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Sodium and Potassium Fluxes and Compartmentation in Roots of *Atriplex* and Oat[1]

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ABSTRACT

K^+ and Na^+ fluxes and ion content have been studied in roots of *Atriplex nummularia* Lindl. and *Avena sativa* L. cv Goodfield grown in 3 millimolar K^+ with or without 3 or 50 millimolar NaCl. Compartmental analysis was carried out with entire root systems under steady-state conditions.

Increasing ambient Na^+ concentrations from 0 to 50 millimolar altered K^+, in *Atriplex*, as follows: slightly decreased the cytoplasmic content (Q_c), the vacuolar content (Q_v), and the plasma membrane influx and efflux. Xylem transport for K^+ decreased by 63% in *Atriplex*. For oat roots, similar increases in Na^+ altered K^+ parameters as follows: plasma membrane influx and efflux decreased by about 80%. Q_c decreased by 65%, and xylem transport decreased by 91%. No change, however, was observed in Q_v for K^+. Increasing ambient Na^+ resulted in higher (3 to 5-fold) Na^+ fluxes across the plasma membrane and in Q_c of both species. In *Atriplex*, Na^+ fluxes across the tonoplast and Q_v increased as external Na^+ was increased. In oat, however, no significant change was observed in Na^+ flux across the tonoplast or in Q_v as external Na^+ was increased. In oat roots, Na^+ reduced K^+ uptake markedly; in *Atriplex*, this was not as pronounced. However, even at high Na^+ levels, the influx transport system at the plasma membrane of both species preferred K^+ over Na^+.

Based upon the Ussing-Teorell equation, it was concluded that active inward transport of K^+ occurred across the plasma membrane, and passive movement of K^+ occurred across the tonoplast in both species. Na^+, in oat roots, was actively pumped out of the cytoplasm to the exterior, whereas, in *Atriplex*, Na^+ was passively distributed between the free space, cytoplasm, and vacuole.

Halophytic plants (*i.e.* those that can survive and reproduce in high salt environments) are thought to absorb and transport inorganic ions, especially Na^+, differently than glycophytes (7, 8). However, there are surprisingly little comparative data between a glycophyte and a halophyte concerning flux rates across specific cell membranes, the electrochemical driving force for various ions, the steady-state ion concentrations in various cell compartments, etc. The purpose of the present study was to provide information of this type using a representative glycophyte (oats, *Avena sativa* L.) and a representative halophyte (*Atriplex nummularia* Lindl.). Such information should help to elucidate the mechanisms of ion transport in these two major groups of plants, and this might ultimately lead to the conversion of a glycophyte into a halophyte or vice-versa, which could have a dramatic effect on where various crops are grown.

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Halophytes generally accumulate more inorganic ions, especially Na^+, than glycophytes, and Na^+ generally accumulates to higher levels in the shoots of halophytes (7, 8). Most glycophytes, on the other hand, accumulate K^+ and exclude Na^+ when availability of both ions is similar or even when Na^+ is higher (8).

According to compartmental analysis and electrochemical measurements, it has been inferred that most cations enter plant cells by an active process. In glycophytes, K^+ is believed to be passively distributed across the tonoplast and passively or actively transported inward across the plasma membrane, however, there are also a few reports that suggest active extrusion of potassium (13, 23). Na^+ seems to be actively secreted from the cytoplasm to the exterior and actively or passively transported into the vacuole. There are also a few reports which suggest an active Na^+ influx into the roots of glycophytes (see 24, and references therein).

In contrast to a large number of investigations on glycophytes, studies of ion fluxes and compartmentation in halophytes are few. Jeschke and Stelter (18, 21) suggested that K^+/Na^+ selectivity is high in the cytoplasm of *Atriplex* and similar to the selectivity in glycophytes. Low Na^+ in the cytoplasm was believed to be achieved by K^+/Na^+ exchange at the plasma membrane and Na^+/K^+ exchange at the tonoplast. The former exchange was found to vary between species and was poor in *Atriplex* (20) and some glycophytes (17). In *Atriplex*, secretion of Na^+ into the xylem was favored, resulting in low Na^+ concentrations in the symplasm (18). Contrary to the findings of Jeschke's group, others (10, 14, 37) have shown that Na^+ concentration in the cytoplasm of tissues of halophytes is rather high, *e.g.* 70 to 150 mM, which is similar to the K^+ concentration (14, 37) or even higher (10). Only one comprehensive study (14), involving efflux analysis and electrochemical measurements, has been conducted on a halophyte species (*Triglochin maritima*). It was shown that both K^+ and Na^+ were passively distributed between the various cellular compartments at external concentrations up to 4 and 100 mM, respectively. At Na^+ concentrations above 100 mM and K^+ concentrations above 4 mM, both ions seemed to be pumped out of the cytoplasm.

In the present study, we have used the same experimental conditions for both oats and *Atriplex* to determine the bidirectional flux rates of both K^+ and Na^+ across the plasma membrane and tonoplast, the unidirectional flux of ions into the xylem, as well as estimating the ion contents of the cytoplasm and vacuole, the permeability coefficients for K^+ and Na^+ at the plasma membrane and tonoplast, and finally the passive or active transport of these ions at the two membranes.

MATERIALS AND METHODS

Plant Cultures. Seeds of *Atriplex nummularia* Lindl. were imbibed overnight in deionized H_2O and germinated in vermiculite. Seedlings were transferred to half-strength Hoagland solution (12) when they were 1 to 2 cm in height (after 2–3

weeks). The solution was adjusted with KH_2PO_4 and K_2HPO_4 to give a final pH of 5.9 to 6.2 and a final potassium concentration of 3 mM. For certain experiments, 3 or 50 mM NaCl were added. The seedlings were grown for an additional 21 d (solutions changed at d 9, 18, and 20) in an environmental chamber with 14-h light/10-h dark, day-night temperatures of 28 and 22°C, respectively, and day-night RH of 60 and 85%, respectively. Light intensity was 500 μE m^{-2} s^{-1}. The solutions were continuously aerated. Water losses were compensated for in the periods between solution changes by adding deionized H_2O.

Seeds of oat (*Avena sativa* L. cv Goodfield) were germinated in vermiculite. After 1 week, the seedlings were transferred to the modified half-strength Hoagland solution. The seedlings were grown for an additional 14 d in an environmental chamber with a day and night temperature of 22°C, day and night RH of 60 and 85%, respectively, a photoperiod of 14 h-light/10-h dark, and light intensity of 215 μE m^{-2} s^{-1}. The solutions were changed on d 11 and 13. Oat seedlings were acclimated to 50 mM NaCl by increasing the salt level gradually; seedlings were transferred to solutions containing 10, 20, 35, and 50 mM NaCl on d 4, 7, 9, and 11, respectively.

Analyses of Root and Exudate Ion Content. Entire root systems of oat and *Atriplex* were washed briefly, blotted with paper towels, and weighed. Ions were extracted in boiling deionized H_2O using 10 ml per g fresh weight. Two successive extractions (15 min each) were performed. Exudates were collected from excised root systems to which a tygon tube had been attached. *Atriplex* plants were cut at the basal part of the stem and oat plants at the mesocotyl. Exudates were collected for 45 to 60 min with glass micropipets. The concentrations of Na^+ and K^+ in the tissue extracts and exudates were determined with a flame-emission spectrophotometer. Fluxes (μmol g^{-1} h^{-1}) of Na^+ and K^+ to the xylem vessels were calculated from the ion concentrations in the exudate, the volume produced in a specific time (see experiments), and the root weight.

Electrical Potential Measurements. Root systems of oat and *Atriplex* were excised as described above and mounted to the bottom of Petri dishes with modeling clay for electrical potential measurements. The different culture solutions served as the bathing solutions. Transmembrane PD[2] were measured with Ag/AgCl glass microelectrodes (filled with 3 M KCl) with tip resistances of 20 to 30 megohm coupled to a WPI (New Haven, CT) amplifier. The reference electrode was Ag/AgCl connected to the bath by an agar bridge. The output of the amplifier was displayed on a Gould Brush model 220 chart recorder. All measurements were performed at 20°C on mature cells 6 to 10 mm from the root tip.

