

It is not all about sodium: revealing tissue specificity and signalling roles of potassium in plant responses to salt stress

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Abstract

Background Salinity is a global issue threatening agricultural production systems across the globe. While the major focus of plant salinity stress tolerance research has been on sodium, the transport and physiological roles of K⁺ in plant salt stress response has received less attention. This review attempts to bridge this knowledge gap. **Scope** The major emphasis is on newly proposed K⁺ signalling roles and plant salt tolerance cell- and tissuespecificity. In addition to summarizing the importance of K⁺ retention for plant salt tolerance, we focus on aspects that were not the subject of previous reviews including (1) the importance of HAK/KUP family of transporters in K⁺ uptake in salt stressed plants and its possible linkage with Ca²⁺ and ROS signalling; (2) control of xylem K⁺ loading in salt stressed plants, control of phloem K⁺ recirculation in salt stressed plants and the potential importance of plant's ability to efficiently coordinate K⁺ signals between root and shoot; (3) the buffering capacity of the vacuolar K⁺ pool; and

(4) mechanisms of restoring the basal cytosolic K⁺ levels by coordinated activity of tonoplast K⁺-permeable channels.

Conclusions Overall, this review emphasises the need to fully understand the newly emerging roles of K⁺ and regulation of its transport for improving salinity stress tolerance in plants.

Keywords Cell- and tissue-specificity · Potassium channels and transporters · Potassium homeostasis · Potassium retention · Programmed cell death · Signalling

Introduction

Soil salinity is a major environmental constrain to crop growth and yield affecting nearly 50% of all irrigated land in the world (Fita et al. 2015). To meet the projected demand of feeding 9.3 billion people at 2050, global agricultural production must be increased by 60% from

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its 2005–2007 levels (van Ittersum et al. 2016). Therefore, understanding the mechanisms underlying plant salt tolerance, especially its ion transport-related traits, would improve breeding robust salt tolerant crop species and thus provide a feasible way to mitigate the possible food shortage in the future.

Traditionally, adverse effects of soil salinity have been associated with Na^+ toxicity, prompting a significant number of studies on this topic (Munns and Tester 2008; Horie et al. 2012; Deinlein et al. 2014; Maathuis 2014; Hanin et al. 2016). However, an increase in Na^+ content is always accompanied by K^+ loss in plants exposed to salt (NaCl) stress. K^+ is an essential macronutrient in plants comprising generally 4 to 6% of its dry matter and is recognized as a rate-limiting factor for crop yield and quality (Dreyer and Uozumi 2011; Zorb et al. 2014). K^+ plays an important role in plant response to both biotic (disease and pests) and abiotic stresses such as drought, salinity, cold, and waterlogging (Wang et al. 2013b; Shabala and Pottosin 2014). Potassium also has a key role in protein synthesis (Fischer 1968), charge balancing, and phloem sugar loading (Gajdanowicz et al. 2011; De Schepper et al. 2013). K^+ deficiency leads to reduced photosynthesis, and the replacement of K^+ by organic osmolytes for the purpose of osmotic adjustment could result in reduced growth (Tsay et al. 2011). A new signalling role of K^+ has recently started to emerge (Anschütz et al. 2014; Rubio et al. 2014). The latter topic is a major focus of this review.

K^+ retention in the cytosol: An overlooked mechanism in plant salt tolerance

Salinity stress induces chronic K^+ deficiency in plants while the capacity of plants to counteract salinity stress strongly depends on K^+ availability (Maathuis and Amtmann 1999). Under salinity stress, NaCl-induced K^+ loss from plants is a common phenomenon, and this event is more pronounced in salt sensitive than tolerant plant varieties (Chen et al. 2007). GORK (guard cell outward rectifying K^+ channel) and ROS-activated NSCC (nonselective cation channels) channels are known to mediate NaCl-induced K^+ efflux from the cytosol to the apoplast (Jayakannan et al. 2013; Wu et al. 2015b). With the onset of salt stress, the plasma membrane potential is rapidly depolarized activating voltage gated GORK channels and resulting in K^+ efflux. Accumulation of ROS under stress conditions could further activate both GORK and ROS-activated NSCC channels inducing more K^+ efflux. This

leads to a rapid loss of K^+ from the cytosol which in turn disrupts the homeostasis of cytosolic Na^+/K^+ ratio, a hallmark of plant overall salt tolerance (Dasgan et al. 2002; Hauser and Horie 2010). In recent years, the ability of various plant tissues to retain K^+ under salt stress (termed cytosolic K^+ retention) has been shown to be an important trait for plant salt tolerance (Table 1). In wheat, K^+ efflux measured from root mature zone after salt application was found to be strongly and negatively correlated with plant yield at the harvest (Cuin et al. 2008). Salt tolerant barley varieties showed 3-fold higher ability to retain K^+ in the roots than the sensitive genotypes (Chen et al. 2007). Smethurst et al. (2008) found that the tolerant lucerne varieties had better root K^+ retention ability than the sensitive counterparts. In barley and wheat, NaCl-induced K^+ efflux in leaf mesophyll was significantly higher in salt sensitive varieties than salt tolerant varieties (Wu et al. 2013, 2015c). Also, salt tolerant bread wheat varieties exhibit significantly higher mesophyll K^+ retention ability than the relative sensitive durum wheat varieties (Wu et al. 2014). Similar results were also reported for *Arabidopsis* (Wu et al. 2018b), poplar (Sun et al. 2009), cotton (Wang et al. 2016a), and brassica (Chakraborty et al. 2016b). Thus, K^+ retention ability in root and leaf tissues appears to be an important and previous largely overlooked trait concomitant to salt tolerance in plants.

However, similar to Na^+ data (Genc et al. 2007), there are some noticeable exceptions from the rule. While the extent of NaCl-induced K^+ efflux from the root correlated with salinity stress tolerance in both wheat (Cuin et al. 2009) and barley (Chen et al. 2007), the magnitude of K^+ efflux even in most tolerant barley variety exceeds the flux value in any of tested wheat varieties, under similar experimental conditions. This comes at a stark contrast with the fact that barley species possess much higher salt tolerance compare with either durum or bread wheat (Munns and Tester 2008). What may be the reason for this discrepancy?

