Physiology

K$^+$ uptake in plant roots. The systems involved, their regulation and parallels in other organisms[☆]

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ABSTRACT

Potassium (K$^+$) is an essential macronutrient for plants. It is taken into the plant by the transport systems present in the plasma membranes of root epidermal and cortical cells. The identity of these systems and their regulation is beginning to be understood and the systems of K$^+$ transport in the model species *Arabidopsis thaliana* remain far better characterized than in any other plant species. Roots can activate different K$^+$ uptake systems to adapt to their environment, important to a sessile organism that needs to cope with a highly variable environment. The mechanisms of K$^+$ acquisition in the model species *A. thaliana* are the best characterized at the molecular level so far. According to the current model, non-selective channels are probably the main pathways for K$^+$ uptake at high concentrations (>10 mM), while at intermediate concentrations (1 mM), the inward rectifying channel AKT1 dominates K$^+$ uptake. Under lower concentrations of external K$^+$ (100 μM), AKT1 channels, together with the high-affinity K$^+$ uptake system HAK5 contribute to K$^+$ acquisition, and at extremely low concentrations (<10 μM) the only system capable of taking up K$^+$ is HAK5. Depending on the species the high-affinity system has been named HAK5 or HAK1, but in all cases it fulfills the same functions. The activation of these systems as a function of the K$^+$ availability is achieved by different mechanisms that include phosphorylation of AKT1 or induction of HAK5 transcription. Some of the characteristics of the systems for root K$^+$ uptake are shared by other organisms, whilst others are specific to plants. This indicates that some crucial properties of the ancestral of K$^+$ transport systems have been conserved through evolution while others have diverged among different kingdoms.

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Introduction

Potassium is an essential macronutrient for plants, composing up to 10% of the plant dry weight (Leigh and Wyn Jones, 1984). It fulfills a number of important functions related to enzyme activation, as well as the neutralization of negative charges, the maintenance of cell turgor, plant growth and organ movement (Marschner, 2012;

see also Anschütz et al., 2014). K$^+$ is taken up by the plant root through the epidermal and cortical cells and once in the stele, it is transported to the shoot and distributed to the leaves (for further details on K$^+$ distribution in plants see also Ahmad and Maathuis, 2014; Wigoda et al., 2014). Most of these processes involve the movement of K$^+$ through the plasma membrane, mediated by different transport systems embedded in the cell membrane.

The K$^+$ concentration in the cytosol of plant cells is maintained at around 100 mM, its optimal level for fulfilling metabolic functions (Britto and Kronzucker, 2008; White and Karley, 2010). In contrast, the K$^+$ concentrations of the soil solution are highly variable, usually in the range of 1 to 0.1 mM, although they can sometimes be even lower (Maathuis, 2009). To a certain extent, plants are able to adjust to different K$^+$ availabilities, developing adaptive responses that mainly involve changes in root architecture and activation or inhibition of K$^+$ transport systems. Agricultural practices attempt to mitigate the variability in nutrient availability using fertilizers to try to maintain nutrients at optimal levels and K$^+$ fertilization is a vital input in agriculture. Even so, intensively cultured land can become K$^+$ deficient (Dobermann et al., 1998; Pal et al., 2001; Rengel and Damon, 2008; Yang et al., 2004) through a greater K$^+$ withdrawal during crop harvest than is supplied, or losses by lixiviation in sandy soils (Pal et al., 2001; see also Zörb et al., 2014). In addition, certain

environmental stresses such as salinity impair K$^+$ nutrition causing deficiency (Alemán et al., 2009b; Botella et al., 1997; Cuin et al., 2003). Furthermore, demand for K$^+$ fertilization is likely to increase; in Africa for example, K$^+$ demands will only be met by doubling the word production of potash fertilizers (Manning, 2010). There is a need to reduce the costs derived from K$^+$ fertilization, and this may be achieved by obtaining crop varieties more efficient in their use of K$^+$ (Rengel and Damon, 2008). Reaching this goal is likely to only be made possible if we can identify and characterize the systems involved in K$^+$ acquisition in plants (Schroeder et al., 2013). In this review, the main properties of K$^+$ uptake at the root level, the molecular systems involved in its transport and their characteristics in comparison with other organisms are presented.

K$^+$ absorption in the root

Major systems for K$^+$ uptake

More than 60 years ago, Epstein proposed that the systems involved in ion transport are enzymes and his group analyzed the kinetics of nutrient uptake in barley roots (Epstein and Hagen, 1952). By applying the concept of enzyme kinetics to the study of root K$^+$ absorption, they observed a biphasic response to the increase in external K$^+$ concentration (Epstein et al., 1963). Their results suggested that at least two transport systems are involved K$^+$ in uptake: a high-affinity system that operates at low external concentrations and a low-affinity system at higher concentrations. This biphasic behavior has since been observed in many plant species, although some exceptions do occur; maize for example, shows a linear non-saturating response in the low-affinity range (Kochian and Lucas, 1982). In the high affinity range of concentrations, K$^+$ uptake is most likely mediated by a K$^+$/H$^+$ symporter, whilst the low-affinity uptake appears to be mediated by inwardly rectifying K$^+$ channels (Maathuis et al., 1997; Maathuis and Sanders, 1996; Rodríguez-Navarro, 2000).