Compartmental Efflux Experiments. For initiating the experiments involving the compartmental analysis, roots of intact seedlings of oat and *Atriplex* were immersed in 100 ml of one-half strength Hoagland solution, with or without NaCl, and labeled with $^{22}Na^+$ or $^{86}Rb^+$. The specific activities of the two isotopes ranged between 0.3 and 5×10^4 cpm $\mu$$mol^{-1}$ (see Tables II, a and b, and III). The absorption period was for 23 to 24 h in the environmental chamber where the plants were grown. After the absorption period, entire root systems were excised and exudate was collected for 15 to 20 min as described above. The roots were then washed briefly in nonradioactive half-strength Hoagland solution, placed in small beakers, and washed (with solution changes noted in the appropriate Figures) for 9 to 12 h in nonradioactive solutions that were vigorously stirred by forced aeration. During the washout period, exudate was collected, measured, and transferred to scintillation vials for counting. At the end of the washout, roots were blotted gently, weighed, and extracted as described above. Samples of extracts, washout solutions, and exudates were counted in a Beckman Liquid Scintillation system 6800 using scintillation cocktail of dioxane, ethoxyethanol, naphthalene, 2,5-diphenyloxazole, and 1,4-bis[2-(5-phenyloxazolyl)]benzene (3). Efflux experiments were carried out at 23°C.

Abbreviations and Symbols used for Flux Analysis. The various symbols and abbreviations used for the flux analysis were as follows:

o, c, v, x: external solution, cytoplasm, vacuole, xylem.

k_c, k_v: rate constants of tracer exchange of the cytoplasm (h^{-1}) and vacuole (h^{-1}).

s_o, s_c, s_v, s_x: specific activity of tracer in the external solution, cytoplasm, vacuole, and xylem (cpm $\mu$$mol^{-1}$).

$t_{1/2c}$, $t_{1/2v}$: half-times for replacement of cytoplasm (min) and vacuole (h) based upon k_c and k_v.

I_c, I_v: apparent tracer content of the cytoplasm or vacuole (μmol g^{-1}).

Q_c, Q_v, Q_x: cytoplasmic and vacuolar ion content (μmol g^{-1}), and xylem concentration (mM).

J_{oc}, J_{co}, J_{cv}, J_{vc}, J_{cx}, J_{xc}: flux from the external solution to cytoplasm, cytoplasm to external solution, cytoplasm to vacuole, vacuole to cytoplasm, cytoplasm to xylem, and xylem to cytoplasm, respectively (μmol g^{-1} h^{-1}).

R, R': net transport into the root and into the xylem, respectively (μmol g^{-1} h^{-1}).

J^*_{cor}: tracer efflux from roots to the external solution through the cortex (*cpm* g^{-1} h^{-1}).

Q^*_{cor}: tracer content in the root, only accounting for tracer loss via the cortex (surface) (cpm g^{-1}).

Q^*_T: total tracer content in the roots, accounting for tracer loss via cortex and xylem (cpm g^{-1}).

Analysis of Efflux Data. The amount of tracers in the different compartments, their specific activities and the membrane fluxes were estimated by the conventional theory and methods (see 36 and references therein). Since transport of ions to xylem vessels should be considered for proper interpretation of membrane fluxes (4, 28, 36), we have accounted for tracer loss to the exudate taking the approach of Davis and Higinbotham (4). Amounts (cpm) of $^{22}Na^+$ or $^{86}Rb^+$ appearing in the exudate were added to the amounts in the corresponding washout solutions. Since sufficient exudate could only be obtained after at least 15 min, the exudate content at earlier times was calculated as the amount per min over the 15-min period, and it was assumed that a linear rate of entry into the xylem occurred. Pitman (28) showed the existence of a lag between the release of tracer from the symplasm and its appearance at the cut surface. The lag was estimated to be 5 min in barley roots. We did not account for it in our calculations since it would have had only a minimal effect. The graphic analysis and calculations were performed as described by Davis and Higinbotham (4) with some modifications in the equations. The equations used for calculations of the various ions fluxes and contents were as follows:

$$J_{co} = k_c I_c + k_v Q_v \quad (1)$$

where Q_v, ionic content of the vacuole, was estimated from the total tissue content measured chemically minus the ion content in other compartments estimated by radioactivity. Since the tissue is regarded as being in steady-state or close to a steady state (see "Results and Discussion"), *i.e.* there was little or no net accumulation of ions by the root cells (36), R' and J_{cv} were defined as follows:

$$R = J_{oc} - J_{co} = J_{cx} - J_{xc} = R' \quad (2)$$

$$J_{cv} = J_{vc} = J_{oc} k_v Q_v / k_c I_c \quad (3)$$

For definitions, see earlier section on abbreviations and symbols. In this study, we did not determine J_{xc}, therefore J_{cx} cannot be estimated (28). Cytoplasmic content (Q_c) was estimated as:

$$Q_c = (J_{co} + J_{cv} + J_{cx})/k_c \quad (4)$$

and the specific activity of the cytoplasm was calculated as:

$$s_c = (J_{oc}\, s_o + J_{vc}\, s_v)/(J_{co} + J_{cv} + R') \quad (5)$$

[2] Abbreviation: PD, potential difference.

RESULTS AND DISCUSSION

Experimental Requirements for the Compartmental Analysis. A few conditions are required for the appropriate interpretation of tracer exchange kinetics as they relate to assessing ion fluxes and compartment contents. The tissue used should be at or very near a steady-state (36). To reach a steady-state condition, seedlings of oat and *Atriplex* were grown for relatively prolonged periods (14 and 21 d, respectively) in the appropriate nutrient solutions. The K^+ and Na^+ content of the tissue and concentrations in the exudate were determined for 2 d prior to the experiment and during the experiment, which consisted of two parts—tracer loading (24 h, roots being intact) and washout (9 h, roots being excised) (Fig. 1). The concentrations of Na^+ and K^+ in exudate and tissue in oat and of K^+ in exudate and tissue of *Atriplex* were steady throughout the 2 d prior to the experiment. The Na^+ content of *Atriplex* increased prior to root excision; however, during the experiment *per se* steady-state conditions prevailed. In contrast to the apparent steady-state in oat and *Atriplex* during the 72 h prior to plant detopping (Fig. 1), a deviation from steady-state occurred after excision, particularly in the case of K^+. Potassium content in both species declined slightly (Fig. 1A), and the K^+ concentration in the exudate of both species also decreased (Fig. 1B). Since there was a decrease in the volume flow of exudate (data not shown), the transport (concentration × volume flow) of K^+ to the xylem declined even faster. In *Atriplex*, sodium concentration increased immediately after root excision and dropped to about the initial level after 6 h.

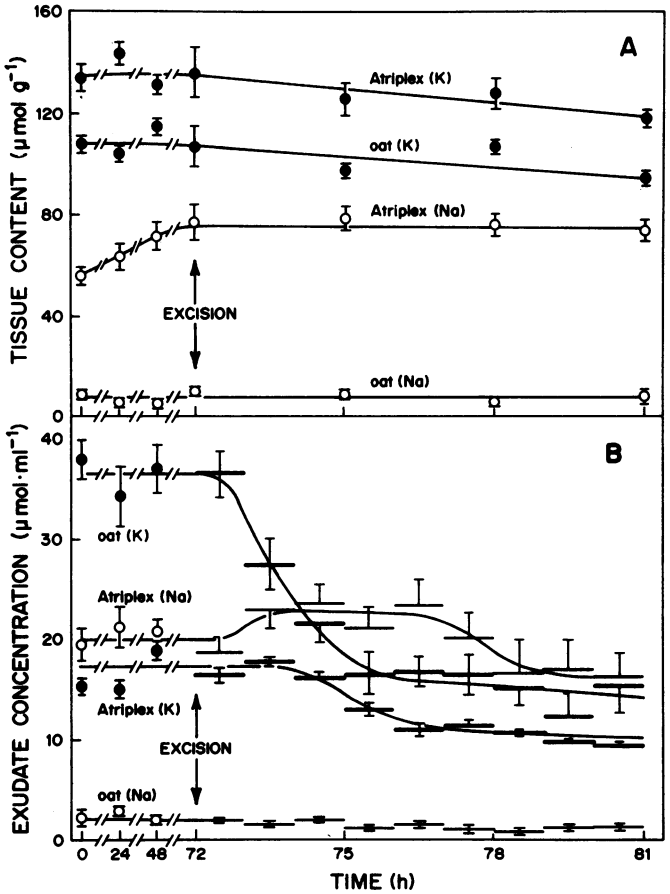

FIG. 1. Tissue content (A) and exudate concentration (B) of Na^+ and K^+ in oat and *Atriplex* roots grown in half-strength Hoagland solution plus 3 mM NaCl 2 d (48 h) prior to the efflux experiment and throughout the flux analysis experiment. The experiment was composed of a tracer loading period (24 h) and a washout period (9 h) in which the root systems were excised (shown by arrow). Values are the mean ± SD of three to five root systems.

