Published January, 1972

^{14}C-Labelled Photosynthate Translocation and Utilization in Cotton Plants[1]

D. A. Ashley[2]

ABSTRACT

Cotton (*Gossypium hirsutum* L.) plant organs were exposed to $^{14}CO_2$ under field conditions to quantitatively evaluate the relative contribution of these organs to fruit development and to obtain information on photosynthate translocation rates. From 87.5 to 91.0% of the photosynthate remained in the sympodia regardless of the vertical position of the sympodia on the main stem or the lateral position of the leaf on the reproductive branch. The primary source of photosynthate for a boll was its subtending leaf with some photosynthate supplied from the associated bracts and from leaves one node removed from the boll. A more rapid rate of photosynthate export was found for main stem leaves than from sympodia leaves. The rate of photosynthate translocation from leaves to other plant parts was slow relative to rates reported for other species with high photosynthetic rates.

Additional index words: Gossypium hirsutum L., Metabolite translocation, Carbohydrate movement.

SOME detailed investigations on metabolite translocation in the cotton plant were conducted in 1928 (14, 15) and later research has contributed some information (4, 8, 21). Nonetheless, little is known about the location and extent of photosynthetic structures required for boll development and maturity. Photosynthate distribution in the early stages of plant development has been described (21). That study showed that upper leaves exported mainly to the stem apex, the lower leaves mainly to the roots, and intermediate leaves in both directions. Biddulph and Cory (2) found similar export patterns in beans (*Phaseolus vulgaris* L.). Apparently, sufficient photosynthate was available during the early stages of development for vegetative growth as well as the small amounts required for reproductive development.

During these early stages of development, most of the photosynthetic structures are relatively young and very active photosynthetically (17) and total leaf area is low so that mutual shading is minimal. However, the critical period in photosynthate supply occurs later in the growth cycle when fruit number and size on the plant increase to the point where the fruit compete strongly with vegetative plant parts for metabolites (13). This phenomenon is evidenced by reduced vegetative growth and continued rapid rate of reproductive development. As the plant develops, the competition for photosynthate becomes more intense, vegetative growth is markedly reduced, and the formation of new fruit buds almost completely ceases and young fruit are abscised.

Photosynthate movement and utilization during this critical period of high photosynthate demand by bolls needs further description. Using plants with a high fruit set and $^{14}CO_2$ tracer technique, Brown (4) found that some photosynthate moved into all developing bolls from all mature leaves on the same reproductive branch and the leaf at the main stem node of sympodium origin. This was one of the earliest attempts at measuring ^{14}C photosynthate translocation to developing cotton bolls, and as such was a good piece of work. However, ^{14}C was monitored by radioautographic techniques and the data were not quantitative, as he points out in the article. Some evidence (8) indicates that the leaf adjacent to the boll supplies the major portion of the photosynthate for boll development. The bracts encasing a fruit may also supply a considerable amount of metabolites to that fruit (16).

The study reported here was conducted to provide quantitative information on the photosynthetic structures contributing to fruit development on cotton plants with a high fruit load and to provide information on the rate of movement of photosynthates from leaves and other photosynthetic structures to the developing fruit.

PROCEDURE

Cotton plants, *Gossypium hirsutum* L., 'Atlas 67,' selected for this experiment were grown in 96-cm rows in field plots. All experiments were conducted during the month of August, and the plants had a large number of developing fruit. The soil from the experimental area was fertile and conventional management practices were used to control weeds and insects. The

[1] Journal Series Paper No. 1105 of the University of Georgia, College of Agri. Expt. Sta., College Sta., Athens, Ga. 30601. Received June 19, 1971.

[2] Assistant Professor, Department of Agronomy, University of Georgia, Athens, Ga.

plots received supplemental irrigation throughout the season to maintain vigorous growth. Special efforts were made to insure that the plants were not subjected to moisture stress during the periods that ^{14}C-photosynthate translocation was measured.

Movement and utilization of photosynthate within the plant were investigated by measuring ^{14}C in various plant parts after exposing selected plant organs to ^{14}C-labeled CO_2. The $^{14}CO_2$ was released from Na_2CO_3 into a 1-liter polyethylene bag which was sealed around the stem or petiole of the organ to receive $^{14}CO_2$. The technique involved the use of a 15-ml serum bottle with a 1-cm hole in its side. The bottle containing the ^{14}C-labeled Na_2CO_3 was placed inside the polyethylene bag and a serum stopper inserted from outside the bag. After the bag was sealed around the plant organ, 1 ml of 1 *M* lactic acid was injected through the serum stopper to release the $^{14}CO_2$. A one-way suction bulb with an attached hypodermic needle was used to distribute and recirculate the CO_2 around the organ within the exposure chamber. In each case, 100 μc of ^{14}C activity were used. The specific activity of the source was 5 mc per m*M*. The CO_2 concentration in the bag was approximately 500 ppm after the release of $^{14}CO_2$. Measurement of photosynthetic CO_2 fixation rate was not made simultaneously with exposure of individual leaves to $^{14}CO_2$; however, separate measurements indicate that the rate of fixation ranged from 18 to 34 mg CO_2 dm^{-2} hr^{-1} in similar leaves and bracts. The oldest leaves usually had the lowest rates.

