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# Potassium Transport in Corn Roots[1]

## IV. CHARACTERIZATION OF THE LINEAR COMPONENT

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### ABSTRACT

**A detailed examination was conducted on the linear, or first-order kinetic component for $K^+$($^{86}Rb^+$) influx into root segments of both low- and high-salt grown corn seedlings (*Zea mays* [A632 × Oh 43]). In tissue from both low- and high-salt grown roots, replacement of $Cl^-$ in the uptake solution by either $SO_4^{2-}$, $H_2PO_4^-$, or $NO_3^-$ caused a significant (50–60%) and specific inhibition of the linear component of $K^+$ influx. The anion transport inhibitor, 4,4′-diisothiocyano-2,2′-disulfonic acid, was found to abolish saturable $Cl^-$ influx in corn roots while causing a significant (50–60%) and specific inhibition of the linear $K^+$ uptake system; this inhibition was identical to that observed when $Cl^-$ was replaced by other anions in the $K^+$ uptake solution. Additionally, the quaternary ammonium cation, tetraethylammonium, which has been shown to block $K^+$ channels in nerve axons, also caused a dramatic (70%) and specific inhibition of the linear component of $K^+$ influx, but this was obtained only in high-salt roots. The reasons for this difference are discussed with respect to the differing abilities of low- and high-salt roots to absorb tetraethylammonium.**

**Our present results indicate that the linear component of $K^+$ influx may occur by a passive process involving transmembrane $K^+$ channels. Fluxes through these $K^+$ channels may be partly coupled to a saturating $Cl^-$ influx mechanism.**

In studies involving the kinetics of uptake for various plant tissues, the majority of the work has focused on the generation of discontinuous isotherms, via either the operation of multiple Michaelis-Menten transport systems, or by complex, multisite carriers. In many of these studies, the presence of a linear component was either ignored or considered to reflect diffusion across the plasma membrane (13 and references therein).

Recently there has been a growing interest in nonsaturating transport kinetics for organic solutes and ions. In contrast to earlier investigations, the more recent literature suggests that the nonsaturating or linear transport component may be a relatively complex process (2, 6, 7, 13–15, 20, 21, 31). Consistent with these results, we have previously demonstrated that in corn roots, the kinetics for $K^+$ influx could be resolved into saturable and linear components (13, 14). Sulfhydryl reagents either had no effect on the linear component, or, in the case of PCMBS[3], caused a significant stimulation, while resulting in complete inhibition of the saturable system.

In the present work, we document a more detailed characterization of the linear component. We were able to selectively inhibit linear component $K^+$ uptake either by varying the accompanying anion, inhibiting $Cl^-$ influx, or by the application of $K^+$ channel-blocking agents. These results are discussed with respect to possible transport mechanisms and the relationship between cation and anion fluxes across the plasmalemma of corn root tissue.

## MATERIALS AND METHODS

**Plant Material.** *Zea mays* seeds (A632 × Oh 43, Crows Hybrid Corn Co., Milford, IL) were imbibed, germinated, and grown by the methods previously outlined (13). Seedlings were either grown on a 0.2 mM $CaSO_4$ solution (low-salt conditions) or 0.2 mM $CaSO_4$ and either 5 mM KCl, $KNO_3$, $KH_2PO_4$, or 2.5 mM $K_2SO_4$ (high-salt conditions). Primary roots of 4-d-old seedlings were used for all uptake experiments.

