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Uptake and Distribution of Sodium and Potassium by Corn Seedlings[1]

I. ROLE OF THE MESOCOTYL IN 'SODIUM EXCLUSION'

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ABSTRACT

The distribution of sodium and potassium throughout corn (*Zea mays* L. [A632 × Crows 3640] × Oh 43) plants is not simply a matter of uptake by cortical cells and irreversible delivery to the xylem for upward transport. We show that sodium, but not potassium, accumulates in the mesocotyl of corn seedlings grown on NaCl medium. Upon transfer to NaCl-free medium, total sodium is reduced by export through the roots but remains at high levels within the mesocotyl. We report experiments which consider uptake from the xylem.

Shoots excised at the seed were allowed to transpire solutions containing ^{22}Na and ^{42}K. Potassium uptake within the mesocotyl was very sensitive to concentration, increasing 27-fold between 1 and 10 millimolar. Sodium uptake was dependent upon the square root of the concentration suggesting active accumulation. At sodium concentrations below 1 millimolar, more than 80% of the sodium in the plant was retained in the mesocotyl. Both the uptake by and retention within the mesocotyl were dependent upon transpiration rate as well as concentration. We discuss the limitations of measuring uptake from a finite, depletable medium. The mesocotyl is a modified root with a cuticularized epidermis. We discuss the feasibility of using this 'plastic-coated root' as a model for root transport studies.

Over the past fifteen years a good deal of progress has been made in understanding the movements of K^+, Cl^-, and Na^+ between an external medium and roots or root segments. Less progress has been made in understanding the distribution and redistribution of ions once they have crossed the endodermis. By far the major effort has been directed toward understanding of the delivery of ions to the xylem (17), and despite evidence to the contrary, summarizing models imply that, once delivered to the transpiration stream, an ion is destined for the shoot (14, 17). The true situation is far more complex. Pate and his coworkers (15) have studied the numerous pathways and chemical alterations which nitrogenous compounds undergo during long distance transport. While the monovalent ions do not change chemical form, it is clear in their case as well that what starts upward may neither get there nor stay there. Shone *et al.* (20) found the ascending transpiration stream in corn to contain less sodium and the root to retain more toward the basal end. Jacoby (8–10), using *Phaseolus vulgaris*, studied the upward movement of sodium, the accumulation in the basal region of the stem, and the subsequent retransport and export through the roots. Similar sodium recirculation was reported for squash by Cooil *et al.* (5). In soybean, discrimination in upward transport is against Cl^- rather than (or in addition to) sodium (13, 21).

It has long been known that glycophytes, including many crop plants, exclude sodium from their shoots, at least at low external sodium concentrations (4). That such discrimination is a phenomenon of importance to survival in some plants is clear from the results such as those of Rush and Epstein who noted that, in tomato (*Lycopersicon esculentum*), breakdown of the sodium exclusion mechanism correlated with death of the plants (18). Therefore, salt tolerance in such plants will be determined, in part, by the effectiveness of the exclusion mechanisms. The transport systems and controls of potassium and sodium distribution are thus problems of both intellectual and practical importance.

With this paper, we begin a series aimed at elucidating the transport phenomena, mechanisms, and controls responsible for distribution and redistribution of sodium and potassium in corn seedlings. In this report, we consider studies of ion accumulation in the mesocotyl and the relationship with sodium exclusion from the shoot, *i.e.* we start with studies analogous to those of Jacoby (8–10). Like the base of the *Phaseolus* stem, this region is active in sodium accumulation. Anatomically, it is similar to the root (7) having a central stele surrounded by an endodermis. When grown in contact with soil or solution, the mesocotyl produces secondary roots from the pericycle. Unlike the root, however, it is cuticularized so that ions cannot be lost to the medium directly through the cortex; all net influx and efflux occur with respect to the xylem and phloem. This affords the possibility, at least in principle, of studying flux of ions outward through the endodermis following accumulation. Such fluxes will be the subject of subsequent studies.

