THE EFFECT OF LEAF AGE AND POSITION ON PHOTOSYNTHESIS AND THE SUPPLY OF ASSIMILATES DURING DEVELOPMENT IN SUNFLOWER

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The pattern of photosynthesis during the development of leaves and the translocation, utilization and storge of assimilates, particularly, during grain filling, are crucial to our understanding of yield in crop plants.

The detailed work in this regard with wheat and barley (see reviews by Wardlaw 1968; Evans et al. 1974), has increased our awareness of the physiological limitations to yield and as a consequence, our ability to discriminate in selecting for characters likely to increase the yield potential of temperate cereals. Our understanding of the carbon balance in other crop plants is quite incomplete, although recent studies in tobacco (Hackett 1973), maize (Tripathy et al, 1972), ryegrass (Ryle 1970), cotton (Ashley 1972), soybean (Penny and Nelson 1970) and sunflower (Vasilevskaya and Ermolaeva 1970) have initiated valuable work in this area.

The work reported in this study was motivated by a similar desire to explore the pattern of carbon fixation and translocation during growth and development of sunflower. In particular we have attempted to measure the effect of ageing and position on the photosynthetic potential of leaves and their contribution to the supply of assimiliates to the inflorescence during grain development under realistic crop conditions.

MATERIALS AND METHODS

Controlled environment studies

Sunflower plants (*Helianthus annuus* L. cv. Peredovik) were grown in large (25 cm diameter) pots under conditions of natural light in a 30/24°C (day/night) temperature regime, with the natural photoperiod extended to 16 h by low intensity incandescent light.

Leaf areas were derived by a non-destructive method involving the regression of length x breadth on area. Rates of photosynthesis were measured by enclosing individual leaves in a perspex assimilation chamber and measuring the flux of CO_2 by infrared gas analysis, following a technique modified from McPherson and Slatyer (1973). Rates of net photosynthesis were measured at optimum temperature (27°C) and under conditions of ambient CO_2 (330 vpm) and saturating irradiance (350 Wm^{-2}. PAR (400—700 nm).

Field studies

Plants of the same cultivar (Peredovik) were studied under field conditions in a stand sown at the rate of 24000 plants ha^{-1} in rows 60 cm apart. Measurements were made on plants selected at random, 8 to 10 days after the commencement of pollination, and during the early stage of rapid grain development. Plants were growing with adequate soil moisture and the weather conditions during the experimental period (March 10 th — 15 th) were as follows :

Mean daily max. temperature	25.1°C
Mean daily min. temperature	9.6°C
Mean daily solar radiation	22.8 MJ m^{-2}
Mean daily sunshine hours	11.5 h

Measurements of stomatal resistance and photosynthesis were taken on ten plants during the middle of the day under conditions of high irradiance (490 Wm^{-2}, PAR). Stomatal resistance was measured on both surfaces of leaves down through the profile, using a diffusion porometer similar to that described by Kanemasu et al. (1969). Short term measurement of photosynthesis were also made on the same leaves by passing a 20 s pulse of $^{14}CO_2$ labelled air of known specific activity and CO_2 concentration over a fixed area of the leaf as described by McWilliam et al. (1973). Values obtained by this technique approximate gross photosynthesis, as the brief exposure allows little time for the labelled carbon to appear as a significant component of the respiratory substrate.

Translocation of photosynthates from leaves in the canopy to the various metabolic sinks in the plant during the period of active grain development was studied by exposing single leaves in the canopy to $^{14}CO_2$ labelled air by means of perspex assimilation chambers, and subsequently determining the movement of the labelled assimilates. Leaves were selected for labelling on matched plants at three different positions in the canopy (upper, mid and lower) representing approximately 90%, 75% and 50% of the total plant height respectively. Forty eight hours after exposure to ^{14}C the entire plants were harvested, partitioned into individual components, oven dried, weighed, ground and small aliquots of each organ acid-digested and the activity released estimated by liquid scintillation spectrometry (Mc William et al. 1973).

RESULTS AND DISCUSSION

EFFECT OF LEAF AGE AND POSITION ON THE AREA AND PHOTOSYNTHETIC CAPACITY OF LEAVES.

The pattern of net photosynthesis measured over the lifespan of individual leaves was similar for all positions on the stem. Typical results for two leaves (No. 14 and 20) taken from the middle of the canopy are illustrated in figure 1.