To further investigate this point, we have analysed the literature data, tabulating reported numbers for the relative value (% control) in root and shoot K^+ content for seven major crop species – wheat, rice, barley, maize, *Vicia faba*, tomato, and cotton – and then plotting these changes against reported salinity tolerance thresholds. The latter was defined as an electrical conductivity of the soil solution at which plant growth starts to decline (see Hedrich and Shabala 2018 for details). As shown in Fig. 1a, a strong and positive correlation was

Table 1 Reported association between K⁺ retention trait and salt tolerance in various plant species

Species	Tissues	Methods/approaches	Reference
Wheat	Root, leaf	K ⁺ fluxes, K ⁺ content	Cuin et al. 2008, Wu et al. 2014
Barley	Root, leaf	K ⁺ fluxes, K ⁺ content	Chen et al. 2005, Wu et al. 2015c
Maize	Root	K ⁺ content	Gao et al. 2016
Cotton	Root	K ⁺ fluxes, K ⁺ content	Wang et al. 2016a
Rice	Root, shoot	X-ray, K ⁺ content	Xu et al. 2011
Lucerne	Root,	K ⁺ fluxes	Smethurst et al. 2008
Poplar	Root	K ⁺ fluxes	Sun et al. 2009
Soybean	Leaf	K ⁺ content	Essa 2002, Lu et al. 2016
Brassica	Root	K ⁺ fluxes	Chakraborty et al. 2016b
Arabidopsis	Root, leaf	K ⁺ fluxes	Bose et al. 2013, Wu et al. 2018b

observed ($r = 0.882$, $P = 0.009$) between amount of K⁺ retained in shoot or leaf under salinity and overall plant performance (salinity threshold measured as an electrical conductivity of the soil solution at which plant growth starts to decline), suggesting the importance of this trait for overall salt stress tolerance. In plant roots, however, this correlation was negative (Fig. 1b). In fact, previous studies report that salt-sensitive species may even increase the overall root K⁺ content compared with non-saline controls (Ai-Rawahy et al. 1992; Hamada 1994; Bulut and Akıncı 2010). This may be indicative that salt-tolerant species possess a better ability to control long-distance K⁺ transport, either by its more efficient xylem loading and delivery to the shoot, or minimising the extent of K⁺ recirculation in the phloem. Both these scenarios are discussed in more detail in the following sections.

Supporting the above notion, recent studies showed that mutualistic fungi can enhance plant salt stress tolerance through upregulation of genes related to K⁺ transport and thus maintain better K⁺/Na⁺ homeostasis. For example, arbuscular mycorrhizal fungi inoculation upregulate the expression of *RbSOS1*, *RbHKT1*, and *RbNHX1*, and significantly improve K⁺ content and reduced Na⁺ content in root and leaf of black locust under 200 mM NaCl (Chen et al. 2017). Similar results were also showed in other plant species inoculated with mutualistic fungi, e.g. *Arabidopsis* inoculated with *Piriformospora indica* (Abdelaziz et al. 2017) and bermudagrass inoculated with *Aspergillus aculeatus* (Xie et al. 2017). Interestingly, while *AtHKT1* (gene encoding a Na⁺ selective transporter) is downregulated in salt stressed *Arabidopsis*, *TsHKT1;2* encoding a K⁺

selective transporter is upregulated in salt stressed halophytic *Arabidopsis* relative, *Thellungiella salsuginea* (Ali et al. 2012, 2013). These findings further emphasise the importance of maintaining K⁺ homeostasis for plant salt tolerance.

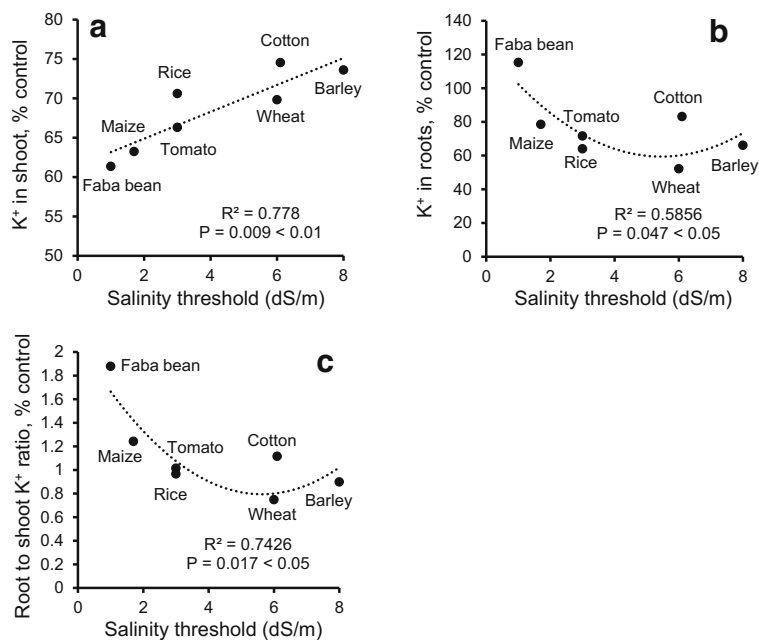
Furthermore, accumulation of compatible solutes e.g. water soluble carbohydrates and amino acids in stem tissue and subsequent remobilization of these compatible solutes to developing grains under salinity stress can decrease plants' dependency on photosynthesis and thus can reduce its yield loss from salt stress (Kerepesi and Galiba 2000; Yang and Zhang 2006; Sharbatkhari et al. 2016). At the same time, potassium availability was critical for accumulation of water-soluble carbohydrates (Krumm et al. 1990) and, specifically, fructans (Livingston et al. 2009). Fructan can account for up to 85% water soluble carbohydrates in wheat stem internodes (Yanez et al. 2017), and a positive correlation between fructan accumulation and higher efficiency of its remobilization and salinity tolerance was reported in wheat (Sharbatkhari et al. 2016). Furthermore, some fructan related enzymes e.g. fructokinase in chloroplast, are activated by K⁺ (Table 2).

