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Dual Mechanisms of Ion Absorption in Relation to Long Distance Transport in Plants

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Summary. The characteristics of ion transport to the shoots of young corn seedlings were studied with respect to the nature of the isotherm through a wide concentration range, the competitive influence of closely related ions upon the transport of a given ion, and the influence of the counter-ion. Both with respect to ^{36}Cl and ^{86}Rb transport, the characteristics of the process in every way resemble uptake by non-vacuolate root tips wherein the plasma membrane is the only membrane involved in absorption, and where system 1 — of the 2 systems which can be shown to participate in absorption by vacuolate tissue — is the only system operative. Net ion uptake by the roots per se was shown to display both the high affinity (system 1) and low affinity (system 2) mechanisms. It is concluded that the symplastic theory of ion movement to the xylem is valid, and that the contention that system 1 operates at the plasma membrane while system 2 functions at the tonoplast is strengthened.

A leading theory regarding the means whereby salts from the environs of plant roots are absorbed and enter the xylem is that of Crafts and Broyer (1, 7), in which it is proposed that ions are actively accumulated across the plasma membrane of the cortical cells, and pass thereafter by diffusion through a cytoplasmic continuum, the symplasm (7, 20), into the stele, where they leak from the stelar parenchyma into the xylem. In this view the primary purpose of the endodermis is to prevent the back-diffusion of ions in the xylary fluid to the environment, through the water free space of the cell wall. At the same time, free diffusion into the xylem from the soil solution is precluded. The Casparian strips provide the means whereby the endodermis fulfills this function (23, cf. 26).

In the last years a large body of evidence has accumulated that net ion absorption by roots and other plant tissues involves a dual or multiple isotherm when uptake is examined through a wide concentration range (8, 9, 10, 11, 13). Recently the proposal has been put forth (25) that the high-affinity, low K_s system (system 1) which operates in the range 0 to 0.5 mM, is involved in ion transport across the plasma membrane, while the low-affinity, high K_s system (system 2), which operates in the range 1 to 50 mM, is related to passage of ions from the cytoplasm to the vacuole. Inherent in the proposal is the postulate that at high concentrations, i.e. at concentrations well in excess of that which saturates system 1, ions enter the cytoplasm by diffusion, at a rate greater than that implemented by system 1 transport. Under these conditions transport across the tonoplast becomes rate limiting, and it is for this reason that the isotherm for vacuolar absorption is discernible even though the 2 systems operate sequentially rather than in parallel.

On the basis of the above considerations it was postulated that since ions which are involved in long-distance transport in the xylem arrive there through the symplasm, the characteristics of long-distance transport should be those of ion movement across the plasma membrane, i.e. of system 1. To examine this question long-distance transport was investigated in 3 ways: by ion movement into the exudate of excised roots, by ion movement from the tips to the base of excised roots, and by ion movement into the shoots of intact corn seedlings. Long-distance transport was found to conform to the criteria which delineate system 1.

Materials and Methods

Corn seeds (*Zea mays*) of the hybrid variety Oh 43 Rf × C 103 Rf (Illinois Foundation Seeds, Inc.) were soaked overnight in running tap water,

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rinsed in distilled water, and germinated and grown in 0.2 mM $CaSO_4$ as previously described (6). Seedlings were raised under artificial light in a 12 hour photoperiod. Absorption and transport of ^{36}Cl and ^{86}Rb (as a label for K) respectively were followed at room temperature in 2 concentration ranges, 0 to 0.5 mM, and 1 to 50 mM, the low and high range respectively. All experimental solutions contained 0.5 mM $CaSO_4$. The pH ranged between 5.6 and 6.0, with an average of 5.8.

Exudation Experiments. Roots were harvested from 7 to 10 days after seed soaking. Primary roots, 8 to 12 cm in length, were excised for use. The excised stumps were each fitted into a length of glass capillary just wider than the root base at the opening, and slightly constricted several millimeters behind. Each root was seated and sealed into its capillary simply by the exertion of gentle pressure upon root insertion. Two such capillaries were held in a rubber stopper, the stopper being fitted into a large test tube so that the 2 roots were bathed in 50 ml of experimental solution. The position of the capillary in the rubber stopper was adjusted so that the level of the experimental solution came to within a mm of where the root passed into the capillary. Each experimental treatment involved 10 roots — 2 in each of 5 test tubes. After 20 to 24 hours, the time required for appreciable exudation, the tared capillaries were weighed to determine the quantity of exudate, and the radioactivity of the exudate was measured. The roots were rinsed in ice cold water for 30 minutes, gently surface dried, weighed, and their radioactivity determined.

