

Potassium Nutrition and Translocation in Sugar Beet¹

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ABSTRACT

The effect of increased net foliar K⁺ accumulation on translocation of carbon was studied in sugar beet (*Beta vulgaris*, L. var. Klein E and US H20) plants. Net accumulation of recently absorbed K⁺ was studied by observing arrival of ⁴²K⁺ per unit area of leaf. Labeled K⁺ was added to give an initial concentration at 2 or 10 millimolar K⁺ in mineral nutrient solution. Because the newly arrived K⁺ constitutes a small part of the total leaf K⁺ in plants raised in 10 millimolar K⁺, export of ⁴²K⁺ by phloem was negligible over the 2- to 3-day period; consequently, accumulation is a measure of arrival in the xylem. In leaves from plants in 2 millimolar K⁺, export by the phloem was estimated to be of the same order as import by the xylem; K⁺ per area was observed to remain at a steady-state level. Increasing the supply of K⁺ to 10 millimolar caused arrival in the xylem to increase 2- to 3-fold; K⁺ per area increased gradually in the mature leaves. Neither net carbon exchange nor translocation of sugar increased in response to a faster rate of arrival of K⁺ over a 6- to 8-hour period. In the absence of short-term effects, it is suggested that K⁺-promoted increase in synthetic metabolism may be the basis of the increased carbon assimilation and translocation in plants supplied with an above-minimal level of K⁺.

promote import into sinks. Haeder and Mengel (9) found that increasing K⁺ supplied to the roots caused increased translocation of carbon to tomato fruits. They observed that increased K⁺ promoted conversion of soluble metabolites to an insoluble form in tomato fruits. Mengel and Viro (16) cited this metabolic conversion in sink tissues as a possible mechanism responsible for the long-term increase in translocation of assimilates observed in plants under increased K⁺ fertilization.

The present study was undertaken to determine if any of the four mechanisms cited above are likely to be means by which K⁺ regulates translocation of assimilate. Increasing the K⁺ available to the roots caused an immediate increase in delivery of K⁺ to the leaves but did not produce a concomitant increase in net CO₂ exchange or export of carbon. The data lead us to conclude that increased K⁺-supply does not promote net carbon exchange or translocation over the short term. Instead, we favor the hypothesis that increased accumulation of K⁺ in sinks and older source leaves promotes synthetic metabolism, which in some manner leads to an eventual increase in net carbon exchange and in export of products of photosynthesis.

MATERIALS AND METHODS

Plant Material. Sugar beet (*Beta vulgaris*, L., var. Klein E and US H20) plants were raised in washed sand and vermiculite watered with mineral nutrient solution (5). The concentration of K⁺ was adjusted to 2 or 10 mM by varying the KCl content. All plants were maintained on a regime of 14-h days at 24°C and 10-h nights at 17°C. Light was provided by fluorescent lamps supplemented with incandescent lamps; photon flux density at leaf level was 350 μE m⁻² s⁻¹ PAR.

One to 2 d prior to a labeling experiment a plant was carefully removed from the container with sand and vermiculite in place. Rooting medium was removed in a large container of tap water by aerating the solution. There was no evidence of extensive root damage nor indication of water stress at the time of the experiment.

Determination of Foliar Concentration. Leaf K⁺ concentrations for plants raised at 2 and 10 mM K⁺ levels were determined by atomic absorption spectrophotometry of acid-digested tissue samples. Eight to 12 samples were removed from the lamina of source leaves with a cork borer of 4.5 mm diameter. Care was taken to avoid including major veins in the samples. Tissue samples were dried at 50°C in a forced-air oven until constant weight was achieved. Dried samples were weighed with a precision of ±0.01 mg and digested by heating with a mixture of concentrated HNO₃, HClO₄, and H₂SO₄ in a ratio of 40:4:1.

