

REVIEW

Cellular mechanisms of potassium transport in plants

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Potassium (K^+) is the most abundant ion in the plant cell and is required for a wide array of functions, ranging from the maintenance of electrical potential gradients across cell membranes, to the generation of turgor, to the activation of numerous enzymes. The majority of these functions depend more or less directly upon the activities and regulation of membrane-bound K^+ transport proteins, operating over a wide range of K^+ concentrations. Here, we review the physiological aspects of potassium transport systems in the plasma membrane, re-examining fundamental problems in the field such as the distinctions between high- and low-affinity transport systems, the interactions between K^+ and other ions such as NH_4^+ and Na^+, the regulation of cellular K^+ pools, the generation of electrical potentials and the problems involved in measurement of unidirectional K^+ fluxes. We place these discussions in the context of recent discoveries in the molecular biology of K^+ acquisition and produce an overview of gene families encoding K^+ transporters.

Introduction

2007 marks the 200th anniversary of the discovery of potassium by the English chemist Sir Humphrey Davy. Since then, much intensive and insightful research has been conducted on this element and its function in the living world. A recent biological highlight of this work was the awarding of the 2003 Nobel Prize in chemistry to R. MacKinnon for elucidation of the structure and function of the *Streptomyces lividans* K^+ channel at the atomic scale (Doyle et al. 1998). Potassium is one of the most abundant elements in plant tissues, comprising about 1–10% of dry matter (Epstein and Bloom 2005). Globally, over 25 MT of potash fertilizer is applied to cropland every year (Minerals Mining and Sustainable Development 2002: http://www.iied.org/mmsd/mmsd_pdfs/065_ifa.pdf), and improved efficiency of potassium acquisition by plants is an important concern among plant scientists (Lynch 2007).

Although sodium can, under some circumstances, partially replace potassium for relatively non-specific functions such as osmoregulation (Marschner et al. 1981, Subbarao et al. 1999), potassium is classified as an essential macronutrient for all plants. Many of the diverse roles of K^+ in plant cells depend on the transport of K^+ through K^+-specific membrane-bound transport proteins. Such functions include the short-term maintenance of electrical potentials across membranes (Cheeseman and Hanson 1979) and turgor-related phenomena such as cell expansion (Dolan and Davies 2004), plant movements (Moran 2007, Philippar et al. 1999), pollen tube development (Mouline et al. 2002) and stomatal opening and closing (Dietrich et al. 2001, Humble and Hsiao 1969). Other well-characterized biological functions of potassium include the activation of numerous enzymes (Suelter 1970), long-distance transport of nitrate (Ben-Zioni et al. 1971) and sucrose (Cakmak et al. 1994) and the charge stabilization of anions within the cell (Clarkson and Hanson 1980). In this review, we focus on the key topics of membrane transport and compartmentation of potassium in plant cells, summarizing the state of knowledge and indicating new directions in potassium research.

Abbreviations – CNG, cyclic-nucleotide-gated channel; HATS, high-affinity transport system; LATS, low-affinity transport system.

HATS and LATS: the two-mechanism model

Research on potassium transport in plant roots includes some of the first instances of the utilization of novel radiotracer technologies in the 1940s. Of particular note were the pioneering studies of Epstein and co-workers, who established that, at low external concentrations (under 1 m*M*), the unidirectional uptake kinetics of K^+ can be mathematically analyzed using a Michaelis–Menten model (Epstein et al. 1963). This led to the assignment of maximal velocity (V_{max}) and half-saturation concentration (K_M) terms to what was initially referred to as 'Mechanism 1' and later as the high-affinity transport system (HATS) for potassium. At external concentrations higher than 1 m*M*, K^+ transport patterns become dominated by a kinetically distinct system, which shows little if any saturation. This linear component of K^+ transport was first termed 'Mechanism 2' by Epstein and later the low-affinity transport system (LATS). The two-mechanism model is depicted in Fig. 1.

The distinct kinetics, energetics and regulatory aspects of HATS and LATS were subsequently worked out in greater detail (Glass and Dunlop 1978, Kochian and Lucas 1982, Kochian et al. 1985, Maathuis and Sanders 1995). Apart from the different external K^+ concentrations at which they operate and the shapes of their associated concentration dependence curves, each system has several unique characteristics. Most importantly, there appear to be distinct mechanisms by which HATS and LATS transporters catalyze the flux of K^+ across the plasma membrane. In the case of HATS, it is likely that K^+ enters the cell via symport with H^+, with a proposed (although possibly variable) 1:1 stoichiometry (Kochian et al. 1989, Maathuis and Sanders 1994, Maathuis et al. 1997), in an energy-dependent process involving the transmembrane proton motive force (Fig. 2). The H^+ and electrical gradients underlying this force are maintained by membrane-bound, ATP-hydrolyzing transporters that pump H^+ out of the cytosol and into the external medium (Cheeseman and Hanson 1980, Cheeseman et al. 1980, Kochian et al. 1989, Maathuis and Sanders 1994, Palmgren 2001, Pardo et al. 2006). The regulation of HATS is accomplished both by limitations to substrate binding with the carrier molecule and by feedback on

