

# Effects of Leaf Position and Plant Age on Photosynthesis and Translocation in Peanut I. Apparent Photosynthesis and $^{14}\text{C}$ Translocation<sup>1</sup>

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## ABSTRACT

Two experiments were conducted to determine the contribution of leaves at different stem positions to photosynthesis of peanut plants, and the change in this contribution with plant age. Apparent photosynthesis (AP) and translocation of assimilated  $^{14}\text{C}$  were determined on leaves 3, 5, and 8 from the tip of a cotyledonary lateral branch of the "Florunner" cultivar of peanut (*Arachis hypogaea* L.) at 80, 110 and 140 days after planting. To determine  $^{14}\text{C}$ -photosynthate translocation individual leaves were exposed for 15 min to  $^{14}\text{CO}_2$  and plants harvested 24 hr later were analyzed for  $^{14}\text{C}$ . Translocation was computed as the percentage of total  $^{14}\text{C}$  in the plant which was in plant parts other than the labeled leaf.

Highest AP was observed for leaf 3, the youngest fully expanded leaf on the branch, and the lowest AP for leaf 8. Leaf 5 exhibited intermediate AP rates. AP decreased with plant age, the average decrease in two experiments being 21 and 58% from 80 to 110 and 140 days, respectively. The decline in AP with plant age was similar in both experiments. The percentage of  $^{14}\text{C}$  translocated from labeled leaves for the two experiments averaged 64% and was not significantly affected by plant age. A significantly greater percentage (76%) of the  $^{14}\text{C}$  fixed was translocated from leaf 3 in Experiment II than from leaves 5 and 8 which averaged 55%. Leaf position had no effect on  $^{14}\text{C}$  translocation in Experiment I. These data indicate that leaves near the periphery of the peanut plant contribute most during pod filling and that the photosynthetic capacity of all leaves decreases during this period.

Key Words: *Arachis hypogaea* L., Photosynthate translocation, Apparent photosynthesis, Leaf position, Plant age.

Peanut (*Arachis hypogaea* L.) is an important food and oil crop in subtropical and tropical areas of the world. It is grown in the southern United States on approximately 600,000 ha. During the period from 1969-1974, yields increased from 1,928 to 2,799 kg ha<sup>-1</sup>. This 45% increase was possible through the development of superior yielding varieties, increased use of more effective pesticides, and improved cultural practices. Further advances in yield are most likely to result from a better understanding of the physiological components of peanut yield.

Little is known about the physiology of peanut, especially physiological determinants of yield. Apparent photosynthesis (AP) rates of peanut are similar

to those of other  $\text{C}_3$  dicot crop species (2, 3, 10). Maximum crop growth rates are also similar to those of other  $\text{C}_3$  crop species (6, 14). Peanut has been shown to have a high  $\text{CO}_2$  compensation concentration (3) and increased AP at low  $\text{O}_2$  concentrations (10) which are characteristic of plants exhibiting photorespiration. In addition, peanut has been shown to have  $^{14}\text{C}$ -photosynthate translocation rates (12) similar to those of other  $\text{C}_3$  crop species.

The contribution of leaves at various stem positions to fruit development has been studied in several species. Ashley (1) found that developing cotton fruit received most of their photosynthate from the nearest leaves and that 90% of the photosynthate produced by a leaf on a fruiting branch remained on that branch 24 hrs later. In wheat it has been found that the flag leaf is by far the most important in supplying photosynthate to the ear (7, 8).

The research reported here was conducted to determine (1) the relative AP rates of peanut leaves at different stem positions and (2) the export of  $^{14}\text{C}$ -labeled photosynthate from leaves at those positions.