Two-Plate Experiments. Excised roots, 9 to 14 cm in length, from 7 to 8 day old seedlings, were taken in groups of 10 (ca 2 g fr wt) and placed with 3 to 4 cm of the tip in a petri dish containing 50 ml of experimental solution, and with approximately 1 cm of their basal end in a small dish, the receiver plate, containing 5 ml 0.5 mM $CaSO_4$. The entire system was kept in a saturated atmosphere. At the end of an experimental period (anywhere from 2–24 hrs) the radioactivity of the contents of the receiver plate was determined, and the roots were divided into apical segments, which had been immersed in the donor plate, and proximal sections, which were outside of the donor plate. The root segments were rinsed and weighed as above, and their radioactivity determined. It is a simple matter to remove the cortex as a unit from excised roots (3, 18, 19) and to obtain cylinders of cortex, and intact steles some 10 cm in length. Both these tissues can be used separately in 2-plate experiments and compared with intact roots.

Intact Seedling Experiments. Filter paper disks 6 cm in diameter were dipped in melted paraffin which was then allowed to harden. Five small holes were punched in each of the paraffined disks, and the primary root of a single seedling was passed through each hole. Sets of 5 seedlings were thus floated on 200 ml of experimental solution contained in 250 ml beakers. Experiments were performed at room temperature on the laboratory bench. All treatments of a given series were carried out at once, so that any variation in temperature and lighting, and hence in transpiration rate, was of no consequence. In experiments involving ^{86}Rb, roots were rinsed in unlabeled experimental solution rather than in water at the end of the experimental period.

Determination of Radioactivity. ^{36}Cl: Roots were thoroughly dried and dropped directly into fluor for liquid scintillation counting. Aliquots of the experimental solutions were dried on circles of Whatman glass filter paper (GF/A) — and the glass paper placed directly into fluor for counting. Alternatively samples were dried on planchets and counted with a gas-flow micromil window detector. Shoots (ca 2 g fr wt) were extracted on a steam bath with 20 ml 40 percent ethanol (v/v) for several hours. The volume was reduced to 10 ml on a steam bath, and 1 ml aliquots were dried on planchets and counted. Standard curves were prepared both for gas-flow and for liquid scintillation counting. In the latter instance standards were prepared both for ions adsorbed on glass filter paper and for ions adsorbed on root tissue. Thus all radioactivity measurements were convertible to comparable quantitative units. Uptake and transport rates were calculated from radioactivity measurements and the determined specific activity of the experimental solutions.

^{86}Rb: Both roots and shoots were extracted for 60 mins in 20 ml 1:50 nitric acid on a steam bath. Aliquots of the extract were pipetted on to glass filter-paper disks together with a drop of polyvinyl alcohol (Du Pont Elvanol grade 51-05) as adhesive, and counted with the gas-flow detector.

Results

As a direct means of studying salt movement into the stelar vascular system, initial studies centered on the transport of ions from the external solution to root exudates, the latter being considered to represent xylary fluid. In the low concentration range exudation is constant with time for at least 24 hours, as is the concentration of Cl in the exudate. By contrast, net uptake into the root per se is apparently completed in roughly 10 hours [cf (14)]. In the low range, Cl is concentrated in the process of movement into the xylem, the so-called accumulation ratio ranging from 200 to approximately 30 as the external concentration increases from 0.02 to 0.5 mM. In the high range there is little evidence of accumulation, the ratio approximating 1.0 (fig 1). The isotherm for Cl transport to the xylary fluid in the low range is hyperbolic, as exemplified by the double reciprocal plot of figure 2, and the K_s for the transport process is

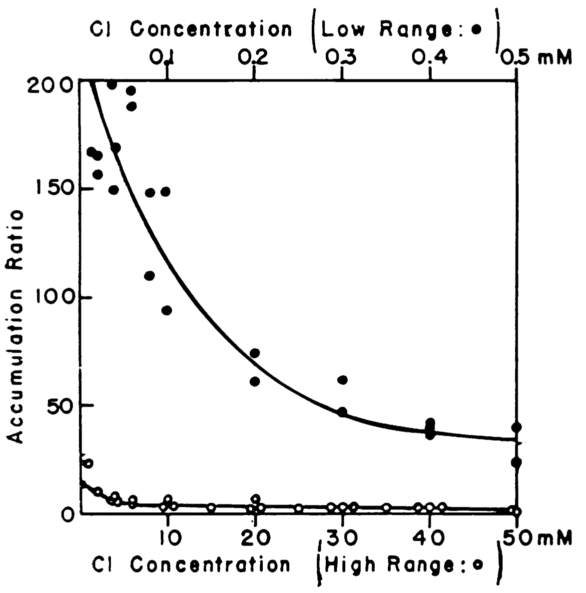

FIG. 1. Accumulation ratio as a function of the external concentration. Accumulation ratio represents the quotient of the Cl concentration in the exudate divided by that of the external solution.

akin to that for uptake by the root per se (table I). A meaningful isotherm is difficult to obtain for the high range in exudation experiments since at high external concentrations water uptake is diminished for osmotic reasons, the salt concentration in the xylary fluid approximating the concentration in the external solution (see fig 1). Consequently both salt uptake and exudation vary with concentration, the latter in a capricious way.