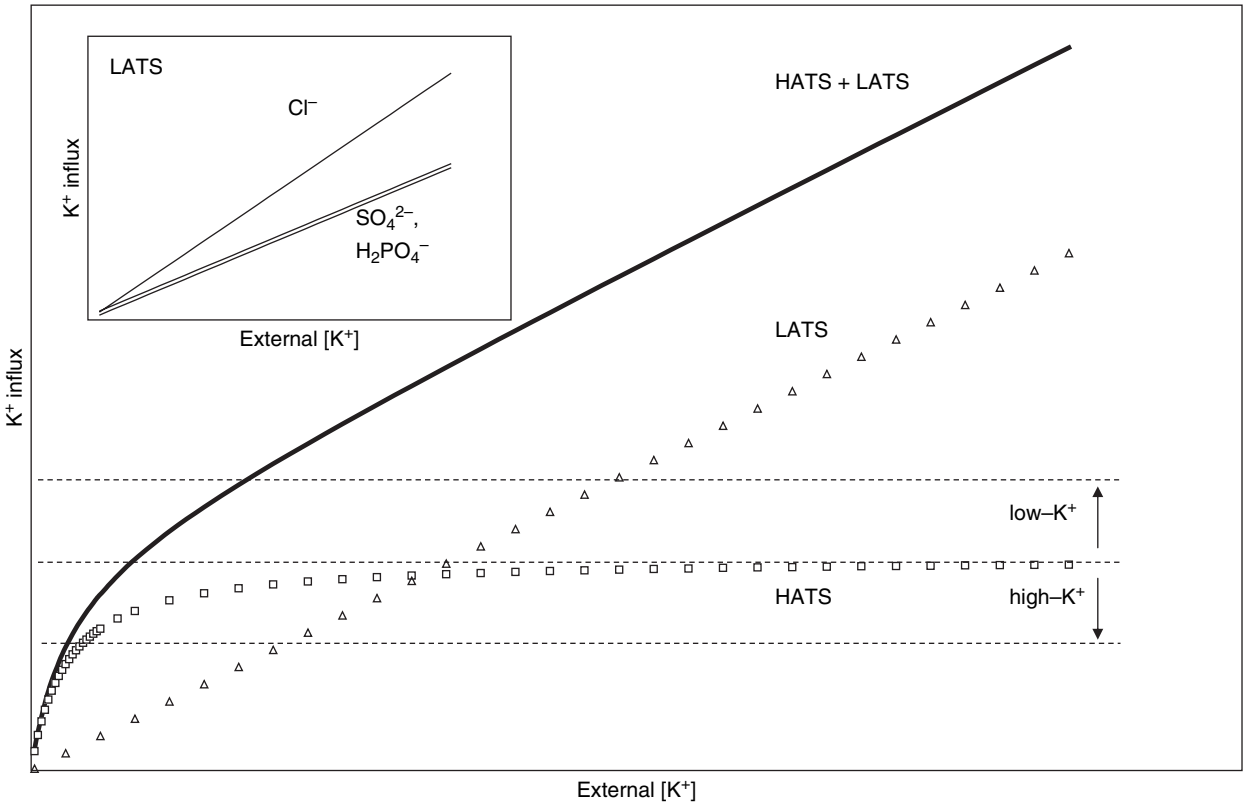

Fig. 1. General schematic of K^+ influx kinetics in plant roots. Isotherms for HATS (open squares) and LATS (open triangles) are indicated, in addition to the combined flux (solid line). Arrows and dashed lines indicate up- and downregulation of HATS, in response to plant K^+ status. Inset: Effect of accompanying anions on low-affinity K^+ fluxes.

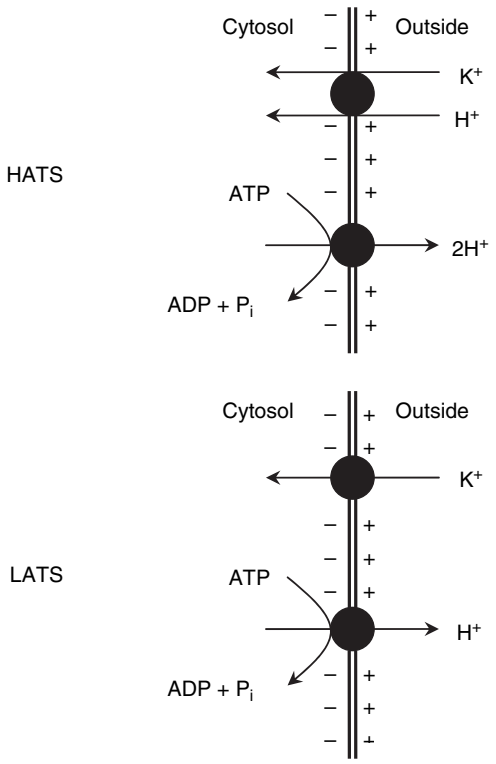

Fig. 2. General mechanisms proposed for K^+ influx into plant cells, via the HATS (upper diagram) and the LATS (lower diagram). In the HATS mechanism, the thermodynamically uphill flux of K^+ is driven by the downhill flux of H^+; charge balance is achieved by the outward pumping of two H^+ by the plasma membrane proton ATPase. In the LATS mechanism, by contrast, an electrogenic uniport of K^+ is electrically balanced by the ATP-driven efflux of one H^+.

gene transcription (Gierth et al. 2005). In the LATS, K^+ is thought to be transported via ion channels (K^+ specific as well as non-selective), which, by forming pores that cross the membrane bilayer, can catalyze thermodynamically downhill fluxes that are at least three orders of magnitude higher than those catalyzed by pumps and carriers (Tester 1990). Thermodynamically, channel activity relies on electrochemical potential gradients for K^+ to drive transport and is regulated by a wide range of agents: membrane voltage (Gassmann and Schroeder 1994), pH (Hoth and Hedrich 1999), cyclic nucleotides (Talke et al. 2003), CO_2-dependent light activation (Deeken et al. 2000), reactive oxygen species (Cakmak 2005) and K^+ itself (Johansson et al. 2006, Liu et al. 2006). The thermodynamic distinction between these two basic types of transporters forms the basis for their designation, in the recently devised transporter classification (TC) system, as class 1 (channel/pore type) for LATS transport, and class 2 (electrochemical potential-driven transporter type) for HATS transport (Busch and Saier 2002).

