

## PHOTOSYNTHESIS AND TRANSPIRATION OF SUNFLOWER CROPS

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## ABSTRACT

The photosynthesis and transpiration of sunflower crops subjected to a range of irrigation sequences were measured over the entire crop cycle using field chambers. The data define the high photosynthetic potential of sunflower which at full cover (LAI 3) reached  $10 \text{ g CO}_2/\text{m}^2/\text{hr}$  with little saturation to global irradiance of  $900 \text{ W}/\text{m}^2$ . Water supply exercised marked control over crop photosynthesis through canopy size more than activity of unit leaf area. Daily photosynthesis was proportional to intercepted radiation ( $5.2 \text{ g CO}_2/\text{MJ}$ ). A 2-weekly irrigation sequence which applied about 50% of pan evaporation introduced a balance which promoted leaf expansion, did induce limited stomatal closure but relieved stress before hastened leaf senescence. On a daily basis, photosynthesis was proportional to transpiration per unit saturation vapour pressure deficit. There was no difference between treatments in daily transpiration efficiency. The data confirm the interpretation of an agronomic analysis that differences between the water use efficiency of the various treatments were a result of differences in soil evaporation rather than in transpiration efficiency.

## INTRODUCTION

The measurement of  $\text{CO}_2$  and  $\text{H}_2\text{O}$  exchange by crops provides an instantaneous view of crop growth and water-use that enables analyses of the short-term response of crops to environmental conditions and crop status. Such analyses are an important adjunct to field experiments of crop performance because they provide an explanation of the accumulated behaviour of crops as measured over the longer term by dry matter harvesting and evaluation of the crop water budget.

## METHODS

The observations were made upon three treatments of a field experiment of the response of sunflower cv Sungold to strategies of irrigation (Connor *et al.* in press). The three treatments are the weekly irrigated and rainfed controls together with a 2-weekly irrigated treatment which received half the irrigation of the weekly control. The crops were sown on December 5, 1981 and reached 50% anthesis 70 days after sowing (DAS). Seasonal rainfall and pan evaporation to 114 days after sowing were 92 and 798 mm respectively. The total water-used by the three treatments, including withdrawal from the soil, was 620, 255 and 420 mm respectively.

Photosynthesis and transpiration of the crops were measured diurnally with a set of four, open-system, field assimilation chambers each of ground area  $1 \text{ m} \times 1 \text{ m}$  maintained with  $1^\circ\text{C}$  of ambient temperature. The chambers remained on the same section of crop for a maximum of three successive days. Leaf area index (LAI) was estimated non-destructively from measurement of the lengths of all laminae in the chambers. For all

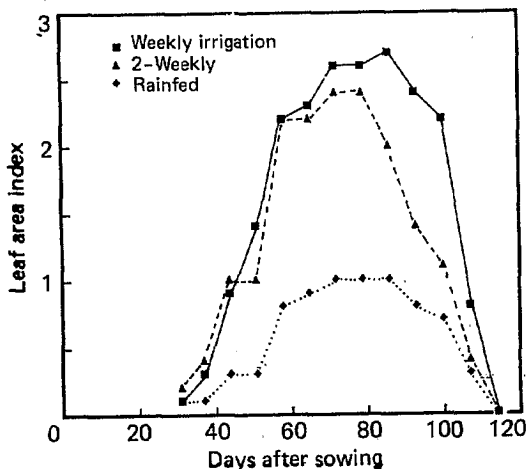
observations reported here the ground surface within the chambers was covered with plastic sheet so that the gas exchange is that of the crop canopy itself i.e. of crop photosynthesis and of crop transpiration.

The mean diffusive conductance of the leaf surface ( $2 \times \text{LAI}$ ) within the chambers was calculated from the measured transpiration rate by assuming that in these well stirred chambers the temperature of all leaves was the same as that of the air leaving the chamber and that the boundary layer resistance was negligible.

