Estimation of Potassium Recirculation in Tomato Plants by Comparison of the Rates of Potassium and Calcium Accumulation in the Tops with Their Fluxes in the Xylem Stream

MICHAEL J. ARMSTRONG AND ERNEST A. KIRKBY[1]
Department of Plant Sciences, The University of Leeds, Leeds LS2 9JT England

ABSTRACT

A procedure to estimate the extent of K recirculation in plants is proposed. This is based on the ratio of the upward fluxes of K to Ca in the xylem sap from root to shoot with the ratio of K to Ca accumulation in plant tops.

In a preliminary investigation the factors influencing the K to Ca ratio in the xylem sap were considered. Tomato plants were grown at three levels of K nutrition and harvested at different times during the 24-hour day period. It was shown that the K to Ca ratio in xylem sap changed dramatically depending on the time of sap collection after decapitation, the values falling from over 2 to less than unity over the 4-hour period of collection. Diurnal effects on exudation were less marked but also of significance. The level of K nutrition was of little importance. It is suggested that a representative xylem sap from tomato plants can best be obtained from samples taken between 15 and 60 minutes after decapitation.

In a second experiment K recirculation was estimated. At nine harvesting stages over a 24-hour period the K to Ca ratio in the xylem sap was invariably higher than the K to Ca ratio of accumulation in the tops over the same period. From this information it was calculated that about 20% of the upward flux of K in the xylem stream resulted from recirculated K.

There is current interest in the possible occurrence of K recirculation in plants, followng the work of Dijkshoorn (7) and Ben Zioni et al. (2). The scheme these authors have proposed is as follows: K^+ and NO_3^- as the major ions taken up by the root are translocated to the shoot in the xylem. The reduction of NO_3^- in the upper plant parts induces OH^- production

$$NO_3^- + 8H^+ + 8e^- \rightarrow NH_3 + 2H_2O + OH^-$$
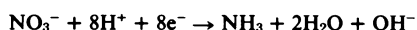
which in turn stimulates malate synthesis and accumulation from P-enolpyruvate (12, 20). Some of the K^+ is then redirected via the phloem to the roots in association with malate ions. In the roots malate is decarboxylated to pyruvate and a negative charge is excreted from the plant as HCO_3^- in exchange for the uptake of a further NO_3^- ion. This is consistent with the general observation that intact plants supplied with NO_3^-–N almost always take up an excess of anions over cations (6, 14, 15). The cycle described above is then repeated. In this way the recirculation of K^+ is postulated to facilitate the uptake and distribution of NO_3^- (2). Experimental evidence of this has been obtained recently by Frost et al. (9) in wheat seedlings.

One means of investigating this recirculation hypothesis is to utilize the well documented difference of behavior of the mobility of K and Ca. K is known to be highly mobile in plants, and is present in both xylem and phloem (10, 21, 23). In contrast, although the level of Ca in the xylem can be high, only very small amounts are found in phloem sap (3, 5, 10). Once Ca is translocated to the tops via the xylem pathway it is not redirected. Indeed, Ca is known to be the most immobile macronutrient (11). A comparison of the K/Ca ratio of accumulation in plant tops with that in the xylem sap should thus provide a means of estimating the extent to which K is recirculated within the plant. If for a given time period there is evidence of a lower K/Ca ratio of accumulation in the tops than in the upward flux, this is indicative of K recirculation in the plant. In other words if K is recirculating, the upward flux of K comprises two components: one directly from absorption from the nutrient medium, and the other from recirculation of K translocated from the tops via the roots. Using this concept we have estimated the extent of K recirculation in tomato plants.

The difficulty in dealing experimentally with the above approach lies in the determination of xylem sap which is representative of the intact plant over a given time period. One accepted method of obtaining xylem sap is by plant decapitation. Sap composition and rate of exudation are dependent on a number of factors including ionic composition of the nutrient medium (18, 24), diurnal effects (22, 25), and the time at which the sample is taken after decapitation (18), as well as other environmental conditions.