MATERIALS AND METHODS

Corn seedlings (*Zea mays* L. [A632 × Crows 3640] × Oh 43; Crows Hybrid Corn Co., Milford IL) were grown in the dark at 29°C on moist paper towels as previously described (6). For experiments to determine salt tolerance and salt effects on growth and internal concentrations, 3-d-old seedlings were transferred to hydroponics and grown in opaque plastic 2.5-L containers on a MSW[4] with or without NaCl (0.75 mM KNO_3, 0.265 mM $KHCO_3$, 1.05 mM $CaCl_2$, 3.2 mM $MgSO_4$, 2.3 mM $MgCl_2$, 0.5 mM $(NH_4)H_2PO_4$, 45 mM NaCl, micronutrients, and Fe). In

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[4] Abbreviations: MSW, modified sea water nutrient solution; ϕ_{xc}, ion flux from the xylem to the symplasm; ϕ_{cx}, ion flux from the symplasm to the transpiration stream.

growth experiments at higher NaCl levels, all nutrients were increased proportionately. Plants were maintained in a growth chamber on a 14-h photoperiod, 27°C/18°C. All solutions were continuously aerated. Potassium content of solutions was monitored daily by flame photometry and corrected by addition of KNO_3. Solutions were replaced weekly. Plants were harvested after 7 or 14 d. Shoots and mesocotyls were separated at the node and weighed; the roots were first washed in ice cold 10 mM $CaCl_2$ for 10 min to allow exchange of the cell wall contents before being blotted and weighed. After oven drying at 80°C, the tissues were reweighed and pulverized. Five 100-mg samples of roots and leaves, and three 50-mg samples of mesocotyls were then ashed at 450 to 500°C until white and resuspended in 0.9 M Mg-acetate for Na^+ and K^+ analysis by flame photometry. Concentrations of sodium, potassium, nitrate, and chloride in the xylem sap were estimated for plants growing on 0 and 45 mM NaCl solutions to serve as a guide for levels to be used in transpiration experiments. Eight-d-old seedlings were detopped and roots were transferred to distilled H_2O to induce exudation. To enhance the probability that collected solution was in the xylem prior to excision, only the first 10 μl of solution were collected from each bleeding root system in these determinations (19). The sodium concentration in the sap entering the mesocotyl was 12.3 ± 7.8 (range 5.8–19.9) mM and the potassium concentration was 6.8 ± 3.6 (range 3.8–11.4) mM. In plants grown without sodium, the potassium concentration was 10.9 ± 1.3 (range 9.9–11.8) mM. Based on this, we selected combinations of 1 and 10 mM potassium and sodium chloride as the basic levels to be used in transpiration studies. Subsequent analysis of exudates for chloride and nitrate showed chloride levels in the high salt plants to be in the range of 2.0 to 3.0 mM. Nitrate levels were 5.3 to 9.8 mM.

For uptake experiments, 3- to 4-d-old seedlings were transferred to soil-filled containers in the growth room and experiments were carried out using 8-d-old seedlings. The plants were cut 2.5 cm below the coleoptile node and immediately transferred to a foil-covered scintillation vial containing 5 ml of labeled solution. About 0.5 cm of the mesocotyl was submerged in the solution. Using neutral red and Evans blue dyes, it was found that penetration of the cortical apoplast after 2 h was restricted to the basal mm of the mesocotyl. Thus, the error introduced into the results by nonvascular uptake was ignored. Four seedlings were placed in each vial, and four vials were used for each treatment. As soon as all the plants were in the vial, an initial weight was taken and the vials were reweighed after the uptake period to determine the transpiration rates. For experiments lasting more than 6 h, solutions were replenished at 4 and 8 h and intermediate transpiration data taken.

Following the uptake period, the plants were transferred to a vial containing unlabeled solution for 5 min. Estimates of the xylem vessel volume from cross-sections of the mesocotyl indicated that this length of time should have been sufficient to allow the labeled solution in the transpiration stream to pass out of the mesocotyl: approximately 4% of the cross-sectional area of the mesocotyl was vessels. In a 2.5-cm segment, this corresponds to a vessel volume of approximately 2.5 μl. In slowly transpiring seedlings, the passage time for this volume was 4 to 6 min. These estimates are approximations due to our inability to determine with certainty the relative maturity and resistances of the conducting elements.