## RESULTS

The crops studied were subjected to distinct irrigation regimes which led to major differences in growth and yield (Connor et al. in press). An important part of the adjustment to water shortage clearly lies in the development and maintenance of crop leaf area. Fig. 1 shows that in the pre-anthesis period, i.e. up to 70 days, there was a progressive but small restriction in the development of leaf area in the 2-weekly irrigated treatment relative to the weekly irrigated control. By contrast the development of leaf area was severely restricted in the rainfed control. Following anthesis there was rapid loss of leaf area in the 2-weekly irrigated treatment relative to the two controls.

Fig. 1 Seasonal patterns of LAI for three irrigation treatments of sunflower



### (a) Diurnal patterns of Crop Photosynthesis and Transpiration.

Data collected on two representative days, 61 and 80 DAS, are presented in Figs. 2 and 3. An important feature of these data is the high rate of  $\text{CO}_2$  assimilation seen especially in the weekly irrigated control which developed the greatest LAI. At  $\text{LAI} = 2$ , a crop assimilation rate of  $9 \text{ g CO}_2/\text{m}^2/\text{hr}$  (Fig. 2a) is equivalent to a unit leaf rate of  $45 \text{ mg CO}_2/\text{dm}^2/\text{hr}$  which is well in excess of the rate of around  $30 \text{ mg CO}_2/\text{dm}^2/\text{hr}$  which characterizes most productive  $\text{C}_3$  species. Connor and Cawood (1978) recorded maximum rates of leaf photosynthesis in potted plants of sunflower cv Hysun grown outdoors under high insolation of  $60 \text{ mg}/\text{dm}^2/\text{hr}$  at global flux density of  $800 \text{ W}/\text{m}^2$ . In the sunflower crops measured here there is little saturation even at high insolation (Fig. 2c).

By 61 DAS (Fig. 2) there was a substantial reduction in the photosynthetic performance of the rainfed relative to the irrigated treatments (Fig. 2a) but the analysis of leaf conductance (Fig. 2b) shows that stomatal closure did not play a dominant role in this response. Nor was there,

CROP GAS EXCHANGE

Fig. 2 (61 DAS)