A preliminary investigation was carried out to study the main factors influencing the K and Ca contents in the sap. These included the level of K supply, the time of sap collection during the 24-h day period, and the change in sap composition in relation to time after decapitation. Information obtained from this experiment was then used in a subsequent investigation to calculate the extent of K recirculation in tomato plants as outlined above.

BASIC THEORY FOR RECIRCULATION CALCULATION

The uptake of a nutrient by a plant over a short period of growth may be represented by the straight line equation:

$$\ln y = at + b \qquad (1)$$

where y = nutrient uptake at time t; a = slope of the line; t = time; b = intercept. From this equation it follows that:

$$a = \frac{1}{y}\frac{dy}{dt}$$

and thus:

the rate of uptake $\dfrac{dy}{dt} = ae^{(at + b)} \qquad (2)$

By substituting values for Ca or K into this equation, their uptake

rates, $(d(Ca))/dt$ and $(d(K))/dt$, may be obtained. For an element which moves unidirectionally upward (i.e. Ca), the upward flux F is equivalent to the rate of uptake from the nutrient medium. Thus:

$$F_{(Ca)} = \frac{d(Ca)}{dt} \qquad (3)$$

For an element which can be recirculated (i.e. K), the upward flux comprises two components: the rate of uptake from the nutrient medium together with the rate at which the nutrient is recirculated:

$$F_{(K)} = \frac{d(K)}{dt} + R_{(K)} \qquad (4)$$

where $R_{(K)}$ is the recirculated fraction of the upward flux $(F_{(K)})$. The upward flux of K $(F_{(K)})$ can be calculated from the product of the [K]/[Ca] ratio in the exudate and the upward flux of Ca $(F_{(Ca)})$. Thus:

$$F_{(K)} = \frac{[K]}{[Ca]} \times F_{(Ca)} \qquad (5)$$

where [K]/[Ca] = ratio of K to Ca concentration in the xylem sap. From equation 3 it follows that:

$$F_{(K)} = \frac{[K]}{[Ca]} \times \frac{d(Ca)}{dt} \qquad (6)$$

The recirculated K component can be obtained by substitution of this expression of $F_{(K)}$ into equation 4:

$$R_{(K)} = \left(\frac{[K]}{[Ca]} \times \frac{d(Ca)}{dt} \right) - \frac{d(K)}{dt} \qquad (7)$$

From the final equation obtained above, it is clear that the value of $R_{(K)}$ can be determined if at any given time the rates of accumulation of K and Ca are known together with the K/Ca ratio in the xylem sap.

MATERIALS AND METHODS

Tomato plants (Lycopersicon esculentum var. Ailsa Craig) were germinated and grown in the glasshouse in a soil-compost mixture. At the four-leaf stage the plants were removed and their roots thoroughly rinsed with distilled H_2O to remove any adhering soil particles. Similar sized plants were then transferred to aerated nutrient solutions held in 52-liter containers.

The plants were grown in a growth chamber at a light intensity of 80 w m^{-2} provided by warm white fluorescent tubes. A RH of about 75% was maintained and a 16-h light, 8-h dark cycle employed at temperatures of 23 and 18 C, respectively.

Xylem sap samples were obtained by decapitating the plants at about 1 cm above the root system. This position was chosen so as to be as near the root system as possible. The stump was fitted with a short length of suitable polyvinylchloride tubing to collect exudate, which was removed by means of a syringe. Evaporation of sap between collections was prevented by covering the top of the tubing with Parafilm. A small number of plants which did not exude were discarded. K and Ca in the sap were estimated by flame emission and atomic absorption spectroscopy, respectively.

In the preliminary experiment, plants were grown in solutions of different K concentrations and harvested at different times during the day. The basic composition of the macronutrient solutions in this experiment was as follows: 10 meq/l $Ca(NO_3)_2$, 2 meq/l $MgSO_4$, 1 meq/l NaH_2PO_4. K was added to the solutions at three different levels of K_2SO_4, i.e. 0.2 meq/l, 1.0 meq/l, and 4.0 meq/l. The micronutrients were added to all three treatments as described previously (15). Sulfate was used as the compensating ion for K$^+$. Sulfate was chosen as it is well established that it has little effect on the uptake of other ions. In order to maintain constant ionic concentrations the solutions were changed daily.