Tissue content and exudate concentrations of K^+ in both species was near a steady-state condition 24 h after root excision, *i.e.* there was little net loss or uptake by the tissue (data not shown). However, in experiments not reported here, compartmental analysis of roots 24 h after excision revealed that $^{86}Rb^+$ fluxes and apparent contents in the tissue were impaired. Values of I_c were 0.75 and 0.45 μmol K^+/g for oat and *Atriplex*, respectively. These values were 18 and 24% of the values for roots that were excised just 20 min prior to the washout period (Table II). In addition, I_v values were 16 and 6% of the values of unexcised roots of oat and *Atriplex*, respectively. These results indicated that the excised tissue, after 24 h, was not in a steady-state condition. This is in agreement with the results of Pallaghy and Scott (26) who reported a decline in the values of the vacuolar and cytoplasmic apparent content of K^+ (I_c, I_v) of excised bean roots.

Because excised roots deviated from steady-state conditions, compartmental analysis should be carried out with intact plants. However, in order to estimate tracer efflux via the xylem, as well as the root surface, it was necessary to detop the plants after tracer loading and to monitor the ion content of the exudate. For evaluating the extent of deviation from the steady-state condition, due to shoot removal, we compared k_c, k_v, I_c, and I_v of only the cortical (surface) efflux of Na^+ and K^+ (*i.e.* Rb^+) in intact plants and in excised roots (Table I). The various parameters for intact plants were generally similar to those in detopped ones. The greatest deviations were as follows: k_c of K^+ in excised roots of *Atriplex* was higher than the value in intact plants. The value for I_v of Na^+ in excised roots of oat was lower than in intact plants. However, since the cortical efflux parameters were basically unaffected by the excision, we assumed that the tissue was still at, or very close to, steady-state prior to excision. It should be pointed out that regular (smooth) efflux curves were obtained when intact plants or excised roots of oat and *Atriplex* were used. One might have expected irregularities in the curves since a decrease in ion flux to the xylem could cause a transient increase in the root surface efflux. For example, irregular efflux curves have been observed by Erlandsson (6) and Jensen and Kylin (15) in intact plants. The latter suggested that changes in ion transport to the xylem, due to variation in transpiration, might vary the efflux of tracer through the surface. In addition, Jeschke and Jambor (19) reported irregularities in efflux from intact seedlings in the presence of potassium, particularly when K^+ was added a few hours before the efflux experiment. They suggested that such irregularities indicated some deviation from a steady-state condition. Our observation of a lack of irregularities in the efflux curves of intact and detopped oat and *Atriplex* also supports our assumption that the tissue is in, or very close to, a steady-state condition.

A further test of the validity of the compartmental analysis is that a plot of log content (Q^*_t) *versus* time and log efflux (dQ^*_t/dt) *versus* time should both yield curves fitted by the same number of components and the same rate exchange constants (23, 36). This similarity is demonstrated for Na^+ rate exchange constants k_c and k_v of the cortical efflux in oat roots (Fig. 2). Curve comparisons were made for the various efflux experiments. The values of k_c of the log content and log efflux plots were usually similar for Na^+ and K^+ in oat and *Atriplex*, however, occasionally there was a discrepancy in the k_v values between the two plots. This was more common for K^+ than Na^+. In general, the two types of plots gave similar results, and it was concluded that both oat and *Atriplex* roots behaved as a three-compartment system (free space, cytoplasm, and vacuole).

The Combined Tracer Efflux, *i.e.* via the Cortex and Xylem.

Table I. *Effect of Shoot Removal on the Cortical (Surface) Efflux Parameters of Na^+ and K^+ (Rb^+) in Atriplex and Oat*

Plants were grown in nutrient solution plus 3 mM NaCl and exposed to tracers while intact. Roots were excised 20 min prior to the washout period.

	Atriplex				Oat			
	Na^+		K^+ (Rb^+)		Na^+		K^+ (Rb^+)	
	Intact	Excised	Intact	Excised	Intact	Excised	Intact	Excised
k_v ($10^3 \cdot h^{-1}$)	6.17 ± 1.1[a]	5.60 ± 1.8	4.22 ± 1.72	3.83 ± 0.42	13.70 ± 3.78	17.6 ± 2.93	4.45 ± 1.49	4.48 ± 1.33
$t_{½v}$ (h)	112.3	123.7	164.2	180.9	50.6	39.4	155.7	154.7
k_c (h^{-1})	0.95 ± 0.19	0.98 ± 0.29	0.73 ± 0.16	1.02 ± 0.21	1.27 ± 0.57	1.64 ± 0.49	0.45 ± 0.07	0.47 ± 0.06
$t_{½c}$ (min)	43.8	42.4	57.0	40.8	32.7	25.3	92.4	88.5
I_v (μmol/g)	18.45 ± 6.45	19.32 ± 5.19	27.76 ± 13.92	33.22 ± 15.1	0.68 ± 0.4	0.43 ± 0.08	19.66 ± 4.47	17.59 ± 6.32
I_c (μmol/g)	0.85 ± 0.25	1.18 ± 0.32	0.89 ± 0.39	1.13 ± 0.64	0.13 ± 0.05	0.1 ± 0.025	1.35 ± 0.57	1.69 ± 0.51

[a] Mean ± SD of six determinations.

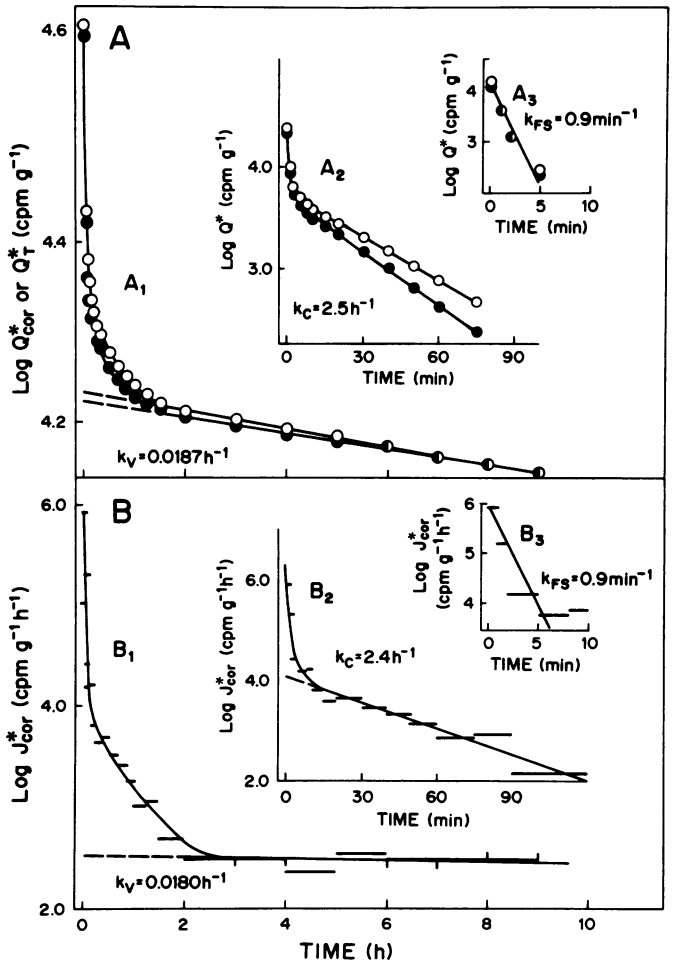

FIG. 2. Loss of $^{22}Na^+$ from root system of oat seedling grown in half-strength Hoagland solution plus 3 mM NaCl, via the surface (O) or surface plus xylem (●). A, loss of tracer content; B, rate of tracer efflux. Insets show: (a) tracer loss from the cytoplasmic component calculated by subtracting the slow (vacuolar) exchange component from the overall curves; (b) tracer loss from the free space calculated by subtracting the slow and the intermediate (cytoplasmic) exchange components from the overall curves.