K^+ acquisition from low external concentrations is usually considered to be an energy-demanding process, while that from high concentrations is energetically passive. On the surface, this view is supported by analyses of the electrochemical potential gradient for K^+ transport into the plant cell, which is defined primarily by the differences in K^+ concentration and electrical potential on either side of the plasma membrane (Cheeseman and Hanson 1980, Szczerba et al. 2006a). K^+ is usually the most abundant cation in the cytosol, with concentrations typically ranging from 40 to 200 m*M* (Kronzucker et al. 2003, Leigh and Wyn Jones 1984, Walker et al. 1996), a condition that could present an energetic obstacle to K^+ entry even under abundant potassium supply, were it not for the electrical charge separation across the membrane (inside negative), which greatly enhances the uptake of cations. However, in very dilute solutions, this electrical pull is insufficient to drive K^+ influx, and an active transport mechanism is thus postulated under such conditions (Cheeseman and Hanson 1980, Maathuis and Sanders 1994).

Nevertheless, if, at higher external concentrations, thermodynamic conditions favor an energetically downhill influx of K^+, a more comprehensive view indicates that this process must still entail cellular energy consumption. This is because for every K^+ ion that enters the cell and is retained, a slight depolarization of the membrane will occur, in turn requiring a subsequent, energy-dependent electrical compensation via the plasma membrane H^+ ATPase. In addition, it has been amply demonstrated that, as potassium provision goes up, increased influx of K^+ is accompanied by a substantial increase in K^+ efflux. Except for the special case in which the thermodynamic gradient for K^+ transport across the membrane is zero (a Nernstian condition – see, e.g. Maathuis and Sanders 1994), a passive influx of K^+ entails that the efflux of K^+ must be directly energy requiring (Szczerba et al. 2006a). The idea that energy demand for K^+ acquisition can occur over a broad range of K^+ supply (1–50 m*M*) is supported by the strong correlations between K^+ uptake and ATP hydrolysis by roots of numerous plant species (Fisher et al. 1970).

Responses to plant K^+ status also distinguish HATS from LATS (Fig. 1). HATS is strongly downregulated under K^+-replete conditions and, conversely, strongly upregulated under K^+ starvation (Glass 1978, Kochian and Lucas 1982). By contrast, influx in the LATS range appears, at least in some studies, to be insensitive to K^+ status (Kochian and Lucas 1982), although, in at least one instance, low-affinity K^+ influx was enhanced by low external K^+ (Maathuis and Sanders 1995). In the latter case, however, the hyperpolarized state of the plasma membrane under low K^+, rather than a specific regulatory

mechanism, may have enhanced the passive, inward, channel-mediated current. In addition, the apparent insensitivity of LATS to plant K^+ status in other work (Kochian and Lucas 1982) may be somewhat misleading because flux underestimates are more prone to occur in the LATS range (Szczerba et al. 2006b); thus, it is possible that LATS-range K^+ influx is generally upregulated with increased K^+ status, a situation similar to the increase in low-affinity NH_4^+ transport that has been repeatedly seen with higher plant N status (Cerezo et al. 2001, Rawat et al. 1999; see below). Armengaud et al. (2004) and Gierth et al. (2005), in transcriptome analyses of *Arabidopsis*, showed that the response of putative K^+ transporter expression to K^+ starvation was largely limited to the strong upregulation of a single high-affinity transport gene, *athak5*, which may be responsible for the majority of high-affinity uptake. In another study examining gene expression in roots of wheat and barley (Wang et al. 1998), the gene encoding the putative K^+ transporter HKT1 was rapidly and strongly upregulated upon K^+ starvation, although the relevance of this gene product to K^+ acquisition has been called into question (Haro et al. 2005, Hayes et al. 2001).

Another notable difference between the two systems is seen in the interaction between K^+ uptake and the presence of other ions. HATS transport can be very sensitive to competitors or toxicants such as NH_4^+ and Na^+, while LATS transport appears to be relatively resistant to their influence (Kronzucker et al. 2003, Maathuis and Sanders 1994, Maathuis et al. 1996, Nieves-Cordones et al. 2007, Pardo and Quintero 2002, Santa-Maria et al. 2000, Spalding et al. 1999). Indeed, the sensitivity of HATS to NH_4^+ is the basis of the surprising finding that channel mediation can contribute to K^+ transport in the high-affinity range (Hirsch et al. 1998; see below). We have recently shown (Szczerba et al. 2008) that the reverse effect is not seen; that, rather, low-affinity NH_4^+ transport in barley roots is substantially reduced when the K^+ supply is increased, offering a partial explanation for the alleviation of NH_4^+ toxicity by elevated external $[K^+]$.

