LETTER TO THE EDITOR

Can K^+ Channels Do It All?

Plant roots absorb K^+ over a wide range of soil K^+ concentrations. The pioneering tracer flux studies for root K^+ uptake conducted by Epstein and coworkers (Epstein et al., 1963) indicated that at least two K^+ transport mechanisms exist, one mediating high-affinity K^+ uptake and the other low-affinity uptake. More recent studies in higher plants, fungi, and charophytic algae have shown that the high-affinity K^+ transport system is expressed under growth in low K^+ conditions, has a very low K_m for K^+ (2 to 20 μM), and is highly electrogenic (depolarizing) in nature (Rodriguez-Navarro et al., 1986; Kochian et al., 1989; Smith and Walker, 1989). K^+ uptake into plants and fungi from low external K^+ concentrations has generally been considered to involve a thermodynamically active process. In fungi, this system has been suggested to be a K^+-H^+ cotransport, while in charophytes evidence in support of a K^+-Na^+ cotransport has been presented (Rodriguez-Navarro et al., 1986; Smith and Walker, 1989). Low-affinity K^+ absorption, which is important at much higher external K^+ concentrations and is thermodynamically passive, has been suggested to be mediated by K^+ channels (Kochian et al., 1985; Schroeder and Fang, 1991).

The recent use of the patch clamp technique to identify and characterize plant ion channels has focused considerable attention on the role of K^+ channels in plant membrane biology. Indeed, some researchers have speculated that high-affinity K^+ uptake could be mediated by inwardly rectifying K^+ channels; if so, all plant K^+ absorption could be mediated by K^+ channels. Hedrich and Schroeder (1989) noted the similarity in the current–voltage relationships between the putative K^+-H^+ cotransporter that mediates high-affinity K^+ uptake in Neurospora and an inward K^+ channel from guard cells. They went on to point out that the very negative membrane potentials (E_m) in Neurospora cells incubated in K^+-free solutions (− 305 mV) could allow for passive K^+ influx via K^+ channels at low external K^+ (i.e., at concentrations greater than 0.6 μM). Although it was not stated directly in this review, the implication was that high-affinity K^+ uptake could involve passive K^+ transport through ion channels.

In the past year, information arising from the cloning and characterization of the first K^+ transport genes in higher plants has also raised questions concerning the nature of the high-affinity K^+ transporter. These K^+ transport cDNAs, designated *KAT1* and *AKT1*, were cloned from Arabidopsis by complementation of a K^+ transport–defective yeast mutant (Anderson et al., 1992; Sentenac et al., 1992). *KAT1* and *AKT1* share extensive sequence similarity but are not allelic, and both share structural features with the Shaker family of voltage-activated K^+ channels in Drosophila and related gene products in invertebrates and vertebrates. Injection of *KAT1* mRNA into Xenopus oocytes confers the expression of inwardly rectifying K^+ channel activity (Schachtman et al., 1992). When these transport cDNAs are expressed in yeast mutants defective in K^+ absorption, they allow growth in solutions containing relatively low concentrations of K^+, 20 μM in the case of *AKT1*. These results suggest that high-affinity K^+ uptake could be mediated by K^+ channels, i.e., that K^+ channels might "do it all" in terms of K^+ absorption into higher plant cells.

Despite these results, an evaluation of the thermodynamics associated with high-affinity K^+ absorption into roots reveals that K^+ absorption from low K^+ solutions cannot be mediated by K^+ channels because it is clearly energetically "uphill." Although very negative E_m values (−200 to −300 mV) can be measured in fungi and root cells under minus K^+ conditions, the presence of even 2 μM K^+ causes a significant depolarization. Thus, the resting E_m in the presence of micromolar K^+ is considerably less negative than the voltages measured in the absence of K^+.

Consider K^+ absorption into low salt–grown maize roots, for which we have previously characterized high-affinity K^+ uptake (Kochian and Lucas, 1982; Newman et al., 1987; Kochian et al., 1989). The steady state net K^+ influx into the maize root, measured using a vibrating extracellular K^+ microelectrode, was approximately 7 pmol cm^{-2} s^{-1}, and the E_m measured simultaneously on the same root epidermal cell had a value of −110 mV. The K^+ activity detected at a position 5 μm from the root surface was 5 μM, which was depleted down from a bulk solution concentration of 25 μM K^+; thus, the K^+ activity at the plasma membrane surface would be even lower than 5 μM. Our labs have recently used double-barreled K^+ microelectrodes to measure cytoplasmic K^+ activity under the same transport conditions and have found that the cytoplasmic K^+ is in the range of 100 to 150 mM (L.V. Kochian, J.E. Schaff, and W.J. Lucas, unpublished results).