## Materials and Methods

Two experiments were conducted: Experiment I at Athens, Ga. in 1972 and Experiment II at Tifton, Ga. in 1973. Seeds of the peanut cultivar "Florunner" were planted on a well-prepared fertile seedbed on May 19, 1972 and May 4, 1973. Seed were spaced 7 or 8 cm apart in the row, with row spacings of 102 cm in Experiment I and 86 cm in Experiment II. Plants were thinned to a spacing of 30 cm in Experiment I at 20 days after planting, but were not thinned in Experiment II. Supplemental irrigation was supplied when necessary in both experiments to prevent moisture stress. Benlate (methyl 1-(butylcarbamoyl)-2-benzimidazolecarbamate) was applied for control of leafspot (*Cercospora arachidicola* and *C. personata*) in Experiment I. Adequate disease control was not achieved and considerable defoliation had occurred by 110 days after planting. Bravo 6F (tetrachloroisophthalonitrile) was applied in Experiment II at 7 to 10 day intervals for leafspot control beginning when the plants were approximately 20 days old and defoliation due to disease was minimal.

Apparent photosynthesis rates of individual leaves 3, 5 and 8, numbering from the apex of one cotyledonary branch, was measured at approximately 80, 110, and 140 days after planting. A minimum of 6 and 8 leaves were used at each position for AP determination for each plant age in Experiment I and Experiment II, respectively. Measurements were made using attached leaves in a plexiglass chamber similar to the air-sealed chamber of Wolf et al. (15). The two halves of the chamber were sealed on three sides leaving space inside the chamber to accommodate the leaf. One end of the chamber was left open to serve as an inlet for the leaf as well as an exit for air from the chamber. A lid with a slot to accommodate the petiole was fitted to the open side of the leaf chamber. Air was passed over the leaf at  $1.5 \text{ l min}^{-1}$ . Approximately  $0.51 \text{ min}^{-1}$  of air was withdrawn through a manifold positioned between the leaf and the chamber outlet. This sample of air was transported to an infrared gas analyzer along with a sample of reference air for analysis of  $\text{CO}_2$ . The re-

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remainder of the air passed through the slot in the lid which accommodated the leaf petiole. Positive pressure inside the chamber and the exiting air around the leaf petiole provided a seal for the chamber against ambient  $\text{CO}_2$ . The air stream was bubbled through water before passing over the leaf and the reference and sample air streams were passed through  $\text{CaSO}_4$  drying columns before entering the gas analyzer. The infrared gas analyzer was calibrated to measure concentration differences up to  $70 \mu\text{l l}^{-1}$  in the sample and reference air streams. Temperature inside the chamber was monitored with a thermocouple positioned under the leaf and was maintained at  $30 \pm 2^\circ\text{C}$  by circulating controlled temperature water through a jacket built into the base of the chamber. All leaf AP measurements were made in full sunlight above  $1600 \mu\text{E m}^{-2} \text{sec}^{-1}$  with leaves in a horizontal position. Leaf area was determined and AP per unit of leaf area (one surface only) was calculated.

Photosynthate translocation was determined by exposing leaves to  $^{14}\text{CO}_2$  at similar positions and plant ages as in the AP study. Six replicates were labeled in an air tight plexiglass chamber with dimensions of  $15 \times 15 \times 7$  cm. A nylon thread network across the base of the lid and in the chamber body maintained the leaf in a horizontal position. The hinged top was closed over an attached leaf during labeling. Rubber gaskets provided an airtight seal and prevented damage to the petiole. A small electric fan surrounded by coiled copper tubing, through which controlled temperature water was circulated, served to maintain the chamber temperature at  $30 \pm 2^\circ\text{C}$  and to circulate the  $^{14}\text{CO}_2$  air. Temperature was monitored by a thermocouple under the leaf.  $^{14}\text{CO}_2$  was generated inside the chamber by injecting 1 ml of 6N HCl into a plastic vial containing  $50 \mu\text{Ci}$  of  $\text{NaHCO}_3$ . The leaf was exposed to  $^{14}\text{CO}_2$  for 15 min during midday in full sunlight.