Although the suppression of high-affinity K^+ transport by NH_4^+ is well established, evidence for the interactions between Na^+ and K^+ is more equivocal: for instance, Maathuis et al. (1996) found that, in a wide range of terrestrial plants (including *Arabidopsis*), the addition of Na^+ either inhibited or had no effect on high-affinity K^+ absorption; by contrast, Spalding et al. (1999) showed that the non-channel-mediated uptake of K^+ into *Arabidopsis* roots (see discussion of AKT1 below), at an external $[K^+]$ of 10 μM, was in fact stimulated by Na^+. The latter finding may indicate a role, if limited, of a proposed Na^+/K^+ exchange mechanism of the HKT1 transporter (Rubio et al. 1995). Our recent work (Kronzucker et al. 2006) shows that, in barley roots, Na^+ suppresses K^+ influx at both 0.1 and 1.5 mM external $[K^+]$, while a reciprocal effect of K^+ on Na^+ influx is not observed; in still more recent experiments (under review), we have found evidence that Na^+ inhibits K^+ influx well into the low-affinity range (up to 40 mM), while such high concentrations of K^+ had no effect on Na^+ transport or compartmentation. A similar lack of effect of K^+ on Na^+ uptake was observed by Wang et al. (2007) in *Sueda maritima*, but strong reciprocal interactions of the two ions were seen in a classic study on barley roots (Rains and Epstein 1967). That the latter study shows results, in the same species, contradictory to ours is likely an indication of the non-steady-state conditions used in that study. This, however, is not to discount such an approach; it is essential to consider both short- and long-term effects of these ionic interactions, particularly with regard to the potentially important role that enriched soil K^+ may play in the amelioration of Na^+ toxicity in glycophytes.

A further aspect of differential ion interaction in the two transport ranges is the effect on the LATS of the accompanying anion (Fig. 1, inset). Epstein et al. (1963), for instance, showed that K^+ (Rb^+) influx in the LATS range was much higher with RbCl than with Rb_2SO_4. Similarly, Kochian et al. (1985) found that the velocity of LATS-range K^+ transport was 60% higher when the counterion was Cl^- rather than SO_4^{2-}, NO_3^- or $H_2PO_4^-$. In neither study was this counterion effect observed in the HATS range.

One final distinction between HATS and LATS transport to be mentioned here is that, under low-affinity conditions, the plasma membrane is much more permeable to K^+, in both the influx and the efflux directions (Pettersson and Kasimir-Klemedtsson 1990, Szczerba et al. 2006a). This increased 'leakiness' results in very high ratios of efflux to influx as $[K^+]_{ext}$ rises through the millimolar range, a phenomenon common to a wide array of nutrient ions (Britto and Kronzucker 2006). One aspect of this high permeability is that K^+ ions can be lost from roots as a result of physical disturbance, possibly because of the engagement of mechanically or stretch-activated channels (Britto et al. 2006, Shabala et al. 2000). Clearly, this ion loss from the plant system can pose a problem for the flux researcher, and its possibility must be taken into account.

In the decades prior to the identification of genes encoding K^+ transport proteins, there was a vigorous debate about whether fluxes in the high- and low-affinity ranges were each catalyzed by specialized transport proteins or, alternatively, by proteins that undergo state changes in response to varying nutritional conditions,

resulting in modified substrate affinities (Borstlap 1981, Nissen 1980). The eventual identification of genetically distinct molecular entities operating in specific parts of the transport range appeared at first to have resolved this issue, until the publication of several reports indicating that individual transporters may have both high- and low-affinity activity. Such dual-affinity behavior has also been reported for the transport of nitrate (Liu et al. 1999) and phosphate (Shin et al. 2004). In the case of potassium, at least three transporters from *Arabidopsis thaliana* appear to have dual (or very broad spectrum) affinities: the carrier AtKUP1 (Fu and Luan 1998, Kim et al. 1998) and the inward-rectifying channels AKT1 (Hirsch et al. 1998) and KAT1 (Brüggemann et al. 1999). AtKUP1, when expressed in yeast cells, shows two half-saturation constants (K_M): one in the range of 22–44 μ*M* external [K^+] and another near 11 m*M* (Fu and Luan 1998, Kim et al. 1998). The mechanism by which the switch between affinities occurs may involve phosphorylation of the transport protein, as has been demonstrated for the switch between affinities of the nitrate transporter CHL1 (Liu and Tsay 2003), and for the change in gating characteristics of the voltage-gated channel AKT2 (Michard et al. 2005). The AKT1 channel was shown to have a dual- (or broad-spectrum) affinity character by allowing growth of *A. thaliana* under conditions where high-affinity K^+ transport was blocked by NH_4^+. In this situation, an inward channel-mediated flux of K^+ was calculated to be thermodynamically feasible even with external [K^+] as low as 10 μ*M*, given a sufficiently hyperpolarized plasma membrane (Hirsch et al. 1998). A recent report by Li et al. (2006) indicates that AKT1 is upregulated at low external [K^+] via a calcium-dependent phosphorylation event, providing further evidence for the role of this channel in 'high-affinity' K^+ influx. In addition, the guard cell channel KAT1 was shown to mediate K^+ uptake from an equally low [K^+], when expressed both in *Arabidopsis* and in yeast cells (Brüggemann et al. 1999).

