PHOTOSYNTHETIC RESPONSE OF SUNFLOWER LEAVES TO PPFD UNDER FIELD CONDITIONS, WITH RELATION TO THEIR AGE AND POSITION

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SUMMARY

Wide variability is often observed for leaf photosynthesis in field conditions. The adaptive responses of tissues to light and senescence are advocated to explain these variations. With the aim to assess the effects of leaf position and leaf age on sunflower leaf photosynthesis (A) during the plant cycle, a field trial was carried out. Leaf conductance (stomatal and boundary layer conductance to CO_2) (Gg), water use efficiency (WUE) and the balance between formed/lost leaf area were also evaluated.
Using an open steady-state portable IRGA system CO_2 exchange rates, relative humidity, temperature and irradiance were detected. Photosynthetic response to PPFD was interpolated with a rectangular hyperbola, obtaining the maximum rate of photosynthesis, calculated at 2000 μmolPh m^{-2} s^{-1} (Amax).
A linear function ($Gg=Gg_0+b$ PPFD) was fitted to Gg vs PPFD relations. Amax, Ggmax (leaf conductance calculated at 2000 umolPh m^{-2} s^{-1}), Gg_0 and "b" were analysed as function of leaf age and leaf position. Strong correlation between A and Gg was found (r=0.598**). Amax was correlated to leaf position and leaf age; Ggmax with leaf position only. The leaf ageing seemed to decrease the intercept value, while the slope was independent from leaf age. The opposite occurred for leaf position. Maximum photosynthetic rate, for each leaf, was found when leaf area reached about 90% of its maximum value.

INTRODUCTION

The C3 sunflower species shows a particular photosynthetic behaviour : high rates of photosynthesis (Hesketh, 1963; Lloyd and Canvin, 1977; English et al., 1979; Merrien et al., 1983), and low stomatal resistance to CO2 diffusion (Potter and Breen, 1980). The sunflower also shows rapid leaf senescence, with a loss of potential photosynthesis and traspiration (Rawson and Constable, 1980). Sunflower leaf photosynthesis, as in other herbaceous species, increases rapidly and reaches the highest level before its maximum expansion (Woodward, 1976; English et al., 1979). Furthermore, leaf size and potential photosynthesis are variable and influenced by different factors such as position of leaf insertion on stem, and temperature and light leaf is exposed to (English et al., 1976; Charles-Edwards, 1981). Shaded leaves on the lowest nodes can have a negative effect on water use efficiency. Rawson e Constable (1980) suggested the higher efficiency in water stress conditions of the plant ideotype in which canopy progressively move upwards.
Studies on the effects of plant ontogeny and leaf position and age in sunflower photosynthetic activity have already been carried out (MacWilliam et al., 1974 English et al., 1979; Rawson and Constable, 1980). There is, however, the nee for a better understanding of leaf photosynthetic behaviour with regards to ag and adaptation to different conditions in the canopy. Many growth models (D

Wit, 1978; Hesketh and Jones, 1980; Charles-Edward, 1982), in fact, exploit the photosynthesis integration of each individual leaf to obtain the crop photosynthesis.

The aim of this study, carried out in the open field, was to extablish the developement of sunflower leaves in terms of formed/lost plant leaf area balance, and to extimate the assimilation rate and leaf conductance with relation to leaf age, position and photosynthetic photon flux density (PPFD).

MATERIALS AND METHODS

The experiment was carried out in 1985 on stony entisoil, with a sandy clay texture, average fertility, no shallow water table and with scarce water retention.

The sunflower crop (cv Romsun HS-301) was planted on April 22, 1985. Plant density was 5 plants m^{-2} in rows of 75 cm apart. The emergence appeared on May 9. The weather was characterized by scarce summer rainfall. It was therefore necessary to irrigate on July 17 (40 mm) and on July 31 (30 mm). Observations were carried out during 6 clear sky days from the vegetative to the beginning of maturity stage (table 1).

Table 1 - Observation dates and phenological stages of crop.

day of measurement		time from emergence (days)	phenolog. stage (1)	pos. range for measured leaves	mean leaf temp.(C)	mean air CO_2 conc.(vpm)
N.	date					
1	June, 19	41	V32	6-23	24.7	294
2	June, 26	48	R1	6-29	29.1	295
3	July, 3	55	R2	9-29	30.4	297
4	July, 11	63	R5.2	18-29	34.0	286
5	July, 23	75	R6	18-37	31.7	293
6	Aug., 9	92	R8	24-37	30.4	297

(1) Schneiter and Miller, 1981.