In both cases the rates of photosynthesis increased to a maximum at approximately 80—90% of full leaf expansion and then declined as the leaf aged and approached senescence.

The maximum rates of net photosynthesis measured on successive leaves up the main stem during their development also increased with time as the plant aged and reached a maximum for leaves in the upper third of the canopy (figure 2). In parallel with this increase in photosynthetic capacity of leaves up the stem, there is also a marked increase in leaf area as illustrated in figure 2, reaching a maximum at about 70% of the final plant height. Above this point the leaves become smaller and are ultimately reduced to the fused green bracts which form the base of the compound inflorescence.

These results indicate that the large, recently developed, active leaves which are produced on the upper part of the stem are the most productive in supplying carbon assimilates during all stages of the plant's growth and development.

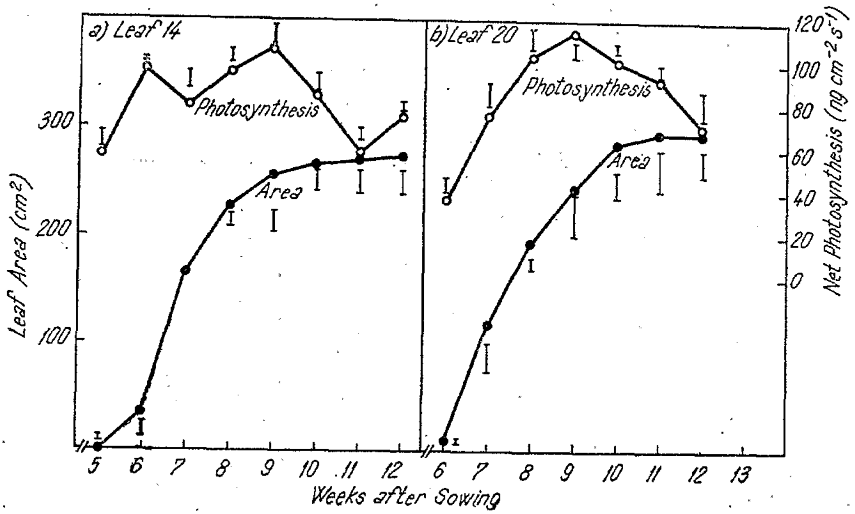

Fig. 1 — Leaf area growth and net photosynthesis measured over the active life of leaves at two positions (based on leaf number) on the stem of sunflower.

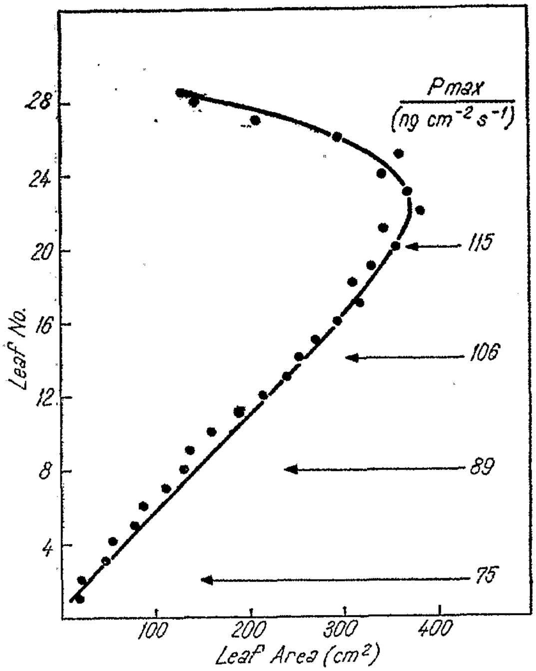

Fig. 2 — Leaf area profile and values for maximum net photosynthesis at various leaf positions on the stem of sunflower plants measured over the course of development from germination to flowering.

PHOTOSYNTHESIS UNDER FIELD CONDITIODS

Profiles of leaf diffusion resistance (r_l) (stomatal resistance) and photosynthesis down through the canopy of plants grown in the field are illustrated in figure 3. At this spacing and stage of development (grain filling), plants retained no living leaves on the lower third of the stem.