**$K^+$ and $Cl^-$ Influx Experiments.** Short-term (10 min) $^{86}Rb^+$ and $^{36}Cl^-$ influx experiments were performed using 2-cm root segments as previously described (13). Briefly, experiments were performed with 2-cm root segments cut from the 1st through 8th cm of the primary root. Root segments were washed (4 h) in solutions of identical composition to their growth solutions to allow for recovery from excision. Uptake was initiated by the addition of $^{86}Rb^+$ (as RbCl, New England Nuclear, Boston) or $^{36}Cl^-$ (as NaCl, ICN Biochemicals, Irvine, CA) and terminated by the vacuum withdrawal of radioisotope solution. Free space radiolabel was removed by either two 8-min washes for $^{86}Rb^+$ or two 5-min washes for $^{36}Cl^-$ in ice-cold 0.5 mM $CaSO_4$ + 1 mM KCl. We have found that these desorption regimes removed approximately 95% of the free space radiolabel while exchanging only about 5% of the intracellular label. Following desorption, root segments were centrifuged (300*g*) for 15 s to remove surface water, and then the roots were weighed into scintillation vials. In order to quantify $^{86}Rb^+$ absorbed by roots, they were incubated (15 min) in 5 ml of 95% ethanol and then 10 ml of 5 mM ANDA were added to each vial. We have found this treatment quite effective in releasing $^{86}Rb^+$ from root segments. Radioactivity was quantified via detection of Cerenkov radiation in a Beckman LS 9800 scintillation counter. For $^{36}Cl^-$ influx studies, root segments were weighed into scintillation vials and then 10 ml of Beckman Ready Solve Hp/b scintillation cocktail (Beckman Industries, Fullerton, CA) was added. Radiocactivity was also

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[3] Abbreviations: PCMBS, *p*-chloromercuribenzene sulfonic acid; ANDA, 7-amino-1,3-naphthalene disulfonic acid; CCCP, carbonyl cyanide *m*-chlorophenylhydrazone; DIDS, 4,4′-diisothiocyano-2,2′-disulfonic acid stilbene; NEM, *N*-ethylmaleimide; TEA-Cl, tetraethylammonium chloride.

quantified using a Beckman LS 9800 scintillation counter.

The effect of the amino-reactive anion transport inhibitor, DIDS (Calbiochem-Behring, Fullerton, CA), on $K^+$ and $Cl^-$ influx in excised root segments was studied. Roots were pretreated for 15 min prior to $^{36}Cl^-$ or $K^+$ ($^{86}Rb^+$) influx with either 1 or 2 mM DIDS in a solution containing 0.2 mM $CaSO_4$ + 5 mM Mes (pH 6.0). DIDS was included in all uptake solutions. Buffer concentration was increased to 5 mM in all uptake solutions in order to maintain the appropriate pH value.

We have previously shown that in our corn root system, $^{86}Rb^+$ is a suitable radiotracer for $K^+$ influx experiments (13).

**$K^+$ Channel-Blocking Agents.** Experiments were performed to investigate the influence of the quaternary ammonium salt, TEA-Cl (Aldrich Chem. Co.), on $K^+$ influx. During the last 30 min of the 4-h wound recovery wash, either high- or low-salt roots were transferred to an identical wash solution containing 10 mM TEA-Cl for pretreatment. Additionally, 10 mM TEA-Cl was included in the uptake solutions.

For experiments investigating the absorption of TEA by low- and high-salt roots, 2-cm root segments were handled as previously described for $K^+$ and $Cl^-$ influx studies. Root segments were placed into 20 ml of aerated uptake solution which consisted of various concentrations of TEA-Cl (1–20 mM). Uptake was initiated by the addition of [$^{14}$C]TEA (as TEA-Br, New England Nuclear Corp.) to a final concentration of approximately $3.7 \times 10^3$ Bq/ml. The subsequent experimental protocol was as previously described for $K^+$ ($^{86}Rb^+$) influx studies.

## RESULTS

**Anion Involvement in Linear $K^+$ Influx.** Early work by Epstein *et al.* (8) demonstrated that in barley roots, Mechanism II $K^+$ influx was dramatically inhibited when $Cl^-$ was replaced by $SO_4^{2-}$ in the uptake solution. Since our linear $K^+$ uptake component functions primarily in the Mechanisms II concentration range, we examined the influence of $Cl^-$ replacement by other anions, on the uptake of $K^+$ in both low-salt and high-salt grown roots. Replacement of $Cl^-$ with $SO_4^{2-}$, $NO_3^-$, or $H_2PO_4^-$ in the uptake solution resulted in a 60% reduction in linear component $K^+$ influx and a 20% reduction in the $V_{max}$ for saturable uptake in low salt roots (Fig. 1). In these roots, the $K_m$ ($K^+$) for the saturable system exhibited no discernible change in response to changes in the accompanying anion (Table I).