Labeled plants were harvested after 24 hr and total  $^{14}\text{C}$  activity determined in the exposed leaf and in all other plant parts. After separation the plant components were frozen, freeze-dried, weighed and ground to pass a 20 mesh screen. A 100 mg subsample of the ground plant tissue was wrapped in an ignition paper and placed in a one liter oxygen enriched suction flask and ignited with a Thomas-Ogg infrared ignition apparatus. Resultant  $\text{CO}_2$  was captured by injecting 10 ml of ethanalamine: ethanol (2:1 v/v) solution into the flask through a serological stopper. After 30 minutes a 1 ml aliquot of the  $^{14}\text{CO}_2$  solution was transferred from the flask to a vial and 15 ml of a solution containing 6.0 g PPO (2,5-diphenyloxazole) and 0.06 g POPOP (1,4-bis 2-(5-phenyloxazole) benzene) per liter of toluene was added. One ml of ethanol was added to the vial to clear the solution. Radioactivity in each vial was determined in a Packard Model 3320 liquid scintillation counter and appropriate corrections for quenching were made. The percentage  $^{14}\text{C}$  translocated was determined as follows:

$$\text{Percent } ^{14}\text{C translocated} = \frac{\text{Total } ^{14}\text{C recovered} - ^{14}\text{C in labeled leaf}}{\text{Total } ^{14}\text{C recovered}} \times 100$$

Analysis of variance was performed on all data to determine if differences due to leaf position or plant age were significant.

## Results

### Apparent Photosynthesis

In Experiment I the highest AP,  $22 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$ , was observed for leaf 3, the youngest fully expanded leaf, of 80 day old plants (Figure 1A). Leaf 8 of 140 day old plants had the lowest AP of  $3.6 \text{ mg dm}^{-2} \text{ hr}^{-1}$ . Plant age had a greater effect on leaf AP than leaf position in Experiment I. The mean AP rate decreased in a nearly linear fashion with increased plant age, although for leaves 3 and 5 the drop from 80 to 110 days was not significant at the 5% level. The average AP rate for all leaf positions was 31 and 73% less for 110 and 140 day old plants, respectively, than for 80 day old plants. There was no significant effect of leaf

position at any plant age. The AP of leaves 5 and 8 was 92 and 71%, respectively, of the rate of leaf 3 when averaged across plant ages.

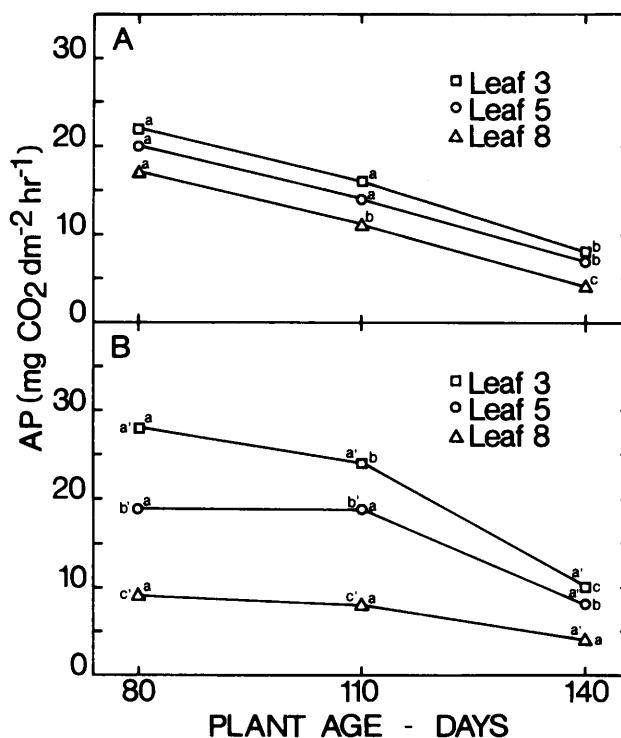


Fig. 1. Apparent photosynthesis (AP) of Florunner peanut leaves as influenced by position on the cotyledonary branch and age of the plant. A. Experiment I. B. Experiment II. Means associated with the same letter are not significantly different at the .05 level. a', b', c' show leaf position effect: a, b, c show plant age effects.

The range in AP for Experiment II was from  $27.9 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$  for leaf 3 of 80 day old plants to  $3.9 \text{ mg dm}^{-2} \text{ hr}^{-1}$  for leaf 8 of 140 day old plants (Figure 1B). AP decreased with plant age as in Experiment I, except that the decrease was much greater from 110 to 140 days than from 80 to 110 days. There was a significant decrease in AP from 80 to 110 days after planting for leaf 3 only; however, AP of both leaves 3 and 5 decreased from 110 to 140 days. There was no significant change in AP for leaf 8 with plant age. AP for leaf 3 at 140 days was only about 36% of that observed for the same leaf position at 80 days. Although AP of leaf 8 declined relatively less than AP for leaves at other positions, it had the lowest value at all plant ages.