The plants were decapitated during the 8th day at three different times, five plants being used at each harvest for each K level. The first group of plants from each treatment was detopped in the middle of the light period. Detopping was carried out for the second group at the beginning of the dark period and for the third group at the end of the dark period.

Using the method already described, exudate samples were collected at 15-min intervals for the 1st h, and then at 30-min intervals for the next 3 h. For each plant harvested weights of exudate were recorded and the concentrations of K and Ca estimated in the individual exudates.

In the second experiment, designed to calculate K recirculation, plants were grown at the intermediate K concentration (1.0 meq/l) using the same nutrient solution composition as in the preliminary experiment.

In order to obtain the rates of uptake of K and Ca, plants were harvested after 4, 6, 9, and 10 days of growth. For the first three harvests, four plants were removed and K and Ca analyzed on the individual plant tops dried at 85 C. Similar estimations were carried out at the outset of the experiment on the original plants. On the final day, nine separate harvests each of four plants were carried out over the 24-h period. Seven harvests were taken in the light and two in the dark. At each sampling period K and Ca were estimated in the dried tops as well as in the xylem sap exudate collected between 15 and 60 min after decapitation.

Standard errors were determined on both yield and cation data. These values all fell within the 95% confidence limits. Standard errors are not included in the results.

RESULTS

Preliminary Experiment: Influence of K and Light Treatment on Exudation. Figure 1 shows the cumulative weights of exudate plotted against the time of exudation for the three K treatments and three sampling periods. The time of day at which the plants were decapitated exerted a dramatic influence on the amount of sap exuded. At all three K levels, detopping in the middle of the light period gave rise to a 2- to 3-fold greater weight of exudate than decapitation at the end of the dark period. Decapitation at the onset of the dark period resulted in intermediate values. The rates of exudation were also different for the three light treatments. For plants harvested in the middle of the light period the rate of exudation was very high at the beginning but decreased with time. A distinct increase in rate of exudation toward the end of the sampling period was observed in plants decapitated at the end of the dark period. For plants detopped at the beginning of the dark period the rate of exudation over the sampling period appeared to be fairly constant. The same pattern of behavior was observed at all three K levels.

The effects of the different levels of K on the exudate weights and rates of exudation were less marked. When sampling from the end of the dark period, the total weight of exudate was somewhat depressed at the lower level of K nutrition.

The K and Ca concentrations in the exudate are shown in relation to time after decapitation for the three K treatments (Table I). The table includes only the two extreme light treatments (sampling at the middle of the light period and the end of the dark period). Sampling at the beginning of the dark period gave intermediate results. The same general pattern was observed at all three K levels in the nutrient medium. The K concentrations started at a comparatively high level, fell slowly (15–60 min) and then dropped off rapidly with time. The rate at which the K concentration fell was particularly rapid for plants decapitated at the end of the dark period. The level of K nutrition had little effect on the Ca concentration in the sap which in most cases was similar to the concentration in the nutrient medium (10 meq/l). A small increase in concentration was observed in samples from
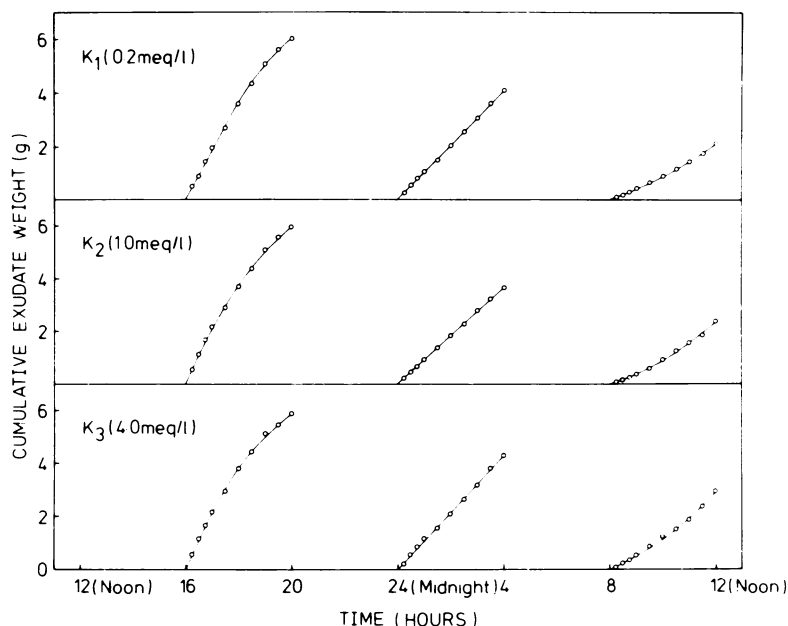
FIG. 1. Influence of time of harvesting and level of K nutrition on accumulated weights of exudates collected over 4-h period after decapitation.