Long-distance transport experiments utilizing the 2-plate technique allowed examination of transport characteristics well into the high range, i.e. to 30 mM, with fewer osmotic difficulties, on the one hand, and on the other, allowed for a separate evaluation of transport in isolated cylinders of cortex and in isolated steles. A further virtue of the 2-plate method was the opportunity to study the basipetal movement of ions into the root segment between the donor and receptor plates. Transport to the leaves of young seedlings offered the most natural, and in the last analysis, the most effective way to study long-distance movement. Results with the 2-plate method were in most every respect similar to those with young seedlings. The results which follow made use of both methods, the choice being determined by the particular nature of the experiment, or by historical precedence, the 2-plate method having led to experiments with seedlings. The point of paramount importance concerns the relative shape of the absorption and transport isotherms in the 2 concentration ranges, whether in intact seedlings or in excised roots. Nevertheless, an appraisal of figures 4, 7 or 9 in relation to figure 5 allows a quantitative comparison of both absorption and transport in the high range in roots of intact seedlings and in excised roots, as well as a comparison of the relative rates of absorption and transport in each case. Figure 3, in turn, permits a measure of the relative rates of absorption and transport in excised roots in the low range, while table I compares the K_s for absorption and trans-

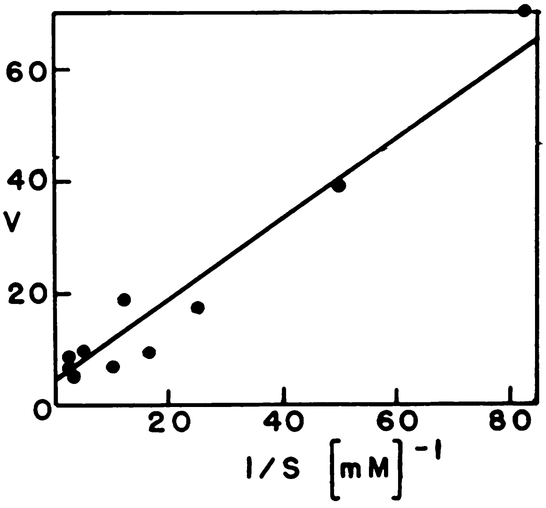

FIG. 2. Double reciprocal plot of the isotherm for Cl transport to the exudate in the low range. Concentration range: 0.01 to 0.5 mM. Transport rate: μeq Cl⁻/hr g fr wt roots.

Table I. *K_s for Absorption and Transport in the Range of System 1*

Ion	Type of Experiment	Absorption	Transport	
		mM		
Cl	Exudation experiment	0.07	0.15	
	2 Plate experiment		Transport to receiver plate	Transport to proximal root section
	Intact roots, low salt status	0.18	0.22	0.21
	Intact roots, high salt status	0.09	0.22	0.08
	Cortex alone	0.13	0.17	0.17
K	Intact seedlings	0.04	0.10	

port in the low range in seedlings and in excised roots.

Table II affirms that long-distance transport through excised whole roots is through the xylem, or at least through the stele. Excised whole roots exude freely, and salt is carried in the exudate at essentially the rate that salt moves proximally in 2-plate experiments.[2] Since excised cortex absorbs Cl as effectively as whole roots (cf fig 3, see table I), yet neither exudes nor effectuates long-distance transport in 2-plate experiments, long-distance transport is apparently confined to the stele. Since, however, decorticated steles as well neither exude nor transport salt along their length, a further word is necessary. While the absorbing capacity of the cortex is much the same in newly excised and in aged tissue, decorticated steles only absorb salt markedly following aging. Freshly excised steles display little differential permeability, and virtually no capacity for absorption (18). The condition of the stele in situ presumably resembles newly decorticated stele. Thus while aged decorticated steles fail to exude, and to carry out long-distance transport, because the stelar parenchyma cells retain the salt they absorb and do not release it to the xylem (table II), freshly excised steles fail to exude because the parenchyma plasma membranes leak, and the parenchyma cells are incapable of providing a concentrated salt solution to the xylem. In the whole root, the cortical cells accumulate salt in the cytoplasm, and pass it centripetally through the symplasm into the stele, where it leaks into the xylem. Osmotic water movement thereupon causes exudation (in excised roots) and long-distance transport. The data of table II are in accord with this view, which implies that the isotherms for ion uptake to the shoot, or to the receiver plate in 2-plate experiments, are in effect the isotherms for salt passage to the xylem.