K⁺ in plant salt stress responses: Emerging new roles

Cytosolic K⁺ efflux as a “metabolic switch”

In addition to being an essential macronutrient, K⁺ is also a major determinant of the cell's fate (Shabala 2009, 2017; Anschütz et al. 2014). This dual role of K⁺ (nutritional and signalling) is poorly understood. As

Fig. 1 Correlation between plant salinity tolerance threshold (measured as the electrical conductivity of the soil solution in which plant growth starts to decline) and the relative amount of K^+ retained in shoots (a) or roots (b) in plants grown under saline conditions (~100 mM NaCl). c Relative change in retained root K^+ vs changes in the shoot K^+ content. Seven common crops (wheat, barley, rice, maize, tomato, *Vicia faba* and cotton) are represented



mentioned above, salinity stress induced K^+ loss is a common phenomenon in plants. K^+ efflux is correlated with electrolyte leakage (up to 80%) (Pavlovkin et al. 1986), a hallmark of stress response in intact plant cells. Cytosolic K^+ efflux has been proposed to play the role of “metabolic switch” by providing inhibition of energy-consuming biosynthesis that releases energetic molecules for defence and reparation needs (Demidchik et al. 2014). This “metabolic switch” role of cytosolic K^+ efflux could be important for salt stressed plants to halt growing and use the available energy to finish a full life cycle.

To further understand the possible role of the cytosolic K^+ efflux as metabolic switch, we looked at the K^+ activated enzymes related to the energy-consuming processes in plant cells. The likely candidates are listed in Table 2. Further studies are needed to understand their activation thresholds, tissue-specific changes in their activity, and associated changes in cytosolic and organelle-specific K^+ concentrations in various species.

Rapid and severe cytosolic K^+ efflux induced programmed cell death

Programmed cell death (PCD) is a common phenomenon in salt stressed plants (Huh et al. 2002; Li et al. 2007; Pan et al. 2016). PCD represents one of the forms of apoptosis (Suzanne and Steller 2013) and facilitates

the removal of redundant, misplaced, or damaged cells. While the physiological role of PCD under saline conditions is still a matter of debate (Huh et al. 2002; Shabala 2009), the causal relationship between K^+ efflux and stress induced PCD is beyond any doubt. Overexpressing antiapoptotic CED-9 gene in tobacco mesophyll has reduced salt-stress induced K^+ leak from this tissue two-fold and resulted in a salt-tolerant phenotype (Shabala et al. 2007b). *Arabidopsis* plants lacking functional GORK channels showed much slower development of the PCD symptoms when treated with NaCl or hydroxyl radicals (Demidchik et al. 2010). *gork-2* mutant also exhibits increased uptake of Rb^+ than Col-0 (Osakabe et al. 2013). The blockage of K^+ efflux channels by TEA reduces the extent of PCD in wild-type *Arabidopsis* roots, suggesting a causal relationship between cytosolic K^+ efflux and PCD development.

K^+ efflux-mediated PCD events are intrinsically related to the ROS generation in stress-affected cells. A decrease in the cytosolic K^+ may stimulate ROS generation though NADPH oxidase (Shin and Schachtman 2004) and peroxidase (Kim et al. 2010) mediated pathways. For example, mutation of an NADPH oxidase gene (*rhd2*) prevents the upregulation of *HAK5* gene that is highly induced by K^+ deficiency, whereas its expression in the NADPH oxidase *Arabidopsis* mutant is restored by application of extracellular H_2O_2 (Shin

Table 2 K⁺ activated enzymes in reactions requiring ATP (Evans and Sorger 1966; Glusker 2006)

Enzymes	Reaction	Involved in	Main location
Acetic thiokinase	Acetate + ATP + COA → acetyl COA + AMP + pyrophosphate	Carbohydrate metabolism	Mitochondria
Acetokinase	Acetate + ATP → acetyl phosphate + ADP	Carbohydrate metabolism	Cytoplasm, mitochondria
Fructokinase	Fructose + ATP → Fructose-1-phosphate + ADP	Carbohydrate metabolism	Chloroplasts
Deoxyguanylic kinase	dGMP + ATP → dGDP and/or dGTP	Nucleic acid and nucleotide metabolism	Mitochondria
NAD synthetase	Desamido NAD + ATP + NH ₄ ⁺ (or glutamine) → NAD + AMP + pyrophosphate (+ glutamate)	Nucleic acid and nucleotide metabolism	Cytosol, mitochondria
Aspartokinase	Aspartate + ATP → aspartyl phosphate + ADP	Amino acid metabolism and protein synthesis	Chloroplasts
Carbamyl phosphate synthetase	CO ₂ + ATP + NH ₄ ⁺ → carbamyl phosphate + ADP	Amino acid metabolism and protein synthesis	Mitochondria, cytosol
Glutamate cysteine ligase	Glutamate + cysteine + ATP → γ glutamyl-cysteine + ADP + phosphate	Amino acid metabolism and protein synthesis	Nucleus
Glutathione synthetase	γ glutamyl-cysteine + glycine + ATP → glutathione + ADP + phosphate	Amino acid metabolism and protein synthesis	Nucleus
Methionine adenosyltransferase	Methionine + ATP → S-adenosyl methionine + triphosphate	Amino acid metabolism and protein synthesis	Cytosol
Formate-tetrahydrofolate ligase	Formate + ATP + tetrahydrofolate → N ¹⁰ ,formyltetrahydrofolate + ADP + phosphate	Folic acid metabolism	Cytosol, mitochondria, chloroplast
Adenosine triphosphatase	ATP + H ₂ O → ADP + phosphate	ATP hydrolysis	Organelle membrane