TABLE I: The influence of the time of harvesting and level of K nutrition on the K and Ca concentrations (meq/l) of exudates collected at different times over the 4 hour sampling period after decapitation

	Time after decapitation (mins)	K_1 0.2 meq/l		K_2 1.0 meq/l		K_3 4.0 meq/l	
		K	Ca	K	Ca	K	Ca
	15	22.8	8.9	23.1	8.7	26.4	8.5
Middle	30	18.9	10.4	20.0	10.3	21.7	10.3
of the	45	16.7	10.8	19.2	10.4	20.9	11.1
light	60	16.1	10.6	18.1	10.6	19.5	11.7
period	120	11.6	10.3	12.8	10.8	13.8	12.1
	240	6.0	11.5	7.6	11.1	10.8	11.8
		K	Ca	K	Ca	K	Ca
	15	23.7	6.0	22.1	7.5	22.2	8.5
End	30	17.6	9.2	19.9	7.0	18.6	12.1
of the	45	13.9	11.8	14.4	10.8	16.2	12.3
dark	60	10.0	13.5	11.9	11.0	13.8	13.5
period	120	6.7	14.3	7.5	13.7	9.5	12.9
	240	6.4	14.1	7.4	12.5	10.1	11.4

plants harvested at either the onset or the end of the dark period. The K/Ca ratio in the xylem sap was thus largely determined by K sap concentration. In all treatments K/Ca ratios fell from a value of about 2 to that of less than unity over the 4-h period of exudation. The high levels of K in the sap accompanied by low Ca concentrations during the first 15-min exudation suggested phloem contamination, which was also indicated by the presence of sugars in these samples. Sampling between 15 and 60 min after detopping appeared to be the most suitable for obtaining uncontaminated xylem sap. At this time contamination from phloem was deduced to be unimportant as sugars were not detected. Moreover, the inorganic cations were found to be almost quanti-

tatively balanced by the inorganic anions, and largely by NO_3^-, an anion which is absent in phloem sap (10, 23). This period was also suitable for sap sampling because of the relative constancy of the K concentration over this time period (Table I).

Table II shows the total amounts of K and Ca in the exuded sap over the 4-h period. This represents the product of the values of Figure 1 and Table I. The amount of K exuded in the sap was highly dependent on the light treatment and to a lesser extent on the level of K nutrition. The highest K content was found in sap from plants decapitated in the middle of the light period at the high K level. The lowest amount was observed at the low K level at the end of the dark period. The Ca contents were largely

TABLE II: Influences of the level of K nutrition and time of harvesting on the total amounts of K and Ca in the exuded sap over the 4 hour period (meq x 10^{-2})