Following the exchange period, the shoot and mesocotyl were separated at the node and the samples were weighed, dried, ashed at 450 to 500°C until white, and counted using a Beckman LS230 scintillation counter.

The uptake solution (and the unlabeled chase solution) contained 1 mM $CaCl_2$ and 1 mM K-phosphate (pH 6.0). NaCl and KCl were added as required to produce the reported concentrations. Sodium was labeled with ^{22}Na (New England Nuclear). Potassium as labeled with ^{42}K (locally produced by irradiation of K_2CO_3 in the central thimble of the TRIGA reactor, University of Illinois Nuclear Engineering Program; samples were neutralized with H_2SO_4 following irradiation). Both labels were present at levels of at least 20,000 cpm/ml of uptake solution at the beginning of the counting period. For double-labeled experiments, samples were recounted after complete decay of the ^{42}K. Initial counts were decay corrected.

RESULTS

Though corn roots show marked selectivity for potassium over sodium (1, 4), exclusion of the latter is not complete and plants grown on solutions containing NaCl will accumulate significant amounts in the shoots. Table I shows the distribution of sodium and potassium in 7- and 14-d-old seedlings grown on MSW, with and without NaCl. Despite sodium accumulation, shoot potassium levels were maintained though root levels declined. A more dramatic correlation between sodium accumulation and loss of potassium was in the mesocotyl region. Preliminary experiments confirmed the finding of Shone *et al.* (20) that the root base also had high sodium levels (data not shown).

Table I suggests that, upon removal of sodium from the growth medium, the levels within the plant as a whole decreased. This was confirmed by analysis of total plant sodium contents (Table II). Table II also shows that the mesocotyl contained a significant portion of the total sodium, and that once accumulated, it was less mobile than leaf or root sodium. Table III compares fresh weights after 7 d at four salinity levels (at 14 d, roots could not be separated for analysis of individual plants). Leaf weight was more affected than root weight, showing statistically significant growth reduction at 45 mM NaCl. Toxicity symptoms (tip necrosis and seedling mortality) were apparent at the 60 mM level. We therefore accepted the 45 mM dilution as an upper level at which corn was tolerant of sodium under our growth conditions and estimated the magnitude of xylem sap concentration (see "Materials and Methods") prior to the following experiments.

When soil-grown seedlings were excised and allowed to transpire labeled solutions, the rate of accumulation of both sodium and potassium in the mesocotyl was linear over a period of at least 4 hours (Figure 1). The data are taken from two experiments in which the total $Na^+ + K^+$ was constant at 11 mM. At each concentration, the uptake of sodium was greater than that of potassium, the difference being more notable at the 1 mM level.

The concentration dependence of sodium uptake over an extended range is shown in Figure 2, and in Figure 3 is shown the percentage of the total label in the plant that was found in the mesocotyl at each concentration. In the 1 to 20 mM sodium range, Figure 2 indicates the sodium uptake rate to be unaffected by potassium level.

Comparing Figures 2 and 3, it is reasonable to consider that, at transpiration stream concentrations less than 1 mM, the mesocotyl is efficient at detoxification and that sodium uptake by the mesocotyl may be limited by the rate at which it is delivered via the transpiration stream. The effects of transpiration rate, particularly as they effect experiments using this system, will be discussed further below.

Table IV compares the rates of sodium uptake and retention in the mesocotyl when nitrate and sulfate were substituted for chloride in the uptake solution. Uptake in the presence of sulfate was slower than in the presence of chloride, similar to the case in roots.

Table V shows the effect of temperature, fusicoccin, an uncoupler, an ATPase inhibitor, and gramicidin on sodium uptake by the mesocotyl. Though temperature had a pronounced effect, neither fusicoccin nor the inhibitors produced a large change. Vanadate, however, had visible deleterious effects on the leaves

Table I. *Sodium and Potassium Concentrations in Plants Grown Hydroponically on Modified Seawater Nutrient Solutions*

Age is time after transplanting to hydroponics; concentrations are given for roots (R), shoots (S = leaves), and mesocotyls (M). Plants grown for 7 d on sodium and transferred to sodium-free solution are designated 45 → 0.

