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Going beyond nutrition: Regulation of potassium homeostasis as a common denominator of plant adaptive responses to environment

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ABSTRACT

Partially and fully completed plant genome sequencing projects in both lower and higher plants allow drawing a comprehensive picture of the molecular and structural diversities of plant potassium transporter genes and their encoded proteins. While the early focus of the research in this field was aimed on the structure–function studies and understanding of the molecular mechanisms underlying K⁺ transport, availability of *Arabidopsis thaliana* mutant collections in combination with micro-array techniques have significantly advanced our understanding of K⁺ channel physiology, providing novel insights into the transcriptional regulation of potassium homeostasis in plants. More recently, posttranslational regulation of potassium transport systems has moved into the center stage of potassium transport research. The current review is focused on the most exciting developments in this field. By summarizing recent work on potassium transporter regulation we show that potassium transport in general, and potassium channels in particular, represent important targets and are mediators of the cellular responses during different developmental stages in a plant's life cycle. We show that regulation of intracellular K⁺ homeostasis is essential to mediate plant adaptive responses to a broad range of abiotic and biotic stresses including drought, salinity, and oxidative stress. We further link post-translational regulation of K⁺ channels with programmed cell death and show that K⁺ plays a critical role in controlling the latter process. Thus, it appears that K⁺ is not just the essential nutrient required to support optimal plant growth and yield but is also an important signaling agent mediating a wide range of plant adaptive responses to environment.

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Abbreviations: ABA, abscisic acid; ABI1, abscisic acid insensitive 1; AIP1, AKT1 interacting protein phosphatase 1; AKT1, *Arabidopsis* K⁺ transporter 1; AtCHX7, cation-proton exchanger 7; AtKC1, *Arabidopsis* potassium channel α -subunit; AtNHX3, sodium/proton (Na⁺/H⁺) antiporter 3; ATP, adenosine triphosphate; BA, benzyladenine; BY-2, bright yellow-2; CBL, calcineurin B-like protein; CCC, Cation-Cl⁻ cotransporter; CED9, mammalian anti-apoptotic CED-9 gene; CIPK, CBL-interacting protein kinase; CNGCs, cyclic nucleotide activated channels; COI1, Coronatine-Insensitive 1; COS, CV-1 (simian) in origin carrying the SV40 genetic material; CPA2, proton antiporter-2; CPK, Ca²⁺ dependent protein kinase; DAMPs, damage associated molecular patterns; EF-hands, family of Ca²⁺-binding proteins; EFR, EF-Tu receptor; E_K, reversal potential of K⁺; FLS2, flagellin sensitive 2; GORK, guard cell outward rectifying K⁺ channel; GRFs, general regulatory factors; HAK5, high-affinity transporter 5; JA, jasmonic acid; K⁺_{in} channel, K⁺ uptake channel; K⁺_{out} channel, K⁺ release channel; K2P, two-pore K⁺ channels (TPK/K2P); KAT1, K⁺ channel *Arabidopsis thaliana* 1; KCO, kalium channel outward-rectifying; KcsA, potassium crystallographically-sited activation channel; KEA5, K⁺ efflux antiporter 5; KST, K⁺ channel from *Solanum tuberosum*; KUP, K⁺ uptake transporter; K_V, voltage-dependent *Shaker*-like potassium channels; KZM1, K⁺ channel *Zea mays* 1; *lks1*, *Arabidopsis* low-K⁺-sensitive mutant; MAMPs, microbe-associated molecular patterns; NADPH, nicotinamide adenine dinucleotide phosphate hydrate; NKT1, *Nicotiana tabacum* K⁺ channel 1; NO, nitric oxide; NORC, Nonselective Outward Rectifying Cation; NRT1.1, *Arabidopsis thaliana* Nitrate Transporter1.1; NSCC, non-selective cation channels; NTORK1, *Nicotiana tabacum* outward rectifier K⁺ channel 1; OPDA, 12-oxo-phytodienoic acid; OST1, open stomata 1; P, pore region; PCD, programmed cell death; PEP1, damage-associated molecular pattern peptide 1; PEPR, PEP receptor 1; PIP, plasma membrane intrinsic proteins; PP2C, phosphatase; PVX, Potato virus X; QUAC, quick anion channel; RCI3, Rare Cold Inducible gene 3; RLK, rich repeat-receptor-like kinase; ROS, reactive oxygen species; SKOR, stelar K⁺ outward rectifier; SLAC, S-type (slow-sustained) anion channel; SNARE, soluble N-ethylmaleimide sensitive factor protein attachment protein receptor; SNF1, sucrose non-fermenting 1 protein kinase; SnrK, SNF1-related protein kinase; SOS1, salt overly sensitive 1; SPIK, *Shaker* pollen inward K⁺ channel; SRK2E, SNF1-related protein kinase; SV channel, slow vacuolar channel; T-DNA, transfer DNA; TM, transmembrane domains; TPC1, Two-pore channel1 (TPC1); TPK, tandem pore K⁺ channel; VK, vacuolar K⁺ channel; VSD, voltage sensitive domain; *ZmEA1*, *Zea mays* EGG APPARATUS1; ZMK1, *Zea mays* K⁺-channel 1.