To perform $Cl^-$ replacement studies on high-salt grown roots, we cultivated the tissue on solutions containing 2.5 mM $K_2SO_4$, instead of the usual 5 mM KCl so that contamination of the uptake solution, via chloride leakage from the tissue, was minimized. Using this tissue, we found that $Cl^-$ replacement resulted in an even more selective inhibition of the linear component. When $Cl^-$ was replaced by $SO_4^{2-}$, $NO_3^-$, or $H_2PO_4^-$, a 60% reduction in the linear component was again seen, while the $V_{max}$ of the saturable component remained totally unaffected (Fig. 2). It should be noted that the apparent $K_m$ ($K^+$) of the saturating system increased from approximately 100 to 145 μM when $Cl^-$ was replaced (Table I).

To determine whether linear component $K^+$ uptake was linked to $Cl^-$ influx, $^{36}Cl^-$ uptake studies were performed. As shown in Figure 3, the kinetics for $Cl^-$ uptake into low-salt roots exhibited both the saturable and linear components. A comparison between the flux data presented in Figures 1 and 3 indicate that the value for $K^+$ ($^{86}Rb^+$) influx is almost double that for $^{36}Cl^-$.

The membrane-impermeable, amino-reactive reagent, DIDS, has been shown to irreversibly inhibit anion uptake in red blood cells. More recently, DIDS has been used to inhibit $Cl^-$ and $SO_4^{2-}$ uptake in corn root protoplasts (16) and was shown to be a reversible inhibitor of $Cl^-$ influx in *Chara corallina* (12). To investigate the effect of DIDS on the kinetics of both $Cl^-$ and $K^+$ influx in low-salt grown corn roots, the following experiments were performed. DIDS, at 1 mM, was sufficient for maximal inhibition of $Cl^-$ influx (data not shown). Furthermore, a pretreatment in 1 mM DIDS for 15 min was necessary to elicit this inhibition. Additionally, as with *Chara*, DIDS inhibition of $Cl^-$ influx was reversible; a 15-min wash without DIDS (in 1 mM $Cl^-$) was sufficient to reverse the inhibition caused by a 60-min DIDS pretreatment. Consequently, all DIDS experiments consisted of a 15-min pretreatment with 1 mM DIDS, followed by the inclusion of 1 mM DIDS in all uptake solutions.

The results of such a DIDS treatment on $Cl^-$ influx are presented in Figure 3. The saturable component for $Cl^-$ influx

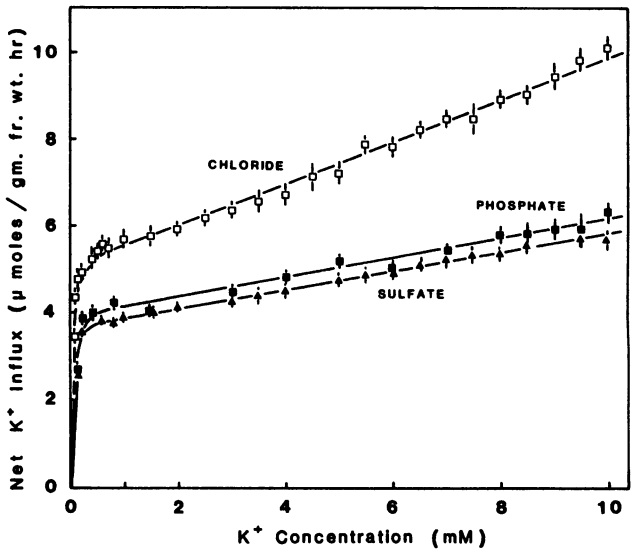


FIG. 1. Influence of the accompanying anion on $K^+$ ($^{86}Rb^+$) influx for corn root segments grown in 0.2 mM $CaSO_4$ (low-salt status). The first order rate coefficients, k, (in μmol g fresh weight$^{-1}$ h$^{-1}$ mM$^{-1}$), for the linear component, were as follows: 0.50 ($Cl^-$), 0.21 ($SO_4^{2-}$), 0.24 ($H_2PO_4^-$). To ensure clarity, the isotherm obtained with $NO_3^-$ as the accompanying anion was omitted. All data points in this figure and subsequent ones are the average of eight replicates and error bars are SE. Points which lack error bars do so because standard errors were smaller than symbols used.