[Na⁺]		Age (d) 7 Na⁺	7 K⁺	13 Na⁺	13 K⁺
mM		*μmol/g fresh wt*			
0	R	3.6 ± 0.4	60.2 ± 3.0	<1	60.8 ± 5.3
	S	1.9 ± 0.1	67.5 ± 2.5	<1	119.4 ± 4.3
	M	1.6 ± 0.1	99.3 ± 7.1	<1	123.8 ± 6.8
45	R	52.0 ± 2.1	63.0 ± 2.7	47.9 ± 2.4	30.4 ± 3.6
	S	39.0 ± 2.8	102.2 ± 3.5	36.2 ± 4.7	88.6 ± 3.5
	M	219.1 ± 11.9	29.8 ± 3.9	208.1 ± 15.4	15.9 ± 0.6
45→0	R			6.0 ± 1.4	55.3 ± 2.8
	S			8.6 ± 1.4	100.9 ± 15.4
	M			159.1 ± 19.4	24.4 ± 6.8
60	R	60.6 ± 3.6	41.0 ± 5.0	49.1 ± 2.3	42.3 ± 3.1
	S	27.5 ± 2.8	85.2 ± 3.5	44.8 ± 3.2	84.2 ± 4.9
	M	166.7 ± 9.3	26.7 ± 2.3	219.0 ± 6.4	19.0 ± 1.4
75	R	56.9 ± 5.1	37.1 ± 3.8	44.2 ± 3.6	41.8 ± 2.5
	S	51.6 ± 3.0	101.1 ± 3.0	69.2 ± 5.2	111.7 ± 7.1
	M	242.4 ± 14.7	23.2 ± 0.7	266 (n = 1)	36 (n = 1)
90	R	45.9 ± 3.8	45.4 ± 4.2	58.3 ± 6.3	40.0 ± 3.5
	S	47.9 ± 5.1	97.5 ± 2.0	98.2 ± 2.3	129.5 ± 2.3
	M	213.4 ± 8.9	21.1 ± 0.3		

Table II. *Fresh Weight, Sodium Content, and Localization within the Mesocotyl in Corn Seedlings Grown 13 Days after Transplanting to Hydroponics at Various Sodium Levels, Determined from Data in Table I and Combined Fresh Weights of Plants Surviving to Harvest*

In all cases, the mesocotyl represented 2 to 3% of plant fresh weight.

[Na⁺]	Fresh Weight/Plant	Na⁺/ Plant	Na⁺ Mesocotyl
mM	*g*	*μmol*	%
45	3.8	174	15
45→0	5.6	62	31
60	3.7	190	13
75	2.9	198	13

Table III. *Root and Leaf Weights of Corn Seedlings Grown for 7 Days on Nutrient Media of Differing Salinity*

Values are means per plant of four groups of four plants at each level.

[Na⁺]	Root Weight	Leaf Weight
mM	*g/plant*	
0	1.96	2.42
45	1.68	1.49
60	1.43	1.02
75	1.16	0.80
LSD (5%)	0.34	0.58

(drying and shriveling) and resulted in a large decrease in transpiration after 2 h (data not shown). Thus, rather than eliminating the possibility of active sodium transport, their lack of effect on uptake may mean only that the inhibitors did not reach the site of that transport.