At each measurement time, biometrical values, photosynthesis and transpiration were taken on 3 tagged plants . Position (number of node starting from the bottom), length and width were detected for each leaf longer than 4 cm. By the previously obtained equation "Leaf Area = 0.692 (Length x Width)$^{1.014}$", leaf expansion was monitored. The emergence date of leaves was obtained by extrapolation. A balance between formed and senesced areas was calculated too.

Five leaves, at different positions on the stem, were chosen from each plant and then grouped as follows: (I) position 6 to 8; (II) position 9 to 11; (III) position 18 to 23; (IV) position 24 to 29; (V) position 31 to 37.

From leaf area measurement, LAI over each tagged leaf, were calculated.

Gas exchange measurements were carried out on the chosen leaves (table 1), during the middle of the day (from 11 to 14 hours). CO_2 exchange rate and transpiration were detected with an open steady-state portable system (ADC). This consists of an air supply unit with a flow meter, a leaf chamber including 6.25 cm^2 of leaf lamina and a differential IRGA. The leaf chamber is equiped

with sensors to detect PPFD, temperature and relative humidity of air exiting the cuvette. The air caugth at a height of 5 m was dehydrated with silica-gel before entering the leaf chamber.

The above-mentioned variables were recorded for four decreasing values of PPFD obtained by exposing to direct insolation the leaves and then shading them with sheats of white paper as suggested by Littleton et al., 1981.

Photosynthesis values obtained for the four PPFD levels were interpolated by a rectangular hyperbola (Acock et al., 1971; Thornley, 1976) and the Gauss iterative method was used to calculate the parameters:

$$A = \frac{a\ PPFD}{1 + (a\ PPFD)/(Am+R)} - R \qquad (1)$$

where: A = assimilation rate ($\mu molCO_2\ m^{-2}\ s^{-1}$);
PPFD = photosynthetic photon flux density ($\mu molPh\ m^{-2}\ s^{-1}$);
a = maximum quantum efficency ($molCO_2\ molPh^{-1}$);
R = diurnal dark respiration ($\mu molCO_2\ m^{-2}\ s^{-1}$);
Am = maximum asymptotic level of A ($\mu molCO_2\ m^{-2}\ s^{-1}$).

In order to compare the photosynthesis in the different situations (leaf age and positions), A values, obtained from the equation (1) with PPFD=2000 (Amax), were considered (Dwyer and Stewart, 1986). This method was used because it was impossible to obtain a full light saturation for the highest leaves in field conditions.

Leaf conductance to CO_2 transfer (Gg, stomatal and boundary layer conductance) was obtained from transpiration rate by using the Long and Hallgren (1985) method. The relation between Gg values and irradiance were fit to the linear function:

$$Gg = Gg_0 + b\ PPFD \qquad (2)$$

where: Gg_0 = stomatal conductance at PPFD=0 ($molCO_2\ m^{-2}\ s^{-1}$);
b = Gg response to PPFD coefficient ($molCO_2\ m^{-2}\ s^{-1}\ \mu molPH^{-1}\ m^{-2}\ s^{-1}$).

This particular model was used because it simplified the hyperbolic one suggested by Jarvis (1981) which did not fit the experimental data. This seems due to the high vapour pressure deficit in the leaf chamber, which probably cause high levels of cuticle transpiration, and to a slower speed in reaching traspiration steady state than photosynthesis (Thornley, 1976; Setter and Flanningan, 1983).

The values obtained for equation (2) with PPFD=2000 (Ggmax) were used to study the way Gg behaved in different experimental conditions.

Water use efficiency (WUE) was calculated by net assimilation (A), transpiration (E) and vapour pressure deficit (VPD) values with the equation: WUE = A/(E/VPD) ($molCO_2\ molH_2O^{-1}\ mb\ VPD$) (cfr. Rawson et al., 1977).

WUE trends in relation to PPFD for each leaf and observation were interpolated by a rectangular hyperbola. This allowed to calculate a reference value for WUE at PPFD=2000 (WUEmax) for every measurement.