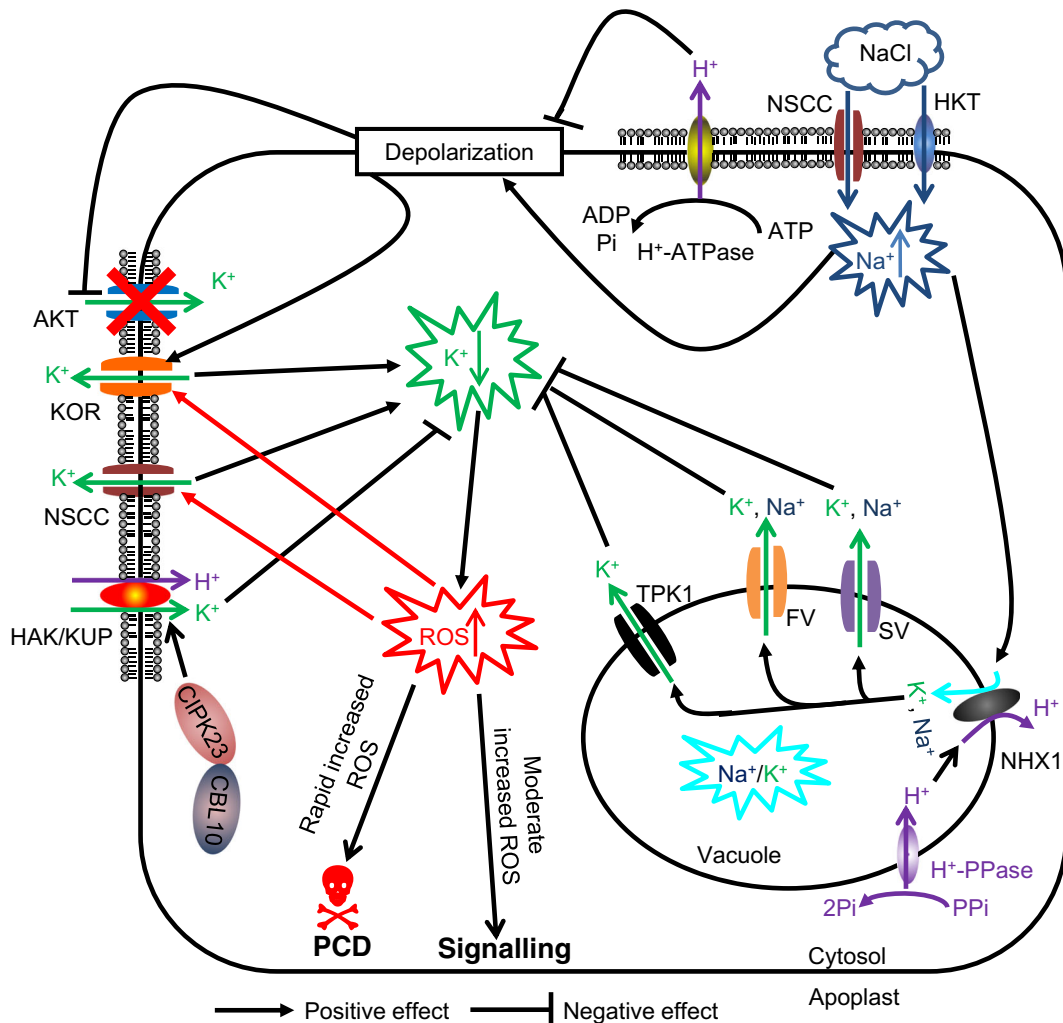


Fig. 2 A schematic diagram depicting membrane transporters mediating NaCl-induced K^+ efflux from the cytosol and its relationship with ROS signaling. K^+ transport across the tonoplast membrane is also shown as a mechanism buffering cytosolic K^+ depletion

and Schachtman 2004). Also, *AtrbohD* and *AtrbohF* mutants have reduced K^+ content compared with WT *Arabidopsis* under salt stress. The NaCl induced decrease of K^+ content could be alleviated by application of exogenous H_2O_2 (Ma et al. 2012). In recent years, the concept of a dual role of ROS in plant biology has been developed and accepted (Miller et al. 2010; Petrov et al. 2015; Mittler 2017). According to this concept, low concentrations of ROS play an important signalling role in plant adaptive and developmental responses, while at high concentrations ROS are detrimental to the integrity of key cell structures and may trigger PCD. Thus, a moderate K^+ decrease could generate a low level of accumulated ROS essential for signalling. This high level of accumulated ROS could in turn activate K^+

efflux channels, thus resulting in more K^+ loss. A more rapid and severe K^+ loss can lead to a high level ROS accumulation resulting acute ROS toxicity and thus PCD in plant cells (Fig. 2). It has also been proposed that superoxide anion could post-transcriptionally regulate GORK channel and allow sustained K^+ effluxes during PCD (Tran et al. 2013). The magnitude and timing of cytosolic K^+ changes might be related to these different outcomes. The cytosolic K^+ spikes likely operate as messengers that signal and shape plant adaptive stress responses including those to salinity (Shabala 2017).

Besides the above mentioned K^+ signalling role, K^+ uptake is also known to be required for proper cell-cycle progression during the transition from G1 to S phase

(Sano et al. 2007), and a threshold level of K^+ is needed for re-enter the cell cycle (Sano et al. 2007, 2009). It has been shown that at G1 phase, a Shaker-type NKT1 inward rectifying K^+ channel was transcriptionally induced in tobacco BY-2 cells, whereas K^+ outward rectifying channel (*NTORK1*) transcripts dominated the S phase (Sano et al. 2009). Together, these results suggest a role of K^+ channels in regulating cell division and cell-cycle progression.

Cell- and tissue- specificity of functional expression of channels and transporters mediating salt-induced K^+ efflux

Plant salt tolerance is achieved by the combination of different salt tolerance mechanisms and sub-traits. The coordination of these mechanisms and sub-traits likely vary widely between plant species. Cell- and tissue-specificity in plant responses to salinity is reported in several plant species including *Arabidopsis* (Dinney et al. 2008), wheat (Wu et al. 2015a, 2018a), and barley (Shabala et al. 2016). For example, Shabala et al. (2006) showed that higher salt sensitivity in the barley root apex compared to mature zone is linked to its higher potency for NaCl-induced K^+ efflux. More details of channel and transporter activities at tissue- specific level still need to be revealed.

K^+ content in the cell represents a balance between K^+ efflux and K^+ uptake. These two processes are mediated by a number of K^+ channels and transporters that are being reported to have cell- and tissue- specificity. NaCl-induced K^+ efflux in barley leaf mesophyll (Wu et al. 2013) and root mature zone (Chen et al. 2007) is mainly mediated by the depolarization activated KOR/GORK channel. However, membrane potential control might not be essential for maintaining K^+ homeostasis in the root elongation zone, where K^+ efflux is mediated mainly by voltage independent NSCC channels, compared with the root mature zone cells where depolarization activated KOR channels play a major role (Wu 2016). Other examples include polyamine-sensitive NSCC channel and ROS-activated NSCC channels in pea mesophyll cells (Shabala et al. 2007a) and root mature zone cells (Bose et al. 2014), and NSCC channels and KOR channels in either wheat mesophyll (Chakraborty et al. 2016a) or root mature zone (Cuin et al. 2012) cells, respectively. Compared with high expression of *McHAK4* in all tissues, *McHAK2* and