Loss of tracer from cytoplasm and vacuole of root cells occurs via the xylem as well as the root surface (cortex). It is important to account for the tracer flux to the xylem in order to accurately assess the various fluxes (4, 19, 28). Pitman (28) has shown that about 75% of tracer diffusion out of barley root cells passed to the solution through the stele; however, this flux was less than 4% in the halophyte *Triglochin maritima* (14). In view of this difference, we analyzed the K^+ and Na^+ fluxes in oat and *Atriplex* by the two methods used by Davis and Higinbotham (4). By one method, the tracer efflux through the root surface only has been plotted, and the various parameters have been calculated. By the other method, the loss of tracer to both the exudate and the root surface were evaluated. Exudation rates were slower in *Atriplex* than in oat and ceased about 4 h after excision when only small amounts of tracers were found in the exudate. Therefore, from that point onward, vacuolar loss occurred only through the root surface (Fig. 3, B and C). Data of Fig. 3, B and C show that tracer movement out of *Atriplex* roots through the xylem was 8 and 16% of the total loss for K^+ (*i.e.* Rb^+) and Na^+, respectively. Root systems of oat exuded for the entire length of the efflux experiment at a steadily declining rate. Large amounts of K^+ (*i.e.* Rb^+) appeared in the exudate—33% of the total (Fig. 3A); in contrast, only 3% of the total Na^+ was transported to the xylem (Fig. 2). The various parameters of the efflux experiments, with or without accounting for the xylem efflux, are compared in Table II. The cytoplasmic specific activity (s_c) did not reach the external specific activity (s_o). Specific activity of the cytoplasm (s_c) was 66–89% of s_o as calculated by equation 5. These lower values are expected because of the removal of ions from the cytoplasm (36). In *Atriplex* roots, s_c for sodium and potassium were similar, and they were also similar for the two methods of estimation. In oat roots, however, s_c values for potassium were higher and therefore more realistic when tracer losses via both surface and xylem were considered. The opposite was true for sodium, although the differences were not large. Both k_c and k_v in oat and *Atriplex* were similar for Na^+ and K^+ with both methods. In oat, I_c for K^+ (*i.e.* Rb^+) was much higher when both surface and xylem fluxes were combined. This was not the case with Na^+. In *Atriplex*, values of I_c for both ions were only slightly higher using the second method. Values of I_v obtained by the two methods were the same in both species. The higher I_c value for K^+ in oat, when xylem data were included, caused higher values for J_{co} and J_{oc}, lower values for J_{vc} and J_{cv}, and slightly higher values for Q_c. The same differences were observed in *Atriplex* for both ions, but to a lesser extent. These data illustrate that in *Atriplex* the error in the compartmental analysis would be minor by neglecting the tracer efflux through the xylem. This was also true for Na^+ in oat roots, however, K^+ transport to the xylem in oats is too high to be neglected. For a unified procedure, both surface and xylem fluxes were combined in both plants in the experiments described below.

Estimates of Na^+ and K^+ Fluxes and Content. Six to nine efflux experiments were conducted for each ion (Na^+ and K^+) for both species grown at one K^+ concentration (3 mM) and at three different NaCl concentrations (0, 3, or 50 mM). The data

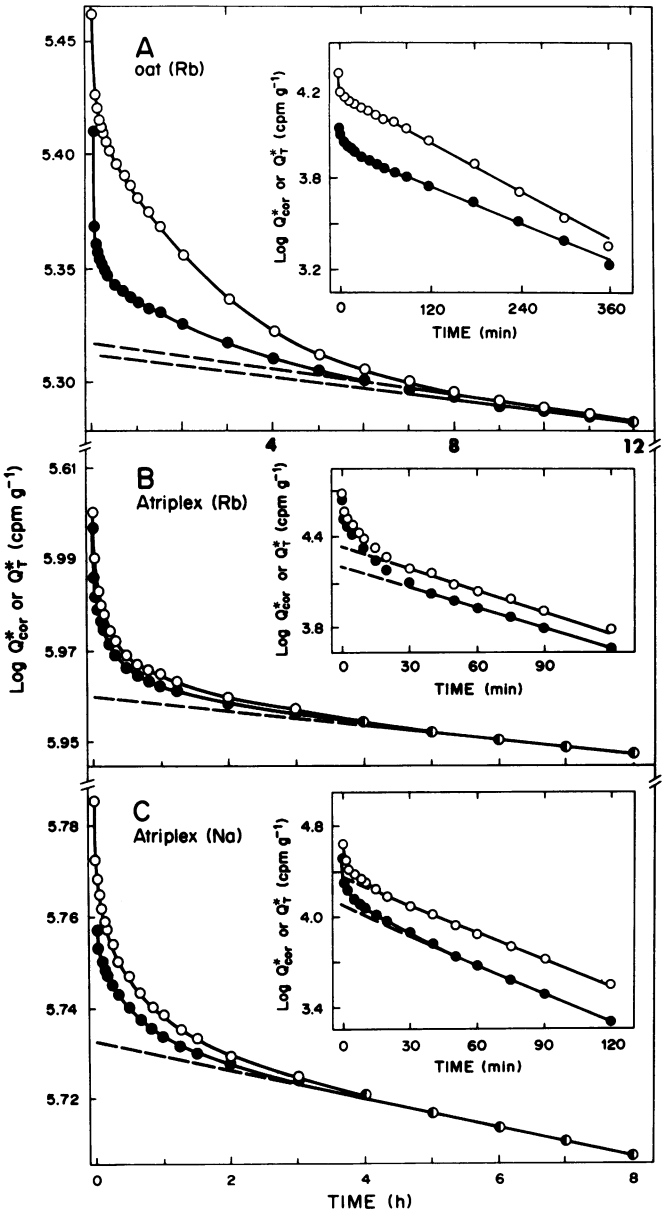

FIG. 3. Loss of $^{86}Rb^+$ from roots of oat (A) and *Atriplex* (B) and loss of $^{22}Na^+$ (C) from roots of *Atriplex* via the cortex (O) or cortex plus xylem (●). Plants were grown in half-strength Hoagland solution plus 3 mM NaCl. Insets show the loss from the cytoplasmic component, calculated by subtracting the slow (vacuolar) exchange component from the overall curves.

are presented in Tables II and III. The values of k_v for K^+ in *Atriplex* were similar to those in oat, however, the values of k_c for K^+ were 2-fold lower in oat. In *Atriplex*, the values of k_v for Na^+ were similar to those for K^+, whereas in oat the k_v for Na^+ was 3- to 4-fold higher than for K^+. These results show that retention of both ions in vacuoles of *Atriplex* roots is similar (note $t_{1/2v}$, Table III) and also similar to that of K^+ in oat roots, whereas the retention of Na^+ in vacuoles of oat root cells was much poorer. The long vacuolar half-time (120–130 h) of Na^+ reported here for *Atriplex* is in contrast to the short half-time (18 h) reported for other halophytes, *i.e. Suaeda* (37) and *Triglochin* (14). In general, k_c and k_v for the two ions, compartments, and plants were not changed when the roots were exposed to different salinity levels (Tables II and III).

The various flux rates and compartment contents were estimated according to equations 1 to 5 and are presented in Tables IV and V for K^+ and Na^+, respectively. Table IV shows that the fluxes of K^+ are similar in roots of oat and *Atriplex* at 0 and 3 mM external NaCl. However, at the higher ambient NaCl concentration (50 mM), K^+ fluxes in oat roots were impaired by about 80%. In particular, the fluxes across the plasma membranes and transport to the xylem were reduced. The concentration of K^+ in the exudate of oat roots did not change at the high salinity; the decrease in transport was due to a reduction in exudate volume flow. In *Atriplex* roots, the high salinity caused only a moderate decrease in K^+ fluxes. In both species, 50 mM NaCl did not affect K^+ fluxes across the tonoplast. Cytoplasmic concentration of K^+ was 2-fold higher in oat roots compared to *Atriplex* roots at 0 and 3 mM external NaCl, however, at the high NaCl concentration the Q_c dropped to a lower value than in *Atriplex*. In *Atriplex*, salinity caused only a slight drop in cytoplasmic potassium (Q_c). Salinity had different effects on vacuolar K^+ (Q_v) in the two species; increasing Na^+ caused a decrease in vacuolar K^+ in *Atriplex* roots but had little or no effect in oat roots. In both species, concentration of K^+ in the xylem was unchanged when plants were grown with different NaCl concentrations in the medium.