RESULTS AND DISCUSSION

Maximum value of leaf area (0.95 m^2/plant, corresponding to a LAI value of 4.75) was obtained in phase R2 (Schneiter and Miller, 1981).

Production of new leaf area ended during phase R5.2 (20% of flowers opened), 63 days after plant emergence. Loss of photosynthetic tissue started about 50 days

after emergence in phase R1 (fig. 1).
The distribution of leaf area during each survey was characterized by the progressive movement of active leaf area towards the top of the plant (fig. 2). Leaves belonging to groups II and III (9 to 23 nodes) were largest in size (fig. 3). Leaf expansion of highest nodes was slower and leaf area was less in comparison to low leaves.
LAI standing over the measured position ranged from 4.4, for the lower leaves, to 0.3 for the higher (tab. 2). Considering that, in sunflower, a canopy with LAI of 2.5-2.7 is able to absorb quite all solar radiation (Merrien, 1988), we can argue that leaf of I and II groups, after June 20 do not contribute positively to assimilation.

Fig. 1 – Number of leaves and Leaf Area/Plant during the experimental period. T=Total leaves, P=Photosynthetically active and S=Senesced leaves.

Net photosynthesis ranged from negative values to maximum values of 27 μmol m^{-2} s^{-1}, with PPFD of 1600-1730 μmolPh m^{-2} s^{-1}.
Photosynthetic saturation was obtained with very low PPFD values (200-300) for both senescent leaves and low leaves. On the other hand, photosynthetic saturation of leaves belonging to groups IV and V was rarely observed (tab. 3).
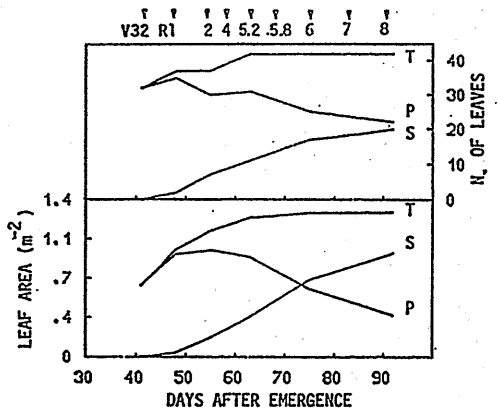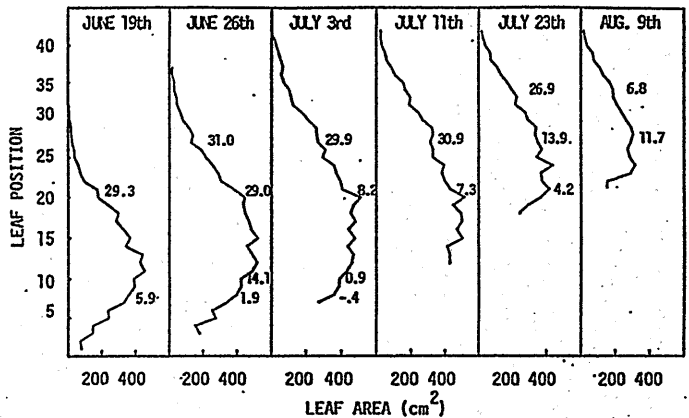

Fig. 2 – Patterns of Photosynthetically active leaf area during the experimental period with relation to their position on the stalk. Amax values determined along the canopy profile are reported.

Table 2 – LAI over each leaf position, for every day of measurement.

day of measurement		leaf position				
N.	data	I(6-8)	II(9-11)	III(18-23)	IV(24-29)	V(31-37)
1	June, 19	2.6	1.9	0.2	0.0	–
2	June, 26	4.1	3.4	1.0	0.3	–
3	July, 3	4.4	4.1	1.7	0.7	–
4	July, 11	–	–	2.1	1.1	–
5	July, 23	–	–	2.3	1.2	0.3
6	Aug., 9	–	–	–	1.1	0.3

Table 3 - PPFD values (μmolPh m^{-2} s^{-1}) at photosynthetic light saturation (about 90% of Amax) for each leaf group and measurement day. Values in the brackets are the maximum PPFD values observed without gaining photosynthetic light saturation.

day of measurement		leaf position				
N.	data	I(6-8)	II(9-11)	III(18-23)	IV(24-29)	V(31-37)
1	June, 19	300	(700)	(1100)	(1500)	-
2	June, 26	200	580	1500	(1400)	-
3	July, 3	-	300	530	(1750)	-
4	July, 11	-	-	500	(1700)	-
5	July, 23	-	-	250	1100	870
6	Aug., 9	-	-	-	800	(1700)

Wide variability and a not clear trend was found for maximum quantum efficiency (a) and R, probably because of the long time required to gain the steady state at low PPFD. Maximum quantum efficiency ranged between 0.018 and 0.068 molCO$_2$ molPh^{-1} whilst R averaged 2.4 μmolCO$_2$ m^{-2} s^{-1}. However, it was observed that "a" rose as the leaves grew older, especially in low leaves.