The effects of transpiration, discussed briefly with respect to Figures 2 and 3, are considered further in Table VI. Potassium uptake was affected to a much greater extent by concentration than was sodium uptake, increasing 27-fold between 1 and 10

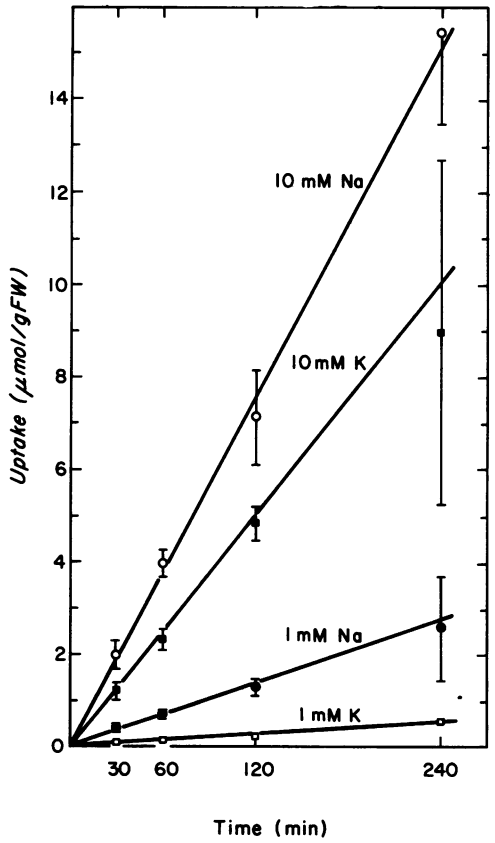

FIG. 1. Time course of sodium and potassium accumulation by mesocotyls of 8-d-old corn seedlings transpiring label medium. Medium contained 1 mM Na^+ (●) plus 10 mM K^+ (■) or 10 mM Na^+ (○) plus 1 mM K^+ (□). Solutions were double labeled with ^{42}K and ^{22}Na. Error bars are SD.

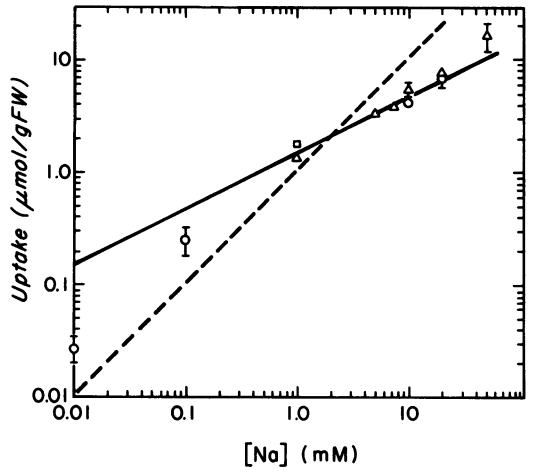

FIG. 2. Sodium uptake *versus* sodium concentration by mesocotyl of 8-d-old corn seedlings transpiring labeled medium. Potassium concentrations were 1 mM (O) and 10 mM (Δ). Solid line has a slope of 0.5, dashed line has a slope of 1.0. Error bars are SD.

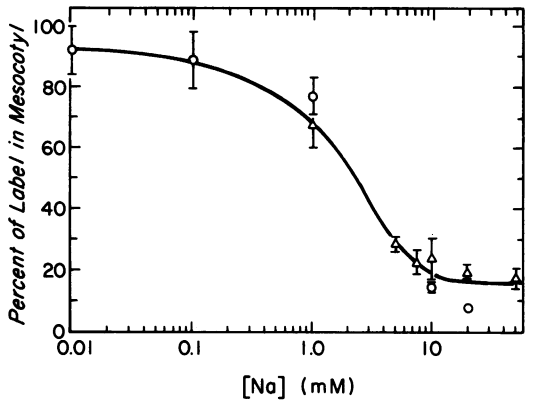

FIG. 3. Retention of ^{22}Na label by mesocotyls of 8-d-old corn seedlings as a function of sodium concentration at 1 mM K^+ (O) and 10 mM K^+ (Δ). Error bars are SD.

Table IV. *Effect of Counter Ion on Sodium Uptake by Mesocotyls*

Transpirational ion levels were 10 mM Na^+, 10 mM K^+. Similar superscripts denote values not significantly different at the 5% level. Mesocotyl retention is per cent of total transpired label in the mesocotyl. Delivery rates were saturating (see below).