Table V shows the fluxes of Na^+ and compartment contents of Na^+ in *Atriplex* and oat roots. In general, Na^+ fluxes and compartment contents were higher in *Atriplex*. Also, in the two species, raising NaCl from 3 to 50 mM caused an increase in almost all parameters of sodium transport. It should be noted, though, that Na^+ fluxes across the tonoplast were increased in *Atriplex* roots but not in oat roots, yet Q_v of sodium increased in both *Atriplex* and oat root cells. The flux of Na^+ from the cytoplasm to the exterior, J_{co}, increased more in oat roots than in *Atriplex*. In addition, sodium concentration in the xylem increased tremendously in oat roots, however, due to low volume flow, very little Na^+ was transported into the xylem.

Transmembrane Electropotential Differences. Transmembrane PD measurements were obtained with microelectrodes, and the data are given in Table VI. It was assumed that the potential differences reported were between the external solution and the cortical cell vacuole. The PD values reported here for oat roots were very similar to the ones reported by Higinbotham *et al.* (11) for oat roots, namely −84 and −71 mv for 1× and 10× nutrient solutions, respectively. In *Atriplex* roots, the PD values were somewhat low but within the range reported for other plant cells (29). PD values around −130 mv have been reported for roots of *Atriplex hastata* (1).

Cytoplasmic Volume and Membrane Surface Area Estimates. Surface area of membranes was needed for estimating permeability coefficients, and the parameters involved in making these estimates are shown in Table VII. Air space volume in roots of *Atriplex* and oat were estimated by measuring the area of the intercellular spaces in hand-cut cross sections of mature roots. Based upon cell diameter and length measurements and considering the cells as circular cylinders, volumes of the cell, the cell wall, protoplast, cytoplasm, and vacuole were estimated. The cytoplasm volume was estimated as 5% of the tissue volume in both oat and *Atriplex* roots, assuming the thickness of the cytoplasm to be 0.5 μm (24). Based upon cell number per g tissue and cell dimensions, the plasma membrane and tonoplast surface areas were calculated. Cell numbers per g roots was 2-fold higher in *Atriplex* than in oat because *Atriplex* cells were shorter and the root diameter was larger; this resulted in a higher (2-fold) membrane surface area per g of tissue in *Atriplex* roots (Table VII).

Flux Ratios and Fit to Ussing-Teorell Flux Ratio Equation. Based upon measured fluxes and PD across the membrane and on ion concentrations on the two sides of the membrane, it is possible to test for active or passive ion distributions with the

Table IIa. *Ion fluxes, Concentrations, and Various Parameters Estimated from Tracer Efflux via Cortex (Surface) or Cortex plus Xylem in Atriplex Roots Grown in Nutrient Solution plus 3 mM NaCl*

Parameter	*Atriplex*			
	K^+ (Rb^+)[a]		Na^+[b]	
	Cortex	Cortex + xylem	Cortex	Cortex + xylem
$k_v \cdot 10^3$ (h^{-1})	4.62 ± 2.22[c]	4.75 ± 2.75	5.91 ± 1.59	5.93 ± 1.60
k_c (h^{-1})	1.17 ± 0.46	0.99 ± 0.32	1.06 ± 0.26	0.97 ± 0.22
I_c ($\mu mol \cdot g^{-1}$)	1.51 ± 0.67	1.89 ± 0.74	1.10 ± 0.33	1.49 ± 0.39
I_v/t ($\mu mol \cdot g^{-1} \cdot h^{-1}$)	1.85 ± 0.23	1.85 ± 0.23	0.86 ± 0.23	0.86 ± 0.23
Q_c ($\mu mol \cdot g^{-1}$)	5.54 ± 1.62	6.76 ± 2.77	2.64 ± 0.41	3.07 ± 0.45
Q_v ($\mu mol \cdot g^{-1}$)	139.7 ± 12.8	139.6 ± 12.8	57.6 ± 12.2	57.4 ± 12.0
J_{oc} ($\mu mol \cdot g^{-1} \cdot h^{-1}$)	4.24 ± 0.97	4.42 ± 0.86	2.14 ± 0.69	2.48 ± 0.78
J_{co} ($\mu mol \cdot g^{-1} h^{-1}$)	2.29 ± 0.74	2.45 ± 0.84	1.54 ± 0.54	1.88 ± 0.62
$J_{cv} = J_{vc}$ ($\mu mol \cdot g^{-1} h^{-1}$)	1.68 ± 0.53	1.70 ± 0.77	0.66 ± 0.30	0.58 ± 0.24
$S_o \cdot 10^{-4}$ ($cpm \cdot \mu mol^{-1}$)	1.2		2.1	
S_c (% of S_o)	79	82	89	86

[a] $n = 8$. [b] $n = 9$. [c] Mean ± SD.

Table IIb. *Ion Fluxes, Concentrations, and Various Parameters Estimated from Tracer Efflux via Cortex (Surface) or Cortex plus Xylem in Oat Roots Grown in Nutrient Solution plus 3 mM NaCl*

Parameter	Oat			
	K^+ (Rb^+)[a]		Na^+[b]	
	Cortex	Cortex + xylem	Cortex	Cortex + xylem
$k_v \cdot 10^3$ (h^{-1})	4.52 ± 1.13[c]	5.09 ± 1.27	14.3 ± 3.8	15.2 ± 3.2
k_c (h^{-1})	0.48 ± 0.10	0.48 ± 0.05	1.77 ± 0.46	1.71 ± 0.44
I_c ($\mu mol \cdot g^{-1}$)	1.72 ± 0.46	4.10 ± 1.12	0.11 ± 0.04	0.12 ± 0.03
I_v/t ($\mu mol \cdot g^{-1} \cdot h^{-1}$)	1.04 ± 0.32	1.05 ± 0.33	0.019 ± 0.002	0.019 ± 0.002
Q_c ($\mu mol \cdot g^{-1}$)	10.5 ± 3.0	11.2 ± 1.9	0.39 ± 0.09	0.41 ± 0.09
Q_v ($\mu mol \cdot g^{-1}$)	110.5 ± 15.1	108.7 ± 14.3	7.66 ± 2.4	7.65 ± 2.4
J_{oc} ($\mu mol \cdot g^{-1} \cdot h^{-1}$)	2.98 ± 0.64	4.19 ± 0.99	0.41 ± 0.09	0.43 ± 0.09
J_{co} ($\mu mol \cdot g^{-1} h^{-1}$)	1.31 ± 0.25	2.52 ± 0.61	0.30 ± 0.11	0.32 ± 0.10
$J_{cv} = J_{vc}$ ($\mu mol \cdot g^{-1} h^{-1}$)	2.00 ± 0.79	1.15 ± 0.29	0.25 ± 0.09	0.25 ± 0.09
$S_o \cdot 10^{-4}$ ($cpm \cdot \mu mol^{-1}$)	1.2		2.1	
S_c (% of S_o)	66	86	72	66

[a] $n = 9$. [b] $n = 6$. [c] Mean ± SD.

Table III. *Various Efflux Parameters for K^+ (Rb^+) and Na^+ in Roots of Oat and Atriplex Grown in Nutrient Solution (3 mM K^+) with or without 50 mM NaCl*

Tracer efflux via xylem was combined with the root surface efflux.