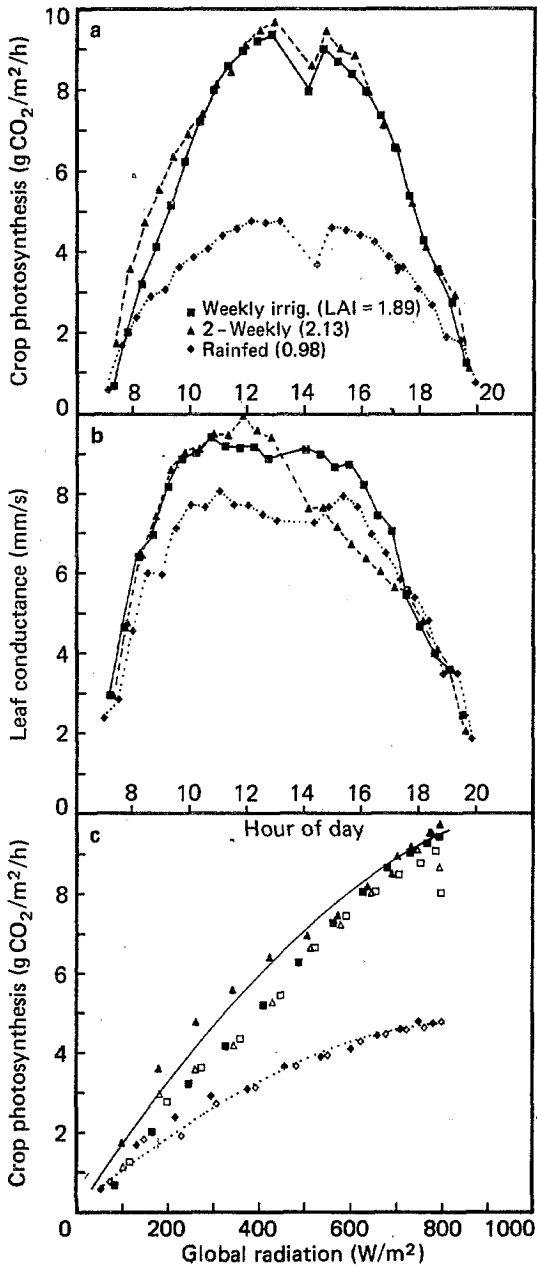


Fig. 3 (80 DAS)

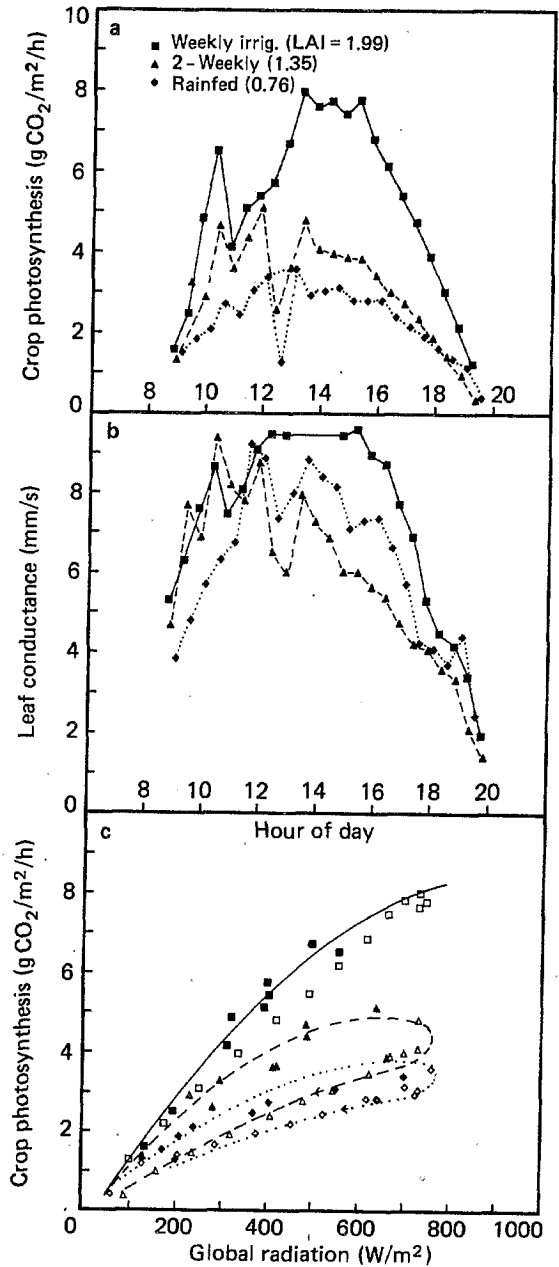


Fig. 2 and Fig. 3 Diurnal pattern of (a) crop photosynthesis and (b) leaf diffusive conductance for the three irrigation treatments of sunflower 61 and 80 days after sowing. The relationship during the day between crop photosynthesis and global flux density is presented in (c) where open symbols depict measurements taken after 1300 hr and in Fig. 3 the arrowed line the diurnal time sequence in the measurements.

despite the prior effect of water supply on canopy growth, any evidence of water stress during the afternoon (Fig. 2c, open symbols).

Although 2-weekly irrigation allowed development of leaf area up to anthesis (70 DAS) water supply was inadequate to maintain leaf area afterwards. In Fig. 3, at 80 DAS, the different photosynthetic performance of the treatments (Fig. 3a) is once again dominated by differences in leaf area rather than by leaf conductance (Fig. 3b). Fig. 3c shows a marked suppression in photosynthetic response in the afternoon to which wilting makes a major but unmeasured contribution.