The position of leaves or other organs on the plant receiving $^{14}CO_2$ include the following: (a) The leaf subtending the first boll on reproductive branches from branch number one at the bottom of the plant to branch 16 at the top of the plant, (b) leaves subtending the first, second and third bolls on reproductive branches which were located in the bottom, middle and top portions of the plant, (c) leaves attached at the junction of the reproductive branch and the main stem in the bottom, middle and top portions of the plant, (d) 10 cm of the terminal growth segments of both reproductive branches and the main stem, and (e) 25-day-old bolls with and without attached bracts. Only one leaf, boll, or terminal shoot on any plant was treated with $^{14}CO_2$. In order to replicate a treatment at a given position on the plant, three plants similar in size and fruit distribution were selected and exposed to $^{14}CO_2$ at comparable locations.

In all cases, the plant organs were exposed to $^{14}CO_2$ for 1 hour and the entire plant was harvested after permitting translocation to occur for selected periods of time. All exposures to $^{14}CO_2$ were begun between the hours of 10:00 AM and 1:00 PM except for the 8- and 24-hour translocation treatments which were begun at 9:00 AM. From 60 to 78% of the total ^{14}C-activity supplied to leaves in the form of $^{14}CO_2$ was recovered in the plant parts. When the bolls, or bolls without bracts, were exposed to $^{14}CO_2$ only 25 and 10% were recovered, respectively.

In the harvest operation each leaf, fruit, and stem segment was sampled separately on the branch containing the $^{14}CO_2$-treated organ and on the branch above and below the treatment branch. The organs on the other branches were separated into three components—leaves, fruit, and stem. The fruit that were sufficiently mature were dried and then separated into seed, lint, and bur. Immediately after harvest, the samples were frozen and maintained at —32 C until lyophyllized. After drying, the plant samples were weighed and finely ground. The ^{14}C activity in all the dried samples was assayed by liquid scintillation techniques. One-tenth gram of the dried ground samples was metered into a black paper wrapper and placed in a wire basket which was suspended in a 1-liter suction flask. The air in the flask was displaced with O_2 and sealed. The sample was ignited by use of a Thomas-Ogg infrared ignition apparatus. After igniting the sample, ethanolaniue-ethanol (1:2 v/v) solution was injected hypodermically through a serilogical stopper at the top of the suction flask for CO_2 capture. Each sample was analyzed in duplicate.

A more detailed analysis of ^{14}C was made of certain plant samples by extracting the dried plant material for 2 hours with boiling ethanol (80%). The amount of ^{14}C was determined on an aliquot of the ethanol extract. The residue from the ethanol extraction was collected on filter paper, washed with ethanol and ^{14}C determined on the dried residue by the ignition process described above.

RESULTS

^{14}C Photosynthate in Treated Sympodium

A high percentage of the photosynthate assimilated by the leaves on a sympodia (reproductive branch) of a heavily fruited cotton plant remained in the same branch. Figure 1 shows that 87.5 to 91.0% of the translocated photosynthate remained in the same sympodia as the source leaf. The percentage remaining in the sympodia was similar whether the source leaf was the leaf subtending the boll in the first position near the main stem or the third leaf more distant from the main stem. Likewise, the percentage remaining was similar whether the source leaf was on a sympodia at the bottom, middle or top of the plant. The data in Figure 1 represent a 2-hour translocation interval. These data appear to be minimum values since the percent of translocated photosynthate remaining on the sympodia with the source leaf increased with time beyond two hours (Fig. 2).