Parameter	*Atriplex*			Oat		
	0 mM NaCl[a]	50 mM NaCl[b]		0 mM NaCl[a]	50 mM NaCl[a]	
	K^+ (Rb^+)	K^+ (Rb^+)	Na^+	K^+ (Rb^+)	K^+ (Rb^+)	Na^+
$k_v \cdot 10^{-3}$, (h^{-1})	3.08 ± 0.48[c]	4.85 ± 1.23	5.32 ± 2.66	4.6 ± 0.73	3.52 ± 0.32	13.7 ± 2.6
$t_{\frac{1}{2}} v$ (h)	231	143	130	151	197	51
k_c (h^{-1})	1.03 ± 0.13	1.32 ± 0.62	1.12 ± 0.16	0.48 ± 0.06	0.42 ± 0.1	1.16 ± 0.32
$t_{\frac{1}{2}} c$ (min)	40	32	37	87	99	36
$I_v/_{tup}$ ($\mu mol \cdot g^{-1} \cdot h^{-1}$)	2.13 ± 0.24	1.13 ± 0.45	1.66 ± 0.43	1.31 ± 0.05	0.53 ± 0.13	0.27 ± 0.05
I_c ($\mu mol \cdot g^{-1}$)	2.68 ± 0.95	1.78 ± 0.65	5.08 ± 1.37	1.31 ± 0.05	0.86 ± 0.3	1.33 ± 0.31
$S_o \cdot 10^{-4}$ ($cpm \cdot \mu mol^{-1}$)	1.0	1.6	0.3	1.0	2.1	5.0
S_c (% of S_o)	88	80	91	89	57	95

[a] $n = 7$. [b] $n = 6$. [c] Mean ± SD of n determinations.

Ussing-Teorell flux ratio equation (34, 35):

$$J^{in}/J^{out} = C_j^o/C_j^i \; exp(z_j \, FE/RT) = a_j^o/a_j^i \qquad (6)$$

where J^{in} and J^{out} are the inward and outward fluxes across the membrane; C^i and C^o are the ion activities in the interior and exterior; a^i and a^o ($= C^o \, exp[zFE/RT]$) are the electrochemical activities on each side of the membrane, F is the Faraday; R the gas constant; T the absolute temperature, and E is the electrical PD across the membrane. This equation tests for independent passive movement of an ion when there is a net flux of an ion across the membrane. When the experimental flux ratio equals or is close to the predicted flux ratio (electrochemical activity ratio), one can conclude that the movement of the ion is passive. When the measured flux ratio is greater or smaller than the predicted, one can assume active transport inward or outward, respectively. The measured flux ratios, which are given in Table

Table IV. *K^+ (Rb^+) Fluxes ($\mu mol \cdot g^{-1} \cdot h^{-1}$) and Compartment Contents ($\mu mol \cdot g^{-1}$ or mM) in Roots of Oat and Atriplex Grown in Nutrient Solution (3 mM K^+) with or without 3 or 50 mM NaCl*

The various parameters were calculated from the data in Tables II and III. The concentrations in the vacuole and cytoplasm were calculated using the volume estimates in Table VI.

Parameter	*Atriplex*			Oat		
	0 mM NaCl	3 mM NaCl	50 mM NaCl	0 mM NaCl	3 mM NaCl	50 mM NaCl
Q_c $\mu mol \cdot g^{-1}$	6.79 ± 1.39	6.76 ± 2.77	4.51 ± 2.14	11.9 ± 0.9	11.2 ± 1.9	4.11 ± 0.77
mM	135.8	135.2	90.2	238	224	82.2
Q_v $\mu mol \cdot g^{-1}$	171.6 ± 1.4	139.6 ± 12.8	126.0 ± 8.6	94.7 ± 16.7	108.7 ± 14.3	90.2 ± 3.2
mM	195.0	158.6	143.2	108.9	124.9	103.7
Q_x mM	28.7 ± 8.8	38.4 ± 6.0	31.7 ± 5.2	20.0 ± 2.6	21.8 ± 3.1	25.9 ± 2.6
R'	2.46 ± 0.86	1.97 ± 0.55	0.90 ± 0.47	1.86 ± 0.43	1.67 ± 0.56	0.16 ± 0.04
J_{oc}	5.77 ± 1.29	4.42 ± 0.86	3.86 ± 1.38	4.92 ± 1.23	4.19 ± 0.99	0.86 ± 0.22
J_{co}	3.31 ± 1.22	2.45 ± 0.84	2.97 ± 1.23	3.06 ± 0.88	2.52 ± 0.61	0.70 ± 0.19
$J_{vc} = J_{cv}$	1.13 ± 0.18	1.70 ± 0.77	1.25 ± 0.79	0.85 ± 0.26	1.15 ± 0.29	0.81 ± 0.23

Table V. *Na^+ Fluxes ($\mu mol \cdot g^{-1} \cdot h^{-1}$) and Compartment Contents ($\mu mol \cdot g^{-1}$ or mM) in Roots of Oat and Atriplex Grown in Nutrient Solution (3 mM K^+) with 3 or 50 mM NaCl*

The various parameters were calculated from the data in Tables II and III. The concentrations in the vacuole and cytoplasm were calculated using the volume estimates in Table VI.

Parameter	*Atriplex*		Oat	
	3 mM NaCl	50 mM NaCl	3 mM NaCl	50 mM NaCl
Q_c ($\mu mol \cdot g^{-1}$)	3.07 ± 0.45	9.91 ± 3.55	0.41 ± 0.09	1.98 ± 0.67
(mM)	61.4	198.2	8.2	38.8
Q_v ($\mu mol \cdot g^{-1}$)	57.4 ± 12.0	108.9 ± 12.0	7.6 ± 2.4	12.2 ± 4.0
(mM)	65.2	123.8	8.7	14.0
Q_x (mM)	17.4 ± 4.5	74.9 ± 8.4	1.3 ± 0.2	38.2 ± 13.5
R'	0.60 ± 0.29	3.44 ± 1.84	0.11 ± 0.07	0.3 ± 0.27
J_{oc}	2.48 ± 0.78	9.79 ± 3.67	0.43 ± 0.09	1.98 ± 0.53
J_{co}	1.88 ± 0.62	6.35 ± 2.33	0.32 ± 0.1	1.68 ± 0.48
$J_{vc} = J_{cv}$	0.58 ± 0.26	1.25 ± 0.58	0.25 ± 0.09	0.22 ± 0.09

Table VI. *Cell Membrane Potentials in Roots of Atriplex and Oat*

Two sets of root systems (I and II) grown at three different NaCl concentrations were measured on three different roots in the region of 6 to 10 mm from the root tip. Number of impalements were 2 to 4 per root.

Ambient NaCl Concentration (mM)		Membrane Potential	
		Atriplex	Oat
0	I	−45.6 ± 6.6[a]	−82.7 ± 6.7
	II	−48.4 ± 5.7	−75.3 ± 3.4
3	I	−60.5 ± 1.2	−83.1 ± 11.4
	II	−58 ± 2.5	−83.1 ± 0.7
50	I	−31.9 ± 2.5	−69.3 ± 6.6
	II	−60.5 ± 3.7	−48.0 ± 9.0

[a] Mean ± SE.

Table VII. *Dimensions of Mature Cortical Cells, Compartments, and Membrane Surface Area of Roots of Atriplex and Oat*

	Atriplex	Oat
Root diameter (μm)	540	464
Cell length (μm)	160	220
Cell diameter (μm)	48	47
Space vol (% of tissue vol)	2	3
Cell vol ($10^4 \times mm^3$)/cell	2.9	3.7
(% of tissue vol)	98	97
Cell wall vol (% of tissue vol)	5	5
Protoplast vol (% of tissue vol)	93	92
Cytoplasm vol (% of tissue vol)	5	5
Vacuole vol (% of tissue vol)	88	87
Cell number/g tissue	7×10^6	2.9×10^6
Plasma membrane surface area ($cm^2 \cdot g^{-1}$)	1,560	880
Tonoplast surface area ($cm^2 \cdot g^{-1}$)	1,520	860

VIII, were calculated from the data in Tables IV and V. Actual flux ratios across the tonoplast equal 1 since J_{vc} and J_{cv} were assumed to be equal in steady-state conditions. Two sets of data (Table VIII) for the predicted flux ratios across the two cell membranes were calculated, one assuming no PD across the tonoplast and the other assuming a PD of +15 mv (vacuole positive). In the latter case, the PD across the plasma membrane was corrected by adding −15 mv to the measured PD. Based upon the differences between the experimental and predicted flux ratios (Table VIII), it seemed that potassium moved inward across the plasma membrane of both species by an active process and moved across the tonoplast passively. Sodium was passively distributed between the three compartments in *Atriplex* roots; however, in oat roots, Na^+ was actively extruded from the cytoplasm across the plasma membrane by an active process. Since the tissue was regarded as being close to equilibrium, *i.e.* no net accumulation of ions and therefore $J_{cv} = J_{vc}$, the Nernst equation could also be used as a test for passive movement across the tonoplast (13). The predicted concentration ratios (on the two sides of the tonoplast) using either $E = 0$ or +15 mv as tonoplast PD, were similar to the experimental ones (data not shown). Or, if one uses the cytoplasmic and vacuolar ion concentrations, the estimated E_{vc} across the tonoplast is in the range of −10 to +25 mv for the two ions in both plants at the various external NaCl concentrations. Since this PD is believed to exist between the cytoplasm and vacuole, it reinforces our conclusion

Table VIII. *Experimental (J_{in}/J_{out}) and Predicted (a_j^o/a_j^i) Flux Ratios across the Plasma Membrane and Tonoplast in Roots of Oat and Atriplex*

The experimental flux ratios were calculated from fluxes given in Tables IV and V. Membrane potential data are the average values given in Table VI. The predicted flux ratios were calculated by the Ussing-Teorell equation (Equation 6 in text) using concentrations given in Tables V and VI. Predicted flux ratios were estimated by assuming a PD across the tonoplast of either 0 or +15 mv (vacuole position).