	Na^+ Uptake	Mesocotyl Retention
	μmol/g fresh wt·h	%
Chloride	3.55 ± 0.59^a	22 ± 5
Nitrate	$2.91 \pm 0.47^{a,b}$	25 ± 9
Sulfate	2.47 ± 0.24^b	24 ± 2

mM. At 1 mM sodium and potassium (equimolar concentrations), sodium uptake was more than 10 times potassium uptake. Using the approximations for xylem volume determined above ("Materials and Methods"), the transpiration rates in lines 1 and 3 of Table VI represent 25, 55, 19, and 9 changes in xylem contents/h, respectively. Thus, the low uptake rate of sodium in line 3b may have been limited by the rate of delivery of ions. The small differences in uptake in lines 1a and 1b, however, imply that uptake is saturable at high delivery rates.

Such complexity would be the expected consequence of two depletion effects. First, unlike studies using roots or other tissues

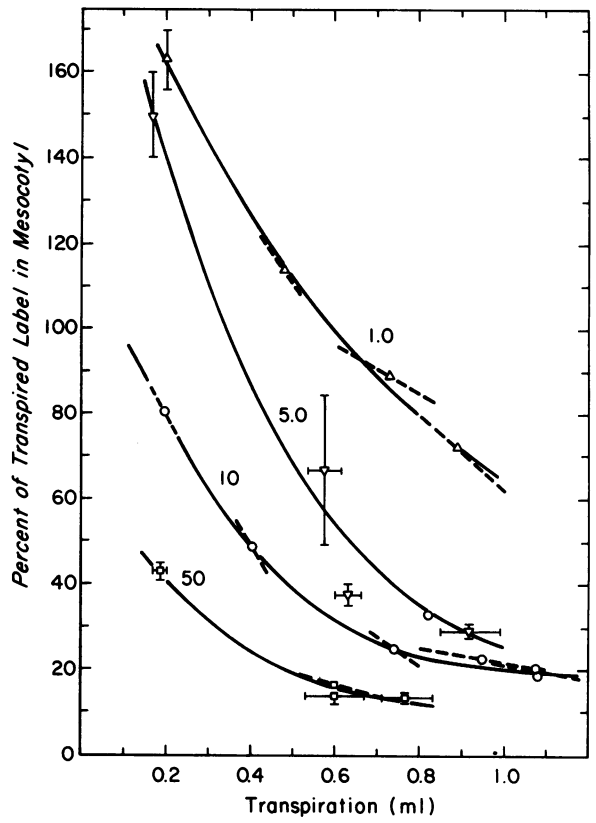

FIG. 4. Percent of transpired label found in the mesocotyl of 8-d-corn seedlings *versus* total transpiration (per group of four plants). Transpiration rates were altered by shading to half and quarter light and darkness. Dashed lines show linear regressions over narrower ranges of transpiration occurring naturally within the four groups per treatment. Solid lines were fit by eye and have no regressional meaning. Potassium was 10 mM, sodium was 1 (Δ), 5 (▽), 10 (O), or 50 (□) mM. Error bars are SD.