Leaf position had a significant effect on AP only at 80 and 110 days after planting. The average AP rate for leaf 3 of 80 and 110 day old plants was  $26 \text{ mg dm}^{-2} \text{ hr}^{-1}$  compared to 19 and 8  $\text{mg dm}^{-2} \text{ hr}^{-1}$  for leaves 5 and 8, respectively. While leaf 8 exhibited less than 50% of the AP of leaf 3 at 140 days, the rates were variable enough that significant leaf position effects were not established.

### Photosynthate Translocation

A significantly greater quantity of  $^{14}\text{C}$  was found in

**Table 1. Total  $^{14}\text{C}$  recovered and translocated after 24 hr and percent  $^{14}\text{C}$  translocated by peanut leaves at three leaf positions and at three plant ages.**

Leaf position	Plant age	Total $^{14}\text{C}$				Translocated <sup>§</sup>	
		Recovered <sup>†</sup>		Translocated <sup>‡</sup>		Exp. I	Exp. II
	days	Exp. I	Exp. II	Exp. I	Exp. II	Exp. I	Exp. II
		-----cpm x 10 <sup>5</sup> -----				-----%-----	
3	80	89	234	63	171 a	60	76
5	80	54	239	44	105 b	71	46
8	80	72	150	44	79 c	60	52
	Mean	72 b*	208 a	50 a	118	64 a	58 a
3	110	108	145	85	114 b	61	78
5	110	115	115	89	67 c	76	59
8	110	281	79	211	40 de	69	53
	Mean	168 a	113 b	128 a	74	69 a	63 a
3	140	137	54	114	43 d	78	74
5	140	67	48	46	26 e	71	55
8	140	105	42	68	27 e	58	64
	Mean	103 b	48 c	76 a	32	69 a	64 a
Means for leaf Positions							
3		111 a	144 a	87 a	109 a	66 a	76 a
5		79 a	134 a	60 a	66 a	73 a	53 b
8		153 a	90 b	108 a	49 a	62 a	56 b

\*Means followed by the same letter are not significantly different at the 0.05 level using least square std. error. When no leaf position x plant age interaction was measured, only main effect means were tested.

<sup>†</sup>15 min assimilation period;  $^{14}\text{C}$  present in plant 24 hr after labeling.

<sup>‡</sup>24 hr translocation period.

<sup>§</sup>Percent translocated was determined as the average for the five or six individual plants per treatment rather than from the mean values of cpm recovered and translocated as shown in this table. Variability among plants in  $^{14}\text{C}$  fixed causes skewness in percentages calculated from mean values of  $^{14}\text{C}$  fixed and translocated.

Experiment I in plants labeled at 110 days (168 x 10<sup>5</sup> cpm) than those labeled at 80 (72 x 10<sup>5</sup> cpm) or 140 days (103 x 10<sup>5</sup> cpm) (Table 1). The quantity of  $^{14}\text{C}$  recovered in the plants was not significantly affected by leaf position, probably due to the wide variability among replicates in the amount recovered.

Neither position of the labeled leaf nor the age of the plant significantly affected the quantity or percentage of  $^{14}\text{C}$ -photosynthate translocated from labeled leaves in Experiment I (Table 1). There was a trend, however, for leaf 5 to translocate a higher percentage at 80 and 110 days and for leaf 3 to translocate a greater percentage at 140 days. The overall average of  $^{14}\text{C}$ -photosynthate translocated from labeled leaves was 86 x 10<sup>5</sup> cpm or 68% of the total recovered. The trans-

location percentage should be considered approximate, since an unknown quantity of  $^{14}\text{C}$  was respired during the 24 hour period from labeling to harvesting the plant.

