

## Leaf Area Index is an Important Determinant of Pre-anthesis Radiation Use Efficiency in Sunflower Crops

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### Abstract

The effects of leaf area index (LAI), as determined by canopy growth and crop population density, on sunflower crop radiation use efficiency (RUE) during the emergence to first anthesis period were evaluated in experiments conducted during three seasons. RUE increased with LAI (range 0.1 to 3.5) from ca. 1 to ca. 3.5 g MJ PAR<sup>-1</sup>. Consequently, RUE achieved close to anthesis was strongly dependent upon plant population density, varying between 1.12 g MJ<sup>-1</sup> at 0.5 pl. m<sup>-2</sup> and 3.09 g MJ<sup>-1</sup> at 5 pl. m<sup>-2</sup>. A model of light interception by sunflower canopies was combined with a module which estimated aerial biomass as a function of irradiance, specific leaf nitrogen (SLN), partitioning to roots, and respiratory costs of biomass synthesis and maintenance. The combined model provided acceptable estimates of crop biomass accumulation and RUE across experiments, time from emergence, and crop population density. Simulations using the model showed that although variations in crop thermal and irradiance regimes, SLN, and partitioning to roots produced shifts in the RUE/LAI relationship, none of these factors was capable of altering the form of the relationship. It is concluded that the effects of LAI on light interception and distribution within the canopy of RUE is the main cause of the observed increase of RUE with LAI.

**Key words:** Sunflower, radiation use efficiency, leaf area index, partitioning, simulation.

### Introduction

Trápani et al. (1992) showed that the radiation use efficiency (RUE) of the sunflower crop during the establishment phase was about one-half of that of the rapid growth (roughly, bud visible to anthesis) phase. This report has since been confirmed (Orgaz et al., 1992; Steer et al., 1993; Giménez et al., 1994). Trápani et al. (1992) concluded that canopy light-saturation (Connor et al., 1985), followed by partitioning to the roots, were the most likely reasons for their results. If changes in degree of light saturation of the canopy were a major cause of variation in RUE, it should be possible to alter the dynamics of crop RUE through manipulation of plant population density.

This paper reports the results of experiments and analyses directed toward resolving this issue. Biomass and LAI dynamics were followed in three experiments, in two of which plant population density was manipulated in order to break the linkage between ontogeny, changes in partitioning to roots, and increase in LAI. In another approach, a simulation model of radiation interception in sunflower crops (Villalobos and Orgaz, pers. comm.) was combined with information on leaf photosynthetic responses to irradiance, specific leaf nitrogen (SLN), and temperature, biomass partitioning to roots, and maintenance and synthesis respiration costs. This combined model, which effectively reproduced

the dynamics of crop biomass and radiation interception, was used to explore the impacts of LAI, incident radiation, temperature, SLN, and biomass partitioning to roots on crop RUE.

### Materials and methods

Three experiments in which the dynamics of biomass accumulation and LAI were followed during much of the emergence-anthesis phase were conducted during 1990 (Exp.1), 1991 (Exp.2) and 1994 (Exp.3) at the Agricultural Research Centre at Córdoba, Spain (38°N, 4°W). These involved irrigated and N-fertilized crops of cv. Arbung E-353 (Arlesa, Spain) growing on a sandy-loam Typic Xerofluvent. Experiments were laid out as complete randomized blocks with three (Exp.2) or four (Exp.1 and 3) replicates. Plant population densities (0.5 to 10 pl.m<sup>-2</sup>), row orientation (N-S or E-W), and planting arrangement ([0.14 m \* 0.70m] to [1.4m \* 1.4m]) were varied within and/or between years to provide a range of crop structures.

Biomass and leaf area index (LAI) were determined at intervals of between three and eight days (Exp.1), one week (Exp.2), and two weeks (Exp.3). Intercepted radiation was estimated from LAI values using the Villalobos and Orgaz (pers. comm.) model. Briefly, this model assumes three categories of leaf surface (suntracking illuminated, immobile illuminated, and shaded), and provides separate estimates of interception of direct and diffuse radiation components for each category of leaf surface, as well as accounting for scattering within the canopy. Model parameters (average shadow projection and maximum LAI values for the suntracking surfaces; extinction coefficients for diffuse and scattered radiation) were calibrated using measurements performed in additional plots of two treatments of Exp. 3, and validated using a further set of plots of different treatments in the same experiment. This validation (Villalobos and Orgaz, pers. comm.) showed that the model can effectively capture the variations in light interception associated with canopy development, planting arrangement and solar zenith angle (Estimated interception = 18.2 + (1.02 \* observed interception),  $r^2 = 0.986$ ,  $n = 160$ , intercept and slope not significantly ( $P = 0.05$ ) different to 0 and 1, respectively, range of observed intercepted radiation: 30 to 1770  $\mu\text{E m}^{-2} \text{s}^{-1}$ ).

