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Effect of Time and Plant K Status on ^{14}C-labeled Photosynthate Movement in Cotton[1]

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ABSTRACT

The effect of time and plant K status on the rate and pattern of photosynthate translocation in 5-week-old cotton (*Gossypium hirsutum* L.) plants was investigated using $^{14}CO_2$ labeling techniques. The cumulative total of ^{14}C-photosynthate translocated from the source leaf increased in a hyperbolic manner with distance during a 2-hour translocation time. The maximum velocity of photosynthate translocation was approximately 50 cm per hour. Decreasing the K content of plants markedly reduced both the quantity and the distance that photosynthate moved from the source leaves. The reduction in photosynthate translocation resulting from reduced K content was obtained before visible K deficiency symptoms appeared on the plant.

Additional key words: **Photosynthate translocation, *Gossypium hirsutum* L., Mineral nutrient deficiency.**

GROWTH of plants is directly dependent on photosynthetic CO_2 reduction and the attendant synthesis of organic compounds. These metabolites must be rapidly translocated to sites of utilization if maximal growth rate is to be attained. The translocation process has been shown to be influenced by a number of environmental and nutritional conditions (4, 7, 16, 21).

Potassium status of plant tissues influences photosynthate translocation (2, 7, 11), and this influence may be an important factor in the growth of cotton plants (15). The effects of K on translocation are of particular concern, since translocation can be retarded at K levels above those that produce visible symptoms of a K deficiency in the plant (7, 15). Other work (1) shows that photosynthate translocation in the cotton plant is relatively slow compared to tropical grasses even under ideal conditions. In addition, K is quite mobile and often moves from older to younger leaves as the plant approaches maturity. Late in the season, when demand for photosynthate by developing bolls is high, the rate of photosynthate movement from older leaves could be impaired by limited K concentration in these leaves.

The information reported in this paper was obtained from experiments designed to (i) characterize the initial time-rate relationships of photosynthate translocation in young cotton plants and (ii) deter-

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mine the effects of plant K status on translocation of photosynthate.

MATERIALS AND METHODS

Cotton (*Gossypium hirsutum* L. 'Atlas 67') seed were germinated in a constant environment chamber and were then transferred to 10-L polyethylene containers filled with Hoagland and Arnon's (9) nutrient solution. Plants were maintained in an upright position by use of a plexiglass lid for the containers. A cork and sponge arrangement in the lid permitted the plants to grow freely through the lid without damage to the stem. The experiments were conducted in a growth chamber with a light intensity of approximately 30,000 lux at midplant. Diurnal temperatures were 30 C for the 16-hour light period and 22 C for the 8-hour dark period. Culture solutions were renewed biweekly.

The experiments to determine the time course changes in photosynthate translocation patterns were conducted on 5-week-old plants. ^{14}C-photosynthate translocation periods of 1/2, 1, 2 and 4 hours were used. Three plants for each translocation period were used.

Procedures for studying effects of K status were the same as for the time course study, except for the development of plants with different levels of K in tissues. Plants with high-K status were grown continuously in complete Hoagland's solution. Medium-K plants were developed by growing them in complete Hoagland's solution for 4 weeks and then in Hoagland's minus-K solution for 1 week. The low-K plants were developed the same as medium-K, except that they were deprived of K for 2 weeks prior to exposing to $^{14}CO_2$ and $^{14}CO_2$ labeling was done on 6-week old plants. The translocation periods in the K status experiment were 1/2 and 1 hour.

The youngest fully expanded leaf of the plant was exposed to $^{14}CO_2$ in both experiments. Exposure to $^{14}CO_2$ occurred in all cases between 9:00 AM and 3:00 PM (EST). The light period began and ended at 5:00 AM and 9:00 PM, respectively. The leaf was enclosed in a plexiglass chamber (20 × 20 × 5 cm) with the petiole extending through a slot in the side of the chamber. Modeling clay was used to seal around the petiole at the chamber wall. $^{14}CO_2$ was released in the chamber by hypodermically injecting HCl through a serological stopper into a Na_2 $^{14}CO_3$ solution within the chamber. The $^{14}CO_2$ was distributed and recirculated around the leaf by use of a oneway suction bulb with an attached hypodermic needle. The leaves were permitted to photosynthesize the ^{14}C-enriched CO_2 for a period of 15 min and then the chamber was removed. The translocation period in all cases consisted of the 15-min period of exposure to $^{14}CO_2$ and the remainder of the time in normal air. The ^{14}C-activity released in the leaf chamber was 25 and 100 μc for the time course and plant K status experiments, respectively. The specific activity of the source was 5 mc/mmole.