Uptake of K⁺. Uptake of K⁺ by sugar beet leaves was followed as accumulation of ⁴²K⁺ in leaves. Leaves were numbered in order of emergence after the cotyledons. Labeled K⁺ was added to the mineral nutrient solution of plants in hydroponic culture as ⁴²KCl. Accumulation of labeled K⁺ in source and sink leaves was monitored by a GM tube positioned near the lower surface of the lamina. In one type of experiment, the plant was maintained in ⁴²K-labeled mineral nutrient solution with K⁺ at 2 mM throughout the duration of the experiment, up to about 60 h. In another type

Various studies provide evidence that K⁺ promotes the translocation of products of photosynthesis in plants (1, 2, 5, 9, 10, 12, 13, 16, 17). This promotion will occur if a higher level of K⁺ nutrition causes one or more of the following to increase: (a) net carbon exchange, (b) phloem loading, (c) transport into cells in sinks, and (d) metabolic conversion of sucrose in sink tissues.

A number of studies have shown that net carbon exchange increases as a result of increased K⁺ fertilization of plants. Low K⁺ appears to reduce net carbon exchange through an increase in both stomatal and mesophyll resistance (15, 18, 19, 22). Two studies (6, 12) showed increased net carbon exchange and a greater proportion of fixed carbon exported to the roots in K⁺-fertilized sugar beets. Generally, data from these and other studies do not permit one to distinguish between direct promotion of net carbon exchange by leaf K⁺ and indirect promotion. For instance, the latter might result from greater leaf expansion or in response to increased export.

Amir and Reinhold (1) presented evidence for promotion of translocation by K⁺ at a point after synthesis of sucrose in mesophyll cells. In a study involving application of K⁺ directly to leaves, Doman and Geiger (5) found a K⁺-stimulated efflux of sucrose from source leaves accompanied by increased export to sink leaves. These studies support the possible involvement of K⁺ in regulating phloem loading.

Because mechanisms for sink unloading are generally not known, it is difficult to specify mechanisms by which K⁺ might

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of experiment, an initial period of labeling in $^{42}\text{K}^+$ -labeled mineral nutrient solution with 2 mM K^+ was followed by a period of labeling with ^{42}K at the same specific radioactivity but with 10 mM K^+ . The concentration of K^+ in the growth solution was measured to determine the extent of depletion in the course of the experiments. For 2 mM $^{42}\text{K}^+$ solutions, concentration of K^+ fell by as much as 40% by the end of the 48 h. Because of shorter times and higher initial concentration, depletion was not a significant factor with the 10 mM $^{42}\text{K}^+$ solutions.

At the termination of an experiment, the lamina of each monitored leaf was removed from the plant and digested by heating it in the acid mixture. Aliquots of solution from each digested leaf were assayed for radioactivity by liquid scintillation counting and for K^+ content by atomic absorption spectrophotometry. All GM and liquid scintillation data were corrected for decay of the isotope. Detection efficiency of GM tubes was determined by comparison of the final GM counts recorded just prior to removal of the blade with the radioactivity per unit area of the leaf as measured by liquid scintillation counting of the digested leaf.

If the leaf grows, a portion of the original lamina area will move out of the direct counting field. Whether the leaf grows or not, the count rate recorded represents the net $^{42}\text{K}^+$ accumulated per unit area of leaf lamina. Calculations and discussion are based on K^+ per unit area rather than K^+ per lamina.

Measurement of Translocation of Photosynthate. Possible changes in export when K^+ supply to the roots was increased, were studied by steady-state labeling with $^{14}\text{CO}_2$ (7). Experimental plants were initially in mineral nutrient solution at 2 mM K^+ . Arrival of photosynthate in a sink leaf on the same orthostichy as the labeled source leaf was measured as accumulation of ^{14}C counts by a GM tube positioned against the sink leaf. After 5 h of $^{14}\text{CO}_2$ -labeling with the roots at the 2 mM K^+ level, the mineral nutrient solution was replaced with one at 10 mM K^+ . Labeling of the source leaf with $^{14}\text{CO}_2$ was continued for approximately 6 h after the increase in K^+ .