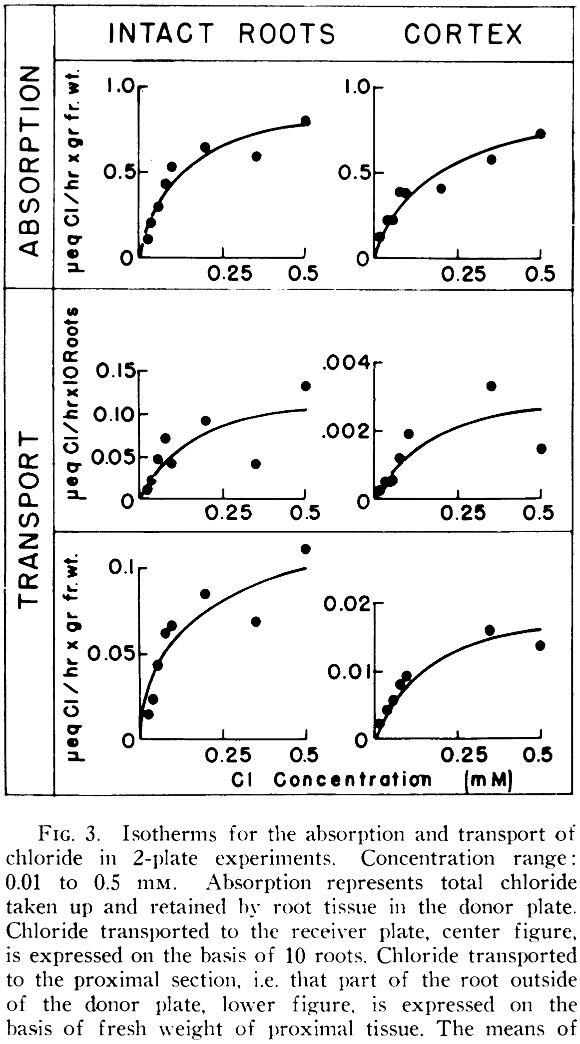

FIG. 3. Isotherms for the absorption and transport of chloride in 2-plate experiments. Concentration range: 0.01 to 0.5 mM. Absorption represents total chloride taken up and retained by root tissue in the donor plate. Chloride transported to the receiver plate, center figure, is expressed on the basis of 10 roots. Chloride transported to the proximal section, i.e. that part of the root outside of the donor plate, lower figure, is expressed on the basis of fresh weight of proximal tissue. The means of expression allow comparison of isotherms while making unnecessary the precise determination of the amount of absorbing tissue.

Isotherms for Absorption and for Transport. The isotherm for both absorption and for long-distance transport of Cl in the low range is invariably hyperbolic, whether determined in 2-plate experiments (fig 3) or with seedlings. In the high range the isotherm for absorption is multiple, much

Table II. *Uptake and Transport of Chloride in Tissues of Excised Corn Roots*

All tissues were aged 24 hours in 0.1 mM $CaSO_4$. 10 Roots weigh approximately 2.0 g fr wt. In 2-plate experiments, the 10 apical segments in the donor plate represent about 1.0 g fr wt. Absorption and transport period were 24 hours at room temperature. External concentration was 0.5 mM KCl.

Absorption and transport of chloride			
Type of experiment	Absorption	Exudation	2-Plate transport
Tissue	µmoles/hr g fr wt		µmoles/hr 10 roots
Decorticated stele	0.43	...	ca 0.0
Cortex	...	...	0.01
Intact root	0.46	...	0.53
Intact root	...	0.34	...

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[2] The absorption and transport values for the various tissue types bear the same relationship to each other when expressed as V_{max} values derived from reciprocal plots of absorption isotherms as when expressed for a single external concentration as in table II.

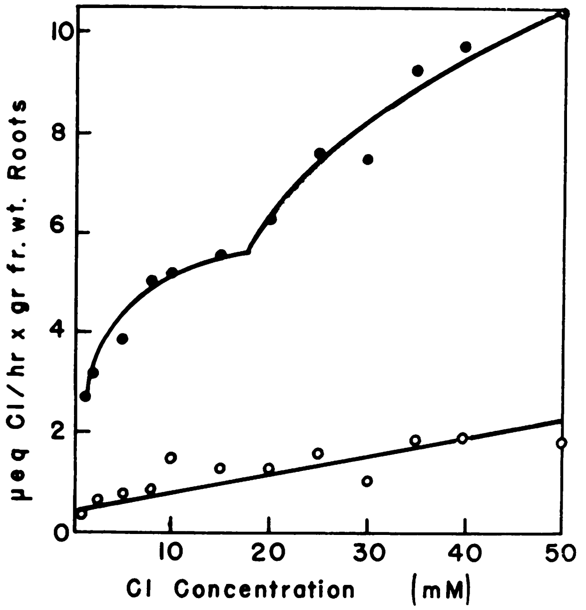

FIG. 4. Isotherms for the absorption and transport of chloride by intact seedlings in the high concentration range. Closed symbols, absorption. Open symbols, transport.