McHAK3 are predominantly present in stems and root tissues in common ice plants (*Mesembryanthemum crystallinum*) respectively (Su et al. 2002). AKT1 and AKT2 contribute equally to the K^+ permeability in *Arabidopsis* mesophyll cells whereas AKT1 contributes predominantly to the K^+ permeability of the plasma membrane in the apical root cells (Dennison et al. 2001). *OsAKT1* overexpression line shows increased K^+ tissue level (Ahmad et al. 2016b) whereas *Atakt1* knockout line exhibits a similar K^+ efflux as Clo-0 under salt stress (Shabala et al. 2006). Furthermore, salt tolerant rice variety has higher relative expression of root *OsAKT1* than the sensitive one under salt stress (Kavitha et al. 2012). Also, in common ice plants, *Arabidopsis* AKT homologs *Mkt1* is root specific, but *Mkt2* is found in leaves and flowers (Su et al. 2001). Together, these results indicate that K^+ retention in plant salt tolerance is regulated in a strict cell- and tissue- specific manner. More attention should be paid to this fact in order to better engineering/breeding crops with stronger K^+ retention ability.

Another important aspect that needs to receive a full attention in the future studies is causal relationship between NaCl-induced K^+ efflux and changes in the cell metabolic profile. Using barley as an example, Shabala et al. (2016) demonstrated that NaCl-induced K^+ efflux from the root apex was about 10-folds higher than that from the mature root zone. At the same time, out of 75 analyzed metabolites, 30 were significantly changed in the root apex. This included 10 out of 25 tested amino acids and seven of 16 organic acids. No such changes, however, were observed in the mature root zone (Shabala et al. 2016). Many of them were shown to modulate ROS sensitivity of K^+ transporters in roots (Cuin and Shabala 2007), or directly gate K^+ channels. For example, salt stress causes a significant (5–6 fold) increase in glutamate (Glu) and glycine (Gly) levels in the barley root apex (Shabala et al. 2016). Plant glutamate receptor-like (GLR) genes are closely related to mammalian ionotropic Glu receptors (Price et al. 2012), which operate as Glu- and Gly-gated NSCCs that catalyze the uptake of K^+ , Na^+ , and Ca^{2+} into neurons (Sohn 2013). It has been proposed that glycine plays a role in the gating of plant glutamate receptors (GLRs) (Dubos et al. 2003). Twenty of 40 NSCC in plants are classified as GLRs (Demidchik and Maathuis 2007; Price et al. 2012; Forde 2014). Thus, the preferential tissue-specific stress-induced increase in the Glu/ Gly levels in the root apex may operate upstream of

Ca²⁺-NADPH oxidase “hub” (Demidchik 2018), shaping cytosolic free Ca²⁺ and ROS “signatures” and affecting intracellular ionic homeostasis. This Ca²⁺-NADPH oxidase “hub” concept implies that stress-induced elevation in the cytosolic free Ca²⁺ induces an increase in the NADPH oxidase-mediated production of ROS in the apoplast. Vice versa, extracellular ROS activate Ca²⁺ influx through Ca²⁺-permeable ion channels, thus forming a self-amplifying mechanism. Another illustration of the causal link between salt stress-induced changes in plant metabolic and ionic profile comes from experiments on halophytes (Kiani-Pouya et al. 2017), showing tissue-specific changes in GABA (3 fold decrease), inositol (1.24 fold decrease) and sucrose (3.19 fold increase) content, and their impact on NaCl sequestration in epidermal bladder cells in *Chenopodium quinoa*.

K⁺ transport in plants under salt stress

Control of K⁺ uptake in salt stressed plants

K⁺ uptake from soil to plants is mediated by channels and transporters (Very et al. 2014; Nieves-Cordones et al. 2016). The typical K⁺ concentration in a soil solution ranges between 0.1 and 1 mM (Wang and Wu 2013) whereas cell cytosolic K⁺ concentration is about 100 mM. Thus, an efficient K⁺ uptake system in plants is required to uptake K⁺ from soil, especially under salinity stress condition. The high affinity of K⁺ uptake mediated mainly by KT/HAK/KUP family and low affinity of K⁺ uptake via channel-based mechanism influence/control K⁺ transport in plants at low and high external K⁺ concentration, respectively (Nieves-Cordones et al. 2010, 2014; Very et al. 2014). The Shaker-type AKT family play the main role in a passive potassium uptake. AKT1 inward rectifying K⁺ channel is shown to be predominantly in roots (Dennison et al. 2001; Ahmad et al. 2016b), whereas AKT2 and AKT1 contributed equally in mesophyll cells (Dennison et al. 2001). AKT2 has two different gating modes and its voltage threshold for activation can be either within the physiological range (gating mode 1), or shifted towards considerably more positive voltages (gating mode 2). Gating mode 1 AKT2 channels behave as delayed K⁺-selective inward rectifiers while gating mode 2 AKT2 channels are K⁺-selective ‘open leaks’ in the physiological range of membrane potential (Michard et al. 2005).

However, the plant plasma membrane potential is significantly depolarized under salt stress, so AKT family mediated K⁺ uptake is thermodynamically not possible, at least at the early salt stress stage. Thus, HAK/KUP K⁺ transporter family plays the main role for K⁺ uptake in plants’ response to salt stress. For example, the stimulation of the relative expression of *McHAK1*, *McHAK2*, *McHAK3* and *McHAK4* genes has been shown in ice plant exposed to high salinity (400 mM NaCl) (Su et al. 2002). Relative expression level of *MeKUP2*, *MeKUP3*, *MeKUP4*, *MeKUP6*, *MeKUP8*, and *MeKUP17* genes is upregulated in salt stressed cassava plant (Ou et al. 2018). *OsHAK21* functions in the maintenance of K⁺ homeostasis and thus salt tolerance in rice plant (Shen et al. 2015). *AtHAK5* and *KUP7* functions in K⁺ deprivation- induced high-affinity K⁺ uptake in *Arabidopsis* roots (Gierth et al. 2005; Nieves-Cordones et al. 2010; Han et al. 2016). Overexpression of *OsHAK5* significantly improved shoot K⁺ accumulation and biomass in overexpression lines under salt stress compared with the WT rice (Yang et al. 2014). Mutation of *OsHAK1-D* resulted in significantly reduced root and shoot K⁺ content and biomass in the rice mutant line (Chen et al. 2015). It should be noted that HAK/KUP transporters are usually regarded as K⁺/H⁺ symporters (Rodríguez-Navarro 2000; Grabov 2007), which requires ATP for H⁺-ATPase pumping of H⁺ to maintain the H⁺ gradient across a membrane. Thus, the availability of ATP and its allocation to plasma membrane might be another factor affecting K⁺ uptake in salt stressed plants. Also, expression of these transporters often decrease under saline conditions (e.g. *AtHAK5* expression in *Arabidopsis*; Nieves-Cordones et al. 2010). However, even under this reduced gene expression conditions these transporters are the only systems involved in high-affinity K⁺ uptake under salinity.