The percent of translocated photosynthate remaining in the sympodia decreased from 91.9% at 1 hour to 89.2% at 2 hours and then progressively increased to 98.6% at 24 hours (Fig. 2). The initial decrease in the percentage retained in the sympodia could logically be attributed to a larger proportion of the total labeled photosynthate being present in a mobile phase. Data to be discussed later (Fig. 3 and 4) show that the activity of the ethanol-soluble fraction was much larger than the activity of the ethanol-insoluble fraction at the end of 2 hours. However, as the translocation time progressed beyond 2 hours, the activity of the insoluble fraction increased rapidly and from 4 through 24 hours the activity of the insoluble fraction exceeded that of the soluble fraction. The foregoing

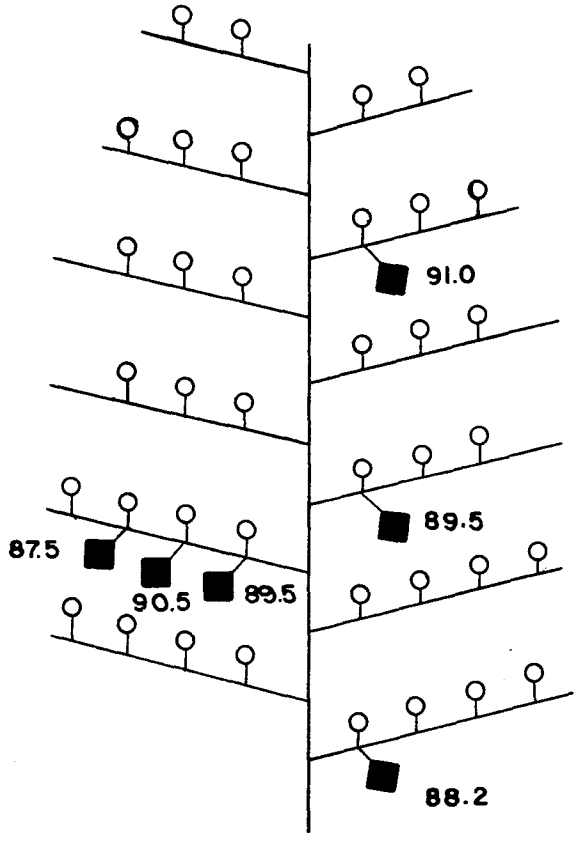

Fig. 1. Percent of translocated photosynthate remaining in treated sympodia when source leaf was at different positions on the plant.

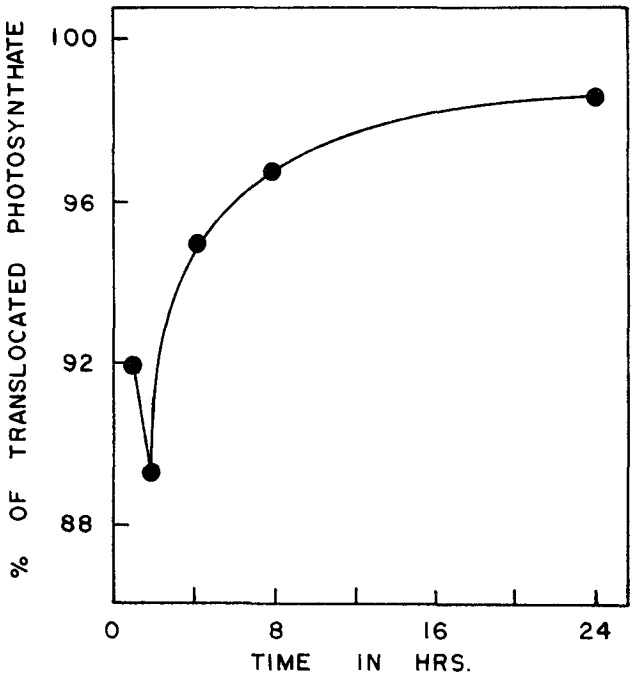

Fig. 2. Time course changes in the percent of translocated photosynthate remaining in the sympodia containing the source leaf.

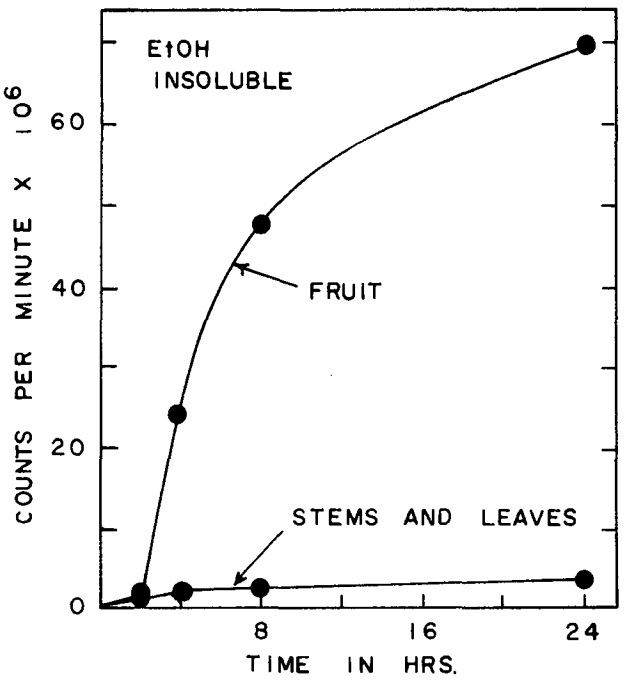

Fig. 3. Time course changes in ^{14}C-activity in EtOH soluble fraction of sympodia components.

explanation of the response obtained in Fig. 2 does not include the possibility of cycling of labeled photosynthate through the main stem and roots of the plant and then back to the source sympodia. Regardless of the specific reasons for the response obtained in Fig. 2, the significant fact remains that more than 89% of the photosynthate translocated from leaves on the reproductive branch remained on the branch throughout the 24-hour exposure period.