The physiological significance of these findings, however, remains unclear. In the case of KAT1, some evidence indicates that the channel inactivates at submillimolar external [K^+], although in a heterologous expression system (mammalian HEK cells; Hertel et al. 2005), although this effect was not observed in *Arabidopsis* itself (Brüggemann et al. 1999). In the case of AKT1, the K_M of Rb^+ uptake by *Arabidopsis* roots (measured as the difference in uptake between wild-type plants and *akt1-1* mutants) was found to be 0.9 m*M* (Gierth et al. 2005), suggesting that AKT1 does in fact normally operate in the low-affinity range. In addition, K^+ uptake by channels relies on the membrane electrical potential as a driving force; the measured potential in the study by Hirsch et al. (1998) was only sufficiently negative in 20% of wild-type cells to drive passive uptake through AKT1. Nevertheless, it has been reported elsewhere that AKT1 may be responsible for 55–63% of K^+ influx in the submillimolar range, again based on differences between wild-type and mutant plants (Spalding et al. 1999). In both examples, however, it is difficult to rule out pleiotropic effects in mutant lines, and thus the conclusions must be appreciated with some caution. Still, it seems clear that considerable kinetic overlap exists among genetically distinct groups of transport proteins.

Moreover, it is beyond question that plant roots have phenotypically plastic systems in place that allow potassium to be extracted from soil solutions that vary considerably in [K^+], reflecting edaphically realistic concentration ranges of 0.1–6 m*M* or even higher in fertilized soils (Adams 1971, Kochian and Lucas 1982, Reisenauer 1966), which can change rapidly in the field, given the substantial impact of soil drying and rehydration.

In retrospect, given the multiplicity of distinct K^+ transport proteins found in plant cells and the number of different cell types found within the root, it is perhaps surprising that the HATS-range concentration-dependence isotherms of K^+ transport into roots fit so well with the Michaelis–Menten model of enzyme kinetics, a model that was initially developed for purified enzymes in solution. Interestingly, protoplasts isolated from maize roots exhibited kinetic patterns of K^+ uptake that were essentially identical to those measured in whole roots (Kochian and Lucas 1983), indicating that root K^+ transport in this range may be dominated by a single protein (Gierth et al. 2005) or by a group of closely related proteins that share similar kinetic characteristics.

Another problematic aspect of the interpretation of influx isotherms is that they are based on measurements that are underestimated because of the simultaneous occurrence of K^+ efflux (Britto and Kronzucker 2001). In the steady state (i.e. when plant growth and experimentation are conducted under the same physicochemical conditions), the degree to which efflux can result in an underestimate of influx depends greatly on external [K^+] concentration. Because of the higher ratios of efflux to influx seen in the LATS range (see above), 'direct', steady-state influx measurements in this range are inherently more prone to inaccuracies than in the HATS range and can lead to substantial underestimates of K^+ influx (Szczerba et al. 2006b). This problem of accurate flux measurements in the LATS is not unique to K^+ because increased efflux at higher external concentrations is seen with several other nutrient ions (Britto and Kronzucker 2006).

This limitation of the direct influx method can be circumvented under some conditions by means of

compartmental analysis, which monitors both efflux and retention of potassium by the plant, in addition to providing information about intracellular pool sizes of K^+ (see below). However, a crucial assumption underlying such analyses is that the plant system is examined under steady-state conditions. Influx isotherms, on the other hand, depict influxes over a range of external concentrations, only one of which represents the steady-state provision. Thus, compartmental analysis cannot by itself resolve the distortions present in such isotherms as a result of simultaneous efflux. While the extent of efflux under non-steady-state conditions has yet to be investigated, preliminary results in our laboratory, from a combination of compartmental and direct influx analyses, indicate that steady-state K^+ efflux is conserved by the plant in the short term, when $[K^+]_{ext}$ is shifted, and that a new steady state requires several hours to be achieved. This information will be used to develop influx isotherms that more accurately reflect plant capacity to transport K^+ and other ions.

Another aspect of K^+ transport research that needs to be approached with caution is experimental work that employs rubidium-86 as a radiotracer for potassium. Justification of the widespread use of $^{86}Rb^+$ as a potassium analogue stems from several reports suggesting that, at least in some cases, there is little discrimination between the two ions (Kochian and Lucas 1982, Läuchli and Epstein 1970, Polley and Hopkins 1979). However, numerous other studies have shown that, on the contrary, $^{86}Rb^+$ is a poor tracer for K^+ in higher plant systems (Behl and Jeschke 1982, Cline and Hungate 1960, de Agazio et al. 1983, Jacoby 1975, Jacoby and Nissen 1977, Kannan and Ramani 1973, Maas and Leggett 1968, Marschner and Schimanski 1968, Schachtman et al. 1992); substantial discrimination between the two elements has also been observed in *Nitellopsis* (MacRobbie and Dainty 1958), *Chlamydomonas* (Malhotra and Glass 1995, Polley and Doctor 1985), *Chara* (Keifer and Spanswick 1978), *Ulva* and *Chaetomorpha* (West and Pitman 1967), as well as in *Escherichia coli* (Rhoads et al. 1977). Moreover, the discrimination between these elements is not uniform across experimental conditions. For instance, two studies have shown that it increases in *Chlamydomonas* with K^+ deprivation. In addition, de Agazio et al. (1983) concluded that, in maize roots, discrimination against Rb^+ is particularly strong in the high-affinity, energy-dependent range of K^+ uptake. A similar conclusion was reached with *E. coli* (Rhoads et al. 1977), in which a 1000-fold discrimination against Rb^+ was seen in the high-affinity K^+ uptake range and a 10- to 25-fold discrimination in two of three low-affinity systems. In the third low-affinity system, K^+ was actually discriminated against, in favor of Rb^+.