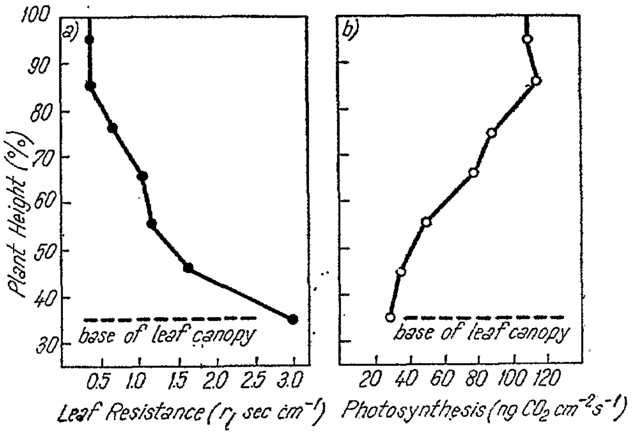

Fig. 3 — Profiles of leaf resistance and photosynthesis in the canopy of sunflower plants grown under field conditions, (a) leaf resistance, (b) photosynthesis.

The r_l values for leaves in the upper portion of the canopy were low and increased down the canopy to reach a maximum in the most mature leaves at the base of the canopy. The profile for photosynthesis is almost a mirror image of leaf resistance, decreasing with depth in the canopy, with values at the base less than 25% of those found for the young active leaves in the upper third of the canopy. Even these values tend to be overestimated as all measurements were made in full sunlight which is rarely achieved at the base of the canopy.

The decline in the photosynthetic potential of leaves down the canopy is a consequence of the increased diffusion resistance and the greater age and position of leaves, which, as indicated earlier, is associated with a marked decline in the rate of photosynthesis.

The rates of „gross“ photosynthesis for the younger leaves in the upper half of the green canopy under field conditions (145 to 155 ng cm^{-2} s^{-1}) were lower, after adjusting for photorespiration, than the maximum rates obtained for glasshouse grown plants under conditions of optimum light and temperature and non-limiting CO_2, however they are comparable with other values recorded for sunflower (El Sharkawy and Hesketh 1964; Warren Wilson 1966) when appropriate adjustments are made to allow for the more favourable conditions under which these measurements were made. These results, together with the information on the distribution of leaf size in the canopy, indicate that the bulk of the assimilate produced during the period of grain development is derived from photosynthesis in the large active leaves in the upper third of the canopy.

TRANSLOCATION

As indicated previously the upper leaves fix more carbon than leaves lower in the canopy but in addition, they also export a greater proportion of this assimilate to various other sinks throughout the plant. The proportion of the labelled assimilates exported from each of the three leaf positions was as follows: upper leaf 77%; mid leaf 72%; lower leaf 48%. The distribution of the labelled assimilate exported from the various levels in the canopy is illustrated in figure 4.

It is quite evident that leaves in the upper and mid positions export a significantly ($P<0.01$) greater proportion of their assimilates (83% and 75% respectively) to the inflorescence (including the developing seed and other parts of the inflorescence) than do leaves at the lower levels (24%). In all cases some activity was retained in the adjacent stem sections. This was particularly high in the case of the lower leaves. Significant movement of assimilate to the roots occurred only when the lower leaves were exposed to labelled carbon, although the figure reported in this case is likely to be an underestimate because of the difficulty of recovering all the root material from plants grown under field conditions.

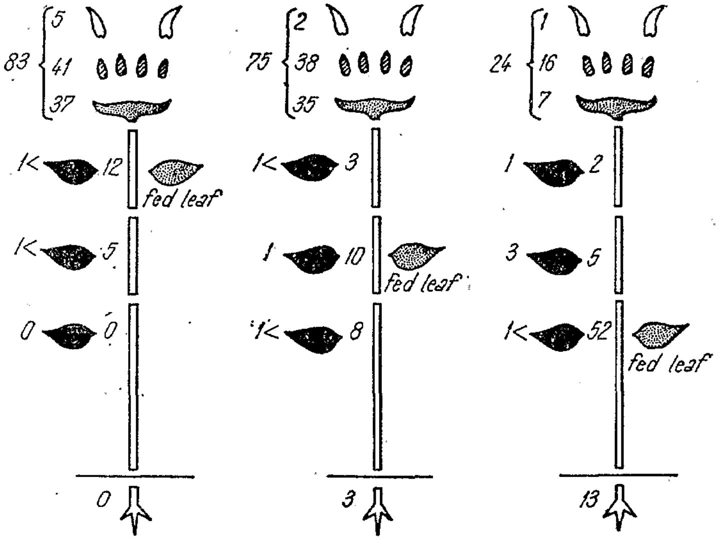

Fig. 4 — Distribution of labelled assimilate from leaves exposed to $^{14}CO_2$ at three positions in the canopy of sunflower during grain developement under field conditions. The values represent the percentage of labelled exports found in the various organs 48 hours after exposure.