Table I. *Influence of Various Experimental Treatments on the Saturable and Linear Components of $K^+$ ($^{86}Rb^+$) Uptake into Corn Root Segments*

Influx isotherms were separated into their saturable and linear components. Eadie-Hofstee plots for saturable curves yielded the following $K_m$ and $V_{max}$ values. Linear regression performed on data points for $K^+$ concentrations from 1.5 to 10 mM yielded the first order rate coefficient (k).

| Salt Status | Experimental Treatment | Saturable Component | | Linear Component |
|---|---|---|---|---|
| | | $K_m$ | $V_{max}$ | (k) |
| | | μM | μmol g fresh wt$^{-1}$ h$^{-1}$ | μmol g fresh wt$^{-1}$ h$^{-1}$ mM$^{-1}$ |
| Low-Salt | $Cl^-$ | 57 | 5.10 | 0.51 |
| | $SO_4^{2-}$ | 50 | 4.05 | 0.21 |
| | $H_2PO_4^-$ | 55 | 4.15 | 0.24 |
| Low-Salt | Control | 50 | 5.25 | 0.40 |
| | 1 mM DIDS | 54 | 4.30 | 0.20 |
| High-Salt | $Cl^-$ | 112 | 2.85 | 0.54 |
| | $SO_4^{2-}$ | 114 | 2.75 | 0.24 |
| | $H_2PO_4^-$ | 150 | 2.70 | 0.25 |
| | $NO_3^-$ | 147 | 2.75 | 0.30 |

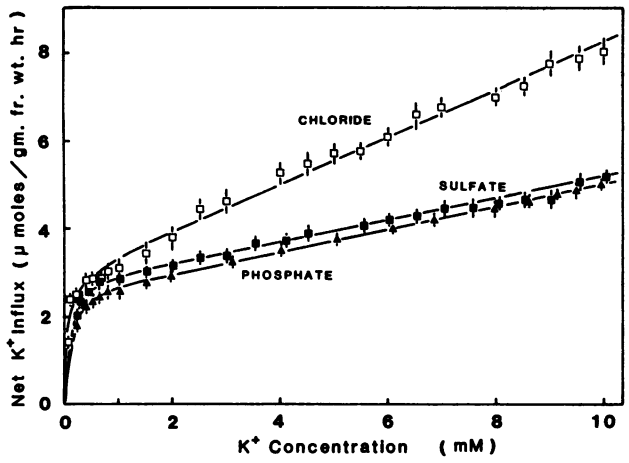


FIG. 2. Influence of the accompanying anion on $K^+$ ($^{86}Rb^+$) influx for corn root segments grown in 0.2 mM $CaSO_4$ + 2.5 mM $K_2SO_4$ (high-salt status). The first order rate coefficients, k (in $\mu$mol g fresh weight$^{-1}$ $h^{-1}$ $mM^{-1}$), for the linear component were as follows: 0.53 ($Cl^-$), 0.24 ($SO_4^{2-}$), 0.25 ($H_2PO_4^-$), 0.30 ($NO_3^-$). To ensure clarity, the isotherm obtained with $NO_3^-$ as the accompanying anion was omitted.

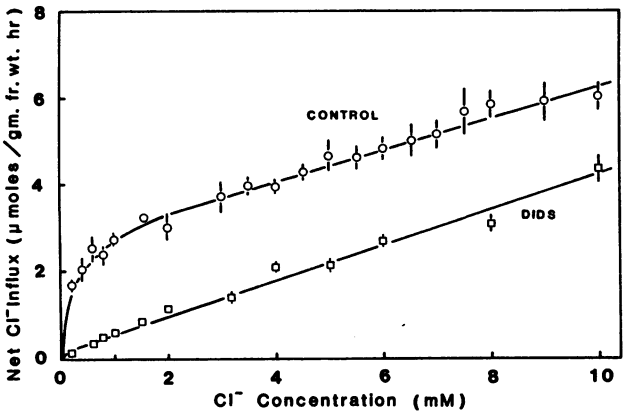


FIG. 3. Influence of 1 mM DIDS on $^{36}Cl^-$ influx for low salt roots. Roots were pretreated with a solution consisting of 1 mM DIDS, 5 mM Mes (pH 6.0), and 0.2 mM $CaSO_4$ for 15 min prior to uptake and 1 mM DIDS was included in all uptake solutions. The first-order rate coefficients, k, for the linear component were as follows: 0.37 (control), 0.41 (DIDS).