Unfortunately, the majority of K^+ transport studies using radiotracers have used $^{86}Rb^+$ instead of $^{42}K^+$. This is largely because of the convenience of using $^{86}Rb^+$, which has a much longer half-life than $^{42}K^+$ (18.65 days vs 12.36 h). For the same reason, studies using $^{86}Rb^+$ rarely involve corroboration of results by use of $^{42}K^+$. Given the numerous instances of Rb/K discrimination, some of the conclusions concerning K^+ transport, arrived at using $^{86}Rb^+$ exclusively, are likely to be incorrect. This problem is compounded by the issue of simultaneous influx and efflux, mentioned above, that may give rise to inaccurate isotherms. A further complication in the measurement of K^+ fluxes is the rarely reported phenomenon of flux alterations caused by physical disturbance of experimental plants, a problem that is particularly pressing in the LATS range (Britto et al. 2006; see above).

Electrical aspects of K^+ transport

Potassium transport is a key component underlying the homeostatic regulation of the plasma membrane electrical potential difference ($\Delta\Psi$) in plant cells. Interestingly, however, a range of set points for $\Delta\Psi$ can be achieved by the cell, depending on factors such as the external concentration of K^+ itself (Cheeseman and Hanson 1979, Etherton and Higinbotham 1960, Hayes et al. 2001, Maathuis and Sanders 1993). Membranes depolarize rapidly in response to increases in external K^+ and hyperpolarize with decreasing $[K^+]_{ext}$. This can be explained by the passive, channel-mediated, electrogenic flux of K^+ either into the cell (causing depolarization) or out of it (causing hyperpolarization). The direction of the flux is determined by the direction of the potassium diffusion potential, which is a function of $\Delta\Psi$ and of the ratio of $[K^+]$ on either side of the membrane. $\Delta\Psi$ shows a roughly linear response to the log of $[K^+]_{ext}$ over several orders of magnitude (e.g. three orders in the study by Etherton and Higinbotham 1960). Thus, plant cells behave very similarly to potassium electrodes within this response range (Fig. 3).

Conversely, plants engage electrogenic K^+ transport that rectifies alterations in $\Delta\Psi$ brought about by other means. For instance, sudden exposure of roots to cations such as Rb^+, Cs^+ and NH_4^+ causes membrane depolarization in root cells of maize, and the subsequent efflux of K^+ counteracts this change (Nocito et al. 2002). This efflux of K^+ is mediated by outward-rectifying K^+ channels; similarly, the influx of K^+ can counteract membrane hyperpolarization via the activity of inward-rectifying channels. Clearly, both types of channels are voltage regulated.

It should be pointed out, however, that the channel-mediated flux of K^+ along its diffusion potential is not

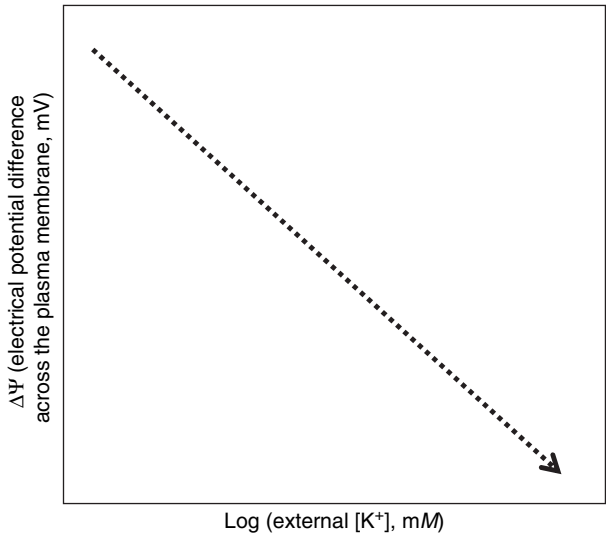

Fig. 3. Potassium-induced plasma membrane depolarization. Plant cells behave like potassium electrodes, adjusting their membrane electrical potentials to variable set points as external [K^+] changes.

a primary generator of $\Delta\Psi$, as it involves merely passive transport. The active transport of K^+, mediated by HATS, also does not contribute to the primary generation of $\Delta\Psi$ but is contingent upon an electrochemical proton gradient to furnish the required energy. Ultimately, the establishment of this gradient by the activity of the plasma membrane H^+-pumping ATPase is the means by which plant cells become electrically polarized (Palmgren 2001), in contrast to animal cells, which generate $\Delta\Psi$ by the ATP-driven counter-exchange of three Na^+ ions and two K^+ ions.

Cytosolic K^+ pools

The cytosolic concentration of potassium is under fairly strict homeostatic control and is maintained by fluxes to and from the soil solution, as well as to and from the storage pool in the vacuole; these fluxes are catalyzed by transporters in the plasma membrane and tonoplast membrane, respectively. The vacuolar K^+ pool is much more dynamic than that of the cytosol, gaining and losing potassium as required to maintain cytosolic K^+ homeostasis (Leigh 2001, Walker et al. 1996). Typically, cytosolic [K^+] is held between 80 and 200 m*M*, although declines in this value have been observed under conditions of K^+ starvation (Walker et al. 1996), salt stress (Hajibagheri et al. 1987, 1988, Kronzucker et al. 2006, Speer and Kaiser 1991), ammonium toxicity (Kronzucker et al. 2003) and aluminum toxicity (Lindberg and Strid 1997). Surprisingly, in our own laboratory, a substantial decline of 40–50% in cytosolic [K^+] was also observed with an *increase* in external [K^+] from an HATS-range value of 0.1 m*M* to an LATS-range value of 1.5 m*M* (Kronzucker et al. 2003; Szczerba et al. 2006a; at higher $[K^+]_{ext}$ this pool was seen to recover). This counter-intuitive finding, determined under steady-state conditions, might be explained by a link between transmembrane K^+ distribution and the shift in K^+ transport from the high-affinity to the low-affinity condition, represented by these two external concentrations of K^+. A fundamental distinction between these conditions is the active transport of K^+ in the HATS range and its passive transport in the LATS. In the latter situation, an electrochemically neutral distribution of K^+ across the membrane may result (Maathuis and Sanders 1993), and this, in conjunction with the potassium-dependent drop in membrane potential, could dramatically alter the distribution of K^+ across the plasma membrane.