The quantity of  $^{14}\text{C}$  recovered in Experiment II decreased from 208 x 10<sup>5</sup> cpm for 80 day old plants to 113 and 48 x 10<sup>5</sup> cpm for 110 and 140 day old plants, respectively (Table 1). This decrease amounted to 46 and 78% less  $^{14}\text{C}$  recovered by leaves of 110 and 140 day old plants, respectively, compared to that recovered by 80 day old plants. Treatment of leaf 8 resulted in significantly less  $^{14}\text{C}$  recovered (90 x 10<sup>5</sup> cpm) on the average than when leaves 3 and 5 were labeled which resulted in an average of 139 x 10<sup>5</sup> cpm recovered. An average of about 62% of the  $^{14}\text{C}$  recovered

was translocated during the 24 hr period (Table 1). A significantly greater percentage (76%) was translocated from leaf 3 compared to leaves 5 and 8 (55%), and this trend was similar at all three plant ages. A leaf position  $\times$  plant age interaction was evident in the quantity of  $^{14}\text{C}$  translocated. The quantity of  $^{14}\text{C}$ -photosynthate translocated was significantly greater for leaves nearer the tip of the cotyledonary branch (Leaves 3 and 5) at the three plant ages, but this trend was progressively less at advanced ages.

## Discussion

Data obtained in this research confirms in peanut the trend observed in other plants for AP to decrease with leaf age. Leaves farther from the tip of the branch were older and had lower AP rates. This trend was significant in Experiment II, but not Experiment I. The greater effect of leaf position in Experiment II may have been due to more shading of leaves 5 and 8 by upper leaves, since plants were thinned in Experiment I, but not in Experiment II. In addition, more defoliation occurred in Experiment I due to leafspot disease which would have reduced mutual shading. There were no lesions on any of the leaves on which AP was measured except at 140 days in Experiment I, where a few lesions were observed on leaf 8. The effects of mutual shading and leafspot in these experiments are, however, unknown. Whatever the effects of mutual shading, they were only on the preconditioning of leaves since all AP measurements were made with leaves exposed to full sunlight.

Younger leaves would be expected to contribute more photosynthate to the plant, but the relative contribution by leaf 3 would probably be greater than estimated because of its more favorable position to available light. The values from the photosynthesis and labeling data minimize differences among leaf positions, since leaves were exposed to full sunlight during AP measurements and labeling. In the undisturbed canopy leaves 5 and 8 would receive less sunlight than leaf 3 and therefore contribute even less to the plant than shown by this study. Percent  $^{14}\text{C}$  translocated was significantly affected by the position of the labeled leaf only in Experiment II. In this experiment leaf 3 exported a significantly greater percentage of  $^{14}\text{C}$  than leaves 5 and 8. Therefore, the contribution of photosynthate from leaves 5 and 8 was limited by both reduced AP and a lower translocation percentage.

Although the effect of leaf position on AP was much greater in Experiment II, the average AP for all leaf positions was similar for the two experiments, differing by 1 mg  $\text{CO}_2$   $\text{dm}^{-2}$   $\text{hr}^{-1}$  or less at 80 and 140 days and 3 mg  $\text{dm}^{-2}$   $\text{hr}^{-1}$  at 110 days. If leaves at nodes 3, 5 and 8 were representative of all the leaves in the canopies in these experiments, then potential AP may have been similar on a leaf area basis in the two experiments. Since the leaf area index was much greater in Experiment II, however, canopy photosynthesis may have been higher than in Experiment I.

The decrease in AP with increased plant age is apparently not due to increased mutual shading since maximum LAI is reached at 80 to 110 days (6, 9, 14). It is more likely caused by increased leaf age or perhaps decreased sink activity. The near linear increase in dry weight of pods during the pod filling period (6, 14) indicates no decrease in the activity of fruit sinks at least up to 130 days in the Florunner cultivar. However, vegetative growth nearly ceases at 80 to 90 days after planting (6, 9) so that the total sink for photosynthate may have been less during pod filling. A decrease in sink strength may also be reflected in total dry matter accumulation patterns in peanuts which show that the highest crop growth rates occur at the end of the vegetative period and the start of fruiting, and then decreases later (6, 9, 14). This pattern is complicated to some extent by leaf loss of unknown magnitude which lowers apparent crop growth rates late in the season.