as described by Elzam et al. (8) while the transport isotherm tends towards the linear (fig 4). Since in passing to the leaves ions are to some extent withdrawn en route into the vacuoles of stelar parenchyma and even into the cortex [see below and cf (29)], the high range isotherm for transport may unavoidably reflect the operation of system 2 to a small extent. Thus the high range isotherm for transport is neither precisely linear, nor exponentially rising, as might be expected for system 1 alone in the high range (25), but is nevertheless grossly different from the absorption isotherm. The high range isotherm for ion movement to the receiver plate in 2-plate experiments is somewhat less linear than that for transport to the shoot, and considerably less hyperbolic than that for root absorption (fig 5). Such a result is to be expected if there is more absorption from the xylary stream by contiguous cells in excised roots than is the case in seedlings, where a more effective transpiration stream expedites movement in the xylem. It will be noted that basipetal transport to the proximal root section is essentially the same as to the receiver plate in 2-plate experiments. Since the cortex is of no consequence in long-distance transport (table II), it follows that the cortex receives salt via the xylem. As with exudation experiments, though less markedly, the effect of changing osmotic pressure on water absorption in the high range is reflected in salt transport, and consequently prevents the accurate determination of a transport isotherm. When so-called high salt roots are prepared by pretreating the seedlings in 40 mM KCl for 26 hours before use, the high range isotherm for basipetal transport is a straight line.

Ion Competition in Absorption and Transport. While the carrier-mediated uptake of a given ion is competitively inhibited by one or more generically related ions (9, 10), the passage of an ion through a membrane by diffusion should remain relatively unaffected by other ions. In this connection it is noteworthy that both the absorption and the long-distance transport of Cl in the low range is competitively inhibited by bromide (fig 6), while only absorption is affected by bromide in the high range (fig 7). In the latter instance competitiveness is readily demonstrated only in the lower part of the range, since the affinity for Cl far exceeds that for Br, and effective inhibition by Br at higher Cl levels would require inordinately high total salt concentrations. The unreliable values in the high range are therefore indicated by broken lines in figure 7.

The Effect of Counter-Ions on Absorption and Transport. In contrast to system 2, system 1 has

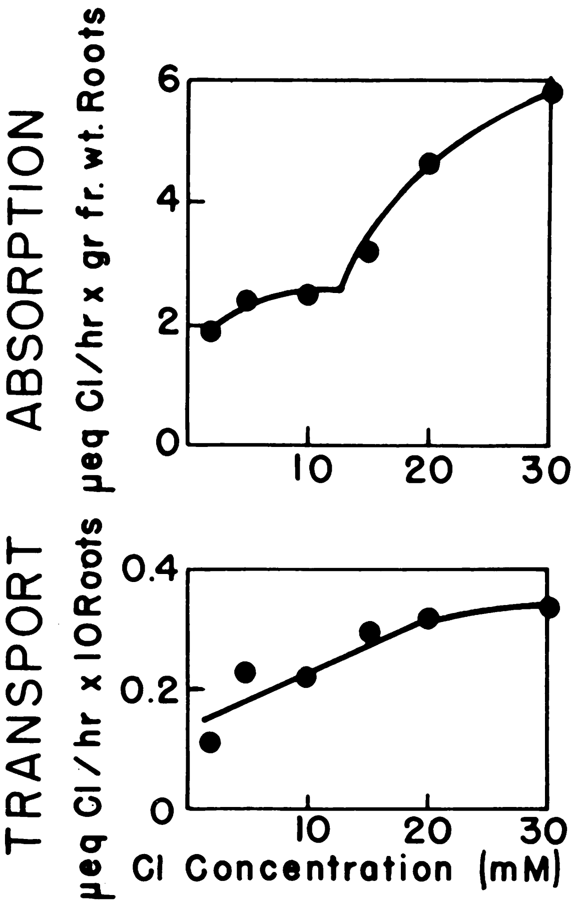

FIG. 5. Isotherms for the absorption and transport of chloride by excised roots in the high concentration range. 2-plate experiment. Absorption and transport as for figure 3.