The distribution of translocated ^{14}C-photosynthate among the aerial plant parts is given in Table 1. In the fruit of the source sympodia the percent of labeled photosynthate present in each the ethanol soluble and insoluble fractions increased with increase in time. The inverse was true of the percentages in the stems and leaves of the source sympodia. The amount of labeled photosynthate found in sympodia other than those containing the source leaves tended to be variable; however, the general trend was toward a decrease in the percent of labeled photosynthate as time increased in each the soluble and insoluble fractions of both fruit and vegetative parts. Again, only a very small percentage of the photosynthate in either the ethanol soluble or insoluble fractions was recovered in any of the plant parts other than the treated branch.

The counts in the ethanol soluble fraction of the fruit on the source sympodia increased rapidly from 2 to 8 hours after a relatively slow buildup of activity in these organs during the initial 2-hour translocation period (Fig. 3). The lag in the initial period was expected because of the time required for the photosynthate to move from the chloroplasts to the vascular elements of the leaf and then through the petiole and the stem before arriving at the fruit on the sympodia. Further evidence of this delay was the changes in ^{14}C-activity in the stems and leaves, primarily the stems. Activity of these organs was almost equal to that of the fruit at the end of 2 hours; however, beyond 2 hours the number of counts in the stems and leaves remained almost constant, whereas the counts of the fruit increased rapidly from 2 to 8 hours. After 8 hours, the number of counts in the fruit continued to increase, but at a reduced rate.

The sequential effects of the initial lag in export of labeled photosynthate from the source leaf was evident from the time course changes in the ethanol insoluble fraction (Fig. 4). The total counts in the ethanol insoluble fraction of fruit and leaves at the end of 2 hours were only $.84 \times 10^6$, whereas the counts in the ethanol soluble fraction reached 10.23×10^6

Table 1. Distribution of ^{14}C photosynthate translocated from source leaves on sympodia.

Translocation time (hrs.)	Percent of ^{14}C activity[a]											
	EtOH soluble						Residue					
	Treated branch[b]			Other branches			Treated branch[b]			Other branches		
	Fruit	Stem + leaves	Total	Fruit	Veg.	Total	Fruit	Stem + leaves	Total	Fruit	Stem + leaves	Total
2	64.5±6.8	32.2±6.2	96.7±1.0	3.3±0.5	0.0	3.3±0.5	65.8±8.6	27.2±4.5	93.0±4.1	6.8±4.1	0.2±0.1	7.0±4.1
4	83.2±6.3	13.7±5.0	96.9±2.3	0.6±0.5	2.5±0.3	3.1±1.6	83.8±6.1	13.8±6.8	97.6±2.3	0.3±0.2	2.1±0.8	2.4±1.2
8	89.3±4.2	8.2±3.6	97.5±3.9	1.5±0.2	1.0±0.1	2.5±0.4	90.1±6.1	7.8±3.9	97.9±2.8	0.6±0.3	1.5±0.5	2.1±1.0
24	94.9±2.8	4.8±0.2	99.7±2.1	0.1±0.1	0.2±0.06	0.3±0.08	96.4±0.8	3.0±0.7	99.4±0.7	0.2±0.02	0.4±0.03	0.6±0.1

[a] Total activity in the EtOH soluble fraction was divided into the activity in each of the plant parts to determine the percentages. Same procedure was used for the residue fraction.
[b] The leaf treated with $^{14}CO_2$ was on this branch.