Besides the possibility of the specificity of HAK/KUP K⁺ transporters at cell- and tissue- level in controlling K⁺ uptake in plants’ response to salt stress, its relationship with other signalling events e.g. Ca²⁺ signature and ROS signalling in salt stressed plants should be also considered in future studies. After onset of salt stress, plant has two cytosolic Ca²⁺ peaks (Schmöckel et al. 2015; Shabala et al. 2015). These cytosolic Ca²⁺ elevation can in turn activate calcineurin B-like (CBL) calcium sensors e.g. CBL4 and CBL10, and thus CIPKs. CBL10-CIPK23 complex activates HAK5 in vivo (Ragel et al. 2015), suggesting that HAK/KUP activities could be regulated by, or associated with, the

Table 3 K⁺ channels and transporters involved in xylem K⁺ loading

K ⁺ channels/transporters	Species	References
NRT1.5/NPF7.3 H ⁺ /K ⁺ antiporter	<i>Arabidopsis thaliana</i>	Li et al. 2017
KUP7 K ⁺ transporter	<i>Arabidopsis thaliana</i>	Han et al. 2016
AtSKOR	<i>Arabidopsis thaliana</i>	Gaymard et al. 1998, Rodenas et al. 2017
OsK5.2 outward <i>Shaker</i> K ⁺ channel	<i>Oryza sativa</i>	Nguyen et al. 2017
OsHAK1 transporter	<i>Oryza sativa</i>	Chen et al. 2015
OsHAK5 transporter	<i>Oryza sativa</i>	Yang et al. 2014
SISKOR	<i>Solanum lycopersicum</i>	Rodenas et al. 2017

change in the cytosolic Ca²⁺ levels in plants' response to salt stress. Similar to Ca²⁺ signature, H₂O₂ signature is another known signalling event in salt stressed plants. CIPK24 interacts with catalases and a H₂O₂ signalling protein NDPK2 (nucleoside diphosphate kinase2) (Verslues et al. 2007), suggesting a possible casual linkage between HAK/KUP activities and ROS signalling events in salt stressed plants. Onset of salt stress results in an elevation of cytosolic Ca²⁺, which could in turn activates CBL calcium sensors and thus CIPKs, leads to an activation of HAK/KUP activities or possible perturbation of H₂O₂ signalling. These observations suggest a possible casual relationship between HAK/KUP mediated high-affinity K⁺ transport and Ca²⁺ signature and ROS signalling (Fig. 2). Also, Raf-like kinase ILK1 interacts with and promotes HAK5 accumulation under osmotic and salt stress conditions in *Arabidopsis* (Brauer et al. 2016).

Xylem K⁺ loading and unloading in salt stressed plants

K⁺ absorbed by roots from soil is transferred to shoot, even under K⁺ deprivation e.g. salt stress. Under non-saline conditions, xylem K⁺ loading can be mediated by passive transport. Shabala et al. (2010) showed that NaCl-induced K⁺ efflux from the xylem parenchyma tissue in barley roots correlated with membrane depolarization and was suppressed by TEA⁺ but not Gd³⁺. This was interpreted as evidence for the operation of depolarization-activated K⁺-selective (e.g. SKOR) channels that activate in a time-dependent manner at membrane potentials slightly positive of the Nernst potential of K⁺ (E_K) (Gaymard et al. 1998). However, channel-mediated xylem K⁺ loading may be not thermodynamically feasible under all conditions. Under control conditions, the membrane potential of barley

stellar root cells was −120 mV, while xylem sap [K⁺] was between 3 and 7 mM, depending on calcium level in the growth media (Shabala et al. 2010). Thus, SKOR-mediated xylem K⁺ loading under these conditions will require cytosolic [K⁺] to exceed 300 mM. This is well above the cytosolic [K⁺] values reported in the literature. Thus, under such conditions active xylem K⁺ loading mechanisms may be required. HAK/KUP transporters are the most likely candidates for this role. Another candidate could be the NRT1.5 H⁺/K⁺ antiporter (Li et al. 2017). It has been confirmed that the presence of NRT1.5 antiporter in roots is important for root-to-shoot translocation of K⁺ (Drechsler et al. 2015), and this NRT1.5 antiporter can suppress nitrate starvation-induced leaf senescence by modulating foliar K⁺ level (Meng et al. 2016). Mutation of NRT1.5 antiporters results in a remarkable defect in K⁺ translocation from root to shoot, especially under low K⁺ conditions (Li et al. 2017). Table 3 summarizes identified K⁺ channels and transporters involved in the xylem K⁺ loading (Gaymard et al. 1998; Yang et al. 2014; Chen et al. 2015; Han et al. 2016; Nguyen et al. 2017; Rodenas et al. 2017; Li et al. 2017).