Table 1 shows values for cytosolic [K^+], obtained from a variety of plant systems and using several analytical methods. Ranges of values, where given, represent the response of the cell to K^+ availability; in many cases, this range is fairly narrow, reflecting the homeostasis of the K^+ pool. Interestingly, the use of widely differing laboratory techniques to determine cytosolic [K^+], including tracer analysis (Pitman and Saddler 1967), longitudinal ion profiling (Jeschke and Stelter 1976), X-ray microanalysis (Flowers and Hajibagheri 2001), the K^+-sensitive fluorescent dye PBFI (potassium-binding benzofuran isophthalate; Halperin and Lynch 2003), K^+-specific microelectrodes (Walker et al. 1996) and cell fractionation (Speer and Kaiser 1991), nevertheless results in reasonably close agreement. This is in contrast to large differences in values obtained using a similar range of methods for other ions such as sodium (Carden et al. 2003, Kronzucker et al. 2006), ammonium (Britto et al. 2001, Lee and Ratcliffe 1991), and nitrate (Britto and Kronzucker 2003, Siddiqi and Glass 2002). The reasons for inconsistent agreement is unclear; the general agreement seen among methods in the case of potassium may be indicative of the homeostatic control of this pool, which may render it more resistant to physical disturbances that may be imposed during experimentation, for example with microelectrode impalement or with tracer elution protocols.

K^+ transport families

In the past decade, there has been substantial progress in the identification of genes encoding K^+ transporters in plants, as can be seen in the plethora of excellent recent reviews on the subject (Ashley et al. 2006, Cherel 2004, Gierth and Mäser 2007, Grabov 2007, Hedrich and Marten 2006, Lebaudy et al. 2007, Rodriguez-Navarro

Table 1. Cytosolic concentrations or activities of potassium, as determined by a variety of methods in several plant systems.

Method	Plant material	$[K^+]_{cytosol}$ (m*M*)	Reference
Efflux analysis	Barley root	92	Pitman and Saddler (1967)
		236	Bange (1979)
		316–320	Behl and Jeschke (1982)
		127–184	Memon et al. (1985)
		40–130	Kronzucker et al. (2003)
		25–200	Szczerba et al. (2006a)
	Onion root	184	Macklon (1975)
	Maize root	99–108	Davis and Higinbotham (1976)
Longitudinal ion profiling	Barley root	110	Jeschke and Stelter (1976)
X-ray microanalysis	Maize root	129–162	Hajibagheri et al. (1987, 1988)
		71–119	Pitman et al. (1981)
Fluorescent dye	Barley protoplasts	65–70	Lindberg (1995)
	Arabidopsis thaliana root hairs	55–60	Halperin and Lynch (2003)
K^+-selective microelectrode	*Acer pseudoplatanus* (suspension cells)	126	Rona et al. (1982)
	A. thaliana root	83	Maathuis and Sanders (1993)
	Barley root	45–83	Walker et al. (1996)
	Barley root (± salt stress)	39–63	Carden et al. (2003)
Cell fractionation	Pea leaf	53	Speer and Kaiser (1991)
	Spinach leaf	147	Speer and Kaiser (1991)

and Rubio 2006, Shabala 2003, Véry and Sentenac 2003). This progress has been made despite a somewhat false start with the discovery of the first putative high-affinity K^+ transporter HKT1 (Schachtman and Schroeder 1994), which is now thought to belong to a group of transporters, the HKT/Trk family, that are clearly implicated in the transport and internal recirculation of Na^+ but appear to be of relatively minor significance to K^+ transport. This revision is an important example of the problems associated with heterologous expression systems (Gierth and Mäser 2007, Haro et al. 2005, Lebaudy et al. 2007), which are used extensively in genetic screening projects. Potentially more promising is the development of plant-based expression systems for physiological studies on specific gene products (Bei and Luan 1998). Nevertheless, the discovery and characterization of HKT proteins have some relevance to K^+ transport, in that, despite being implicated in high-affinity cation transport, their molecular architecture is similar to that of bona fide low-affinity K^+ transporters (Shaker and KcsA-type channels). In both types of transporter, membrane–pore–membrane (MPM) motifs are found, with conserved residues within the pore loop area functioning as an ion selectivity filter (Mäser et al. 2002; see below).

At present, it appears clear that the high-affinity range of transport in plants is dominated by the activity of transporters from the KT/HAK/KUP family, which were identified based on sequence homologies to transporters from bacteria (Schleyer and Bakker 1993) and fungi (Bañuelos et al. 1995), as well as through mutant complementation studies. These transporters have 10 to 14 transmembrane regions (Gierth and Mäser 2007) and probably catalyze K^+ transport by engaging a potassium/proton symport mechanism, as has been shown for the *Neurospora crassa* HAK1 gene product (Haro et al. 1999). In *Arabidopsis*, microarray analysis has shown that several members of this family are upregulated by K^+ starvation, conforming to the phenotype of HATS upregulation; of these, AtHAK5 is particularly strongly upregulated and may be the most important contributor to high-affinity K^+ uptake (Gierth et al. 2005). In addition to K^+ uptake, there appear to be several other roles for transporters in this group, specifically in the distribution of auxin (Vicente-Agullo et al. 2004) and in cell expansion (Elumalai et al. 2002), two processes that, clearly, are intimately connected (Jones et al. 1998). The relationship between potassium transport and these other functions requires further study.