At the end of the predetermined translocation time the plants were harvested by cutting at the root-shoot junction. The treated leaf was removed at the blade-ptiole junction and the petiole and the main stem were cut in 2-cm sections. All parts of the plant were quickly frozen and lyophilized and the dry weight was recorded. The aerial plant parts were prepared for analyses by grinding to pass a 20-mesh screen.

One-tenth gram of each sample was refluxed in 20 ml of aqueous 80% ethanol solution for 2 hours, and the solid and liquid phases were separated by filtration. In this manuscript the liquid extract and the solids will be referred to as the ethanol soluble and insoluble materials, respectively. The filtrate was made to volume with absolute ethanol. The dried residue was placed into a black paper wrapper and suspended in a wire basket inside a 1-liter suction flask. The air in the flask was displaced with O_2 and the flask was sealed. The sample was ignited by an infrared ignition apparatus. After igniting the sample, ethanolamine-ethanol (1:2 v/v) was injected for CO_2 capture through a serological stopper at the top of the suction flask. Each sample was analyzed in duplicate by use of liquid scintillation techniques. Appropriate counting efficiency and quench corrections were made. The K content of plant tissues was determined by standard flame photometric techniques.

Throughout the paper the leaf exposed to $^{14}CO_2$ will be referred to as the source leaf. The ^{14}C-front will refer to the most distant point down the main stem from the source leaf that ^{14}C-labeled photosynthate was detected.

Table 1. Time course change in ^{14}C activity in the source leaves.

Time interval	Activity in counts min^{-1}* × 10^5		
	Ethanol soluble	Ethanol insoluble	Total
1/2 hour	15.24 ± 3.19	1.53 ± 0.88	16.77 ± 4.07
1 hour	13.58 ± 4.72	1.22 ± 0.34	14.80 ± 4.39
2 hour	9.86 ± 0.54	1.65 ± 0.32	11.52 ± 0.66
4 hour	5.96 ± 0.32	3.04 ± 0.44	9.00 ± 0.29

* Standard deviation presented for each entry.

RESULTS AND DISCUSSION

Time Course of Photosynthate Translocation

Photosynthate in Source Leaf

The time course changes in ^{14}C-activity in the source leaves are presented in Table 1. There was a marked decrease in the ethanol soluble components remaining in the source leaf as the translocation time increased from ½ to 4 hours. The quantities of ^{14}C-photosynthate in the leaf-soluble fraction at 1, 2, and 4 hours were 89.1, 64.7 and 39.1%, respectively, of that present in the source leaf at ½ hour. Patterns of ^{14}C-photosynthate accumulation in the ethanol-insoluble component of the source leaf were somewhat different from those of the soluble fraction (Table 1). The average ^{14}C-content in the insoluble fraction increased from 1 through 4 hours' translocation time; however, at ½ hour the ^{14}C-content was somewhat larger than at 1 hour. The relatively large variability in counts at ½ hour, as indicated by the standard deviation, is a possible contributing factor in this apparent anomaly.

The total ^{14}C-activity remaining in the source leaf (Table 1) decreased with increase in time after exposure to $^{14}CO_2$ as has been reported in other studies (19, 20). When the total activity in the source leaf of Table 1 is added to the total activity of the translocated photosynthate in Figure 1, the result is a lower amount of activity recovered in the plant shoots at 2 and 4 hours than at ½ and 1 hour. This was primarily a result of export of the labeled photosynthate from the shoot to the roots and respiratory $^{14}CO_2$ loss from the plant. However, the magnitude of neither of these parameters was determined in these experiments.

Photosynthate Translocated from Source Leaf

Translocation patterns of ^{14}C-labeled photosynthate from the source leaves to the shoots of cotton plants are presented in Fig. 1 for ½-, 1-, 2-, and 4-hour periods. The total amount of labeled photosynthate translocated from the source leaf and recovered in the shoots of the plants progressively increased up to the 2-hour translocation time. After 4 hours, however, the total amount of activity in the shoot was somewhat less than after 2 hours. The same general response was present in the ethanol soluble fraction of the shoots. On the other hand, the ^{14}C-activity in the ethanol insoluble fraction progressively increased through the 4-hour period. These response patterns are apparently due to the fact that at the end of 1 hour only trace amounts of ^{14}C-labeled photosynthate had entered the roots, whereas, at the end of 2 and 4 hours successively larger quantities of ^{14}C-label were entering the roots.