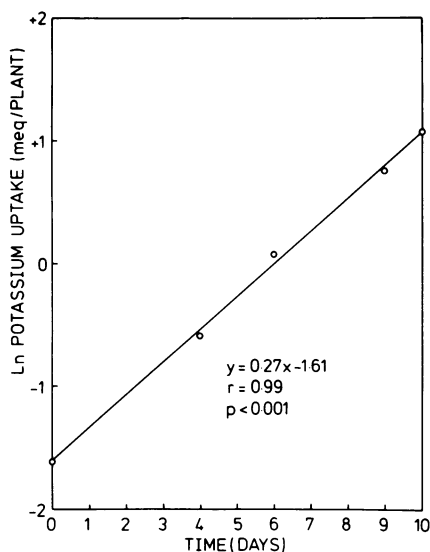|	Middle of the Light Period		Start of the Dark Period		End of the Dark Period	
K_1 (0.2 meq/l)	K	7.7	K	5.6	K	1.8
	Ca	6.5	Ca	5.4	Ca	2.9
K_2 (1.0 meq/l)	K	8.8	K	5.2	K	2.1
	Ca	6.4	Ca	4.6	Ca	2.9
K_3 (4.0 meq/l)	K	9.8	K	6.2	K	3.4
	Ca	6.7	Ca	5.6	Ca	3.7

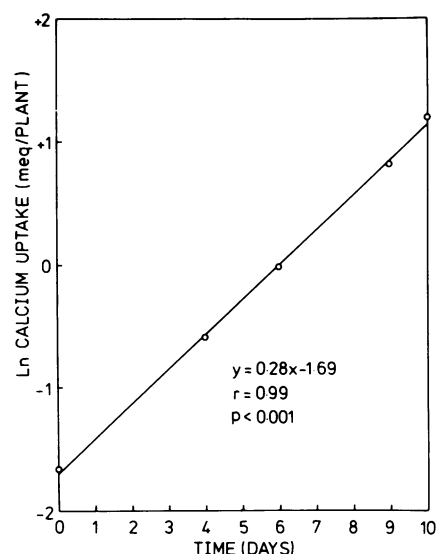FIG. 2. Natural logarithm of K content of tomato plant tops plotted against time.

FIG. 3. Natural logarithm of Ca content of tomato plant tops plotted against time.

determined by the light treatment. The effects resulting from K supply were less marked.

From this preliminary experiment two important conclusions were reached concerning the K recirculation calculation: (a) in order to obtain a representative xylem sap, samples should be taken between 15 and 60 min after decapitation; (b) the very clear diurnal effect on the K/Ca ratio in the sap must be taken into account in the recirculation calculation.

Second Experiment: Uptake Rates of K and Ca. Figures 2 and 3 show the natural logarithms of the K and Ca contents, respectively, of tomato plant tops plotted against time for the second experiment. In both cases a very good linear plot was obtained from the 52 samples of plant tops analyzed. The regressions of ln of K and Ca contents on time were both highly significant ($r = 0.99$, $P < 0.001$).

Table III shows the rates of uptake of K and Ca obtained by substituting the values from Figures 2 and 3 into equation 2:

$$\frac{dy}{dt} = ae^{(at + b)}$$

As expected, the rates of uptake of K and Ca increased with

increasing plant size. There was little difference between the comparative rates of accumulation of K and Ca. This probably reflects the much higher concentration of Ca than K in the nutrient medium.

K/Ca Ratio in Xylem Sap. The K and Ca concentrations and the K/Ca ratio of the xylem exudate are shown in Table IV. The samples were obtained from tomato plants decapitated at different times throughout the 24-h period of the 10th day of growth, as already described. At all sampling times during both the light and dark periods, the K concentration was always found to be in excess of the Ca concentration. This resulted in a K/Ca ratio invariably greater than unity. Although the K and Ca concentrations of the exudates did not change appreciably during the 24-h period, the K/Ca ratio varied considerably (1.42–1.10) because of the cumulative effects resulting from differences in K and Ca concentrations.

To obtain a representative K/Ca exudate ratio the K and Ca concentrations were integrated over the whole 24-h period. These integrated values for K and Ca were 15.01 meq/l and 12.35 meq/ l, respectively, thus giving a K/Ca ratio of 1.22.