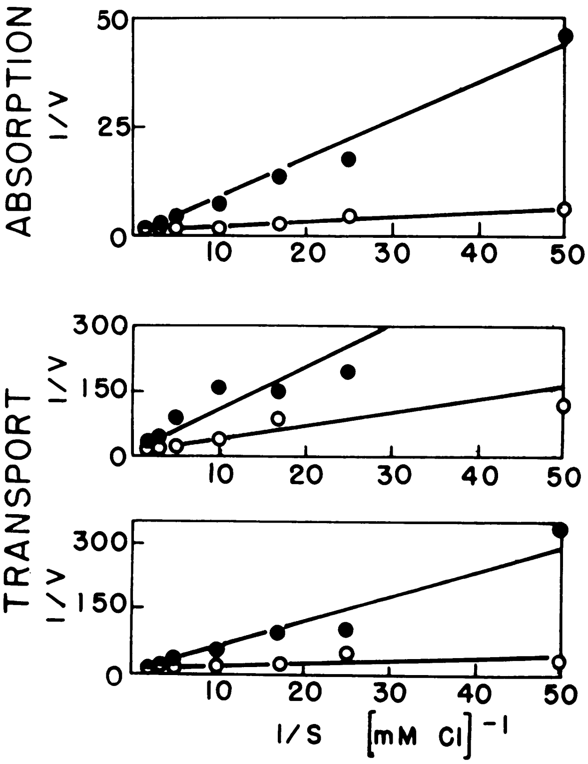

FIG. 6. Competitive inhibition by bromide of chloride absorption and transport by excised roots in the low concentration range. 2-Plate experiment. Double reciprocal plots. Absorption and transport as for figure 3. Open symbols, chloride only. Closed symbols, 2.5 mM Br throughout. v = μeq Cl$^-$/hr g fr wt for top and bottom figures; μeq/10 roots for central figure.

been shown to be indifferent to the nature of the counter anion in the absorption of Rb (10). Similarly Cl uptake was demonstrated to be relatively little affected by the counter anion in the range of system 1 while proving markedly susceptible to the type of cation in the range of system 2 (25). Figure 8 demonstrates that both absorption and long-distance transport of Cl in the low range are much the same whether Cl is presented as the K or Ca salt. On the other hand, while transfer to the shoot in the high range is indifferent to the nature of the cation, absorption by the root is emphatically less from the Ca than from the K salt (fig 9).

The characteristics of K absorption and long-distance transport are much the same as for Cl (fig 10). Thus the isotherms for both absorption and transport to the shoot are hyperbolic in the low range. In the high range, uptake by the root displays a multiple hyperbolic isotherm while long-distance transport is linear with concentration. While both processes are indifferent to the counter anion in the low range, only long-distance transport is relatively unaffected by the nature of the anion in the high range; K absorption in the high range is much greater from KCl than from K_2SO_4.

Discussion

Of the major theories regarding the means whereby salt from the milieu is delivered to the stele of plant roots, and more particularly to the xylem, one theory suggests that salts impinge upon the endodermis by diffusion through the free space, and are subsequently secreted into the xylem by endodermal and stelar parenchyma cells, while the other maintains that salts are actively absorbed into the cytoplasm of the cortex cells and pass to the xylem by diffusion within a cytoplasmic continuum, the symplasm (1, 7, 20). The first view assigns no role to the cortex in long-distance transport, i.e. transport to the shoot, relegating the electro-osmotic work which is done to the endodermis, and perhaps to stelar parenchyma as well. The second view considers the cortex as a gathering agency which both collects and concentrates ions as a preliminary to delivery to the xylem. It is further demanded that accumulation must take place in the cytoplasm of the cortex parenchyma, and there is considerable independent evidence to indicate that such is the case (12, 21, 22, 24). The passive movement of ions from the symplasm to the xylem is attributable to the marked drop in the differential permeability of the living cells within the stele, i.e. the leakiness of their plasma membranes (18), while the retention

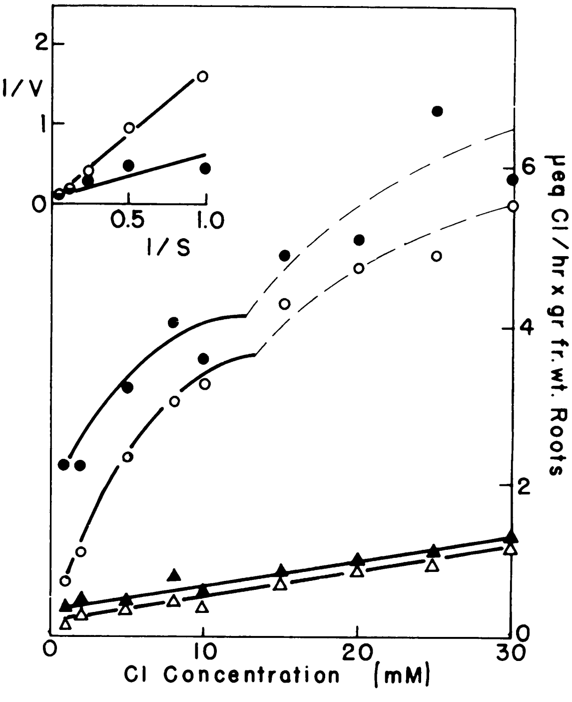

FIG. 7. Competitive inhibition by bromide of chloride absorption and transport by intact seedlings in the high concentration range. Closed symbols, chloride only. Open symbols 10 mM Br throughout. Circles, absorption; triangles, transport. Insert graph: double reciprocal plots, concentration range 1 to 10 mM.