RESULTS

Arrival of K^+ in Source Leaves. Net accumulation of K^+ in leaves of a sugar beet plant, measured as $^{42}\text{K}^+$ accumulation, is presented in Figure 1. The plants used in the five experiments of this type were raised in mineral nutrient solution that contained 10 mM K^+ and transferred to a 2 mM solution at least 24 h prior to the experiment. To begin the experiment, the plants were placed in a solution containing 2 mM K^+ labeled with $^{42}\text{K}^+$. Because of the large amount of K^+ in the leaves, only a small proportion of the leaf K^+ is labeled with $^{42}\text{K}^+$ initially. For instance, after 66 h of labeling, the total K^+ which had arrived by the xylem for the leaves described in Figure 1 was only approximately 12% of their K^+ content. Consequently, little $^{42}\text{K}^+$ is exported initially and the observed rate of net accumulation is equivalent to the rate of arrival of K^+ in the xylem.

The validity of this interpretation is supported by the observation that heat girdling of the petiole did not cause an increase in the net accumulation of $^{42}\text{K}^+$ in the blade of that leaf (Fig. 1). Rates of arrival of K^+ from the mineral nutrient solution, calculated from data in Figure 1, are given in Table I. The calculations are based on the assumption that the arriving K^+ has the same specific radioactivity as the $^{42}\text{K}^+$ supplied to the roots. Consequently, the values are minimal estimates of net K^+ accumulated.

Older leaves showed a pronounced change in the rate of arrival of $^{42}\text{K}^+$ following transition between light and dark (Fig. 1). Arrival in the light was 5 to 10 times that during darkness. The change in rate with a change in illumination is smaller with decreasing leaf age and is practically absent in source leaves which only recently have begun to export. Transpiration from individual leaves was not measured so it is not possible to say to what extent these changes in $^{42}\text{K}^+$ -arrival rate are correlated with changes in

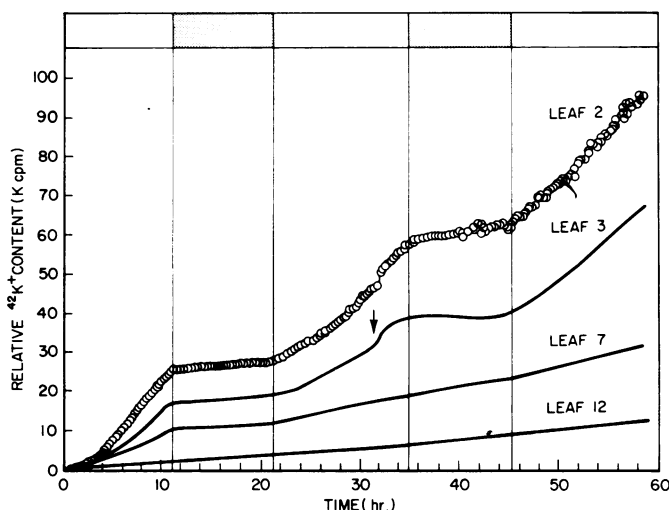


FIG. 1. Net accumulation of ^{42}K per area in four leaves of a sugar beet plant. The K^+ concentration in the mineral nutrient solution at time 0 when ^{42}K was added was 2 mM. Labeling began approximately 3 h after beginning of illumination. Heat killing of a segment of petiole of leaf 3 is indicated by the arrow. Individual values of the count rate are shown for leaf 2. Count rates have been corrected for half-life and data for leaves 3, 7, and 12 have been multiplied by factors which make the final count rates portray the relative ^{42}K content of the leaves at the end of the experiment. The time course for each leaf represents the change in ^{42}K per area of leaf as discussed in the text. To convert slopes to rates of accumulation per unit area, the slopes for leaves 2, 3, 7, and 12 should be multiplied by 0.0650, 0.0800, 0.123, and 0.633 $\mu\text{g K}^+ \text{dm}^{-2} \text{cpm}^{-1}$ respectively.

Table I. Rates of Transfer of K^+ into and out of Sugar Beet Leaves

Rates are for a plant kept in 2 mM K^+ throughout the labeling period. The rate of arrival of K^+ was practically unchanged following killing of a zone of leaf 3 petiole, on day 2.