The distance that the labeled photosynthate moved from the $^{14}CO_2$-treated leaves followed patterns similar to those for cumulative total counts. After ½ hour, the ^{14}C-photosynthate front in the soluble fraction had only advanced to a distance of 20 cm from the treated

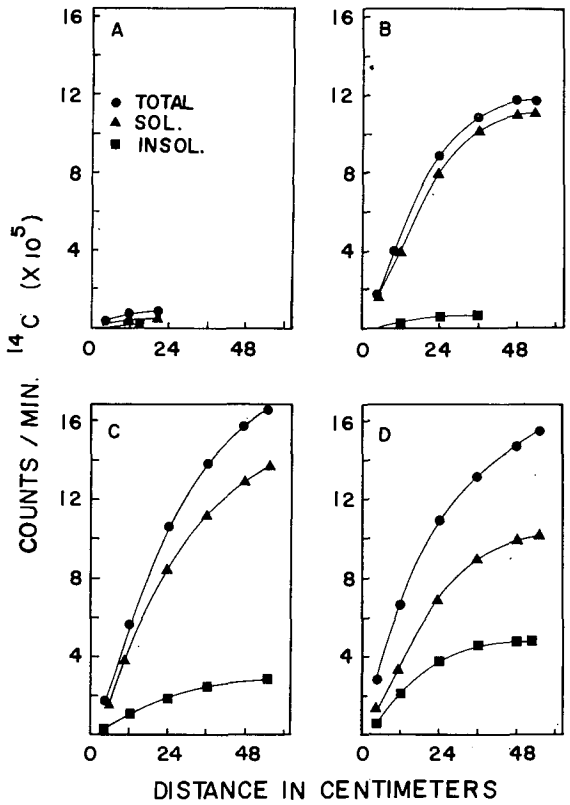

Fig. 1. Radioactivity at various distances from source leaf after different translocation periods. Graphs A, B, C, and D refer to 1/2-, 1-, 2-, and 4-hour translocation periods, respectively.

leaf (Fig. 1A). There was only a small amount of label recovered in the ethanol insoluble fraction, yet traces were found at 14 cm from the treated leaf in this fraction. At the end of 1 hour the ^{14}C front of the soluble fraction had reached a distance of 52 cm, and that of the insoluble fraction, 33 cm (Fig. 1B). The major portion of the activity in the ethanol soluble fraction was present in the first 38 cm. At the end of 2 and 4 hours, apparently significant amounts of ^{14}C-labeled photosynthate had passed the root-shoot junction in both fractions (Fig. 1C and D).

Geiger and Swanson (5) have shown distribution patterns in soybeans that were similar to those obtained in this study with cotton. They found that photosynthate was converted to an insoluble form and accumulated in storage pools along the conducting tissues toward the sink. The insoluble constituents appeared to accumulate within or adjacent to the sieve tubes. They found the amount of insoluble photosynthate to be dependent upon time and the amount of labeled photosynthate translocated.

Velocity of Photosynthate Movement

In studies with $^{14}CO_2$ labeling techniques, the velocity of photosynthate movement has been computed on the basis of the maximum distance that ^{14}C-activity had moved from source leaves in unit time. It was evident from the data of Fig. 1 that the velocity of movement in this study was at least 50 cm $hr.^{-1}$. It is difficult to assign a precise value for velocity of photosynthate movement in these studies, since the entire leaf was exposed to $^{14}CO_2$. Photosynthate fixed in areas remote from the leaf-petiole junction had to move as much as 12 cm across the leaf before being deposited in the petiole. For greater precision in velocity measurement, point-source labelling on the leaf with $^{14}CO_2$ or petiole feeding of ^{14}C-sucrose have been used (10, 18); the validity of these techniques is open to question, however, especially the technique involving leaf removal and petiole feeding of labeled carbohydrates.

