The recent cloning (Anderson et al., 1992; Sentenac et al., 1992) and electrophysiological characterization (Schachtman et al., 1992) of plant inward-rectifying K⁺ (K⁺,in) channel cDNAs has brought new excitement to the field of plant K⁺ transport. K⁺ is a major macronutrient for plants and is the most abundant cellular cation. K⁺ uptake across the plasma membrane is, therefore, of general interest in regard to plant nutrition, movements, growth, development, and metal stress. Inward K⁺ channels have been suggested to contribute to proton pump–driven K⁺ uptake into plant cells (Schroeder et al., 1984, 1987). This letter addresses recent questions regarding the importance of K⁺,in channels for cellular K⁺ uptake (Kochian and Lucas, 1993; Maathuis and Sanders, 1993).

Classical tracer flux studies have shown that higher plant cells possess at least two mechanisms for K⁺ uptake. Based on kinetic analyses, a high-affinity K⁺ uptake mechanism with an apparent K⁺ equilibrium dissociation constant (Kₑ) of approximately 10 to 20 μM was identified that saturates at approximately 0.2 mM external K⁺, and low-affinity mechanisms with a Kₑ for K⁺ of 4 to 16 mM were identified that allow enhanced K⁺ uptake at extracellular K⁺ concentrations greater than 0.3 mM (Epstein et al., 1963). Several studies have indicated that the activity of the high-affinity mechanism is reduced at elevated K⁺ concentrations, such that the low-affinity mechanisms presumably contribute significantly to K⁺ uptake when apoplastic K⁺ concentrations are >0.3 mM.

Schroeder and colleagues (Schroeder et al., 1987; Schroeder and Fang, 1991) have suggested that K⁺,in channels represent a major component of the low-affinity K⁺ uptake mechanism. Biological and physiological studies of K⁺,in channels have shown that they are well suited to serve as an efficient mechanism for K⁺ uptake at K⁺ concentrations >0.3 mM with kinetics similar to those of the low-affinity mechanism (Schroeder and Fang, 1991). The driving force for K⁺,in channel–mediated K⁺ uptake is provided by the negative membrane potential maintained by the proton-extruding plasma membrane proton pump.

One approach to estimating the contribution of K⁺,in channels to K⁺ uptake is to determine the cytosolic and external K⁺ activity and the cell membrane potential. In principle, channel-mediated K⁺ uptake is thermodynamically possible whenever the cell membrane potential lies negative of the K⁺ equilibrium (Nernst) potential. With 100 mM K⁺ in the cytosol and 1 mM extracellular K⁺, for example, a membrane potential more negative than −116 mV is required for K⁺,in uptake.
channel-mediated $K^+$ uptake. With 0.1 mM extracellular $K^+$, a membrane potential more negative than -174 mV is required for $K^+$ uptake. Recent experiments in transformed yeast suggest that plant $K^+_{in}$ channels are capable of accumulating $K^+$ even with only 0.65 μM extracellular $K^+$ (Sentenac et al., 1992) (this would require a membrane potential of approximately -290 mV, based on an estimated cytosolic $K^+$ activity of 60 mM). These results and previous findings (Schroeder and Fang, 1991) did not lead to the conclusion that high-affinity $K^+$ uptake in plants is mediated by passive $K^+$ transport through ion channels, as implied in a recent commentary (Kochian and Lucas, 1993). The results do, however, support biophysical conjectures suggesting that one function of $K^+_{in}$ channels may be to serve as a backup system for high-affinity $K^+$ uptake (Schroeder and Fang, 1991), for example, when the plant high-affinity mechanism is genetically or environmentally disabled. In addition, the $K^+_{in}$ channel cannot be the high-affinity $K^+$ transporter because the transporter in higher plant cells saturates at ~0.2 mM $K^+$, whereas the $K^+_{in}$ channel saturates at >50 mM extracellular $K^+$ (Schroeder and Fang, 1991). Furthermore, the high-affinity mechanism depolarizes the membrane potential sufficiently at low external $K^+$ to require an active transporter (Glass and Dunlop, 1979; Newman et al., 1987). The important question, therefore, is whether $K^+_{in}$ channels promote $K^+$ uptake in a range of external $K^+$ concentrations that is physiologically relevant for $K^+$ uptake into various plant cell types.