Leaf Number	Rate of K^+ Import by Xylem						Entire period
	Area	Day 1	Night 1	Day 2	Night 2	Day 3	
	dm^2	$\mu\text{g K}^+ \text{dm}^{-2} \text{h}^{-1}$					
Source leaves							
2	0.74	153	19	112	5.7	173	99
3	0.86	224	13	172	36	178	102
7	0.55	143	31	80	42	78	65
Sink leaf							
12	0.12	NA	70	108	133	167	117

transpiration.

Transfer of K^+ by the Phloem. Export of K^+ from source leaves was estimated from measured values for sucrose export and ratios of K^+ to sucrose reported for phloem sap. Mengel and Haeder (17) reported a ratio of 30 to 40 μg sucrose/ $\mu\text{g K}^+$ in phloem sap from *Ricinus*. In an extensive table of K^+ concentrations in phloem sap, Ziegler (23) reports values which are largely between 1,000 and 2,500 $\mu\text{g K}^+ \text{ml}^{-1}$. On the basis of a value of sucrose concentration of 10% w/v, a reasonable estimate (23), the ratio of sucrose to K^+ is 40 to 100 μg sucrose/ $\mu\text{g K}^+$. Export from source leaves used in this study averaged 3,000 μg sucrose $\text{dm}^{-2} \text{h}^{-1}$ during the day and 1,800 μg sucrose $\text{dm}^{-2} \text{h}^{-1}$ at night. If values of 30 to 100 μg sucrose/ $\mu\text{g K}^+$ are used for phloem sap, K^+ export is estimated to be between 30 and 100 $\mu\text{g K}^+ \text{dm}^{-2} \text{h}^{-1}$ during the day and 18 to 60 $\mu\text{g K}^+ \text{dm}^{-2} \text{h}^{-1}$ at night. These values are similar to the K^+ arrival values reported in Table I. It appears likely that K^+ is being exported at rates comparable to rates of arrival in the xylem. For plants grown at 2 mM K^+ , the supply of K^+ per unit area of

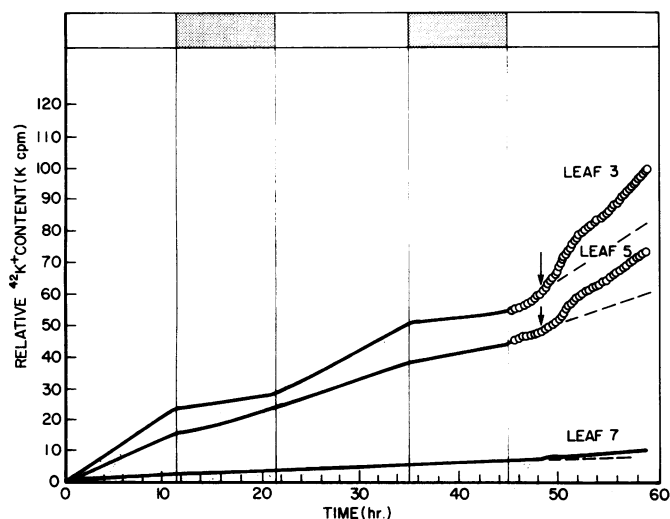


FIG. 2. Net accumulation of ^{42}K per area of leaf in three leaves of a sugar beet plant. Potassium concentration, which was initially 2 mM, was raised to 10 mM at the time indicated by the arrow. Time 0 is the same as for Figure 1. Counts for leaves 5 and 7 were multiplied by factors as described in Figure 1. Conversion factors are 0.0585, 0.128, and 0.858 $\mu\text{g K}^+ \text{dm}^{-2} \text{cpm}^{-1}$ for leaves 3, 5, and 7, respectively.

Table II. Effect of Increasing K^+ Concentration in Mineral Nutrient Solution on Arrival of Potassium in Sugar Beet Source Leaves

Plant was transferred from nutrient solution with 2 mM K^+ to one with 10 mM K^+ at the same specific radioactivity. Rate in 2 mM K^+ = 100%.