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Essentiality of potassium

Potassium is the second most abundant mineral nutrient in plants comprising between 2% and 10% of the plant dry weight (Leigh and Wyn Jones, 1984; Tisdale et al., 1993). Globally, the annual above ground parts of crops (phytomass) contain 60 million tons of potassium (Romheld and Kirkby, 2010). It is essential to plant growth and, consequently, to crop production (see Zörb et al., 2014, in this issue for more details on the importance of K⁺ in agriculture). Potassium essentiality is related to its key role as a major inorganic osmoticum and its impact on leaf movement, stomatal opening and closure, and axial growth and tropisms (Marschner, 1995; Shabala, 2003). Potassium is also essential as a counterion for the charge balance of ion transport across the plasma- and intra-organellar membranes (Dreyer and Uozumi, 2011; Shabala, 2003). Potassium availability is critical to control the process of photoassimilate loading into the phloem (Ache et al., 2001; Gajdanowicz et al., 2011). Last but not least, there are over 70 enzymes the activity of which was shown to be sensitive to K⁺ (Marschner, 1995). The importance of potassium to crop production has long been recognized, with potassium fertilisers, traditionally derived from livestock manure and wood ashes, being supplied for over 250 years. Since 2000, global potash demand has grown by 40%, with over 50 M tons of potash produced in 2012 (Fertecon, 2013).

Historical aspects of K⁺ transport research

The pioneering work of Emanuel Epstein (1963) had shown that potassium uptake in plants is comprised of a high-affinity and a low-affinity component. Accumulation of potassium from low micromolar sources against steep concentration gradients usually describes high-affinity transport. In plants, this influx of K⁺ is probably energized through a symport with protons (for more details on the K⁺ uptake from the soil see Nieves-Cordones et al., 2014, in this issue). Proton driven potassium transporters thus provide for uphill transport of potassium ions by often three orders of magnitude *i.e.* by 2–3 pH units (the reader is referred to Gierth et al., 2005, and references therein). In contrast to K⁺/H⁺ symporters, K⁺ channels mediate facilitated diffusion of potassium ions across biological membranes. Typically, opening and closing transitions – a process called gating – of most K⁺ channels is controlled by changes in membrane voltage. Upon opening of a given number of K⁺ channels potassium flux is determined by the driving force for potassium, in other words the chemical and electrical potential difference across the membrane. Plant potassium channels were first identified by the patch-clamp technique in guard cell protoplasts and pulvinus motor cells (Hedrich et al., 1987; Iijima and Hagiwara, 1987; Moran et al., 1984, 1988; Satter and Moran, 1988; Schroeder et al., 1984). Subsequent studies have led to the identification of potassium channels in plasma as well as vacuolar membranes from all plant cell types investigated (Ache et al., 2000; Dunkel et al., 2008; Hedrich and Becker, 1994; Hedrich and Schroeder, 1989; Latz et al., 2007a; Schroeder and Hedrich, 1989; Schroeder et al., 1984; Ward and Schroeder, 1994). It was, however, not before the late eighties when the first potassium channel genes were cloned in *Drosophila* (Timpe et al., 1988) and took until 1992 when the first plant potassium channels were cloned – the K⁺ channel *Arabidopsis thaliana* 1 (KAT1) and the *Arabidopsis* K⁺ transporter 1 (AKT1), two K⁺ channels sharing structural homology to *Drosophila* *Shaker* channels (Anderson et al., 1992; Jan and Jan, 1997; Sentenac et al., 1992). Yeast complementation assays could show that plant potassium uptake channels are able of rescuing growth in K⁺ transport deficient yeast mutants even in the micromolar range of potassium supply (Becker et al., 1996; Bertl et al., 1998; Brüggemann et al., 1999). Heterologous expression of the *Arabidopsis* KAT1 channel