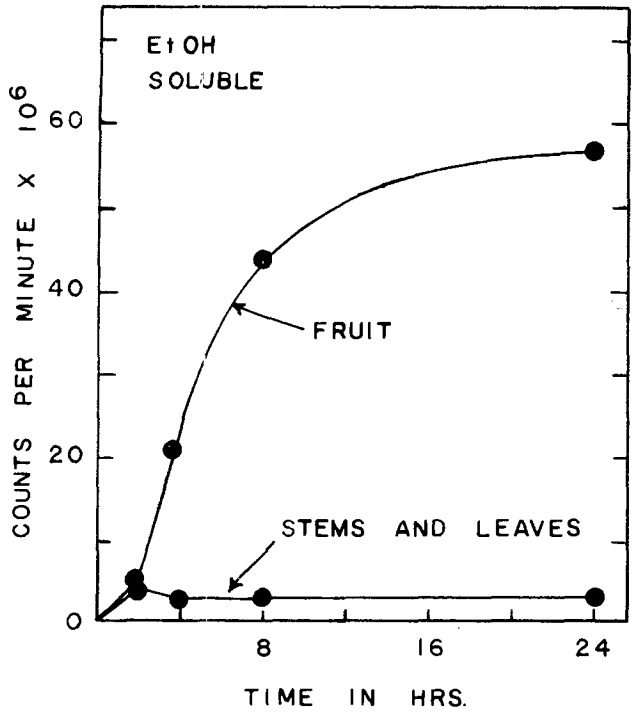

Fig. 4. Time course changes in ^{14}C-activity in EtOH insoluble fraction of sympodia components.

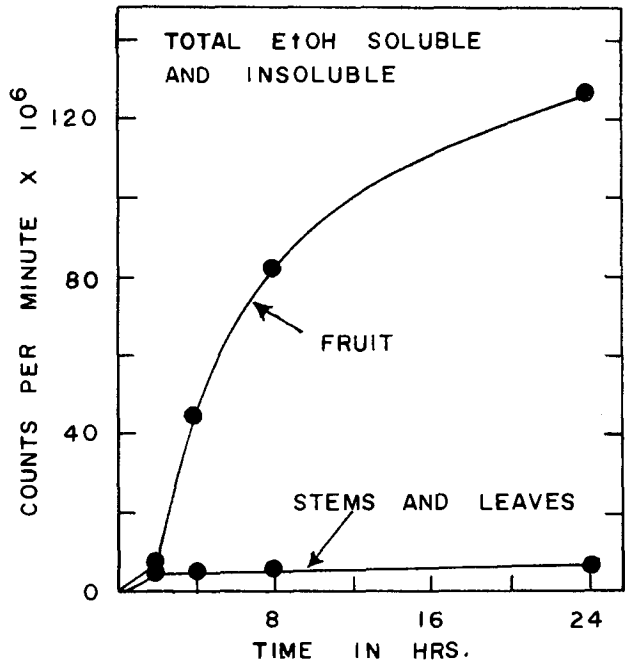

Fig. 5. Time course changes in ^{14}C-activity in EtOH soluble plus insoluble fractions of sympodia components.

during the same time. This trend was expected since the labeled photosynthate had to be delivered to the metabolic sites before synthesis of the insoluble components was initiated. The counts in the ethanol insoluble fraction increased very rapidly during the period from 2 to 8 hours. This is similar to the increase in the ethanol soluble fraction; however, the rate of increase in the insoluble fraction was much greater than in the soluble fraction during the same period. The number of counts in the insoluble fraction of the stems and leaves approached a maximum at the end of four hours and remained relatively constant through 24 hours.

The time course changes in the total counts of both fractions (soluble + insoluble) in sympodia components gave a response curve (Fig. 5) that was intermediate between the curves of the respective fractions when presented alone. The lower counts in the insoluble fraction during the initial time period was offset by the higher counts in the soluble fraction. Likewise, the higher counts in the insoluble fractions during the later translocation periods was offset by the lower counts in the soluble fraction. The total counts in both the ethanol soluble and insoluble fractions of the stems and leaves increased during the initial 2-hour period and then remained fairly constant thereafter.

^{14}C-Distribution Among Fruit

Thus far, the data have shown that a very high percentage of the photosynthate produced by any given leaf on a sympodia remained in the same sympodia. The data further indicate that the fruit was the ultimate sink for a high proportion of that photosynthate remaining on the sympodia and this proportion increases with time after ^{14}C labeling. The next point of interest was the pattern of photosynthate import by the different bolls on a given sympodia. The data in Table 2 show that a majority of the total photosynthate translocated to the fruit went to the boll immediately adjacent to that leaf. Smaller percentages of the labelled photosynthate moved to the other bolls of this sympodia. This same general response was present whether the boll was in the first, second, or third position out on the sympodia from the main stem toward the terminal. There was a definite tendency for the bolls one node removed from the source leaf toward the sympodia terminal to import a higher percentage of the photosynthate than the fruit farther out on the sympodia. On the other hand, when the source leaf subtended the boll in the third position the reverse was true. In the latter case the boll in the second position imported a higher percentage of the labeled photosynthate than the boll in the first or fourth position. With regard to the data in Table 2, the boll adjacent to the source leaf was 20 to 30 days old in all cases; therefore, these bolls were in a highly active state of growth with high demands for photosynthate import.