NaCl (mM)	Ion	Cell Compartment	J_{in}/J_{out}	E_{cv} = 0 mv		E_{cv} = 15 mv	
				E (mv)	a_j^o/a_j^i	E (mv)	a_j^o/a_j^i
Oat							
0	K^+	Cytoplasm	1.6	−79	0.3	−94.0	0.54
		Vacuole	1.0	0	2.2	+15	1.2
3	K^+	Cytoplasm	1.7	−83.1	0.37	−98.1	0.68
		Vacuole	1.0	0	1.79	+15	0.98
	Na^+	Cytoplasm	1.2	−83.1	10.1	−98.1	18.5
		Vacuole	1.0	0	0.94	+15	0.52
50	K^+	Cytoplasm	1.2	−58.6	0.48	−73.6	0.69
		Vacuole	1.0	0	0.79	+15	0.43
	Na^+	Cytoplasm	1.2	−58.6	13.5	−73.6	24.6
		Vacuole	1.0	0	2.77	+15	1.52
Atriplex							
0	K^+	Cytoplasm	1.7	−47.0	0.14	−62	0.26
		Vacuole	1.0	0	0.70	+15	0.38
3	K^+	Cytoplasm	1.8	−59.2	0.24	−74.2	0.43
		Vacuole	1.0	0	0.85	+15	0.47
	Na^+	Cytoplasm	1.3	−59.2	0.52	−74.2	0.96
		Vacuole	1.0	0	0.94	+15	0.52
50	K^+	Cytoplasm	1.3	−46.2	0.21	−61.2	0.38
		Vacuole	1.0	0	0.61	+15	0.33
	Na^+	Cytoplasm	1.5	−46.2	1.59	−61.2	2.9
		Vacuole	1.0	0	1.6	+15	0.88

Table IX. *Permeability Coefficients (P) for K^+ and Na^+ across the Plasma Membrane and Tonoplast of Cortical Cells of Atriplex and Oat*

P_K and P_{Na} values were calculated according to the Goldman net flux equation (see text). Membrane surface values are given in Table VII. PD values across the tonoplast are estimated to be +15 mv and across the plasma membrane as in Table VIII.

Ambient NaCl (mM)	Ion	$P_j \times 10^8$ cm·S^{-1}			
		Atriplex		Oat	
		Plasma membrane	Tonoplast	Plasma membrane	Tonoplast
0	K^+	0.16	0.14	0.10	0.34
3	K^+	0.10	0.26	0.09	0.40
	Na^+	4.70	0.21	1.12	1.21
50	K^+	0.22	0.21	0.38	0.34
	Na^+	1.30	0.24	0.40	0.69

of passive movements of both ions across the tonoplast in root cells of both species.

Permeability Coefficients. Sodium and potassium permeability coefficients were compared in oat and *Atriplex* roots (Table IX), using the Goldman net flux equation (9). Since this equation can be applied to passive fluxes, the outward fluxes of K^+ and the inward fluxes of Na^+ were used for calculating the permeability coefficients across the plasma membrane and outward fluxes of both ions across the tonoplast by the following equations:

$$J^{in} = -P_j\, z_j FE\, C_j^o/RT(1 - exp\, z_j\, FE/RT) \quad (7)$$

$$J^{out} = P_j\, z_j\, FE\, C_j^i\, exp(z_j\, FE/RT)/RT(1 - exp\, z_j\, FE/RT) \quad (8)$$

P_j is the permeability coefficient and other notations are as used before. P_K values for both membranes were similar in roots of oat and *Atriplex*. P_{Na} values were higher than P_K values in both plants, particularly for the plasma membrane of *Atriplex*. P_K and P_{Na} values were in the range reported for other plant membranes (27).

DISCUSSION

First applications of the compartmental analysis in plant tissue were for giant algal cells where it was shown that the cell wall, cytoplasm, and vacuole behaved as three compartments in series (25). This technique has subsequently been applied many times to various plant tissues. However, concern about the validity of this procedure was raised regarding the heterogeneity and organization of certain tissues (36). It was shown, for instance, by Behl and Jeschke (2) that the cytoplasm exchange of ions of the meristematic region of roots was different than that of the differentiated region. Root tissues differ also from algal cells because roots can absorb ions at the outer surface and secrete them internally into the xylem. This means that even at steady-state conditions a net flux of ions is passing through the root cells. The first to acknowledge and account for this difference was Pitman (28) who measured ion fluxes from the cortex and at the cut end of excised roots. This method was used by Jeschke (16) and Macklon (24). Jeschke and Jambor (19) and Davis and Higinbotham (4) have also used roots of intact plants, measuring ion uptake and transport to shoots. In the present study, we show that for highly transported ions such as potassium, a serious error

would have resulted if transport via the stele had not been taken into account (Table II). If we had only taken the surface efflux into account, the conclusions made concerning the driving force for ion fluxes would have been correct, however, when we included the xylem component the magnitude of the differences between low and high salinity were much greater (see Tables II and IV). In *Atriplex*, due to low ion transport to the xylem, the various ion fluxes and contents were similar for the two sets of data, *i.e.* with or without accounting for tracer loss in the exudate (Table II). The differences in tracer movement via the stele between oat and *Atriplex* agree with other reports where the importance of ion transport to the xylem in compartmental analysis has been demonstrated in glycophytes (4, 19, 28) but seemed to be negligible in halophytes (14). The use of $^{86}Rb^+$ as a tracer for K^+ in the compartmental analysis also needs to be mentioned. There have been doubts expressed about $^{86}Rb^+$ being a satisfactory tracer for K^+ (2, 15), however, we used $^{86}Rb^+$ instead of $^{42}K^+$ because of the short half-life of $^{42}K^+$ and the length of the experiments.

In this study, we attempted a comprehensive comparison of potassium and sodium fluxes in roots of *Atriplex* and oat. Comparative studies with a halophyte and a glycophyte are few (18, 21), and there are very few comprehensive ion transport studies on halophytes (14). The results presented here, regarding fluxes of K^+ and Na^+ in oat roots, confirm our knowledge of ion transport and compartmentation in glycophytes (13, 23), *i.e.* potassium is actively pumped across the plasma membrane and passively distributed across the tonoplast, but sodium is actively exuded across the plasma membrane and moves passively or actively into the vacuole. Concentrations of K^+ and Na^+ in both main compartments (cytoplasm and vacuole) are in the range of 100 to 200 mM K^+ and 10 to 70 mM Na^+.