Calculation of Recirculation Fraction of Upward K Flux ($R_{(K)}$). Using the calculated K/Ca ratio in the xylem sap at day

TABLE   III: Uptake rates of K and Ca (meq/day) in tomato
                 plant tops in relation to time after
                 transfer to the nutrient solution

Time (days)	$\frac{dK}{dt}$	$\frac{dCa}{dt}$
4	0.16	0.16
6	0.27	0.28
8	0.47	0.49
10	0.81	0.85

TABLE   IV: The K and Ca concentration (meq/l) and K/Ca ratio
                of xylem exudate from decapitated tomato plants
                sampled from 15 - 60 minutes after decapitation
                (average of 4 plants) over the 24 hour day period

	├─────────── LIGHT ───────────┼── DARK ──┤							
				24 Hour Period				
	0	3	5	7	10	12	14	17	21
K	15.7	15.3	15.3	15.5	14.1	14.2	14.0	16.1	15.3
Ca	11.9	10.8	11.3	12.6	11.9	12.0	12.7	13.3	12.1
K/Ca	1.32	1.42	1.36	1.22	1.18	1.18	1.10	1.21	1.26

TABLE   V: Recirculated K values expressed as meq/day
                and as a % of the total upward K flux in
                relation to the day of harvest. The results are
                calculated on the K/Ca exudate ratio of the
                10th day

Time (Days)	$F_{(K)}$	$\frac{dK}{dt}$	$R_{(K)}$ meq/day	$R_{(K)}$ % Total Upward Flux
10	1.04	0.81	0.23	22
8	0.60	0.47	0.13	22
6	0.34	0.27	0.07	21
4	0.20	0.16	0.04	20

10, the total upward flux of K can be calculated according to equation 6:

$$F_{(K)} = \frac{[K]}{[Ca]} \times \frac{d(Ca)}{dt}$$

This now allows the recirculated K value ($R_{(K)}$) to be estimated from equation 7:

$$R_{(K)} = \left(\frac{[K]}{[Ca]} \times \frac{d(Ca)}{dt}\right) - \frac{d(K)}{dt}$$

Table V shows the recirculated K values in relation to the day of harvest, expressed both in meq/day and as a percentage of the total upward K flux. Strictly speaking, as the K/Ca ratio used in this calculation was determined at day 10, the calculated $R_{(K)}$ values are applicable only to this day. Inasmuch as numerous analyses of the sap of decapitated young tomato plants in this laboratory have given results comparable with those at day 10, we feel justified in extending the calculation as shown. The results

clearly demonstrate that in the young tomato plant only about 20% of the total upward flux of K originates from K recirculated from the tops. The rate appears not to change greatly with plant age.

DISCUSSION

The results in the preliminary experiment indicate that xylem sap representative of the intact tomato plant can best be obtained by sampling between 15 and 60 min after decapitation. Using this information and taking into account the considerable diurnal variation in exudation, the extent of K recirculation in tomato plants was calculated in the second experiment.

The driving force for the uptake of water from the root surface to the xylem vessels is the water potential gradient across the root. In decapitated plants showing root pressure this gradient largely results from osmotic effects. The metabolic uptake of ions and their secretion into the xylem vessels lower the osmotic potential

of the sap and depress its water potential thus inducing water influx. The results of the preliminary experiment shown in Figure 1 are consistent with this view. The highest weights of exudate were collected in the light period when energy was available from the tops to stimulate metabolic ion uptake. The lower rate of exudation in the dark can be accounted for by a lack of energy available to promote ion uptake. The rate of exudation, however, appears to be dependent not only on the energy availability in the roots. This is apparent from the observed increase in the rate of exudation after decapitation of plants harvested at the end of the dark period (Fig. 1). This effect is independent of the tomato plant tops and indicates a possible diurnal effect which may possibly be controlled by changes in root permeability. Evidence of a diurnal effect of root resistance to water flow has been observed by other authors (1, 19) who found a minimum during the day and a maximum at night. Our observations are in agreement with these findings.