in *Xenopus laevis* oocytes confirmed patch-clamp studies on protoplasts and revealed the typical features of a voltage dependent, K⁺ selective ion channel. In contrast to its animal homologs known at the time, KAT1 turned out to function as a voltage dependent K⁺ uptake channel (inward rectifier) rather than a K⁺ release channel (outward rectifier). Following their functional and molecular identification, plant potassium channels were found in all plant cells and tissues investigated to date. This suggests a housekeeping role of these transport proteins. Since potassium salts represent the most important osmotically active ions in plants, the control of potassium fluxes through K⁺ channels is pivotal for many physiological processes. Grass coleoptiles and guard cells have evolved as model systems to study the role of K⁺ channels in irreversible and fast plant growth processes on one side and reversible stomatal movements on the other. Furthermore, root hairs and pollen tubes represent model systems for studying the regulation of potassium homeostasis in polar, tip growing cell types (see below and reviews by Chen et al., 2008a; Hedrich and Marten, 2006; Lebaudy et al., 2007; Roelfsema and Hedrich, 2005; Szczerba et al., 2009; Véry and Sentenac, 2002; and references therein).

Diversity of potassium transport systems

A genome wide survey revealed seven major families of *Arabidopsis* cation transporters (75 genes in total) which mediate K⁺ transport across plant membranes. These include: (i) *Shaker*-type K⁺ channels (9 genes); (ii) two-pore K⁺ channels (6 genes); (iii) putative K⁺/H⁺ antiporters (6 genes); (iv) KUP/HAK/KT transporters (13 genes); (v) HKT transporters (1 gene); (vi) cyclic-nucleotide-gate channels (20 genes); (vii) glutamate receptors (20 genes; Maser et al., 2001; Shabala, 2003; Véry and Sentenac, 2002). The last two groups are often combined into a group of so-called non-selective cation channels, NSCC (Demidchik and Maathuis, 2007), as these channels are permeable to not only K⁺ but also other cations (see also Demidchik, 2014; Pottosin and Dobrovinskaya, 2014; in this issue for more details on NSCCs).

Recent studies have shown that K⁺-selective channels represent targets as well as components of cellular signaling transduction networks, thereby drawing an appearing picture that extends their typical role in potassium transport and nutrition toward novel aspects such as cell cycle control, fertilization or cell death. Thus, the major focus of this review is on the structural and regulatory aspects of K⁺ channels, although the role of K⁺ transporters is also brought into context.

Structural aspects of K⁺ channels

Potassium channels were among the first structurally resolved transport proteins in mammalian systems, where they are subdivided into three distinct structural classes (Fig. 1; MacKinnon, 2003). This is also reflected in the genome of the model plant *A. thaliana* which encodes 15 putative K⁺ channels. Among them, nine members are structurally related to the class of voltage-dependent *Shaker*-like potassium channels (K_V), which exhibit 6 transmembrane domains (TM) and one pore (P) region (Fig. 2), five members share structural homology to voltage-independent, two-pore K⁺ channels (TPK/K2P), which are characterized by a 4TM/2P topology, and a single member, KCO3, encodes a potassium crystallographically-sited activation channel (KcsA)-like potassium channel (Hedrich et al., 2011; Lebaudy et al., 2007). KcsA-type channels exhibit the most simple structure (2TM/1P) and are even found in plant viruses, but appear absent from the poplar or rice genome. In contrast, *Shaker*-like channels as well as two-pore K⁺ channels are conserved in higher plant genomes, even though in varying numbers (for review see Ward et al., 2009). While TPK

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