenance respiration at the beginning of the season (around 70% at 36 DAE) and then decreased to a lower values (25-40%) by the end of the season.

The simulated 7 day average of the RUE (Figure 5) shows that this coefficient was very small at the beginning of the season, but it increased rapidly to its maximum of  $1.8 \text{ g.MJ}^{-1}$  around 35 DAE. From then on there was a gradual decrease up to the end of the season.



## DISCUSSION AND CONCLUSIONS

The average time for full expansion of a Faba bean leaf found in this study was very similar to results found by DENNETT *et al.*, (1978).

There is a lack of studies on assimilation by different leaf classes in legumes. However, the few reported studies in other crops revealed the same general behaviour as found in this study. Assimilation of cotton plants was found to be mainly due to the young leaves up to a crop LAI of 2.3 (WULLSCHLEGER & OOSTERHUIS, 1992). As the crop aged, there was a shift towards older leaves with the middle part of the canopy giving a greater contribution to canopy assimilation.

The small contribution (%) of mature leaves to canopy assimilation and their large contribution to crop maintenance respiration found in this study are very consistent with the idea that higher crop yield may be achieved by reducing maintenance respiration of mature leaves (AMTHOR, 1989).

The insight provided by Monteith's model (MONTEITH, 1977) of a linear relationship between crop dry weight and intercepted solar radiation provided a very useful approach to study the link between plant growth and environment. However, as was pointed out in introducing the concept (MONTEITH, 1977) and in later publications (RUSSELL *et al.*, 1989), this relationship can be affected by several environmental and physiological factors.

Therefore, the results presented in this study may reflect that at the beginning of the season, a crop with a small LAI (which means fewer and younger leaves) was light saturated and therefore gave small values of RUE.

As a canopy ages, later in the season, Lower values of RUE were achieved. The reason for that might be the increasing in the amount of older leaves and also in the crop maintenance respiration.

The variation in RUE found in the simulation presented in this study results are in line with several physiological studies and experimental results (AMTHOR, 1989; LAMBERS, 1985; WHEELER *et al.*, 1993).

These variations in RUE in response to physiological changes in the canopy, are a strong evidence, contrary to that proposed by DEMETRIADES-SHAH *et al.*, 1992, that this coefficient can be effective in predict crop growth. The main reason being the fact that its changes can be explained by physiological and environmental variations and therefore can be predictable.

The model presented in this paper brings together some physiologically based assumptions with some empirical ones in an attempt to keep a sensible level between detail and functionality. One of its main characteristics is to give, for a given LAI, information about the amount and of assimilatory capacity of the different layers considered. This simple feature allows the study of effects of

environment on the canopy leaf class dynamics and evaluation of its effects on crop productivity .

The model presented and discussed in here revealed that to a sensible approximation it is possible to incorporate details of leaf age-class dynamics in a simple simulation model. The inclusion of such feature in crop models improves the understanding of the relationship between photosynthesis, respiration and growth in an ageing canopy.

However, it seems clear that more studies associating field experiment and crop modelling are needed to define the best way to describe canopy expansion, light interception and assimilation in models of crop growth improves the understanding of the relationship between photosynthesis, respiration and growth in an ageing canopy.

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