Leaf Number	Area dm^2	Rate of K^+ Import by Xylem		Relative Arrival after Increase %
		In 2 mM K^+ $\mu\text{g K}^+ \text{dm}^{-2} \text{h}^{-1}$	In 10 mM K^+	
Source leaves				
3	1.19	77	191	248
4	0.95	100	274	274
5	0.56	99	290	293
Sink leaf				
7	0.07	94	243	259

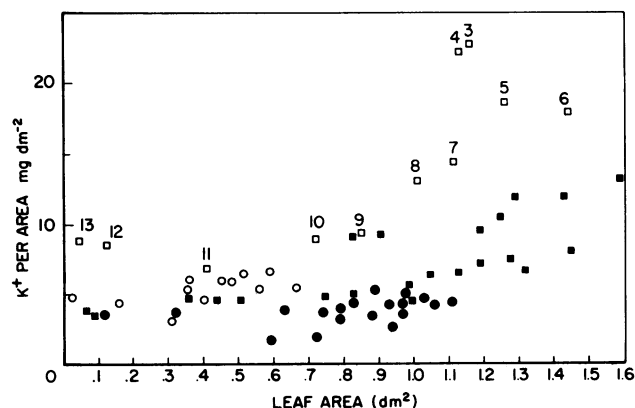


FIG. 3. Potassium content per unit area for the leaves of four sugar beet plants, two supplied with 2 mM K^+ (○, ●), the other two with 10 mM K^+ (□, ■). Each symbol represents an individual plant. The largest leaves in each group are up to 7 weeks older than the smallest. An example of the correlation of leaf size with leaf age is shown for one plant; numbers above symbols are leaf number starting with the first leaf to appear after the cotyledons.

leaf appears to be at steady-state.

Import of K^+ following Increased Supply. Increasing K^+ concentration in the mineral solution increases the rate of delivery of K^+ to the leaves (Fig. 2; Table II). Rate of K^+ arrival, measured as net accumulation of $^{42}\text{K}^+$, was followed in three leaves of a plant which was placed in 2 mM $^{42}\text{K}^+$ -labeled K^+ for 48 h and then transferred to 10 mM of the same specific radioactivity. Arrival of labeled K^+ began to increase 5 to 10 min after K^+ concentration was raised in the mineral solution. Increasing the concentration of K^+ supplied to the roots (while holding specific radioactivity of potassium delivered to the leaves. This occurrence would necessitate that the specific radioactivity of the K^+ available for export to the leaves would be considerably less than that of the K^+ supplied. However, over the 2 d prior to the shift in concentration, there is not a systematic increase in the rate of $^{42}\text{K}^+$ arrival in the leaves. This increase would be expected if the specific radioactivity of the pools available for export from the roots is low and is increasing because of turnover. When the supply of K^+ to the roots was raised, a transient increase in rate of K^+ arrival was observed (Fig. 2). Following the transient, the rate of arrival declines, and this new rate is considered to represent arrival under the higher K^+ nutrition. The 5-fold increase in K^+ supplied produced a 2- to 3-fold increase in arrival of $^{42}\text{K}^+$ in the leaves used in the five experiments of this type.

The K^+ content was measured for each leaf of two sets of plants. One set of two plants was grown in nutrient solution containing 2 mM K^+ , and the other set in 10 mM K^+ (Fig. 3). As was predicted from the rates of import and export of K^+ (Table I), the amount of K^+ /unit area was similar for all the leaves from a given plant in 2 mM K^+ . The younger leaves from the plants in 10 mM K^+ contained similar but slightly higher amounts of K^+ /unit area of leaf. In the older, larger leaves of plants in 10 mM K^+ , K^+ content per unit area increased with size. The oldest leaves for each group of plants were of similar age but those from the plants with high K^+ nutrition had up to 4 times as much K^+ /unit area as those with low K^+ nutrition.

Translocation Rate Following Increased K^+ . The rate of translocation into a developing sink leaf, measured by means of steady-state labeling with $^{14}\text{CO}_2$, did not change following increase of K^+ concentration surrounding the roots from 2 to 10 mM (Fig. 4). The increase in K^+ concentration in the mineral nutrient solution failed to cause a change in the rates of import and net carbon exchange over 4 to 6 h in all four experiments of this type. K^+ arrival in source leaves was observed to increase within 5 to 10 min after the change in K^+ supply in similar plants. Export of carbon from the source leaves also remained constant following increase in K^+ supplied to the roots (Fig. 4).