A model that simulates light interception, photosynthesis and conversion to biomass was formulated and used to explore the impact of the various factors which might affect RUE on the dynamics of this variable. Daily values of LAI, daily radiation integrals and maximum and minimum temperatures are the only inputs to the model, which consists of two modules. The first module, the Villalobos and Orgaz (pers. comm.) model of radiation interception, was used to simulate the interception of light and its distribution within the canopy. Intercepted PAR estimates generated by this model in the course of Exp. 3 tallied well with observations (see above) and this module is not discussed further here.

The second module of the model generated estimates of crop gross photosynthesis and respiration, partitioning the resultant biomass into aerial and below ground compartments. Gross photosynthesis for each category of leaf surface was simulated using the appropriate response functions for irradiance and specific leaf nitrogen (SLN) (Connor et al., 1993), maximum photosynthesis response to temperature (Horie, 1977, Paul et al., 1990), and quantum efficiency response to temperature (Ehleringer and Pearcy, 1983). Daytime temperature dynamics were simulated using a sine curve. Incoming radiation was assumed to vary as a function of the observed daily integral and the daily radiation dynamic above the atmosphere (Gates, 1962). Basic simulations were performed using a SLN of 2 g N

$\text{m}^{-2}$ , appropriate for a crop well supplied with N growing at Córdoba (Giménez et al., 1994). Values of canopy gross photosynthesis were estimated with a 0.5-h time step commencing each day when the solar zenith angle reached  $90^\circ$ .

Conversion of gross photosynthesis to biomass was made using the concepts and parameter values outlined by Penning de Vries et al., (1983) and published and unpublished data on organ composition. Maintenance respiration response to temperature was assumed to have a  $Q_{10}$  of 2. Biomass was partitioned between lamina and non-lamina organs using a modification of the partitioning coefficients reported by Trápani et al. (1994).

## Results

Weather conditions varied quite widely between experiments with mean daily temperature increasing from close to  $16^\circ\text{C}$  at the start of Exp. 3 to close to  $29^\circ\text{C}$  at the end of Exp. 1, with radiation showing a similar trend between about 17 to roughly  $27 \text{ MJ m}^{-2} \text{ d}^{-1}$ . Within each experiment and treatment the range of biomass and LAI values between the start and end of the observations was important, and in Exps. 2 and 3 manipulation of plant population density at sowing had significant ( $P = 0.05$ ) effects on both variables.

The slope of the overall observed aerial biomass/intercepted PAR relationship for crops sown at population densities above  $2 \text{ pl.m}^{-2}$  increased with cumulative intercepted PAR, particularly for values  $> 120 \text{ MJ m}^{-2}$  (Fig. 1). This plot, however, tends to mask the differences in the dynamics of change in RUE (i.e. the slope of the biomass/intercepted PAR relationship) between population density treatments. Thus, mean RUE (estimated from curves fitted to the biomass/intercepted radiation plots) during the interharvest period ending at anthesis was between  $2.04$  and  $2.66 \text{ g MJ}^{-1}$  for crops sown at  $2 \text{ pl m}^{-2}$  and between  $3.22$  and  $2.96 \text{ g MJ}^{-1}$  for crops sown at  $5 \text{ pl m}^{-2}$  in Exps. 2 and 3, respectively. Under the extreme population density of  $0.5 \text{ pl m}^{-2}$  in Exp. 2, there was very little change in RUE (mean value  $1.12 \text{ g MJ}^{-1}$ ) between the start and end of the observation period.

Values of observed RUE, calculated for interharvest intervals, increased with LAI in all experiments and treatments from initial values of ca.  $1 \text{ g MJ}^{-1}$  to close to  $3.5 \text{ g MJ}^{-1}$  for values of LAI of ca. 3 (Fig. 2). Scatter of the points about the trend line increased with LAI (and plant biomass), as is to be expected for estimates of RUE calculated on the basis of inter-harvest increments of biomass.

The model overestimated pooled observed biomass values for the three years by just under 13% (Fig. 3). This effect was largely due to observations for the two cooler years (i.e. Exps. 2 and 3), the slope of the regression for 1990 did not differ significantly ( $P = 0.05$ ) from 1. The tendency toward overestimation was consistent across the observed range of biomass; the intercept values for individual years did not differ from zero ( $P = 0.05$ ).

The preceding tests show the model is a useful tool with which to explore the effects of the various crop and environmental factors on crop RUE for these sets of experimental data. We conducted analyses using the model to compare the simulation for Treatment 1, Exp. 3 ( $10 \text{ pl.m}^{-2}$ , N-S rows,  $\text{SLN} = 2 \text{ g N m}^{-2}$ ), with others in which values for radiation receipt, SLN, temperature and partitioning to roots were varied one at a time. Simulated values of biomass, intercepted radiation and RUE were calculated for the interharvest intervals used in Exp. 3.