Ion Fluxes at Low Salinity (0 or 3 mM NaCl). *Atriplex* roots transport potassium similarly to oat roots under low salinity. Flux rates across the two membranes and transport to the xylem were very similar (Table IV). In addition, the driving forces were similar, *i.e.* active inward movement of K^+ across the plasma membrane and passive in both directions across the tonoplast (Table VIII). P_K values for the plasma membrane were similar in both species; for the tonoplast they were higher in oat roots (Table IX). Potassium was more concentrated in the vacuoles than in the cytoplasm of *Atriplex* root cells. In oat root cells, K^+ was more concentrated in the cytoplasm (Table IV). Sodium fluxes and contents in *Atriplex* root cells were much different than in oat. First, Na^+ fluxes across the plasma membrane, *i.e.* J_{oc} and J_{co} and transport into the stele, *i.e.* R' were about 5-fold higher in *Atriplex* roots than in oat roots. Similarly, Na^+ fluxes across the tonoplast, J_{cv} and J_{vc}, were about 2-fold higher in *Atriplex* than in oat roots (Table V). Second, sodium fluxes across both membranes in both directions were passive in *Atriplex* roots, whereas in oat roots this was true only across the tonoplast; active outward movement of sodium occurred at the plasma membrane (Table VIII). Third, cytoplasmic and vacuolar concentrations in *Atriplex* roots were 5- to 7-fold higher and the xylem concentration was 13-fold higher than in oat roots (Table V). P_K and P_{Na} values for both membranes (Table IX) indicated that membranes of oat root cells, at low Na^+ levels, were more permeable to Na^+ than to K^+. This was also the case for the plasma membrane of *Atriplex* root cells but not for the tonoplast. P_{Na} was higher in *Atriplex* roots than in oat roots and this was in agreement with the high flux of sodium in *Atriplex* roots and other halophytes (7, 8, 14, 31). At the low level of salinity, sodium had no significant effect on the different fluxes and contents of potassium in both plants (Table IV).

Ion Fluxes at High Salinity (50 mM NaCl). Growing oat and *Atriplex* seedlings in relatively high salinity of 50 mM NaCl (moderate for *Atriplex* but nearly lethal for oat) resulted in different fluxes and compartment contents for K^+. In oat, exudation, and by consequence potassium and sodium transport into the xylem, nearly stopped because of the high osmotic potential of the solution. Plasma membrane fluxes of K^+, J_{co} and J_{oc}, and cytoplasmic content decreased dramatically (Table IV) which paralleled an expected increase in Na^+ fluxes and concentrations (Table V). These results were consistent with the findings of Rains and Epstein (30) who showed that in barley roots, sodium, at high concentrations, competes well with potassium. For oat at high salinity, there were only slight changes in fluxes of both ions across the tonoplast J_{cv} and J_{vc} and in the vacuolar content, Q_v; concentration of K^+ increased in the xylem, however not as dramatically as Na^+. These results indicated that Na^+ does not interfere with potassium fluxes at the tonoplast or into the xylem in the same way it does at the plasma membrane. However, it should also be pointed out that the Na^+/K^+ ratio in the cytoplasm (0.47) was much lower than the ratio in the external solution (17). In contrast to oat roots, the same external concentration of NaCl caused only a moderate drop in cytoplasmic content of K^+ and in the fluxes of K^+ across the plasma membrane of *Atriplex* roots (Table IV). This lack of effect of salinity on K^+ fluxes occurred while Na^+ fluxes and content increased by about 3-fold (Table V). These results were similar to the findings of Rains and Epstein (31) on leaves of the mangrove *Avicennia marina* (a halophyte). They found that K^+ was preferred over Na^+ even at high external concentrations of NaCl.

K^+-Na^+ Selectivity. Selectivity for K^+ with respect to Na^+ ($S_{K,Na}$) was defined by Pitman (29) as the ratio between potassium uptake (or tissue content) and its external concentration divided by the same ratio for sodium. When $S_{K,Na}$ is greater than 1, there is a preference for potassium and when less than 1, Na is preferred. $S_{K,Na}$ values were calculated for shoot tissues (21, 32) using external concentrations of potassium and sodium. However, this could be misleading since transport to the shoot, as well as movement to the vacuole, is determined by the cytoplasmic ion concentrations and not directly by the external ion concentrations. Another way of estimating selectivity values, based upon external and cytoplasmic concentrations as well as flux rates, is presented in Table X where the effect of salinity on selectivity for K^+ with respect to Na^+ is shown. At low salinity, the selectivity for potassium relative to sodium at the plasma membrane of oat root cells was much higher than that at the tonoplast and the symplasm xylem boundary. This indicates that potassium is preferentially accumulated in the cytoplasm and sodium is preferentially accumulated in the vacuole. In addition, in oat roots there is little, if any, preferential transport of potassium to the shoot. Similar conclusions were reached when we calculated $S_{K,Na}$ values (as in Table X) from data for other glycophytes, *e.g.* oat coleoptile (27), onion (24), and corn roots (4, 5). In *Atriplex* roots at low salinity, $S_{K,Na}$ of the plasma membrane, tonoplast, and the symplasm/xylem interface were similar, and substantially lower than the $S_{K,Na}$ for the plasma

Table X. *Effect of External Concentrations of NaCl on Selectivity ($S_{K,Na}$) for Atriplex and Oat Roots*

Values are calculated from data given in Tables IV and V by the following equation

$$S_{K,Na} = (J_{jK}^+/J_{jNa})/(K^+/Na^+)$$

where J values are the fluxes of the ions across membrane j and K^+ and Na^+ are the concentrations in the external solution or cytoplasm, respectively.

Membrane/Flux	$S_{K,Na}$			
	3 mM external NaCl		50 mM external NaCl	
	Atriplex	Oat	*Atriplex*	Oat
Plasma membrane (J_{oc})	1.8	9.7	6.8	7.2
Tonoplast (J_{cv})	1.3	0.2	2.2	0.2
Symplasm/xylem (R')	1.5	0.6	0.6	0.3

membrane of oat roots. At higher salinity, the $S_{K,Na}$ at the plasma membrane was similar in oat and *Atriplex* roots. The higher $S_{K,Na}$ at the plasma membrane as compared to the tonoplast in *A. nummularia*, and the increase of this factor at higher salinity, agrees with recent findings in *Atriplex spongiosa* (33) and *A. hortensis* roots (21). In the first report, x-ray microanalysis in meristematic and vacuolated cells showed a higher selectivity for potassium with respect to sodium in the cytoplasm as compared to the vacuole. In the second report, $S_{K,Na}$ for net ion fluxes to the roots increased with increasing salinity. Furthermore, $S_{K,Na}$ values in *T. maritima* (calculated from 14) show higher preference for K^+ in the cytoplasm then in the vacuole; at higher salinities, $S_{K,Na}$ increased in the cytoplasm and was stable in the vacuole.

Selectivity for potassium in plant tissues, at the plasma membrane, can be achieved, according to Jeschke (16), in two ways: selective uptake of K^+ in preference to Na^+ and by K^+/Na^+ exchange; the former might play an important role in roots of sunflower and onion and the latter in wheat and barley (17). We cannot distinguish between these possibilities from our data. Moreover, with respect to these alternatives, we cannot distinguish between two possible effects of Na^+ on K^+ fluxes: selective uptake of sodium in preference to potassium or Na^+-induced efflux of K^+. The data in Table X suggest that Na^+/K^+ exchange or replacement by competition is more efficient at the plasma membrane of oat root cells than of *Atriplex* root cells, and that the tonoplast of *Atriplex* root cells does not discriminate potassium with respect to sodium as well as oat root cells do. Jeschke *et al.* (20) reached similar conclusions. Based upon transport of endogenous K^+ via the xylem and longitudinal ion profiles, these authors concluded that vacuolar Na^+/K^+ exchange occurred in *A. hortensis* roots but not intact seedlings of barley and corn. However, a Na^+/K^+ exchange was observed in excised roots of these glycophytes suggesting that supply of potassium or energy (carbohydrates) via the phloem controls this exchange.

To cope with high salinity, halophytes must possess a way to adjust osmotically, and this can occur by accumulation of organic materials such as oxalate, proline, and glycinebetaine (7, 32), or by massive ion accumulation. Excess ions are sequestered mainly in leaf cell vacuoles and/or secreted to the exterior by salt glands. Another important characteristic is the need to avoid elimination of essential nutrients such as potassium when the plant is bathed in Na^+. Preferential uptake of potassium with respect to sodium has been shown to occur in halophyte leaves (31) and is now suggested also in halophyte roots. Others have reported a preferential uptake of K^+ in halophytes (7, and references therein). Since halophytes appear to have a preferential potassium transport mechanism, as well as a massive transport system for sodium, they clearly have a more elaborate apparatus for cation uptake than to glycophytes. In addition, it will be of great interest to determine whether the lack of a Na^+ efflux pump at the plasma membrane in *Atriplex* found in our studies is true for other halophytic plants.

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