DISCUSSION

Patterns of Source Leaf Potassium Transfer. Increasing the K^+ available to the roots by at least 5-fold was found to produce a 2- to 3-fold increase in delivery of K^+ to the leaves by the xylem (Fig. 2; Table II). There appears to be some rejection of K^+ at the root-soil interface or retention of K^+ by the roots or both. Bowling (3) found that roots of *Ricinus* sequestered up to 99% of the absorbed K^+ ; this did not become available for transport by the xylem subsequently. The fact that the increase in arrival in the leaves is relatively less than the increase in K^+ supplied suggests that a greater proportion of K^+ is rejected or sequestered by the roots with the higher K^+ supply.

Several pieces of evidence support the view that in leaves which are not yet in the phase of very slow growth, K^+ per unit leaf area is near steady state (Fig. 3). Arrival in the xylem (Table I) is similar to estimated rates of export by the phloem. Also, K^+ /unit area of leaf blade does not increase in rapidly growing leaves, but it goes up in leaves that have all but stopped expanding if K^+ is

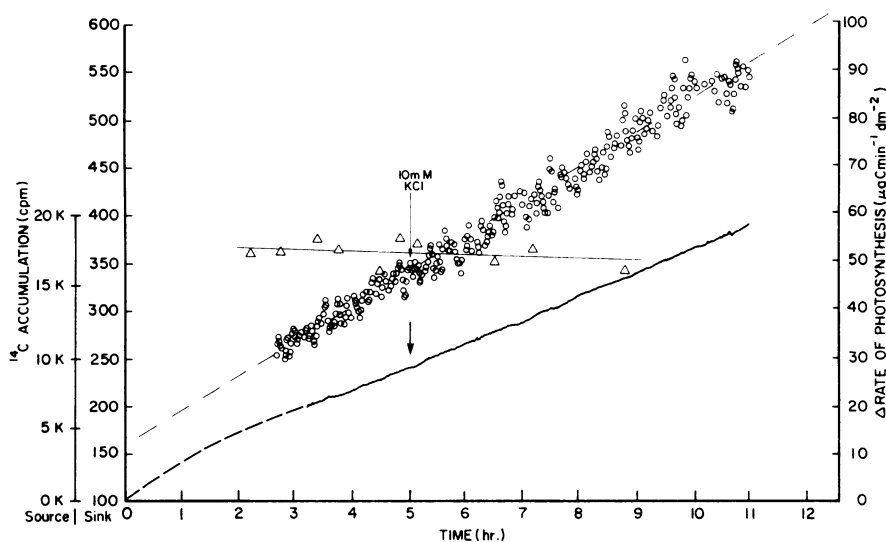


FIG. 4. Net carbon exchange in a source leaf and translocation of ^{14}C -labeled products of recent photosynthesis in a sugar beet plant following increased K^+ nutrition. At the arrow the original mineral solution containing 2 mM K^+ was replaced with one at 10 mM. Export is unchanged, indicated by a steady rate of accumulation of ^{14}C in the source leaf (7) (recorder tracing); import is also unchanged, indicated by steady accumulation of ^{14}C in a sink leaf (○).

supplied beyond a minimally sufficient level (Fig. 3). The amount of K^+ arriving in a leaf during the course of a day is equivalent to only a small proportion of the leaf K^+ , precluding sudden changes in concentration in a leaf. Adjustment of uptake and export by roots and of export of K^+ by the phloem together with the large store of leaf K^+ cause leaf K^+ content to remain nearly constant or to accumulate gradually. Although K^+ accumulates in older leaves when it is in abundant supply, it does so slowly. It seems reasonable to suppose that export of K^+ to sink regions also increases when K^+ per unit area arriving in source leaves goes up. Consequently, an abundant supply of K^+ likely results in increased K^+ nutrition for sink regions as well as source leaves.