The use of constant values of daily radiation receipt, temperature, and SLN, selected to represent the upper and lower extremes of the ranges the crop was exposed to during the season (radiation, temperature) or reported in the literature (SLN) produced shifts in the RUE/LAI relationship with respect to the standard simulation, but did not affect the form of the relationship (data not shown).

Higher partitioning coefficients to the roots in the early stages of crop growth have sometimes been invoked to explain low values of RUE at this stage (e.g. Ferraris and Charles-Edwards, 1986; Giménez et al., 1994). We used the model to explore this issue not only by using constant high (0.22, characteristic of the emergence-bud visible phase in the standard simulation) and low (0.08, characteristic of the bud visible-anthesis phase in the standard simulation) values for the partitioning coefficient to root, but also by using values of 0.33 and 0.44 for the emergence-bud visible phase. These variations in the pattern of partitioning produced the expected shifts in the RUE/LAI relationship, but had little effect on the tendency for RUE to increase with LAI (Fig.4). The shape of the aerial biomass/intercepted radiation relationship for these simulations (data not shown), strongly resemble those of Fig.1. Although the value of the partitioning coefficient does affect RUE, in all combinations simulated the slope of relationship increases with intercepted PAR, similar to the pattern seen in Fig.1.

### Discussion

Results of model analyses are consistent with the notion that RUE, and its variation during the pre-anthesis phase of the crop season, is largely determined by LAI through its effect on radiation distribution within the canopy. Environmental factors such as temperature and radiation, or physiological ones such as SLN and partitioning to roots, have fairly limited impacts. These results extend previous reports by showing the importance of population density in determining peak values of RUE achieved during the emergence-anthesis phase. Thus the change of RUE at bud visible found by Trápani et al. (1992) was probably a particular case of a general phenomenon, rather than an indication of an ontogenetically determined change in crop functioning.

The tendency of the model to overestimate biomass in the cooler years is consistent with the lack, in the model, of any control that reflected acclimation responses to growth temperatures. Additional contributions to this bias might have arisen from the use of constant, rather than a temperature-influenced (Brouwer, 1983), partitioning coefficient to roots. Small changes in the value of the partitioning coefficients or the maintenance respiration requirements would have sufficed to eliminate the bias, but no strong experimental evidence in favour of other values was available, leading us to discard this option. In any case, the magnitude of the bias is insufficient to modify the import of our analyses.

The conservativeness of the form of the RUE/LAI relationship in simulations in which partitioning to roots was varied (Fig.4) shows that the seasonal changes in RUE observed in medium- to high-population density crops (Fig.1) must arise from other causes. When we used the data of Gimenez et al. (1994) as inputs to our model, we estimated increases in gross photosynthesis RUE of between 15 % (low N treatments) and 40 % (high N treatments) between (approximately) bud visible and anthesis. This result contrasts with Gimenez et al.'s inability to simulate substantial changes in daytime RUE with crop development or canopy size using a simple, fixed-extinction-coefficient model to estimate daytime gross photosynthesis. Thus, it appears that the difference in the results obtained using the two approaches should be sought in the estimate of intercepted radiation and its distribution among leaf surfaces of the canopy rather than in respiration or

partitioning to roots.

The association between RUE and LAI which our results have established for sunflower in the pre-anthesis phase have important implications for crop simulation models, water use and yield. If our conclusions are valid, any limitation to canopy development, e.g. lack of nutrients or water or low population density, carries with it an implicit penalty in terms of RUE, a penalty which is independent of any direct effect of these limitations on leaf assimilation rate or fractional interception. Our results also suggest that crops with sparse canopies may have a lower transpiration efficiency per unit crop surface than crops with high LAI. Our findings further indicate that the use of constant RUE values in crop simulation models, particularly in crops which achieve low maximum LAI values, requires re-evaluation.

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#### Figures

Fig. 1. Observed aerial biomass/intercepted radiation relationship for crops included in the three experiments. Data points for the highest values of intercepted PAR for crops grown at 0.5 and 2 pl m<sup>-2</sup> represent harvests made at anthesis.

Fig. 2. Observed radiation-use efficiency/LAI relationship for crops included in the three experiments. Line is fitted linear regression ( $y = 1.004 + [0.69 * x]$ ,  $r^2 = 0.67$ ).

Fig. 3 Estimated/observed relationship for aerial biomass of all crops included in the three experiments. Solid line indicates the 1:1 ratio, dashed line the fitted linear regression ( $y = 10.21 + [ 1.126 * x ]$ ,  $r^2 = 0.99$ ).

Fig. 4. Response of the simulated RUE/LAI relationship to variations in biomass partitioning to roots for Treatment 1, Exp. 3. Values shown next to symbols are partitioning coefficient to roots. Where two values shown next to a symbol, these are for the emergence-bud visible and bud visible-anthesis phases. Standard simulation (Std) shown as thick line, constant values of PCR shown as continuous thin line.