Low leaf conductance was never a feature of these crops. Conductance rarely fell below 7 mm/s during daylight hours from the base value of around 10 mm/s (Figs. 2b, 3b).

(b) Daily Gas Exchange.

Observations of daily photosynthesis were made over 29 days of the crop growing season. The daily photosynthetic rate/unit leaf area (Fig. 4) shows a gradual decline in unit photosynthetic activity which is constant between treatments. The seasonal decline in daily radiation and differences between crops in leaf area index, leaf display and stomatal condition all contribute to this decline and may operate unequally between and within treatments during the course of the growing season.

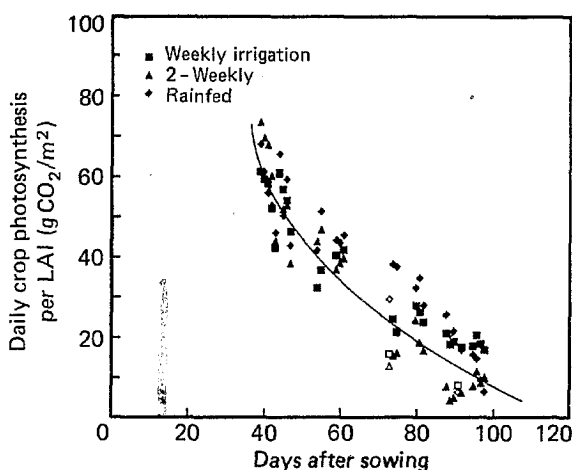


Fig. 4 Seasonal change in daily crop photosynthesis per unit LAI. Open symbols are for three days when global radiation fell below 15MJ/m<sup>2</sup>.

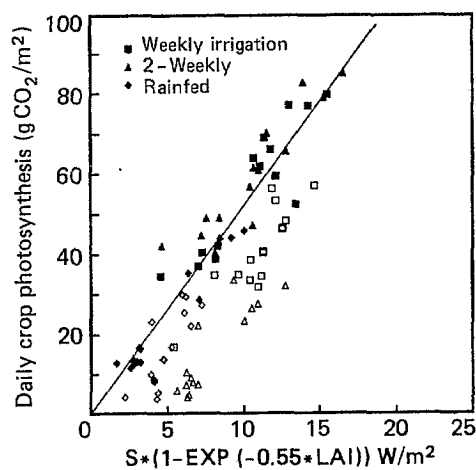


Fig. 5 Daily photosynthesis plotted against a transform of daily global radiation and crop LAI which estimates the amount of radiation intercepted daily by the crop. The open symbols are for measurements taken after anthesis. The line fitted to the observations taken up to anthesis has a gradient of 5.24 g CO<sub>2</sub>/MJ (R<sup>2</sup> = 0.96, n = 42).

Some resolution of the nature of this daily photosynthetic response is achieved in Fig. 5 where daily CO<sub>2</sub> assimilation is plotted against an

estimate of daily radiation intercepted by the crops. The line of best fit ( $R^2 = 0.96$ ,  $n = 42$ ) and hence the value of 0.55 for the parameter of the exponential term in LAI was estimated from the data for all treatments in the period up to 70 DAS. This line suggests that the difference between daily  $CO_2$  uptake between the treatments is dominated by the interception of radiation and hence not by factors, other than shading, which affect activity of unit leaf area. The estimate of photosynthetic activity for this period (*i.e.* gradient of line) is 5.24 g  $CO_2$ /MJ). Fig. 5 also shows how the efficiency of photosynthetic conversion falls in the post-anthesis period, and also how differences are generated between treatments. The effect is most marked in the 2-weekly treatment in which lower leaf conductance and hence lower activity/unit leaf area accompanied the most rapid leaf senescence.