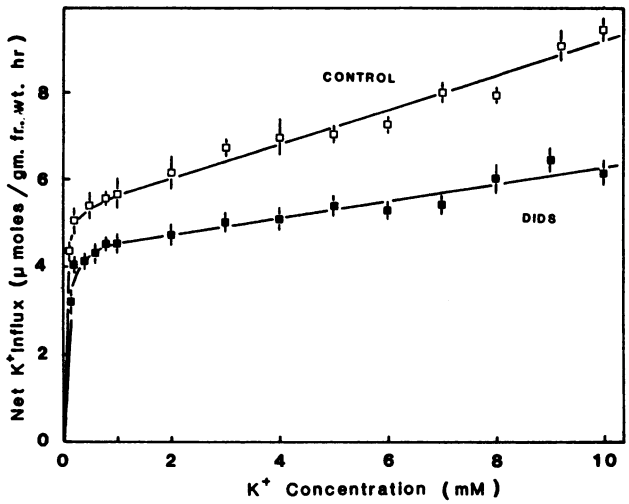


FIG. 4. Influence of 1 mM DIDS on $K^+$ ($^{86}Rb^+$) influx for low-salt roots. See Figure 3 for the experimental conditions. The first order rate coefficients, k, for the linear component, were as follows: 0.40 (control), 0.19 (DIDS).

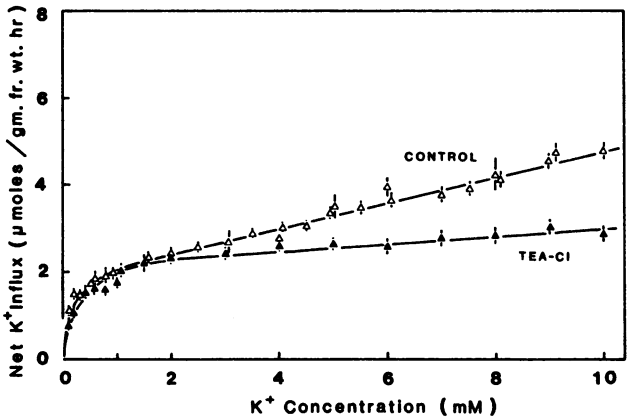


FIG. 5. Influence of 10 mM TEA-Cl on $K^+$ ($^{86}Rb^+$) influx for high-salt roots. Roots were pretreated with a solution containing 10 mM TEA-Cl, 5 mM KCl, and 0.2 mM CaSO4 for 30 min prior to uptake and 10 mM TEA-Cl was included in all uptake solutions. The first order rate coefficients, k, for the linear component were as follows: 0.31 (control); 0.09 (TEA-Cl).

was abolished following DIDS exposure, while the linear component was left unchanged. In Figure 4, the influence of this same DIDS treatment on $K^+$ ($^{86}Rb^+$) uptake into low-salt roots is illustrated; a significant inhibition (60%) of the linear component for $K^+$ influx was observed. The $V_{max}$ ($K^+$) was only moderately reduced (20%), while the $K_m$ was unaffected (Table I). The $K^+$ uptake kinetics in DIDS-treated roots were almost identical to the kinetics observed when $Cl^-$ was removed from the uptake solution (Fig. 1).

**$K^+$ Channel-Blocking Agents.** In studies involving $K^+$ uptake in *E. coli*, it has been suggested that the linear component for $K^+$ uptake is due to the operation of $K^+$ channels in the plasma membrane (27). It has long been established that the membrane of giant nerve fibers support both $K^+$ and $Na^+$ currents that are mediated via ion-specific channels. It is also well documented that quaternary ammonium salts, such as TEA, cause a specific decrease in $K^+$ conductance in these tissues (30).