The three different levels of K supply had little effect on the accumulated exudate weights (Fig. 1). This may be considered as surprising. However, it must be remembered that the roots were exposed to large volumes of solution which were changed daily so that the K levels in the nutrient solution were largely maintained. These findings are in agreement with reports which indicate that optimum plant growth can occur at very low levels of K around the roots, provided that the concentrations are maintained (17). Our results differ from experiments which have compared exudation from K-deficient and K-nondeficient plants where large differences in exudate amounts have been observed (18). A slight effect of the low K level (0.2 meq/l) in depressing exudation was observed only in plants harvested at the end of the dark period where a lack of energy probably limited K uptake.

The dependence of K concentration and uptake on available metabolic energy is demonstrated clearly in Tables I and II. In all treatments a rapid and dramatic fall in the concentration of K occurred after decapitation (Table I). This implies that even after a very short time, the presence of metabolites from the tops became the limiting factor in K uptake.

In direct contrast, the results for Ca show a remarkable constancy in concentration over the 4-h sampling period in all treatments (Table I). This confirms the fact that the uptake of Ca is much less dependent on metabolic energy. The somewhat higher accumulation of Ca observed in the exudates of samples taken from plants harvested in the dark may possibly result from a K/Ca uptake antagonism. When K uptake is depressed, the uptake of other cations is known to be increased (16). This higher accumulation of Ca also indicates a component of Ca uptake which is independent of water movement.

The results obtained in the second experiment demonstrate that the K/Ca ratio of the xylem sap was always greater than the K/Ca accumulation ratio in comparative plant tops. This observation is indicative of K recirculation in the plant as proposed by Ben Zioni et al. (2) and Dijkshoorn (7).

Our results indicate that in tomato plants about 20% of the upward flux of K in the xylem stream originates from K translocated from the tops via the roots. This means that most K taken up from the nutrient medium by the roots remains in the tops. This is in agreement with our earlier observations for tomato plants (14) and is also supported by the work of Breteler and Hänish ten Cate (4).

In a previous publication the extent of K recirculation was calculated from excess anion over cation data by whole plants. A maximum possible figure for K recirculation was obtained (13). This was based on the proposition that all of the HCO_3^- excreted from the plant roots (excess anion uptake) was derived from organic acid anions accompanying K on its downward movement in the phloem. These data for tomato plants are in the same order as those found using this procedure. It may therefore be concluded

that in tomato plants adequately supplied with K, the extent of K recirculation is low. This means too that in this species, K recirculation does not play a major role as a mechanism of controlling the uptake and upward movement of NO_3^- as proposed by Ben Zioni et al. (2).

There is some evidence that K recirculation may be of greater significance in other plant species. In the grasses and cereals, for example, the total uptake of anions is approximately twice that of cations (6, 8). This implies a very high OH^- efflux from the roots which could suggest an important role for K recirculation in these plants. The extent to which this OH^- efflux is derived either from organic acid anions associated with recirculated K, or as a direct consequence of NO_3^- reduction in the roots has yet to be established. Clearly, if NO_3^- is reduced in the roots a NO_3^-/OH^- exchange could occur without involving K translocation in the plant.