As discussed above, plasma membrane is depolarized under salinity condition (at least at the early stages) and, thus, suppresses the activity of hyperpolarization activated AKT channels. In this case, xylem K⁺ loading should be executed by voltage independent channels/transporters e.g. KUP7 transporters (Han et al. 2016) or depolarization activated K⁺ channels/transporters e.g. SKOR (Gaymard et al. 1998; Rodenas et al. 2017). The *Shaker*-like outward K⁺ rectifying SKOR channel is expressed in the pericycle and the xylem parenchyma in roots (Gaymard et al. 1998). This channel is sensitive to H₂O₂ (Garcia-Mata et al. 2010), suggesting a probable linkage between salt stress ROS signalling and xylem K⁺

loading in salt stressed plants. Upon the acute depolarization of plasma membrane induced by salinity, SKOR in xylem parenchyma cells can be rapidly activated to mediate K^+ loading xylem. After the plasma membrane potential is restored by increased H^+ -ATPase activity, SKOR mediation of K^+ release from root stelar cells to xylem by membrane depolarization is suppressed. Then, accumulated ROS under salinity could in turn activate SKOR channels to allow xylem K^+ loading. This may require a highly coordinated mechanism to ensure efficient xylem K^+ loading in salt stressed plants. However, patch-clamp experiments of barley stellar tissue suggested that SKOR plays a little role in xylem K^+ loading under stress conditions (Shabala et al. 2010), implying involvement of some other transporters. One of the possible candidates may be HAK/KUP transporters. KUP7 showed a strong expression in root stelar tissues (Han et al. 2016). However, operation of HAK/KUP K^+/H^+ symporters relies on electrochemical H^+ gradients across the plasma membrane that require ATP-dependent H^+ pumping. At the same time, a reduction of ATP content is always observed in salt stressed plants (Ma et al. 2010; Wu et al. 2018b; Yu et al. 2018), limiting involvement of HAK/KUP transporters in xylem K^+ loading in salt stressed plants. Besides above mentioned SKOR and HAK/KUP transporters, NORC (non-selective outward rectifying channels in xylem parenchyma cells), which is permeable to both Na^+ and K^+ , could be another candidate involved in xylem K^+ loading in salt stressed plants (de Boer and Wegner 1997; De Boer 1999; Zepeda-Jazo et al. 2008; Shabala et al. 2010). However, due to NORC's ability to mediate Na^+ influx and K^+ efflux, tolerant barley varieties show significantly lower NORC activity in root epidermal protoplasts than sensitive counterparts under salt stress (Zepeda-Jazo et al. 2008), suggesting that NORC might not be a good candidate for xylem K^+ loading in salt stressed plants.

K^+ unloading in leaves also affects the distribution of K^+ in plants. Compared with K^+ loading, our knowledge of the mechanisms controlling K^+ unloading in leaves is still limited. One of the channels involved in this process could be K^+ inward rectifying channels e.g. AKT and KAT channels. For example, besides root epidermis, *OsAKT1* show strong localization in the xylem (Li et al. 2014), suggesting that besides its role in K^+ uptake from soil, it might also involve in xylem K^+ unloading. Furthermore, CHX14, a plasma membrane low affinity K^+ efflux transporter, has been proposed to export high concentration of K^+ out of xylem into xylem

parenchyma cells (Zhao et al. 2015). Besides K^+ unloading through channels and/or transporters, Botha et al. (2008) found that xylem unloading of membrane-impermeant probes could only occur through the xylem vessel-xylem parenchyma pit membranes, suggesting that endocytosis across xylem vessel-xylem parenchyma pit membranes could be another complementary pathway for K^+ unloading. This mechanism may be essential under saline conditions, when transport through transporters or channels could be compromised by depolarized plasma membrane and limited ATP. Also, salinity stress is known to induce bulk endocytosis in plant cell (Leshem et al. 2007; Li et al. 2011; Baral et al. 2015a, b; Garcia de la Garma et al. 2015; Zwiewka et al. 2015), suggesting the possible complementary role of the endocytosis pathway in K^+ unloading in salt stressed plants.

Phloem K^+ recirculation in salt stressed plants

Besides xylem K^+ loading and unloading, K^+ recirculation through the phloem is important to maintain K^+ homeostasis in plant roots. This could be very likely a case for plants under salt stress since root K^+ uptake is disrupted. For example, under saline condition, xylem loading of K^+ from flag leaves into developing fruits might be impaired due to the decreased transpiration stream. Phloem recirculation of K^+ might contribute in fulfilling this gap to help finishing a complete life cycle. As a highly mobile nutrient in phloem, a large amount of K^+ delivered to the shoot is returned back to the root (Marschner et al. 1996). Armstrong and Kirkby (1979) calculated that about 20% of the upward flux of K^+ in xylem stream was resulted from recirculated K^+ via phloem of tomato plants. In some species e.g. barley and castor bean, the portion of recirculated K^+ from phloem to root can be up to 85% (Jeschke et al. 1991; Marschner et al. 1996). The physiological rationale behind K^+ cycling via phloem is a feedback control of the radial K^+ uptake by roots. The voltage-gated hyperpolarization activated AKT2 K^+ channels are known to play a role in phloem loading and unloading (De Schepper et al. 2013; Sklodowski et al. 2017), and their activity could be suppressed in salt stressed plants since plant cell plasma membrane is significantly depolarized, at least at the early stage of salinity stress. The expression of *AKT2* has been shown to decrease in wild-type rice plants under salt stress (Schmidt et al. 2013). Thus, not AKT but other types of K^+ channels and transporters

should play a main role in phloem K^+ recirculation of salt stressed plants. KZM1 (K^+ channel *Zea mays* 1) and VFK1 (*Vicia faba* K^+ channel 1) Shaker-type channels were shown to mediate K^+ uptake into the phloem of maize (Philippar et al. 2003) and K^+ unloading from phloem (Ache et al. 2001), respectively. Su et al. (2002) showed low expression of *MchAK4* in phloem cells in non-stressed ice plant (*Mesembryanthemum crystallinum*) leaves and that its expression was stimulated predominantly in the phloem cells in salt stressed leaves. Thus, regulation of phloem K^+ recirculation in salt stressed plants could be likely achieved by manipulating the expression pattern and activity of Shaker-type K^+ channels or HAK/KUP transporters.

As mentioned early, unlike a strong and positive correlation observed between the amounts of K^+ retained in shoots or leaves in common crops and their salinity tolerance threshold, a negative correlation exists for the total root content (Fig. 1b). Moreover, the overall root K^+ content increased under saline conditions in some sensitive species such as *Vicia faba* (Hamada 1994; Bulut and Akinci 2010) and tomato (Ai-Rawahy et al. 1992). A very significant negative correlation ($r = 0.86$, $P = 0.017 < 0.05$) is observed between the relative changes in the retained root K^+ and changes in the shoot K^+ content (Fig. 1c). One of the possible explanations for this relationship might be an increased amount of K^+ returning to roots via phloem, on the expense of the shoot. This is consistent with observations that phloem recirculation rate of K^+ is decreased in salt stressed tolerant barley (Wolf and Dieter Jeschke 1987) but is increased in salt-sensitive pea (Wang et al. 2016b) plants. This suggests that control of K^+ recirculation in the phloem could represent another mechanism for plant salt tolerance. Surprisingly, this trait has never been targeted by plant breeders, despite its obvious essentiality for plant energy balance. Indeed, a failure to coordinate K^+ signals between root and shoot could induce a futile cycle of phloem K^+ recirculation, reducing energy availability allocated towards plant growth.