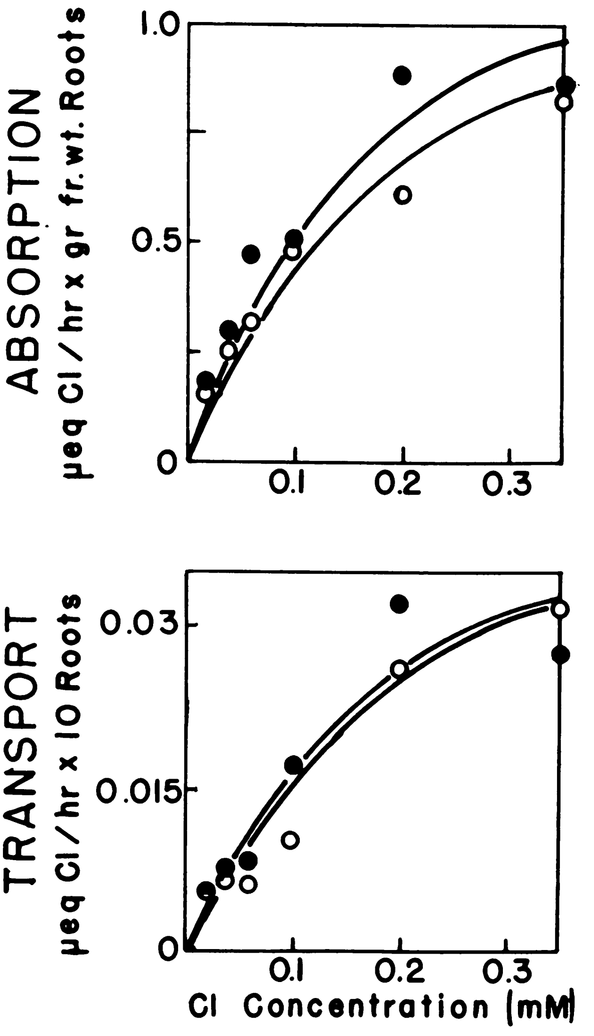

FIG. 8. The effect of the counter-cation on chloride absorption and transport by excised roots in the low concentration range. 2-Plate experiment. Closed circles, KCl; open circles, $CaCl_2$. Absorption and transport as for figure 3.

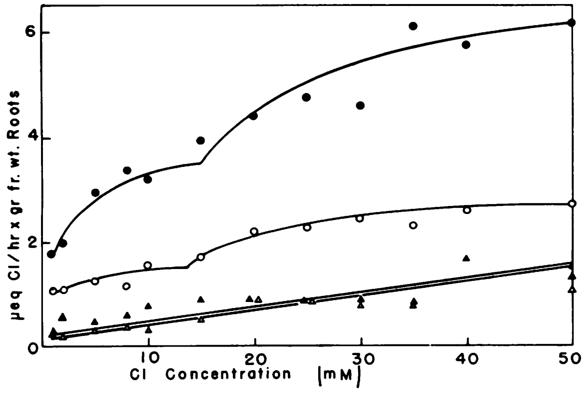

FIG. 9. The effect of the counter-cation on chloride absorption and transport by intact seedlings in the high concentration range. Circles, absorption. Triangles, transport. Closed symbols, KCl; open symbols, $CaCl_2$.

of salts in the xylem is considered to depend upon the presence of the Casparian strips in the endodermis (7, 26).

Several considerations favor the second alternative. 1) Disruption of the continuity between the cortex and the stele markedly decreases salt transfer to root exudates (20). 2) The rate of salt appearance in the exudate of high salt roots is essentially equal to the rate of salt uptake by these roots (5, 14). If salt transfer to the xylem were limited by the activity of the endodermis, the rate of uptake in the high range necessarily imputed to the endodermis would be far in excess of the maximal absorption rates (2–4 μeq/g fr wt/hr) prevalently observed in a great variety of roots and other plant tissues. 3) Under conditions where total absorption is much the same, high salt roots pass the bulk of the salt which they absorb to the xylary fluid, while low salt roots sequester a large part of the salt they take up in the root cell vacuoles (5, 14, 15). If the endodermis and stelar parenchyma were primarily responsible for the transport of salt into the stele, the over-all salt status of the root would be of little consequence, and the vacuoles of the cortical cells of low salt roots would not serve as a diversionary sump for salts en route to the xylem.

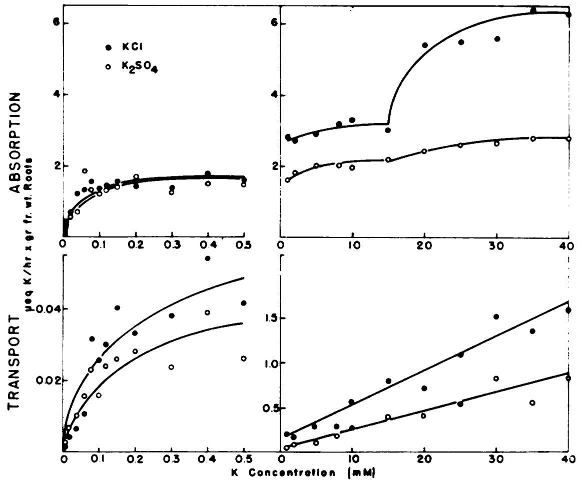

FIG. 10. Potassium absorption and transport by intact seedlings in the low and high concentration ranges. Closed circles, KCl; open circles, K_2SO_4.