This pattern of translocation of carbon assimilates from leaves in the canopy during grain filling reflects the relative stregths of the various metabolic sinks in the plant at this stage of its development. It also indicates that the upper portion of the canopy is largely responsible for the supply of assimilates to the inflorescence during the grain filling period. A similar conclusion was reached by Vasilevskaya and Ermolaeva (1970) working with potted plants of sunflower at an earlier stage of floral development.

CONCLUSIONS

Rates of photosynthesis of sunflower (cv. Peredovik) leaves measured by infra-red gas analysis increased with time from leaf emergence and reached a maximum when leaves had expanded to approximately 80 to 90% of their final size. Maximum rates for a particular leaf were maintained only for short periods and thereafter declined steadily as the leaf reached full size and progressed through to senescence. In addition to the effect of physiological maturity, the position of the leaf on the main stem also influenced its ultimate photosynthetic capacity. Leaves at the base of the plant were considerably smaller and had a lower maximum rate of photosynthesis than those developed higher on the stem.

Measurements of photosynthesis in the leaf canopy of field grown crop plants (*using* $^{14}CO_2$) *during the period of active grain development* gave a similar pattern. Rates for the lower leaves at light saturation were only 25% of the rates for the leaves in the upper portion of the canopy, which is a consequence of their greater physiological age and also their stomatal resistance. With the reduced size of lower leaves and the normal light profile experienced under field conditions, these differences would be even greater than those reported.

Associated measurements to determine the pattern of translocation of ^{14}C labelled assimilates during active grain development indicated that the leaves in the upper half of the canopy exported approximately 75% of their current photosynthate of which 83% moved to the inflorescence. By comparison lower leaves exported only 50% of their assimilate and the majority of this remained in the adjacent stem or was exported to the roots.

These results indicate that the larger, active leaves in the upper part of the canopy provide most of the carbon assimilated during growth and development, and following anthesis, are largely responsible for the supply of the assimilate to the inflorescence during the grain filling period.

This type of information on the pattern of photosynthesis and translocation during growth and development of the crop is of value for devising strategies to achieve the optimum crop architecture in an attempt to maximise yield under field conditions.

REFERENCES

Ashley, D. A., 1972, Crop Sci., *12*, 69.
El Sharkawy, M. A. and Hesketh, J. D., 1964, Crop Sci., *4*, 514.
Evans, L. T., Wardlaw, I. F. and Fischer, R. A., 1974, In Crop Physiology (Ed. L. T Evans), Cambridge Univ. Press, Cambridge.
Hackett, C., 1973. Aust. J. Biol. Sci., *26*, 1057
Kanemasu, E. T., Thurtell, G. W. and Tanner, C. B., 1969, Pl. Physiol. Lancaster, *44*, 881.
McPherson, H. G. and Slatyer, R. O., 1973, Aust. J. Biol. Sci., *26*, 329.
McWilliam, J. R., Phillips, P. J. and Parkes, R. R., 1973, C.S.I.R.O. Aust Div. Pl. Ind. Tech. Pap., No. 31.
Penny, P. and Nelson, C. D., 1970. Canad. J. Bot., *48*; 1033.
Ryle, G. I. A., 1970, Ann. appl. Biol., *66*, 155.
Tripathy, P. C., Eastin, J. A. and Schrader, L. E., 1972, Crop. Sci., *12*, 495.
Vasilevskaya, V. K. and Ermolaeva, E. Y. A., 1970, Vest. Leningr. Univ. Biol. *1* : 33 (Cited in Field Crop Abst. *24* : 1169. 1971).
Wardlaw, I. F., 1968, Bot. Rev., *34*, 79.
Warren Wilson, J., 1966, Ann. Bot., NS *30*, 753.