Up to node 11 Amax rose only to 5.6 and 14 μmolCO$_2$ m^{-2} s^{-1} for groups I and II respectively and quickly decreased with leaf senescence.

At the 1st and the 2nd measurement, the III group of leaves (from 6 to 13 days old) showed an high photosynthetic rate of about 29 μmolCO$_2$ m^{-2} s^{-1}; in the next period (from R1 to R2 stages) the photosynthetic rate decreased to 8.2 μmolCO$_2$ m^{-2} s^{-1}. From R2 to R6 phases the reduction was less noticeable and net photosynthesis reached zero 42 days after leaf emergence.

The highest Amax value was obtained in leaves belonging to group IV (about 31 μmolCO$_2$ m^{-2} s^{-1}) from R1 to R5 phase when these leaves were 8 to 23 days old. Furthemore, these leaves showed high photosynthetic activity (above 12 μmolCO$_2$ m^{-2} s^{-1}) till 52 days after emergence (physiological maturity, phase R8).

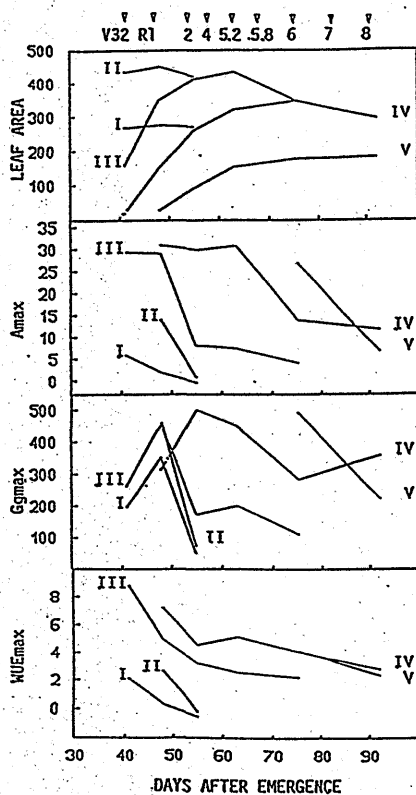Fig. 3 - Leaf Area (cm^2), Amax (μmolCO$_2$ m^{-2} s^{-1}), Ggmax (molCO$_2$ m^{-2} s^{-1}) and WUEmax (molCO$_2$ (molH$_2$O (mbVPD)$^{-1}$)$^{-1}$ 100). Leaf position on the stalk are referred too (I=low leaves V=upper leaves).

In the 5th measurement the leaves on the highest nodes (V) showed an average photosynthetic rate (27 μmolCO$_2$ m^{-2} s^{-1}) higher than those of the previous group. However, the further loss of their photosynthetic rate was more rapid. Although there seems to be no direct physiological control of stomata on photosynthesis (Jarvis and Morrison , 1981; Raschke, 1979; Jones 1985; Farquhar and Sharkey, 1982), an high level of correlation between A and Gg (r=0.680 **) was found in all observations.

Ggmax values (fig. 3) showed a similar trend for each group, with an increasing phase during leaf expansion followed by decreasing values. Maximum Ggmax, which ranged from 400 to 500 mmolCO$_2$ m^{-2} s^{-1} for all leaf groups.

Maximum WUEmax (about 7-9 molCO$_2$(molH$_2$O(mbVPD)$^{-1}$)$^{-1}$ 100) was observed for III and IV group till to R1 stage. The WUEmax (see fig. 3) had increasing values from the base of the canopy to the top. In respect to leaf age water use efficiency showed in all cases an earlier decreasing than Amax. In fact WUEmax gained the minumum about 13 days after leaf emergence and Amax about after 32. Water use efficiency rose when PPFD increased with an asymptotic trend similar to A vs. PPFD but it reaches the maximum at lower irradiance levels than A. In groups I and II, 90% of WUE maximum level was obtained with 100-500 PPFD; group III required 800-1200 PPFD while in the highest leaves (IV and V) maximum level was reached only in aged leaves (at 500-800 PPFD).