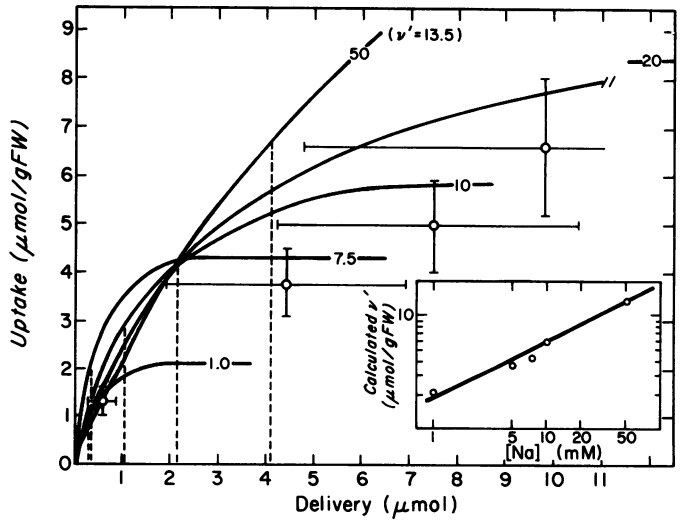

FIG. 5. Sodium uptake *versus* delivery (defined as concentration × transpiration for a group of four plants) at five sodium levels and constant potassium (10 mM). Curves are from linear regression estimates using Eadie-Hofstee transformations. Vertical dashed lines designate delivery rates for half maximal uptake. Error bars are SD and indicate the range of delivery and uptake rates used for analyses. Inset shows maximal calculated uptake rate ν' *versus* concentration; the solid line has a slope of 0.5.

Table V. *Effect of Temperature and Chemical Modifiers on Sodium Uptake and Retention by Corn Mesocotyls, from Transpired Medium at 10 mM Sodium plus 10 mM Potassium over a 4 Hour Uptake Period*

Temperatures were altered by chilling the medium or by augmenting the light with concomitant heating. Temperatures are those of the solutions.

Treatment	Uptake	Mesocotyl Retention	Transpiration
	μmol/g fresh wt·h	%	*μl/plant·h*
Control (25°C)	4.1 ± 0.3	50 ± 3	60 ± 6
Cold (2°C)	0.85 ± 0.15	12 ± 4	42 ± 13
Heat (35°C)	7.1 ± 0.2	44 ± 4	105 ± 9
Fusicoccin (10 μM)	4.7 ± 0.6	60 ± 20	62 ± 10
DNP[a] (50 μM)	4.7 ± 0.4	59 ± 3	55 ± 4
DCCD (50 μM)	4.5 ± 0.3	42 ± 1	73 ± 5
Gramicidin (125 μM)	2.8 ± 0.4	36 ± 3	89 ± 9
Vanadate (3.3 mM)	2.6 ± 0.3	44 ± 3	55 ± 28[b]

[a] DNP, dinitrophenol; DCCD, dicyclohexylcarbodiimide.
[b] Initially high rate fell to near zero after 3 h.

Table VI. *Sodium and Potassium Uptake Rates and Percentage of Total Transpired Label Retained by the Mesocotyl over a 2-Hour Uptake Period*

Corresponding transpiration rates are given for each set of plants. Data are means ± SD ($n = 4$ except line 3b: $n = 8$).

	[K^+]	[Na^+]	Uptake		Retention		Transpiration
			K^+	Na^+	K^+	Na^+	
	mM		*μmol/g fresh wt·h*		%		*μl/plant·h*
1a	1	1	0.139 ± 0.009	1.87 ± 0.10	6 ± 1	77 ± 6	69 ± 20
1b				1.70 ± 0.23		39 ± 2	146 ± 13
2	1	10	0.095 ± 0.008	4.14 ± 0.19	4 ± 1	14 ± 2	84 ± 8
3a	10	1	3.13 ± 0.50	1.27 ± 0.17	18 ± 1	78 ± 4	50 ± 6
3b			2.42 ± 0.19	0.64 ± 0.08	33 ± 4	93 ± 2	23 ± 3
4	10	10	4.03 ± 1.15	4.11 ± 0.30	28 ± 7	36 ± 4	50 ± 11

in an effectively infinite volume of medium, the internal volume of the mesocotyl is small and depletable. Second, as depletion of the transpiration stream occurs, a diffusion gradient should be established increasing the entry of sodium to the mesocotyl over the rate calculated from transpiration alone. The combined result of these two effects at four sodium levels is shown in Figure 4. Using a minimum of 16 points (each representing a group of four plants) with the range of transpiration rates shown, a kinetic analysis of sodium uptake *versus* delivery (*i.e.* transpiration × concentration) was performed at each sodium concentration using Lineweaver-Burk and Eadie-Hofstee transformations. The results (Fig. 5) were similar with both methods yielding highly significant regression coefficients at each concentration except 5 mM, confirming that uptake at any given concentration reached a maximum when the replacement rate of ions was rapid. It should be reemphasized that, in the time period under consideration here, dyes penetrated the cortex through the cut surface of the mesocotyl to a distance of only about 1 mm. Thus, apoplastic movement and uptake by the cortex is not a reasonable explanation for these results.