When bolls with bracts attached or removed were treated with $^{14}CO_2$ a high percentage of the activity remained in that same boll (Table 3). However, the total amount of $^{14}CO_2$ reduced by bolls with attached bracts was much larger than when the bracts were removed. The bracts have a much greater number of stomata than the boll walls, therefore the bracts have a higher CO_2 fixation capacity than the boll walls.

^{14}C-Photosynthate in Source Leaves

The data presented in prior segments of this manuscript have been devoted to that ^{14}C-photosynthate which had moved from the source leaf to other plant

Table 2. Percent of the total activity in translocated photosynthate of the sympodia present in bolls at different positions on the source sympodia.

Translocation time	Boll position on sympodia*		
	1	2	3
(hrs)			
2	61.2 ± 9.8**	12.9 ± 6.4	0
4	43.8 ± 7.6**	20.7 ± 7.1	15.7 ± 4.6
8	59.4 ± 6.6**	22.8 ± 5.0	9.8 ± 3.8
24	56.3 ± 7.1**	31.3 ± 2.5	7.1 ± 5.7
2	2.0 ± 1.1	48.9 ± 6.9**	16.8 ± 7.5
2	4.6 ± 0.8	12.0 ± 6.0	60.3 ± 8.0**

* Position 1 is the first boll adjacent to the main stem and positions 2 and 3 are successive bolls toward the sympodia terminal.
** Denotes that this boll was in the axis of the source leaf.

Table 3. ^{14}C-activity in bolls exposed to $^{14}CO_2$ with bracts attached and removed.

Organ exposed to $^{14}CO_2$	Activity in boll	Total activity in plant
		CPM
Boll with bracts	98.8 ± 1.2	26,691,031 ± 3,168,215
Boll without bracts	94.6 ± 1.1	2,855,021 ± 70,938

Table 4. The percent of the total labeled photosynthate remaining in source leaves located on the sympodia and main stem after a 2 hour translocation period.

Vertical position on plant	Labeled photosynthate remaining	
	Sympodia leaf	Main stem leaf
Bottom	88.2 ± 4.7	66.3 ± 1.4
Middle	89.5 ± 3.6	57.9 ± 2.6
Top	91.0 ± 4.2	58.7 ± 3.2

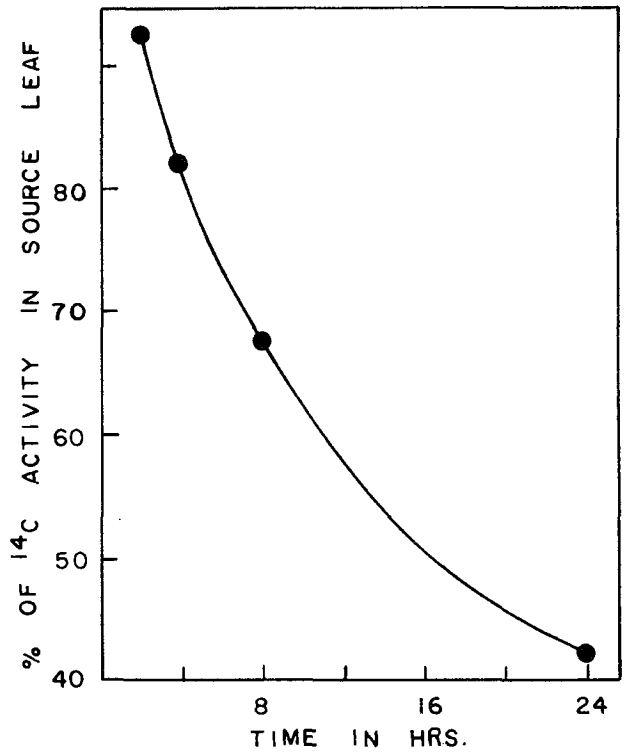

Fig. 6. Percent of total ^{14}C-photosynthate remaining in source leaf at time intervals through 24 hours.

parts. The data in Fig. 6 show the percent of the total ^{14}C-photosynthate remaining in the source leaves at different time intervals over a 24-hour period. The labeled photosynthate remaining in the source leaf decreased progressively throughout the 24-hour period. This type of response was expected; however, it is interesting to note the relatively slow rate of export from the source leaves. Two hours after the leaves were exposed to $^{14}CO_2$, 92.3% of the ^{14}C-photosynthate remained in the source leaf, after 8 hours, 67.9% remained and even after 24 hours 42.5% remained in the source leaf. In comparison, 80% of the photosynthate is translocated within a 4-hour period in corn (*Zea mays* L.) (11) and sugarcane (*Saccharum Sp.*) (9). On the other hand, slow rates have been reported also for other species (5, 12, 18).