To further elucidate the relationship between $Cl^-$ uptake and the linear component of $K^+$ influx, we investigated the effect of the $K^+$ channel-blocking agent, TEA-Cl, on the kinetics of $K^+$ influx for both low- and high-salt roots. Roots were pretreated in 10 mM TEA-Cl for 30 min, and then 10 mM TEA-Cl was included in all uptake solutions. In high-salt roots, TEA caused a dramatic (75%) and specific inhibition of the linear component (Fig. 5); consistent with our earlier findings for anion replacement and DIDS experiments, the saturable component remained unaffected. The TEA results suggest that $K^+$ channels may be involved in linear component $K^+$ uptake into high-salt roots. However, although low-salt roots possess a similar linear component for $K^+$ influx, in the present studies this component was insensitive to TEA (data not shown).

In an attempt to resolve the discrepancy between the linear component TEA-sensitivity in these tissues, we measured [$^{14}C$] TEA influx into high- and low-salt roots. We found that over a TEA concentration range of 1 to 20 mM, influx into high-salt roots was approximately twice that obtained on low-salt roots (Fig. 6). This observed difference in TEA transport capability may result in higher TEA cytoplasmic levels in high-salt roots. These elevated cytoplasmic TEA levels may be sufficient to block $K^+$ channels in high-salt roots, while the reduced TEA influx in

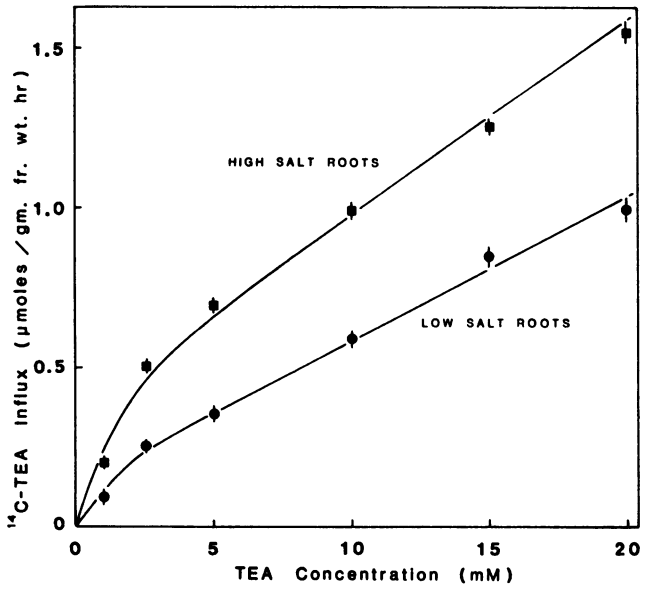


FIG. 6. Uptake of [$^{14}$C]TEA-Cl in low-salt (●) and high salt (■) corn root segments. Experimental protocol was identical to that used for $K^+$ ($^{86}Rb^+$) uptake studies (see "Materials and Methods").

low-salt roots may result in cytoplasmic TEA concentrations that are not high enough to influence $K^+$ channels. Of course, this situation is predicated on the condition that TEA would have to act at the cytoplasmic face of the plasmalemma in order to block $K^+$ channels in corn roots.

**Influence of $Na^+$ on Linear Component $K^+$ Influx.** Epstein *et al.* (8) demonstrated that in low-salt roots, Mechanism I for $K^+$ influx was quite specific for $K^+$ or $Rb^+$, while Mechanism II could be competitively inhibited by $Na^+$. We therefore investigated the influence of 3 mM NaCl on the $K^+$ uptake kinetics in both low- and high-salt roots. In low-salt roots, 3 mM $Na^+$ caused a significant reduction (50%) in linear component $K^+$ uptake, while having little effect on the saturable component (data not shown); this result is in agreement with previous studies conducted in barley roots (8). However, in high-salt roots, 3 mM $Na^+$ had absolutely no effect on either the linear or saturable components of $K^+$ influx (data not shown). These results are similar to those previously obtained by Pitman *et al.* (23–25), who found that in the Mechanism II concentration range, high-salt roots showed a much greater selectivity for $K^+$ over $Na^+$ than did low-salt roots. Therefore, in our low-salt grown roots, linear uptake may be mediated by a general cation channel; however, in high-salt roots, linear uptake appears to be due to a more specific $K^+$ channel.