The nearly constant  $^{14}\text{C}$  translocation percentage with plant age also indicates that the decrease in AP was matched by decreased sink strength. Increases in sink size relative to photosynthate supply have been shown to increase the percentage of translocation (13). There was a slight increase in the percentage of  $^{14}\text{C}$  translocated as plants aged from 80 to 110 and 140 days, but the difference was not statistically significant. Therefore, the efficiency of photosynthate translocation from peanut leaves is apparently not impaired by increased plant age as was postulated by McCloud (9).

An alternative explanation for the decreased AP with plant age may be that nitrogen content of the leaves decreases during pod filling (11), due to competition by pods which are rapidly accumulating N at this time (11). Apparent photosynthesis appears to be closely associated with leaf N content in many species (5) and in soybean the decline in AP with leaf age is associated with decreases in leaf N (4). Whatever the cause for decreased AP during pod filling, it is apparent in the experiments reported here that photosynthesis decreases but that the percentage of  $^{14}\text{C}$  translocated is relatively constant.

## Literature Cited

1. Ashley, D. A. 1972.  $^{14}\text{C}$ -labeled photosynthate translocation and utilization in cotton plants. *Crop Sci.* 12:69-74.
2. Bhagsari, A.S. and R. H. Brown. 1976. Photosynthesis in peanut (*Arachis*) genotypes. *Peanut Sci.* 3:1-5.
3. Bhagsari, A. S. and R. H. Brown. 1976. Relationship of net photosynthesis to carbon dioxide concentration and leaf characteristics in selected peanut (*Arachis*) genotypes. *Peanut Sci.* 3:10-14.
4. Boote, K. J., R. N. Gallaher, W. K. Robertson, K. Hinson and L. C. Hammond. 1978. Effect of foliar fertilization of photosynthesis, leaf nutrition and yield of soybeans. *Agron. J.* 70: 787-791.
5. Brown, R. H. 1978. A difference in N use efficiency in  $\text{C}_3$  and  $\text{C}_4$  plants and its implications in adaptation and evolution. *Crop Sci.* 18:93-98.

6. Enyi, B. A. C. 1977. Physiology of grain yield in groundnuts. *Exptl. Agric.* 13:101-110.
7. Evans, L. T. and H. M. Rawson. 1970. Photosynthesis and respiration by the flag leaf and components of the ear during grain development in wheat. *Aust. J. Biol. Sci.* 23:245-254.
8. Evans, L. T., I. F. Wardlaw and R. A. Fischer. 1975. Wheat. In *Crop Physiology — Some Case Histories*. L. T. Evans, ed. Cambridge Univ. Press, New York, pp. 101-150.
9. McCloud, D. E. 1973. Growth analysis of high yielding peanuts. *Proc. Soil and Crop Sci. Soc. Fla.* 33:24-26.
10. Pallas, J. E. and Y. B. Samish. 1974. Photosynthetic response of peanut. *Crop Sci.* 14:478-482.
11. Radford, A. J. 1972. Dry matter accumulation and nutrient uptake patterns of the peanut plant (*Arachis hypogaea* L.). M. S. Thesis. Univ. of Georgia.
12. Stephenson, R. A., R. H. Brown and D. A. Ashley. 1976. Translocation of  $^{14}\text{C}$ -labeled assimilate and photosynthesis in  $\text{C}_3$  and  $\text{C}_4$  species. *Crop Sci.* 16:285-288.
13. Thorne, J. H. and H. R. Koller. 1974. Influence of assimilate demand on photosynthesis, diffusive resistances, translocation and carbohydrate levels of soybean leaves. *Plant Physiol.* 54:201-207.
14. Williams, J. H., J. H. H. Wilson and G. C. Bate. 1975. The growth of groundnuts (*Arachis hypogaea* L. cv. Makulu Red) at three altitudes in Rhodesia. *Rhod. J. Agric. Res.* 13:33-34.
15. Wolf, D. D., R. B. Pearce, G. E. Carlson, and D. R. Lee. 1969. Measuring photosynthesis of attached leaves with air sealed chambers. *Crop Sci.* 9:24-27.

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