Export from Main Stem Leaves

There was some evidence that the position of the leaf on the plant influenced the rate of photosynthate export from the source leaf (Table 4). These data show that at the end of 2 hours, approximately 90% of the ^{14}C-photosynthate remained in the sympodia leaves; whereas, approximately 60% remained in leaves of the main stem at the end of the same period. The same general response occurred whether the main stem leaves or the sympodia leaves were in the bottom, middle, or top portion of the plant canopy. The reasons for the differences in export rate from main stem and sympodia leaves are not readily apparent. It is possible that the morphology of the two leaves at the stem-petiole junction differ sufficiently to cause a difference in the rate that photosynthate exits from the petiole and source leaf, or it could simply mean that the leaves situated on the main stem are associated with vascular elements exhibiting a greater mass flow phenomena than leaves on the sympodia. Neither of the foregoing postulates is supported by data in this report. Nonetheless, the data indicate that caution should be exerted in interpreting translocation data which come from main stem leaves only.

The distribution patterns of labeled photosynthate from main stem and sympodia leaves differed somewhat. The sympodia in the axil of the main stem leaves imported 60.4 ± 3.2% of the photosynthate from this leaf during a two hour translocation period. Most of the photosynthate entering the sympodia was found in the fruit with smaller amounts in the stems. As discussed previously, at least 87.5 ± 3.7% of the photosynthate translocated from sympodia leaves remained on that sympodia (Fig. 2). The translocated photosynthate not present in the axillary sympodia of the main stem leaves was found in the main stem and sympodia above and below the source leaf.

^{14}C-Distribution from Terminal Segments

When 10-centimeter terminal segments of sympodia or main stem branches were exposed to $^{14}CO_2$ a very high percent of the photosynthate was retained in the treated segment (Table 5). The distribution patterns of labeled photosynthate from the main stem and sympodia terminals were similar. Only a small amount of the photosynthate produced in the terminal segment was exported to the developing bolls and fruit on the plant. Of course, the amount of photosynthate imported by the fruit would be expected to increase somewhat with time. Even though this in-

Table 5. Distribution of ^{14}C-photosynthate produced in terminal growth segments of the plant.

Type of terminal	Distribution of ^{14}C-photosynthate			
	$^{14}CO_2$ treated terminal	Main stem or sympodia stem	Other vegetative parts	Fruit
Main stem	82.8 ± 5.7	13.7 ± 5.04	2.39 ± 1.2	1.10 ± 0.7
Sympodia	87.06 ± 6.6	10.66 ± 2.0	1.12 ± 0.6	1.16 ± 0.3

[a] Terminal segments exposed to $^{14}CO_2$ for one hour and plants harvested after two additional hours.

crease would be expected, it was apparent from these data that the terminal portions of the plant sympodia and main stem supply only a small amount of photosynthate to the fruit of these plants. Similarly, the leaves subtending developing bolls on the sympodia exported very small amounts of photosynthate to the terminal growth segments on the plant.

DISCUSSION

The leaf adjacent to the boll apparently was the prime source of photosynthate for boll growth on plants which contained a large number of fruit (Table 2). Significant amounts of photosynthate also were supplied to a given boll from leaves located one node away from that boll. In addition, some photosynthate was supplied to the boll by its associated bracts with lesser amounts coming from the chlorophyll of carpel tissue (Table 3) (16). Since only small amounts of photosynthate moved from one sympodia to another (Fig. 1 and 2) and only minor amounts of photosynthate from terminal branch segments moved to the fruit (Table 5), it appears that a leaf-to-boll ratio of 1:1 could be a realistic estimate of the source-sink relationship in these plants. This may not be adequate for maximum growth rate since other information (1) indicates that, under certain temperature regimes, an inadequate supply of carbohydrates was available for boll growth and respiration where a relatively large number of bolls are on the plant. The fact that adjacent photosynthetic tissues supply a major portion of photosynthate for reproductive development has been demonstrated in a number of species (13, 19, 20).

The relatively small number of leaves and other photosynthetically active organs directly contributing to boll development could be associated with the slow rate of translocation. It is reasonable from a physical standpoint to assume that most of the available photosynthate in a plant with a heavy fruit load could be consumed locally in boll growth as rapidly as it moves from the leaves. This would leave only a small surplus to be translocated greater distances. This concept was supported by the data of Fig. 6 which showed that translocation of photosynthate from leaves was relatively slow. The slow rate of photosynthate translocation is one physiological response which is characteristic of a photosynthetically inefficient group of plants (3). Other responses in the cotton plant characteristic of inefficient plants are a measurable photorespiration (7) and a large enhancement in CO_2 fixation rates at low O_2 levels (10).