DISCUSSION

In this paper, we have considered the uptake of sodium and potassium by the mesocotyl region of corn seedlings. The results indicate this region is important in the control of sodium transport to the leaves, at least during this period of development. After 8 d growth on a 45 mM sodium medium, the mesocotyl represented approximately 5% of the fresh weight of the plant but contained 25% of the total sodium in the plant. In this role, it is similar to the lower stem of *Phaseolus vulgaris* (8).

Quantitative consideration of the sodium removal capacity of the mesocotyl must take into account both the concentration of sodium and the retention or passage time of the ions in the mesocotyl region. That both factors are important is shown by Table VI and Figures 4 and 5. As transpiration-driven flow was increased, external limitations on the rate of sodium uptake by the mesocotyl were reduced and the sodium transport systems operated at the maximum possible rate at each concentration (Fig. 5). At low flow rates, on the other hand, an experimental limitation was encountered in that uptake was significantly higher than the apparent delivery of ions via transpiration. This was due to the movement of ions down the diffusion gradient and the high conductivity of the vessels. Disregarding these experimental limitations in the excised shoot system would lead to significant misinterpretation of the interrelationship between sodium uptake, sodium concentration, and transpirational delivery rate.

The results presented here may be compared to those of root uptake experiments, with the important caveat that, with roots, ions are delivered to the tissue from an essentially infinite, well-stirred external medium; whereas, in the mesocotyl experiments, the medium is internal, of small volume, and essentially unstirred, even at high transpiration rates. At equivalent rates of ion delivery, sodium uptake by the mesocotyl was considerably higher than potassium uptake (Fig. 1) and the proportion of the

sodium removed from the transpiration stream was much greater than that of the potassium removed (Table VI). Both the linearity of the sodium uptake with time (Fig. 1) and the apparent discrimination in favor of sodium accumulation over potassium represent distinct differences between the present experiments and those previously reported using low salt roots (1).

The shape of the uptake *versus* concentration curve in Figure 2 and of the saturated uptake relationship shown in Figure 5 (insert) are also noteworthy differences from roots (1). In root experiments, the line had a slope of approximately 1 on a logarithmic plot as would be expected for the passive permeation situation otherwise supported for that tissue. In the mesocotyl, as shown by the solid line in Figures 2 and 5, the slope on a logarithmic plot was approximately 0.5; influx was proportional to the square root of the sodium concentration. By association, this suggests that active transport may be involved since a similar slope was found for potassium uptake in low salt roots (2) as well as other systems where active transport has been established (*e.g.* 3). If active transport is involved, it remains to be seen which cells are specifically involved and what the mechanisms of flux to other cell types within the mesocotyl are. As this tissue is rather heavily cuticularized and the stele itself is surrounded by a well-developed endodermis, determination of cell potentials for electrophysiological analysis will be difficult.

Using the notation of Pitman (16, 17), we have been considering ϕ_{xc}, the flux from the xylem back to the symplasm. Pitman considered only the net chloride flux at this barrier (16), due to the inaccessibility of the individual fluxes. Jeschke *et al.*, following Pitman, have also considered the next flux at this barrier using sodium and potassium in barley and sunflower, but they have included the specific, additional assumption that this represented only ϕ_{cx}, *i.e.* that ϕ_{xc} was negligible (11, 12). Clearly, this assumption is incorrect in the case of corn. Taken with the results of Shone *et al.* (20), it is not unreasonable to expect that the same transport systems are present in both the root and mesocotyl stelar regions, and the mesocotyl may be useful, therefore, as a model, or 'plastic-coated' root for studies of efflux from the xylem. We explore this possibility further in the following paper by separating the stele from the cortex following the uptake period. It will be seen that intracellular compartmentation and transport in cells of the stele are very different from that in the root cortex, and that ion-specific barriers to movement within the symplast, particularly at the endodermis, control the distribution and redistribution of sodium to a much greater extent than potassium.

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