## DISCUSSION

**Relationship between Anion Transport and Linear $K^+$ Fluxes.** The linear component dominates $K^+$ uptake in the concentration range where most researchers feel uptake occurs via a thermodynamically passive process. This feature, in conjunction with the linear concentration dependence for uptake, has caused numerous workers to dismiss the linear component for solute uptake as a physiologically insignificant process, *i.e.* the result of diffusion into either the apoplast of plant tissues, or across the plasmalemma.

However, in the present study, we have shown that it is possible to selectively inhibit the linear component for $K^+$ uptake, either by inhibiting $Cl^-$ influx, or by the application of $K^+$ channel-blocking agents. The results from the $Cl^-$ replacement experiments suggest that there is a coupling between the presence of $Cl^-$ in the uptake solution and linear $K^+$ influx. It has been documented previously that $K^+$ influx from solutions containing $K_2SO_4$ is significantly lower than from KCl solutions (8, 23). Anion uptake may co-limit cation influx, and since $Cl^-$ is absorbed more rapidly than $SO_4^{2-}$, $K^+$ influx should be greater from KCl solutions. However, the similarity between $Cl^-$ (Fig. 3) and $NO_3^-$ (9) influx values obtained on corn roots suggests that a more complex situation may exist. We have shown that substitution of either $SO_4^{2-}$ or $NO_3^-$ for $Cl^-$ resulted in a similar reduction in the linear component of $K^+$ influx (Figs. 1 and 2), which suggests that the observed response may be specific for $Cl^-$ rather than a general coupling to anion transport.

The results of the experiments examining the influence of DIDS on the kinetics of $^{36}Cl^-$ and $K^+$ ($^{86}Rb^+$) influx offer additional support for the involvement of $Cl^-$ with linear $K^+$ uptake. The kinetics for $K^+$ influx following DIDS treatment (which abolished saturable $Cl^-$ influx) were almost identical to the kinetics observed when $Cl^-$ was removed from the uptake solution (Figs. 1 and 3). These results strongly suggest that linear component $K^+$ influx is linked to saturable $Cl^-$ uptake. It has been proposed that $Cl^-$ influx in plants is mediated by a proton-$Cl^-$ co-transport system (10, 19, 28). Hence, it seems reasonable to speculate that saturable $Cl^-$ influx is due to a proton-$Cl^-$ symport which is inhibited by DIDS, and is coupled, in some manner, to a linear $K^+$ transport system.

**Nature of the Linear Component.** Our TEA experiments allow us to speculate on the molecular nature of the transport system involved in nonsaturating (linear) $K^+$ influx in corn roots. The observation that 10 mM TEA caused a dramatic and specific inhibition of linear $K^+$ influx in high-salt roots (Fig. 5) clearly suggests that $K^+$ channels are involved. However, we were intrigued by the lack of TEA sensitivity observed for low-salt root linear $K^+$ influx. It is possible that, as in *Chara* (11, 18), the exposure to higher external levels of $K^+$ experienced by high-salt roots, causes a conformational change at the outer surface of the $K^+$ channels, which facilitates TEA binding (blockage).

An alternative explanation for the TEA insensitivity found in low-salt roots is that this tissue behaves in a similar manner to nerve axons, where it is necessary to inject TEA into the axoplasm to block $K^+$ channels (1, 30). A transport system for the uptake of the quaternary ammonium salt, choline, has been demonstrated in the roots of higher plants (22). Hence, the different TEA responses exhibited by high- and low-salt roots could be explained on the basis of the greater [$^{14}$C]TEA influx into high-salt roots (Fig. 6), which would develop higher levels of cytoplasmic TEA. If this were the case, $K^+$ channels could be involved in linear $K^+$ influx in both low- and high-salt roots; only in high-salt roots would the cytoplasmic TEA concentration rise to a level high enough to block $K^+$ channels at the cytoplasmic face of the plasmalemma.

The involvement of channels in linear $K^+$ influx, as opposed to enzyme-like carriers, would provide the most straightforward explanation for a carrier-mediated transport process that is difficult to saturate. A water-filled protein channel could incorporate such properties as specific radius, electrostatic properties at its mouth, and chemical- or voltage-induced conformational changes (gating), in such a way as to impart to it substrate specificity and control.