LITERATURE CITED

1. BARRS HD, B KLEPPER 1968 Cyclic variations in plant properties under constant environmental conditions. Physiol Plant 21: 711–730
2. BEN ZIONI A, Y VAADIA, SH LIPS 1971 Nitrate uptake by roots as regulated by nitrate reduction products in the shoot. Physiol Plant 24: 288–290
3. BIDDULPH O, SF BIDDULPH, R CORY, H KOONTZ 1958 Circulation patterns for ^{32}P, ^{35}S and ^{45}Ca in the bean plant. Plant Physiol 33: 293–300
4. BRETELER H, C HÄNISCH TEN CATE 1978 Ionic balance of root-shoot nitrate transfer in dwarf bean. Physiol Plant 42: 53–56
5. BUKOVAC MJ, SH WITTWER 1957 Absorption and mobility of foliar applied nutrients. Plant Physiol 32: 428–435
6. COÏC Y, C LESAINT, F LE ROUX 1961 Comparaison de l'influence de la nutrition nitrique et ammoniacale combinée ou non avec une déficience en acide phosphorique, sur l'absorption et le métabolisme des anions-cations et plus particulièrement des acides organiques chez le maïs. Comparison du maïs et de la tomate quant à l'effet de la nature de l'alimentation azotée. Ann Physiol Vég 3: 141–163
7. DIJKSHOORN W 1958 Nitrate accumulation, nitrogen balance and cation-anion ratio during the regrowth of perennial ryegrass. Neth J Agric Sci 6: 211–221.
8. DIJKSHOORN W 1962 Metabolic regulation of the alkaline effect of nitrate utilization in plants. Nature 194: 165–167
9. FROST WB, DG BLEVINS, NM BARNETT 1978 Cation pretreatment effects on nitrate uptake, xylem exudate and malate levels in wheat seedlings. Plant Physiol 61: 323–326
10. HALL SM, DA BAKER 1972 The chemical composition of Ricinus phloem exudate. Planta 106: 131–140
11. HANGER BC 1979 The movement of calcium in plants. Commun Soil Sci Plant Anal. In press
12. HIATT AJ, JE LEGGETT 1971 Ionic interactions and antagonisms in plants. In EW Carson, ed, The Plant Root and its Environment. University Press of Virginia, pp 101–134
13. KIRKBY EA 1974 Recycling of potassium in plants considered in relation to ion uptake and organic acid accumulation. In Plant Analysis and Fertilizer Problems. Proc 7th Int Colloquium, Hanover, Federal Republic of Germany, pp 557–568
14. KIRKBY EA, AH KNIGHT 1977 Influence of the level of nitrate nutrition on ion uptake and assimilation, organic acid accumulation, and cation-anion balance in whole tomato plants. Plant Physiol 60: 349–353
15. KIRKBY EA, K MENGEL 1967 Ionic balance in different tissues of the tomato plant in relation to nitrate, urea or ammonium nutrition. Plant Physiol 42: 6–14
16. LEGGETT JT, WA GILTERT 1969 Magnesium uptake by soybeans. Plant Physiol 44: 1182–1186
17. MENGEL K, H FORSTER 1971 Der Einfluss der K-Konzentration der Nährlösung auf die Ertragsbildung, die Qualität und den K-Aufnahmeverlauf bei Hafer. Plant Soil 35: 65–75
18. MENGEL K, R SIMIC 1973 Effect of potassium supply on the acropetal transport of water, inorganic ions and amino acids in young decapitated sunflower plants (Helianthus annuus). Physiol Plant 28: 232–236
19. PARSONS LR, PJ KRAMER 1974 Diurnal cycling in root resistance to water movement. Physiol Plant 30: 19–23
20. RAVEN JA, FA SMITH 1976 Nitrogen assimilation and transport in vascular land plants in relation to intracellular pH regulation. New Phytol 76: 415–431
21. TAMMES PML, J VAN DIE 1964 Studies on phloem exudation from Yucca flaccida Haw. I. Some observations on the phenomenon of bleeding and the composition of the exudate. Acta Bot Néerl 13: 76–83
22. VAADIA Y 1960 Autonomic diurnal fluctuations in rate of exudation and root pressure of decapitated sunflower plants. Physiol Plant 13: 701–717
23. VAN DIE J, PML TAMMES 1975 Phloem exudation from monocotyledonous axes. In MH Zimmermann, JA Milburn, eds, Transport in Plants. I. Phloem Transport. Springer-Verlag, Berlin, pp 196–222
24. WALLACE A, AM ABOU-ZAMZAM, E MOTOYAMA 1971 Cation and anion balance in the xylem exudate of tobacco roots. Plant Soil 35: 433–438
25. WALLACE A, RT ASHCROFT, OR LUNT 1967 Day-night periodicity of exudation in detopped tobacco. Plant Physiol 42: 238–242