The minimum velocity of photosynthate movement of 50 cm hr^{-1} observed in this study could be higher than that found for cotton grown in field conditions. This study involved the use of solution culture techniques with optimum temperature and abundant moisture, nutrients, and oxygen, which resulted in succulent plant growth. Plants grown under field condition seldom have such ideal growth conditions. As will be shown in subsequent sections of this report, restrictions in nutrients available for plant growth can markedly alter the velocity of photosynthate movement. Restrictions of this nature could exert an influence on translocation in the plant without visual plant response.

Effect of K on Photosynthate Translocation

From the data presented in the previous section of this report it appeared that a translocation period of 1 hour was suitable for investigating the effects of K on translocation in plants of comparable size and stage of development. During this translocation time ^{14}C-photosynthate did not reach the root-shoot junction; therefore, measurement of the total amount and maximum distance of photosynthate movement from the source leaf could be accomplished in plants with different K contents.

Photosynthate Translocated from Source Leaf

Decreasing the K content of 5- to 6-week old cotton plants reduced photosynthate translocation from leaves (Table 2). In a 30-min translocation period plants with low-K translocated 52.7% as much photosynthate from the source leaf as did plants high in K. When time periods for translocation were extended to 1 hour, the low-K plants translocated only 17.8% as much photosynthate as did high-K plants. Even the medium-K plants with no visual deficiency symptoms translocated only 46.9% as much labeled photosynthate in 1 hour as high-K plants.

The amount of translocated photosynthate in the ethanol insoluble fraction was relatively low in comparison to the soluble fraction at all three levels of plant K (Fig. 2). A slightly larger portion was in the insoluble fraction of high-K than in the low- and medium-K plants. Since the relative amounts converted to the stable insoluble plant materials were not greatly affected by plant K, it appears that synthesis of cellular components from photosynthates subsequent to their transport from the source leaf did not exert much, if any, influence on the responses to variable plant K.

Moderate K deficiency in plants stimulates the respiration rate (12). This is possibly due to an uncoupling of respiration from oxidative phosphorylation, thereby reducing the useful energy generated per unit of respiration (13, 14). Richards (17) found that as K deficiency progresses from slight to severe respiration

Table 2. Effect of plant K status on ^{14}C-activity in the source leaf, in translocated photosynthate and in plant shoot.

Treatment	Leaf K content %	^{14}C-activity in counts min^{-1}*, × 10^6		
		Source leaf	Translocated	Total in shoot
High-K 30 min.	2.57 ± .15	64.45 ± 14.56	0.56 ± 0.08	64.98 ± 14.54
Low-K 30 min.	0.55 ± .07	62.58 ± 5.34	0.29 ± 0.15	62.87 ± 4.12
High-K 1 hr.	2.59 ± .60	64.89 ± 4.71	3.88 ± 1.37	68.77 ± 4.12
Med-K 1 hr.	1.18 ± .10	49.35 ± 7.82	1.82 ± 0.68	50.57 ± 6.29
Low-K 1 hr.	0.44 ± .17	52.07 ± 2.86	0.69 ± 0.25	52.77 ± 2.61

* Standard deviation presented for each entry.

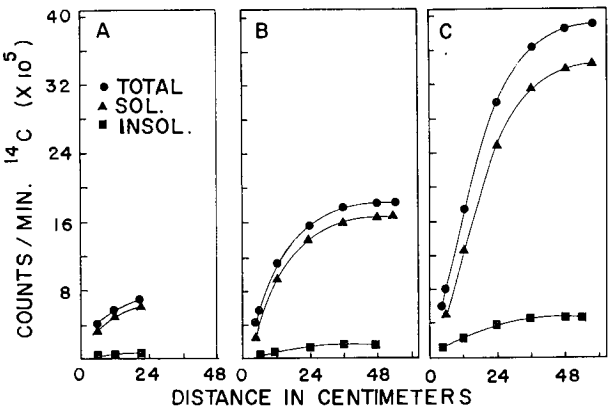

Fig. 2. Translocation of ^{14}C-photosynthate from source leaves in plants with different K status. Graphs A, B, and C refer to data from low-, medium-, and high-K plants, respectively, after a 2-hour translocation period.

reaches a maximum and then declines under extreme K deficiency. The decline was probably due to the depletion of oxidizable substrate. Respiratory rates were probably accelerated in the plants of the low- and medium-K treatments in the present study, since they would be classified as slightly to moderately deficient. This type of response would logically contribute to the differences in ^{14}C activity recovered in the low- and high-K plants at the 1-hour translocation time (Table 2).