An increasing number of molecular approaches and tools have provided researchers with the means of elucidating the molecular entities involved in root K+ uptake. The initial functional characterization was based on the expression of cDNAs that encode putative K$^+$ transport systems in heterologous organisms such as yeast or *Xenopus* oocytes, and also on studies of the expression patterns of the corresponding genes. These studies pointed toward a member of the KT/HAK/KUP family, named HAK1 in some species such as barley (Santa-María et al., 1997), rice (Bañuelos et al., 2002) or pepper (Martínez-Cordero et al., 2004), or HAK5 in others such as *Arabidopsis* (Rubio et al., 2000) or tomato (Nieves-Cordones et al., 2007), as a candidate for the high-affinity K$^+$ uptake system. For the low-affinity one, an inwardly-rectifying K$^+$ channel of the Shaker family, AKT1 (Lagarde et al., 1996; Sentenac et al., 1992), has been postulated. Using *Arabidopsis* T-DNA insertional knock-out mutants that disrupt the genes encoding the HAK5 and the AKT1 K$^+$ transport systems, a clear demonstration for the role of each of them has been possible (Hirsch et al., 1998; Qi et al., 2008; Rubio et al., 2008; Spalding et al., 1999). While AtHAK5 seems to be the only system for K$^+$ uptake at external concentrations below 10 μM, both AtHAK5 and AKT1 mediate uptake in the range of 10–200 μM. At higher concentrations, AKT1 largely contributes to K$^+$ uptake, with other systems, probably non-selective cation channels (NSCCs), contributing when the external K$^+$ concentration is sufficiently high (Alemán et al., 2011; Caballero et al., 2012; Rubio et al., 2010; see also Pottosin and Dobrovinskaya, 2014).

These results show clearly that a channel was indeed operating in the high-affinity range of concentrations, as described by Epstein et al. (1963). These results are surprising, but they can be clarified when the bioenergetic properties of cell-walled eukaryotic cells are considered. The soil concentration of K$^+$ is between 0.1 and 1 mM and cytoplasmic K$^+$ is approximately 100 mM (Britto and Kronzucker, 2008; White and Karley, 2010), so K$^+$ enters the root cell against its concentration gradient. To be energetically favorable, the plasma membrane of plant cells is energized by the activity of a H$^+$-ATPase that, by consuming ATP, pumps H$^+$ out of the cell. Thus, a potential consisting of a H$^+$ gradient (ΔpH) (pHext = 5.5, pHcyt = 7.3) and an electrical gradient (ΔV_m, negative inside) is created. As a cation, K$^+$ can be passively driven into the cell down the ΔV_m; a process that can occur via a secondary transport system such as a uniport, as for example, an inward-rectifying K+ channel, i.e., AKT1. The membrane potential of a plant cell not only depends on the action of the H$^+$-ATPase, but it is also greatly affected by the depolarizing effect of K$^+$-uptake through these channels. Thus, the membrane potential also depends on the external K$^+$ concentration (Wang and Wu, 2010) and a weak linear relationship between the membrane potential and the log of [K$^+$]ext, over several orders of magnitude, has been observed (Cheeseman and Hanson, 1979; Etherton and Higinbotham, 1960; Maathuis and Sanders, 1993).

The limit to which a K$^+$ channel can concentrate K$^+$ in the cell depends on both the values of the K$^+$ gradient and the ΔV_m across the plasma membrane. By using multibarreled microelectrodes, the cytosolic K$^+$ activity, pH and the membrane potential of epidermal and cortical root cells have been determined in barley grown under different K$^+$ supplies; in plants grown at 5 mM K$^+$, the resulting ΔV_m of −83 mV allowed a passive system that was sufficient for accumulating K$^+$ (Walker et al., 1996). Studies with other species and differing growth conditions have also reported ΔV_m values negative enough to allow passive K$^+$ uptake from lower external K$^+$ concentrations (Caballero et al., 2012; Nieves-Cordones et al., 2008; Volkov and Amtmann, 2006). Indeed, membrane potentials more negative than −200 mV have been reported in tomato (Nieves-Cordones et al., 2008) and *Arabidopsis* (Spalding et al., 1999) K$^+$-starved plants. These ΔV_m values would allow passive K$^+$ uptake from an external concentration as low as 30 μM K$^+$: a concentration much lower than initially thought (White and Karley, 2010). By using the *hak5* and *akt1 Arabidopsis* knock-out mutant lines described above, the external K$^+$ concentration that sets the limit for passive K$^+$ uptake has been accurately established (Coskun et al., 2013; Pyo et al., 2010; Rubio et al., 2008). Below 100 μM K$^+$, the AtHAK5 transporter and the AKT1 channel are the only systems involved in K$^+$ uptake (Rubio et al., 2010); *athak5* plants, with the AKT1 channel as the only remaining system for K$^+$ uptake, can take up K$^+$ and grow at K$^+$ concentrations as low as 30 μM (Pyo et al., 2010; Rubio et al., 2008). This is likely due to the highly hyperpolarized membrane potentials registered in root cells of these *athak5* plants when deprived of K$^+$ (our unpublished results). At external K$^+$ concentrations lower than 30 μM, an active system, probably a K$^+$–H$^+$ symporter like the high-affinity HAK5 transporter, needs to be evoked (Maathuis and Sanders, 1994; Walker et al., 1996). Under such conditions, the ΔpH needs to be considered along with the electrical membrane potential, in order to understand how the high concentrative capacities can be reached by the plant. Indeed, pepper and tomato plants are capable of depleting K$^+$ at external concentrations below 0.1 μM (Martínez-Cordero et al., 2004; Nieves-Cordones et al., 2007); and tomato plants grown in hydroponics under a constant supply of 20 μM K$^+$ show similar vegetative growth parameters than when grown with 1 mM K$^+$ (our unpublished results).

K$^+$ sensing and regulation of K$^+$ transport systems

Sensing of and response to K$^+$ by the plant appears to be mediated by a number of different means. These include the cell