Autoradiographic experiments involving the movement of $^{35}SO_4$ into the stele of corn roots and air roots of Epidendrum imputed an active role in ion transport to the endodermis and to the stelar parenchyma (19, 27, 28) because the non-living xylem elements appeared to be the most heavily labelled on an over-all basis, suggesting an active secretion of $^{35}SO_4$ from contiguous living cells. However, the method, while permitting the assessment of the relative radioactivity of the various root tissues, was of insufficient resolving power to distinguish between the vacuole, cytoplasm and the water free space of the cell wall. Hence the relative concentration of $^{35}SO_4$ in the symplasm was undeterminable, and the foregoing considerations leave open the interpretation of the cited experiments, and permit a reevaluation consistent with the views presented herein.

On the basis of what has been said it is to be expected that movement of ions into the xylem will reflect solely the characteristics of movement of ions across the plasma membrane of the cells of the root cortex. In this connection the point has previously been made that in roots where absorption through a wide concentration range is characterized by a dual isotherm, uptake at very low concentrations, implemented by the so-called high-affinity, low K_s system, is controlled by passage through the plasma membrane. Absorption at high concentrations in turn, implemented by the low-affinity, high K_s system, reflects the kinetics of transport across the tonoplast (25). The latter judgment was made on the basis of the observation that non-vacuolate root tips manifest system 1 alone, while vacuolate root tissues evince both systems. Furthermore, salt uptake by vacuolated root segments in the low concentration range displays all the features of system 1.

In the studies herein, the passage of ions to the shoot of young corn seedlings has been shown to reflect the attributes of system 1. In the low concentration range, long-distance transport to the shoot is characterized by a hyperbolic isotherm, by the competitive inhibition of the transport of a given ion by a closely related ion, and by the indifference of ion uptake to the nature of the counter-ion. In the high concentration range, long-distance transport displays an essentially linear isotherm, shows no competitive inhibition of ion uptake, and manifests an indifference to the counter-ion, as in the low range. By contrast, root absorption per se in the high range is hyperbolic with concentration, competitive with respect to generically related ions, and sensitive to the counter-ion. Thus, in the high range, root absorption reflects vacuolar uptake, i.e. ion passage across the tonoplast, while long-distance transport reflects the passage of ions into the symplasm, i.e. across the plasma membrane. The implication that only the plasma membrane is involved in long-distance transport, while both plasma membrane and tonoplast are involved in net uptake by the root, is further substantiated by the fact that root uptake is doubled when the external concentration is raised from the low to the high range, while long-distance transport is increased 10 times. Pitman (22) has recently emphasized the paramount role of the cytoplasm in salt transport across the cortex.

The conception of long-distance transport which has been presented represents a reaffirmation and extension of the theories of Crafts and Broyer (7), Arisz (1), and Lundegardh (20). In addition to verifying the presumption that symplastic transport, wherein the entire cortex participates, delivers salts to the xylem, the experiments herein make the additional point that of the dual systems operating in net uptake by the root, it is solely the high-affinity, low K_s system which accumulates ions across the plasma membrane and which is therefore involved in symplastic, and ultimately long-distance, transport. It is a feature of salt movement through the plasma membrane that when the external concentration markedly exceeds the concentration for maximal uptake by system 1, salt movement across the plasma membrane proceeds by diffusion (25). It is the latter phenomenon which explains the isotherms for long-distance transport in the high range. Diffusion in the symplasm rather than diffusion through the plasma membrane might have been considered the rate-limiting event leading to the linear isotherm for long-distance transport. However, on the one hand absorption by nonvacuolate root tips displays the same linear isotherm (25), and on the other, the rate of vacuolar accumulation in low salt roots is virtually equivalent to xylem transport in high-salt roots (5, 15), an observation strongly implying that it is passage across the plasma membrane which is rate-limiting in both cases. Finally, it may be said that much of the historical contention regarding the question of whether long-distance transport is a metabolically implemented process [see (4)] or is a combination of passive movement and active transport (16, 17) may be resolved in terms of the hypothesis being offered. In the low concentration range, a range encountered in the soil solution in nature (2), absorption into the symplasm is active, and hence long-distance movement displays the features of active transport. In the high range, a range frequently encountered experimentally, movement into the symplasm is in large measure passive, and the consequences thereof are reflected in long-distance transport.

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