Relation of Potassium Nutrition to Export. Four bases for promotion of translocation by increased supply of K^+ were proposed in the Introduction. Results from this study and previous work provide information which is useful in constructing and testing working hypotheses concerning roles of K^+ in phloem translocation.

Promotion of Net Carbon Exchange. Although there are a number of reports that net carbon exchange goes up when K^+ nutrition is increased (15, 17, 18, 19, 22) there is insufficient evidence to identify the mechanism involved. Increased rate of arrival of K^+ in the xylem does not appear to enhance net carbon exchange in a source leaf within a 6- to 8-h period (Fig. 4).

Increased K^+ nutrition may promote net carbon exchange over a longer period. Factors which could give rise to a higher rate of photosynthesis/unit area of lamina include increased leaf thickness, development of additional photosynthetic apparatus, and an increase in its efficiency. Additional factors which could produce a higher rate of net carbon exchange per plant include growth in area of individual leaves and increased rate of initiation of leaves. The possibility that K^+ may enhance net carbon exchange by one of those longer-term effects is being studied.

Promotion of Phloem Loading. Several studies have shown that increased K^+ supply to source leaves promotes transfer of products of photosynthesis to minor vein sieve tubes (1, 5, 11). Increased arrival of K^+ in source leaves did not appear to increase translocation of newly assimilated carbon over a 6- to 8-h period (Fig. 4). It is likely that the increase in concentration of K^+ in the source leaf free space was too small to bring about the mechanism reported by Doman and Geiger (5).

Several authors have described possible roles of K^+ in transport

of sucrose across membranes (4, 8). We believe that the presence of sucrose-proton-cotransport systems in the plasma membranes of mesophyll cells and sieve tube-companion cell complexes provides a basis for maintaining stoichiometric balance between sucrose loaded into minor veins and the efflux of sucrose in the vicinity of these veins. The electroosmotic gradient of protons across the plasma membrane determines a steady-state ratio between sucrose inside the cell and sucrose in the free space. In such a system, events which increase the concentration of sucrose in mesophyll cytoplasm will cause efflux of sucrose from mesophyll into the free space, which will in turn promote loading, without need for direct intervention of K^+ . Similarly, processes which lower sieve tube sucrose concentration will ultimately increase sucrose efflux from adjacent mesophyll. Recent studies suggest that K^+ is important as an environment which conditions the functioning of the sucrose transport system (8) and also serves as a means of charge transfer to stabilize membrane potential (4). Mengel and Haeder (17) suggest that increasing K^+ concentration in the sieve tubes promotes export but additional study is needed.

Promotion of Sink Activity. Although increased K^+ supply did not cause the rate of import into a sink to go up on the short term, it may cause translocation to increase gradually. Besides accumulating in the older source leaves, K^+ probably is recirculated in larger amounts to sink regions when K^+ nutrition is increased. In young shoots, added K^+ may promote cell division, resulting in larger leaves and a more rapid initiation rate. In the taproot, K^+ has been proposed to be important in sugar transport (21); increased K^+ may promote unloading in the beet. The role of K^+ as a cofactor in synthetic metabolism is well established (20). Increased sink region K^+ may speed the conversion of sucrose to synthetic metabolites and thus promote translocation into those sinks enriched in K^+ . Enhancement of synthesis of protein, lipid and cell wall in growing regions appears to result from a higher K^+ supply (9, 17). Kramer *et al.* (14) observed a substantial accumulation of K^+ around nodes prior to initiation of growth of axillary buds in decapitated stems.

Currently we are looking for longer term effects of increased K^+ accumulation in source leaves and its redistribution to sinks on net carbon exchange, partition of assimilated carbon within source leaves and its allocation among various parts of the sugar beet plant.