As Cohen (7) has pointed out, such a channel-mediated process may eventually saturate at high substrate concentrations. However, in his system (amino acid uptake into mouse brain slices), at high substrate levels, the medium changes from isotonic-buffered saline to hypertonic-buffered amino-acid saline. Any observed changes in transport kinetics may therefore be due to changes in media composition. The same applies for $K^+$ influx into corn roots. We have followed $K^+$ influx from a range of KCl concentrations up to 50 mM. At these high $K^+$ levels, we still saw no evidence for saturation, although the slope of the linear

component did decrease slightly. We were reluctant to study uptake from solutions of higher concentration, because we felt that at such ionic and osmotic levels, possible alterations in the membrane lipid/protein structure would make data interpretation doubtful.

**Relationship between $K^+$ Influx and $E_m$.** An important fact that is often ignored when analyzing $K^+$ influx kinetics is the relationship between changes in external $K^+$, $K^+$ influx, and cell membrane potential ($E_m$). It is generally accepted that $E_m$ comprises a large component of the driving force for $K^+$ influx, particularly at higher external $K^+$ levels (3, 4). It has also been well documented that as external $K^+$ concentrations are increased, depolarization of $E_m$ occurs, and the driving force for passive $K^+$ influx through the $K^+$ channel would be reduced (3, 4). Thus, the influence of $E_m$ on channel-mediated $K^+$ influx must be considered. The most detailed study to date concerning $K^+$ influx in plant roots from an electrophysiological viewpoint was conducted by Cheeseman *et al.* (3–5). They investigated the influence of anoxia, proton ionophores, and ATPase inhibitors on $K^+$ influx and $E_m$ over a range of $K^+$ concentrations. Based on their studies, they proposed that over low $K^+$ concentrations, uptake was an active and electrogenic process linked to a $H^+$-ATPase. At $K^+$ levels above approximately 1 mM (*i.e.* the range where the linear component dominates), they suggested that $K^+$ influx occurs via a passive electrophoretic uniport mechanism. This system mediates passive $K^+$ influx and is insensitive to ATPase inhibitors. It is quite possible that this second system described by Cheeseman *et al.* is the putative $K^+$ channel system responsible for linear $K^+$ uptake.

**Physiological Role for the Linear Component?** It has been noted that linear substrate influx often occurs over a concentration range which exceeds the levels normally experienced by roots in the soil, and so it is difficult to assign a physiological role to this system. For example, in corn roots, the linear component for $K^+$ influx becomes significant at $K^+$ levels above 1 mM. Reisenauer (26) has pointed out that the majority of soil $K^+$ is below 2 mM. What then would be the significance of a transport mechanism that operates at substrate levels rarely experienced by the plant? The answer to this question may come from transport studies conducted on *E. coli* and *Neurospora*. In both organisms, it has been well documented that multiple carrier systems are often involved in the transport of a single solute. These organisms tend to combine constitutive, low affinity, high capacity transport systems with derepressible high affinity systems; phospate or glucose uptake into *N. crassa* are excellent examples of this strategy (17, 29). These systems give the organism the adaptive advantage to most effectively obtain nutrients whose concentrations may vary considerably over a period of time. A root growing through the soil may often experience extermely low $K^+$ levels. Therefore, a high affinity system may be necessary in order for the plant to satisfy its requirements for this essential nutrient. However, if the growing root encounters a localized region of high soil $K^+$, the high affinity system may not have the capacity to utilize the excess $K^+$. In such a situation a low affinity system, represented by the linear component, would allow the plant to effectively utilize these pockets of high soil $K^+$. In this way, the plant may maintain a relatively efficient method of dealing with its varying environment.

## CONCLUSIONS

We have previously shown that it is possible to selectively inhibit the saturable component for $K^+$ influx into corn roots through the application of sulfhydryl modifiers (13, 14). Based on our earlier studies, we proposed that the complex $K^+$ uptake kinetics we observed were due to the combined operation of two transport systems, one saturable and one exhibiting linear, or first-order kinetics. In the present study, we have conducted a more detailed characterization of the linear component for $K^+$ influx. The selective inhibition of the linear component by either inhibiton of saturable $Cl^-$ uptake, or by the application of $K^+$ channel-blocking agents, suggests that this tranport process may represent flux through $K^+$ channels. It would also appear that these putative $K^+$ channels are coupled, in some way, to a saturable $Cl^-$ transport system.

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