The requirement for a plant of sufficient stature to physically support the fruit load is an obvious fact (6). However, the data from the present investigations indicated that much of the vegetative growth commonly present on the cotton plant was ineffective in supplying metabolites for fruit development during the period of critical demands. It is highly possible that in some instances the excess vegetative growth, through mutual shading of the leaves adjacent to the developing fruit, greatly reduces the rate of movement and total amount of photosynthate supplied to the fruit. Further investigations of this phenomenon, as well as alternate sources of photosynthate supply where the primary sources are removed, are needed to provide evidence on this point.

REFERENCES

1. Baker, D. N., J. D. Hesketh, and W. G. Duncan. 1971. The simulation of growth and yield in cotton: 1. Respiration and carbon balance. Crop Sci. 11:394-398.
2. Biddulph, O., and R. Cory. 1965. Translocation of ^{14}C metabolites in the phloem of the bean plant. Plant Physiol. 40:119-129.
3. Black, C. C., T. M. Chen, and R. H. Brown. 1969. Biochemical basis for plant competition. Weed Sci. 17:338.
4. Brown, K. J. 1968. Translocation of carbohydrates in cotton; Movement to fruiting bodies. Ann. Bot. 32:703-713.
5. Clauss, Heinz, D. C. Mortimer, and P. R. Gorham. 1964. Time-course study of translocation of products of photosynthesis in soybean plants. Plant Physiol. 39:269-273.
6. Eaton, F. M. 1955. Physiology of the cotton plant. Ann. Rev. Plant Physiol. 6:299-328.
7. El-Sharkawy, M. A., R. S. Loomis, and W. A. Williams. 1967. Apparent reassimilation of respiratory carbon dioxide by different plant species. Physiol. Plant. 20:171-186.
8. Egamberdyev, A. E., K. A. Aliev, and Yu S. Nasyrov. 1963. On the movement of the products of photosynthesis (C^{14}) from the leaves to the bolls in cotton. Temat. Sbor. Otd. Fiziol. Lit. Biofiz. Rast. Akad. Nauk Tadsh. S. S. R. 4:36-41.
9. Hartt, C. E., and H. P. Kortschak. 1967. Translocation of ^{14}C in the sugarcane plant during the day and night. Plant Physiol. 42:89-94.
10. Hesketh, J. D. 1967. Enhancement of photosynthetic CO_2 assimilation in the absence of oxygen, as dependent upon species and temperature. Planta 76:371-374.
11. Hofstra, G., and C. D. Nelson. 1969. The translocation of photosynthetically assimilated ^{14}C in corn. Can. J. Bot. 47:1435-1442.
12. Hofstra, G., and C. D. Nelson. 1969. A comparative study of translocation of assimilated ^{14}C from leaves of different species. Planta (Berl.) 88:103-112.
13. Ludwig, L. J., T. Saeki, and L. T. Evans. 1965. Photosynthesis in artificial communities of cotton plants in relation to leaf area. 1. Experiments with progressive defoliation of mature plants. Aust. J. Biol. Sci. 13:1103-1118.
14. Mason, T. G., and E. J. Maskell. 1928. Studies on the transport of carbohydrates in the cotton plant. 1. A study of diurnal variation on the carbohydrates of leaf, bark, and wood, and the effects of ringing. Ann. Bot. 42:189-255.
15. Mason, T. G., and E. J. Maskell. 1928. Studies on the transport of carbohydrates in the cotton plant. II. The factors determining the rate and the direction of movement of sugars. Ann. Bot. 42:571-636.
16. Morris, D. A. 1965. Photosynthesis by the boll wall and bracteoles of the cotton plant. Emp. Cot. Grow. Rev. 42: 49-51.
17. Muramoto, M., J. D. Hesketh, and C. D. Elmore. 1967. Leaf-growth, leaf aging, and photosynthetic rates of cotton plants. Proc. Beltwide Cot. Prod. Res. Conf. pp. 161-165.
18. Shiroya, M., G. R. Lister, C. D. Nelson, and G. Krotkov. 1961. Translocation of ^{14}C in tobacco at different stages of development following assimilation of $^{14}CO_2$ by a single leaf. Can. J. Bot. 39:855-864.
19. Thorne, Gillian N. 1965. Photosynthesis of ears and flag leaves of wheat and barley. Ann. Bot. 29:317-329.
20. Thrower, S. 1962. Translocation of labeled assimilate in the soya bean. II. The patterns of translocation in intact and defoliated plants. Aust. J. Biol. Sci. 15:627-641.
21. Tuichibaev, M., and A. S. Kruzhilin. 1965. Translocation of the labeled assimilates from cotyledon cotton leaves (K. A. Timiryazev Inst. Pl. Physiol.) Fiziol. Rast. 12:357-360.