LITERATURE CITED

1. AMIR S, L REINHOLD 1971 Interaction between K-deficiency and light in ^{14}C -sucrose translocation in bean plants. *Physiol Plant* 24: 226-231
2. ASHLEY DA, RD GOODSON 1972 Effect of time and plant K-status on ^{14}C -labeled photosynthate movement in cotton. *Crop Sci* 12: 686-690
3. BOWLING DJF, PE WEATHERLEY 1964 Potassium uptake and transport in roots of *Ricinus communis*. *J Exp Bot* 15: 413-421
4. CHO B-H, E KOMOR 1980 The role of potassium in charge compensation for sucrose-proton-symport by cotyledons of *Ricinus communis*. *Plant Sci Lett* 17: 425-435
5. DOMAN D, DR GEIGER 1979 Effect of exogenously supplied foliar potassium on phloem loading in *Beta vulgaris* L. *Plant Physiol* 64: 528-533
6. FARLEY RF, AP DRAYCOTT 1974 Growth and yield of sugar beet in relation to potassium and sodium supply. *J Sci Food Agric* 26: 385-392
7. GEIGER DR, BR FONDY 1979 A method for continuous measurement of export from a leaf. *Plant Physiol* 64: 361-365
8. GEIGER DR, RT GIAQUINTA 1982 Translocation of photosynthate. In Govindjee, ed, *Photosynthesis—Carbon Assimilation and Plant Productivity*. Academic Press, New York, In press
9. HAEDER H-E, K MENGEL 1972 Translocation and respiration of assimilates in tomato plants as influenced by K nutrition. *Z Pflanzenernähr Bodenkd* 131: 139-148
10. HARTT CE 1969 Effect of potassium deficiency upon translocation of ^{14}C in attached blades and entire plants of sugarcane. *Plant Physiol* 44: 1461-1469
11. HAWKER JS, H MARSCHNER, WJS DOWNTON 1974 Effects of sodium and potassium on starch synthesis in leaves. *Aust J Plant Physiol* 1: 491-501
12. IL'YASHUK EM, AS OKANENKO 1970 Effect of potassium on translocation of photosynthetically assimilated $^{14}\text{CO}_2$ in sugar beets. *Sov Plant Physiol* 17: 361-366
13. JAMES WO 1930 Studies on the physiological importance of the mineral elements in plants. I. The relation of potassium to the properties and functions of the leaf. *Ann Bot* 44: 173-198
14. KRAMER D, MO DESBIEZ, JP GARREC, M THELLIER, A FOURCY, JP BOSSY 1980 The possible role of potassium in the activation of axillary buds of *Bidens pilosus* L. after decapitation of the apex. *J Exp Bot* 31: 771-776
5. LONGSTRETH DJ, PS NOBEL 1980 Nutrient influences on leaf photosynthesis. *Plant Physiol* 65: 541-543
16. MENGEL K, M VIRO 1974 Effect of potassium supply on transport of photosynthates to the fruits of tomatoes (*Lycopersicon esculentum*). *Physiol Plant* 30: 295-300
17. MENGEL K, H-E HAEDER 1977 Effect of potassium supply on the rates of phloem sap exudation and the composition of phloem sap of *Ricinus communis*. *Plant Physiol* 59: 282-284
18. O'TOOLE JC, K TREHARNE, M TURNIPSEED, K CROOKSTON, J OZBUN 1980 Effect of potassium nutrition on leaf anatomy and net photosynthesis of *Phaseolus vulgaris*, L. *New Phytol* 84: 623-630
19. PEOPLES TR, DW KOCH 1979 Role of potassium in carbon dioxide assimilation in *Medicago sativa*, L. *Plant Physiol* 63: 878-881
20. RAINS DW 1976 Mineral metabolism. In J Bonner, J Varner, eds, *Plant Biochemistry*. Academic Press, New York, pp 569-573
21. SAFTNER RA, RE WYSE 1980 Alkali cation/sucrose cotransport in the root sink of sugar beet. *Plant Physiol* 66: 884-889
22. TERRY N, A ULRICH 1973 Effects of potassium deficiency on the photosynthesis and respiration of sugar beet. *Plant Physiol* 51: 783-786
23. ZIEGLER H 1975 Nature of transported substances In MH Zimmermann, JA Milburn, eds, *Transport in Plants, Vol 1 Phloem Transport*. Springer-Verlag, Berlin, pp 59-100