Using these measured parameters, one can calculate the electrochemical potential for K^+ (μ_{K^+}) in the cytoplasm versus the solution at the root surface (using 100 mM as a conservative value for cytoplasmic K^+). This calculation indicates that μ_{K^+} in the cytoplasm is approximately 14 kjoules/mol *higher* than μ_{K^+} in the external solution. This large outwardly directed electrochemical potential gradient for K^+ indicates that K^+ channels could not facilitate K^+ uptake from a solution containing 5 μM K^+; high-affinity K^+ uptake must, therefore, involve either a K^+-ATPase or a secondarily coupled active K^+ uptake system (K^+-H^+ or K^+-Na^+

LETTER TO THE EDITOR

cotransport). For μ_{K^+} to be at equilibrium between the cytoplasm and external solution, the external K^+ activity must be increased to approximately 1.4 mM. Thus, it is highly unlikely that any possible increases in the K^+ activity within the root cell apoplasm (due, for example, to the negatively charged plasma membrane surface or to cell wall interactions) would be of sufficient magnitude to alter the direction of the thermodynamic gradient for K^+. Maathuis and Sanders (1993) have recently conducted a similar thermodynamic analysis of K^+ absorption into Arabidopsis roots, using double-barreled K^+ microelectrodes to measure cytoplasmic K^+ activities. They arrived at the same conclusions as those presented here for maize. That is, they found that at low external K^+ concentrations, K^+ uptake is mediated by a thermodynamically active process.

In conclusion, plant K^+ channels are clearly of fundamental importance to K^+ transport into and within the plant, and the recent cloning of putative K^+ channel cDNAs has provided valuable information concerning the nature of these channels. However, their operation cannot mediate active, high-affinity K^+ uptake into the root. In fact, recent findings in our labs on the characteristics of the *KAT1*-encoded transporter expressed in Xenopus oocytes and yeast cells indicate that this system does not have the same transport properties as the high-affinity system previously characterized in maize roots. Therefore, one puzzle that needs to be solved involves the expression of *KAT1*, an apparent K^+ channel cDNA, in yeast. Why does the expression of this transporter confer on K^+ uptake–defective yeast mutants the ability to grow on low external K^+? Another essential challenge for future studies will be to identify the molecular components that are involved in active K^+ transport into the root symplasm.

Leon V. Kochian
U.S. Plant, Soil, and Nutrition Laboratory, USDA-ARS
Cornell University
Ithaca, NY 14853

William J. Lucas
Section of Plant Biology
University of California
Davis, CA 95616

REFERENCES

Anderson, J.A., Huprikar, S.S., Kochian, L.V., Lucas, W.J., and Gaber, R.F. (1992). Functional expression of a probable *Arabidopsis thaliana* potassium channel in *S. cerevisiae*. Proc. Natl. Acad. Sci. USA **89,** 3736–3740.

Epstein, E., Rains, D.W., and Elzam, O.E. (1963). Resolution of dual mechanisms of potassium absorption by barley roots. Proc. Natl. Acad. Sci. USA **49,** 684–692.

Hedrich, R., and Schroeder, J.I. (1989). The physiology of ion channels and electrogenic pumps in higher plants. Annu. Rev. Plant Physiol. Plant Mol. Biol. **40,** 539–569.

Kochian, L.V., and Lucas, W.J. (1982). Potassium transport in corn roots. I. Resolution of kinetics into a saturable and linear component. Plant Physiol. **70,** 1723–1731.

Kochian, L.V., Xin-Zhi, J., and Lucas, W.J. (1985). Potassium transport in corn roots. IV. Characterization of the linear component. Plant Physiol. **79,** 771–776.

Kochian, L.V., Shaff, J.E., and Lucas, W.J. (1989). High-affinity K^+ uptake in maize roots: A lack of coupling with H^+ efflux. Plant Physiol. **91,** 1202–1211.

Maathuis, F.J.M., and Sanders, D. (1993). Energization of potassium uptake in *Arabidopsis thaliana*. Planta **191,** in press.

Newman, I.A., Kochian, L.V., Grusak, M.A., and Lucas, W.J. (1987). Fluxes of H^+ and K^+ in corn roots: Characterization and stoichiometries using ion-selective microelectrodes. Plant Physiol. **84,** 1177–1184.

Rodriguez-Navarro, A., Blatt, M.R., and Slayman, C.L. (1986). A potassium-proton symport in *Neurospora crassa*. J. Gen. Physiol. **87,** 649–674.

Schachtman, D.P., Schroeder, J.I., Lucas, W.J., Anderson, J.A., and Gaber, R.F. (1992). Expression of an inward-rectifying potassium channel by the *Arabidopsis KAT1* cDNA. Science **258,** 1654–1658.

Schroeder, J.I., and Fang, H.H. (1991). Inward-rectifying K^+ channels in guard cells provide a mechanism for low affinity K^+ uptake. Proc. Natl. Acad. Sci. USA **88,** 11583–11587.

Sentenac, H., Bonneaud, N., Minet, M., Lacroute, F., Salmon, J.-M., Gaymard, F., and Grignon, C. (1992). Cloning and expression in yeast of a plant potassium ion transport system. Science **256,** 663–665.

Smith, F.A., and Walker, N.A. (1989). Transport of potassium by *Chara australis*. I. A symport with sodium. J. Memb. Biol. **108,** 125–137.