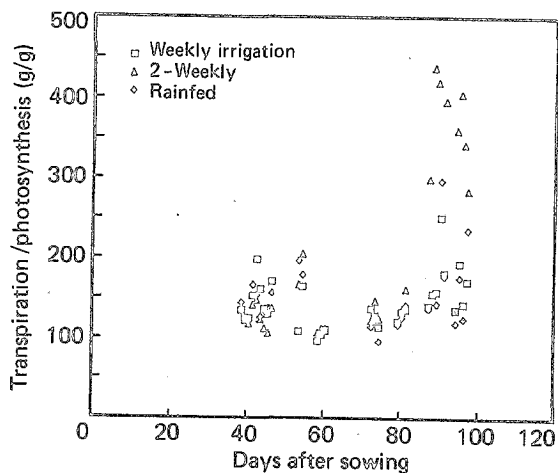


Fig. 6 Seasonal trend of daily transpiration ratio for the three treatments over the growing season.

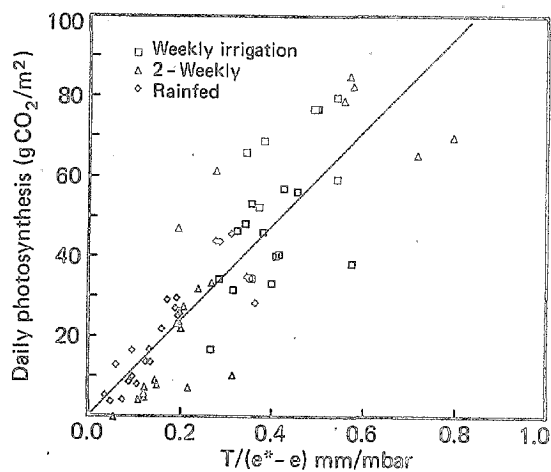


Fig. 7 Daily crop photosynthesis plotted against the ratio of daily transpiration to daily mean saturation vapour pressure deficit. The line fitted to all observations has a gradient of 119 g  $CO_2/m^2$  (mm/mb) ( $R^2 = 0.86$   $n = 66$ ).

The daily ratio of transpiration to photosynthesis *i.e.* the transpiration ratio, is presented in Fig. 6. The wide range reflects the influence of environmental factors operating differentially upon the two processes concerned. During the pre-anthesis period the mean daily ratio is about 150g/g and this is maintained until late in the season when, as has been shown, the photosynthetic capacity of individual leaves fell.

The plot of daily photosynthesis against the ratio of daily transpiration (T) to mean daily saturation vapour pressure deficit ( $e^*-e$ ) (Fig. 7) is essentially an estimate of the mean daily crop conductance. Over all data ( $n = 66$ ) the line of gradient 119 g  $CO_2/m^2$  (mm/mb) is fitted with  $R^2 = 0.86$ . This gradient is the "k" of Tanner and Sinclair (1983) and is consistent with the data that they have assembled, lying as it does at the boundary between  $C_3$  and the more water-efficient  $C_4$  species.

## DISCUSSION

The high photosynthetic capacity of sunflower that is achieved under conditions of adequate water supply is substantially reduced as the availability of water falls. The restriction to assimilation by water shortage is dominated by the effect on the development and maintenance of leaf area rather than by its unit activity. Analysis of leaf conductance (Fig. 2,3) and the photosynthetic conversion of intercepted energy (Fig. 5) both show the relatively consistent activity of unit leaf area across treatment of distinct LAI. Leaf conductance was maintained high in all treatments, even during wilting.

Crop transpiration was related to vapour pressure deficit with no difference between treatments (Fig. 7). This confirms a separate analysis of the accumulation of biomass and crop water-use which suggested that differences in soil evaporation and not transpiration efficiency were the basis for the observed differences in crop water-use efficiency in these experiments.

The observations stress the importance during the crop cycle of morphological as opposed to physiological responses to water shortage. The relative contribution of stomatal activity and wilting to the diurnal behaviour of crop photosynthesis in water stressed crops remains to be assessed.

## ACKNOWLEDGEMENT

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