Potassium Effect on Total $^{14}CO_2$ Fixed by Plants

Although translocation was altered by the supply of K to the plant, photosynthesis was affected to a much smaller degree, if at all. The data in Table 2 show that the total $^{14}CO_2$ fixed by the plants was less in the medium- and low-K plants than in high-K plants for the 1-hour translocation time. On the other hand, total ^{14}C-activity was approximately the same in the low- and high-K plants at the 30-min translocation time. Even though a small reduction may have occurred in the amount of $^{14}CO_2$ fixed by leaves medium and low in K, this reduction was relatively small in comparison to the effects of decreasing K on the translocation of photosynthate (Table 2 and Fig. 2). This is in agreement with Hartt and Burr's (8) study with sugarcane (*Saccharum officinarum*) in which they found that photosynthesis did not decrease until the K concentration in the blade fell below 0.4% of the dry weight. With other experiments, Hartt (7) has shown that translocation decreased as K was decreased, but photosynthesis was not affected. Baver et al. (2) also found in direct $^{14}CO_2$ labeling experiments that translocation of recent photosynthate products from K-deficient leaves was impaired more than the rate of CO_2 fixation. On the other hand, Jackson and Volk

Table 3. Effect of K on the percentage of translocated ^{14}C-photosynthate recovered at 10-cm intervals from the source leaf.

Treatment	Component of activity	% recovery of ^{14}C-activity				
		10 cm	20 cm	30 cm	40 cm	50 cm
High-K 30 min.	S*	59.6	91.1	99.2		
	I**	61.3	93.1			
	Total	60.0	91.0			
Low-K 30 min	S	93.4				
	I	86.9	92.9			
	Total	92.7				
High-K 1 hr.	S	30.9	70.0	90.5	97.3	99.6
	I	50.0	84.1	96.8	99.4	99.9
	Total	33.0	71.7	91.3	97.6	99.7
Med-K 1 hr.	S	58.7	90.6	98.4	99.8	
	I	59.4	89.6	96.5	97.7	
	Total	58.7	90.5	98.3	99.6	
Low-K 1 hr.	S	86.0				
	I	93.0				
	Total	86.7				

* S = ethanol soluble fraction. ** I = ethanol insoluble fraction.

(12) concluded that photosynthesis could be restricted at leaf K concentrations of 1.5 to 2%.

Velocity of Photosynthate Movement

Both the quantity and distance of photosynthate translocated were affected by the K content of the plant (Table 3). After 30 min translocation, plants with high-K translocated ^{14}C-photosynthate a maximum distance of 36 cm with 91% of the radioactive translocate within 20 cm (Table 3) of the treated leaf. Low-K plants, however, translocated labeled photosynthate a maximum distance of 28 cm with almost 93% of the radioactive translocate being within 10 cm of the leaf-petiole junction.

In translocation periods of 1 hour, low-K plants translocated photosynthate a maximum distance of 20 cm (Fig. 2A) with 86.7% of the photosynthate in the first 10 cm (Table 4). Plants with high-K translocated a maximum distance of at least 56 cm (Fig. 2C) with a little more than 90% of the radioactive photosynthate within 30 cm of the treated leaf (Table 3). A few counts were still evident in sampled sections down to the root, but only traces of the radioactive translocate were present in the roots of the high-K plants. Medium-K plants translocated a maximum distance of 50 cm (Fig. 2B) with 90.5% of the radioactive translocate remaining in the first 20 cm (Table 2).

In summary, K deficiency reduced both the quantity and velocity of photosynthate translocation. These results are similar to those of Hartt (6), in which she also found the amount and velocity of transport were affected by K supply in sugarcane. In a similar study Ill'yashuk and Okaninko (11) found that the ^{14}C-photosynthate movement from leaves to roots of sugarbeets (*Beta saccharifera*) was reduced by inadequate potassium.

From these results, it was concluded that K definitely had an effect on translocation in the cotton plant. Whether it has a direct effect, as proposed by Hartt (7) and Spanner (20), or an indirect effect as suggested by Evans and Sorger (3) could not be determined from the data. It is possible that K could have both direct and indirect effects on translocation. Indirectly, it could affect such factors as growth, activity of enzymes, as well as loading and unloading of phloem elements at the source and sink. Directly, effects could involve the development of an electrical potential across sieve plates or within the sieve tubes that would facilitate photosynthate movement.

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