A significant correlation was found between Amax and leaf age (r = -0.730**) and between WUEmax and leaf age (r = -0.705**). This correlation did not occur with leaf position. Leaf age and intercept value of global conductance (Gg$_0$) were also found associated (r = -0.349*). When analyzing multiple linear regressions (tab. 4), both leaf position and age were significant in estimating Amax (R = 0.801) and Gg$_0$ (R = 0.493). The effect of position on Ggmax was better explained by Gg$_0$ than by the relation slope between Gg and PPFD (b) tab. 4). Parameter "b" varied little, averaging 0.62 molCO$_2$ molPh^{-1}.

Table 4 - Multiple linear regressions between photosynthetic and transpiration variables, leaf age (AGE) and position (POS).

N.	dependent variable	intercept	coefficient for: AGE		POS		multiple reg. coeff. (R)	
1	Amax	17.9	-0.61	**	0.71	**	0.801	**
2	Ggmax	64.5	-3.66	ns	13.99	*	0.483	*
3	Gg$_0$	100.3	-2.98	*	6.67	*	0.493	*
4	WUEmax	7.05	-0.107	**	0.02	ns	0.705	**
5	WUEmax	7.33	-0.105	**			0.704	**

(*) Significant at P $\leqslant$ 0.05;(**) significant at P $\leqslant$ 0.01;ns=not significant.

CONCLUSIONS

At the end of July most of the leaf area present was a result of leaves formed after mid-June. This was because of rapid leaf area formation and contemporary loss due to senescence which started in phase R1.

The lowest leaves had scarce photosynthesis rate and showed hight maximum quantum efficiency and photosynthetic saturation with low light intensity.

CO_2 leaf conductance showed an increasing trend in the expansion phase of leaves and then settled and decreased together with photosynthesis. In non-excessive senescent leaves as irradiance rose the conductance rose with similar rate in all situations, while a maximum was not found.

WUEmax also increased as PPFD rose, reaching maximum levels depending on leaf age. It did not vary much with relation to position and decreased rapidly as the leaf grew older.

Senescent leaves on the first nodes do not contribute to assimilation, even though they are green in colour, and have a certain amount of transpiration. This could indicate that a plant growth model with a rapid leaf turn-over can be advantageous for limiting water losses. On the other hand, Amax decrease and the high rate of photonic efficiency in senescent and shaded low leaves, allow them to adapt to low PPFD.

Therefore, plants which have a high leaf turn-over should maximize photosynthetic productivity with relation to water use, while a plant with high leaf duration could reduce the biomass waste, increase the harvest index and better exploit radiation with leaves suited to different light conditions.

It is still not clear, however, if there is incompatibility between leaf adaptation to low light conditions and leaf duration.

ACKNOWLEDGMENTS

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A STUDY ON PHYSIOLOGICAL LIFE PERIOD OF SUNFLOWER LEAVES

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Observations conducted on physiological life period of various leaves of a snack sunflower cultivar Sandaomei, with a maize cultivar Jingza 6 as control, showed that the sunflower had more leaves (52), compared with maize (22), rapid leaf emergence (1-2 days against 2-7 days for maize); however, the averaged physiological life period for leaves in the whole growth period (46.4 days against 65.1 days) and for leaves after flowering (29 days against 53.2 days) were all shorter.

The physiological life period for sunflower cotyledons was 22.5 days. Whereas, the physiological life period for true leaves of sunflower increased upwardly with leaf number counting from the first true leaf and was longest of 58.4 days for the 35th leaf, and decreased progressively with leaves on the higher position starting from the 36th leaf. Eight leaves (including 2 cotyledons) withered and died before flowering and the life period of the remaining leaves, after flowering, averaged 29 days which was 62.5% (81.7% for maize) of the total physiological life days, with the longest of 45.8 days for the 44th leaf and a progressive decrease in the upper and lower positioned leaves, after flowering. These results could be applied in production to intensify management on fertilizers and water at flower budding to flowering for preventing early senescence and prolonging physiological life period of leaves to increase efficiency of photosynthesis and kernel yield.