In guard cells, many studies have supported the hypothesis (Schroeder et al., 1987) that $K^+_{in}$ channels constitute a major component of the low-affinity $K^+$ uptake mechanism mediating physiological $K^+$ uptake fluxes with apoplastic $K^+$ concentrations >0.3 mM (for review, see Assmann, 1993). $K^+_{in}$ channels have been characterized in various plant cell types (for review, see Tester, 1990), and the free $K^+$ concentration in cell walls of various tissues was found to range from approximately 1 to 15 mM (Bowling, 1987; Zucker-Lowen and Satter, 1989; Long and Widder, 1990). This is in the range important for $K^+$ uptake by $K^+_{in}$ channels.

As to $K^+$ uptake by roots from the soil, a careful study of Arabidopsis root cells recently concluded that, based on thermodynamic constraints, $K^+_{in}$ channels could play a role in $K^+$ uptake only at external $K^+$ concentrations above 1 mM (Maathuis and Sanders, 1993). This is slightly higher than the limit of approximately 0.3 mM $K^+$ proposed by Schroeder and Fang (1991) based on patch clamp experiments. We believe that this small but physiologically significant difference can be resolved if correction factors for measurements of the membrane potential are considered. Patch clamp experiments have shown that the membrane resistance of plant and animal cells is approximately 10 times greater than expected from classical microelectrode studies (Marty and Neher, 1986). For example, typical plant and animal cells have whole-cell membrane resistances of >20 GΩ (~0.07 S m⁻²) at the low ion concentrations used in membrane potential measurements (Marty and Neher, 1985; Schroeder and Fang, 1991). Classical membrane potential recordings with high-quality impalement resistances of 500 MΩ (Goldsmith and Goldsmith, 1978; Marty and Neher, 1985) would therefore result in apparent membrane potentials 20 to 40 mV more positive than the actual plant cell resting potential after consideration of proton pump current densities and plasma membrane coupling. Higher impalement resistances should be possible in selected recordings. A correction by 20 to 40 mV does not invalidate the many excellent microelectrode studies from which important insights have been gained. However, it suffices to lower the limit on the extracellular $K^+$ concentration for channel-mediated $K^+$ uptake from 1.4 or 1 mM (Kochian and Lucas, 1993; Maathuis and Sanders, 1993) to 0.3 to 0.45 mM. Is an extracellular $K^+$ concentration of 0.3 mM and above physiologically relevant when looking at $K^+$ uptake by roots? Soils show a broad distribution of solution $K^+$ concentrations, ranging from 0.2 to 10 mM (Fried and Shapiro, 1961). Reisenauer (1964) found that over 90% of 155 soil samples had solution $K^+$ concentrations above 0.3 mM $K^+$. Barber (1984) analyzed 142 soil samples that had been collected with an emphasis on soils with low $K^+$ levels and reported that 30% showed more than 0.3 mM $K^+$. The $K^+$ concentration at the outer surface of the cell membrane can be lower than the bulk solution concentration due to depletion. Because of sublinear Michaelis-Menten kinetics of $K^+$ uptake, this effect should be more important at low micromolar $K^+$ concentrations than at higher concentrations. Compared to 80% depletion at 25 μM extracellular $K^+$ (Kochian and Lucas, 1993), it can be estimated that at 0.3 mM $K^+$, depletion would amount to only about 30% of the bulk $K^+$ concentration. Furthermore, plant roots gain access to undepleted soil regions by growing branch roots and root hairs. For the above reasons, an immediate extracellular $K^+$ concentration range of 0.3 to 1 mM seems physiologically relevant for a contribution to $K^+$ uptake from the soil.

In conclusion, data indicate that $K^+_{in}$ channels can serve as a major component of the low-affinity $K^+$ uptake mechanism across the plasma membrane of various higher plant cell types, such as guard cells. Furthermore, $K^+_{in}$ channels may function as a backup system at intermediate $K^+$ concentrations when the high-affinity mechanism is disabled. $K^+_{in}$ channels are extremely efficient $K^+$ transporter proteins that, in conjunction with the plasma membrane proton pump, can adapt to wide fluctuations in the extracellular $K^+$ concentration and at the same time contribute to membrane potential control. Interestingly, the use of $K^+_{in}$ channels as uptake transporters might contribute to important physiological problems such as Na⁺ toxicity at high mM...
The identification of the active high-affinity function, and the cloning of the Arabidopsis K+ channel genes KAT1 and AKT1. The identification of the active high-affinity K+ uptake mechanism(s) and, perhaps, additional low-affinity mechanisms will also be necessary. A combination of biochemical and molecular genetic studies can now be used to unequivocally answer the open questions and suggestions discussed above and will undoubtedly uncover additional new functions and properties of plant transporters.

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