In addition to the major contribution to high-affinity K^+ transport made by KT/HAK/KUP transporters and the minor possible involvement of HKT/Trk transporters, there is growing evidence that two large, related families of electroneutral cation–proton antiporters, CPA1 and CPA2, are also responsible for non-channel-mediated K^+ transport (Brett et al. 2005, Gierth and Mäser 2007). So far, however, the functional attributions of these proteins have been largely for the transport of Na^+, one prominent example being the tonoplast transporter NHX1 (a CPA1-type protein), which can confer salinity tolerance, most likely by enhancing the Na^+ flux to the vacuole (Apse et al. 1999). Another example from the CPA1 family is the SOS1 protein, which also plays an important role in salt

tolerance by catalyzing Na^+ efflux from the cell (Shi et al. 2000). Nevertheless, NHX1 (and similar proton antiporters) has been shown to be responsible for vacuolar K^+ loading, as well as for Na^+ transport across the tonoplast, although it appears to have lower specificity for K^+ (Zhang and Blumwald 2001); the tandem-pore TPK1 channel may be more important for the trans-tonoplast movement of K^+, particularly in its release from guard cell vacuoles (Gobert et al. 2007). At least two CHX proteins from the CPA2 family appear to be involved in K^+ homeostasis and pH regulation (Gierth and Mäser 2007), properties that are tied together mechanistically via the counter-exchange of K^+ and H^+ (Britto and Kronzucker 2005).

Potassium-selective channels have been identified at the molecular genetic level as multimers composed of α-subunits belonging to three major families: the Shaker, TPK (tandem-pore) and Kir (inward-rectifying)-like families (Lebaudy et al. 2007). Of these, the best characterized, and possibly the most functionally important, is the family of Shaker-type channels. The tetrameric channel is composed of four α-subunits arranged around a central pore (Zimmermann and Sentenac 1999). Each subunit consists of six hydrophobic, transmembrane segments, with a region of positively charged amino acids on the fourth segment acting as a voltage sensor, and a pore domain between the fifth and sixth segment containing the highly conserved GYGD (glycine-tyrosine-glycine-aspartate) motif, a key characteristic of potassium selectivity filters (Véry and Sentenac 2003).

In addition to the above-mentioned families of K^+-specific channels, K^+ currents can also be conducted via non-selective cation channels (Demidchik and Maathuis 2007), a heterogeneous group that includes the Shaker-like, cyclic-nucleotide-gated channels (CNGs). Twenty CNGs have been found in *Arabidopsis* (Talke et al. 2003), one of which, the putative K^+ channel AtCNGC10, was recently found to profoundly influence growth and starch accumulation (Borsics et al. 2007). By contrast, only nine Shaker-type channel genes have been identified in *Arabidopsis*, but, because Shaker subunits can form heteromers, the structural–functional diversity of these proteins may be vast (Lebaudy et al. 2007). A vivid demonstration of this was seen in the case of transformation of *Xenopus* oocytes with five Shaker genes, the resulting gene products being shown to polymerize indiscriminately, suggesting the presence of a major source of K^+ channel diversity in plants (Dreyer et al. 1997, Xicluna et al. 2007).

Apart from their primary role in mediating potassium uptake from the soil, particularly under K^+-replete conditions, potassium channels have a wide range of functions within the plant. One major role, mentioned above, is the short-term maintenance of electrical potential gradients across cell membranes, in which K^+ channels operate in concert with electrogenic pumps (including the plasma membrane H^+ ATPase) and chloride transporters (Gradmann and Hoffstadt 1998). Because K^+ channels are electrogenic in mechanism, all can contribute to the polarization state of the cell, but the voltage-gated channels have regulatory components that render them more specifically suited to this function. These channels are generally of the Shaker type, for both inward- and outward-rectifying fluxes (Lebaudy et al. 2007). Shaker channels have also been shown to function in the xylem loading of K^+ (SKOR channels; Gaymard et al. 1998), as well as in phloem loading and unloading (AKT2/3; Deeken et al. 2000, 2002, Lacombe et al. 2000).

To conclude this review on cellular K^+ transport in plants, we wish to highlight three very recent discoveries in the literature, which illustrate the utility of molecular biology to unravel physiological phenomena of broad interest to plant biologists. In one example (Yu et al. 2006), the activity of the AKT2 channel homologue SPICK2 was shown to be a likely participant in the turgor-related movements of *Samanea* motor cells, acting differentially in extensor and flexor halves of the leaf pulvinus, depending on the phosphorylation state of the transporter. In another example (Sano et al. 2007), K^+-dependent cell turgor influencing different phases of the cell cycle appears to be reciprocally controlled by the inward-rectifying K^+ channel NKT1 during the G1 phase, and the outward-rectifying K^+ channel NTORK1 during the S phase. Finally, Gazzarrini et al. (2006) showed that the *Chlorella* virus MT325 encodes both water channels and K^+ channels that appear to work synergistically in the host, providing both an osmotic driving force (cellular K^+ accumulation) and a pathway for water flow into the cell. These examples indicate the ongoing progress in demonstrating critical functions for potassium pools and transporters in plant systems.

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