Replenishing cytosolic K^+ from the vacuolar pool

Once signalling via K^+ is completed, plants need to restore cytosolic K^+ concentration back to pre-stress level, to enable normal cell metabolism. Given that the operation of AKT uptake channels may be compromised by depolarized membrane potential, plants may rely on HAK/KUP family of K^+/H^+ symporters.

Because their transport capacity is about three orders of magnitude lower than that for ion channels (Gadsby 2019), it is unlikely that the cell will be able to rapidly compensate GORK channel-mediated K^+ loss by operation of existing HAK/KUP transporters. As this HAK/KUP based process is relatively slow (hours timescale), the rapid termination of K^+ signalling plants needs to rely on K^+ supply from internal stores. Indeed, higher TPC1 (SV channel) transcript levels were reported in plants grown under saline conditions (Choi et al. 2014). Overexpression of a vacuolar two pore K^+ channel *PeTPK1* in tobacco cells resulted in less K^+ loss and higher biomass than the wild type cells under salt stress (Wang et al. 2013a). The largest K^+ depot in the cell is a vacuole. Thus, vacuolar K^+ release should represent an important component of stress-induced K^+ signalling and cytosolic K^+ mechanism.

Potassium release from vacuoles may be mediated by three types of tonoplast channels: K^+ -selective TPK (two pore potassium) channels, and slow- (SV) and fast- (FV) activating non-selective cations channels (Pottosin et al. 2003; Gobert et al. 2007; Pottosin and Dobrovinskaya 2014). Isayenkov et al. (2015) found that overexpression of *TPKa* increased salt tolerance in rice. Indeed, *OsTPKa* is upregulated by 4-folds in salt stressed rice plants, whereas no significant change of *OsTPKb* was found (Isayenkov et al. 2011). Ahmad et al. (2016a) also showed that overexpression of *TPKb* channel increased the ratio of K^+ between the cytosol and the vacuole. A salt stress induced stimulation of TPK1 channel has been shown in *Arabidopsis* (Latz et al. 2013) and tobacco (Hamamoto et al. 2008). The FV and SV channels may act as “safety valves” controlling K^+ distribution between cytosol and vacuole (Pottosin and Dobrovinskaya 2014). Application of salt triggers the release of Ca^{2+} into cytosol and thus contributes to the activation of TPC1 in *Arabidopsis* (Evans et al. 2016). An enhanced salt stress tolerance and increased leaf chlorophyll content were observed in *TPC1* (SV channel) overexpression line (Choi et al. 2014). Interestingly, a 6-folds’ transient increase of *TPC1* transcript levels was found in salt stressed *Arabidopsis* shoots, whereas a sustained decrease was found in salt stressed roots (Choi et al. 2014). Bonales-Alatorre et al. (2013) showed that reduced FV and SV channel activity in salt stressed halophyte quinoa is essential to prevent a futile Na^+ leak from the vacuole to the cytosol followed by its sequestration by NHX exchanger. Having SV and FV channels active may be

important to replenish cytosolic K^+ depletion; however, it comes with a danger of having uncontrollable Na^+ leak (Fig. 2). So, the ideal scenario is to increase K^+ selective TPK activity but decrease K^+ non-selective SV (TPC1) activity at the same time. TPK1 channel is known to be activated by 14–3–3 proteins (Latz et al. 2007), whereas 14–3–3 proteins drastically reduces the SV channel currents (Van den Wijngaard et al. 2001; Latz et al. 2007). This suggests a possibility of coordination between TPK and TPC channel activity by 14–3–3 proteins. For example, by increasing expression of 14–3–3 proteins and their delivery to tonoplast, TPK channel can be activated alongside with the inactivation of TPC channels, leading to replenishing cytosolic K^+ from the vacuolar pool, while avoiding Na^+ back leak to the cytosol from the vacuole.

How big is the vacuolar buffering K^+ capacity? The reported concentrations of vacuolar K^+ in plant cells are usually in the range of 120 to 250 mM (Walker et al. 1996; Cuin et al. 2003). At the same time, cytosolic K^+ concentrations are approximately 100 mM and drop under saline conditions to 40–50 mM (Cuin et al. 2003; Shabala et al. 2006). From thermodynamical point of view, vacuolar K^+ concentration cannot be lower than the cytosolic one, if a passive loading mechanism is envisaged. Thus, to be used as a cytosolic K^+ pool buffer, vacuolar concentration can drop by about 200 mM (from 250 to 50 mM). Assuming a typical cell being 40 μm in diameter, and a vacuole occupying 90% of the cell volume, then the vacuolar volume is $3.35 \times 10^{-14} m^3$, and the cellular surface area is $5 \times 10^{-9} m^2$. Hence, the amount of K^+ the vacuole can give away by dropping its K^+ content by 200 mM is $6 \times 10^{-12} mol$. At the same time, the reported mean net K^+ efflux from plant roots are in the range of 50 to 200 $nmol m^{-2} s^{-1}$ (Chen et al. 2007; Cuin et al. 2009; Sun et al. 2012). Thus, the amount of time the cell can “buy” relying on vacuolar K^+ pool will be:

$$T = \frac{A}{F \times S}$$

Where T = time the buffering can sustain (sec); A = amount of vacuolar K^+ available to buffer cytosolic K^+ loss (mol); F = mean net K^+ efflux across the plasma membrane ($mol m^{-2} s^{-1}$); S = cell surface area (m^2).

Putting appropriate numbers into the equation above, one can yield values between 100 and 400 min (or ~1.5 to 7 h), depending on the accepted flux values. Obviously, these numbers are not big enough to be

considered seriously from the perspective of long-term plant adaptation. However, several hours of buffering may be sufficient to complete the signalling process and increase the amount of transcripts for high affinity transporters, to increase K^+ uptake and restore the cellular K^+ pool volume.

Concluding remarks

Compared with sodium, potassium has always been treated as a “Cinderella”, in terms of its role in the overall salinity stress tolerance. This situation has started to change in the last 10–15 years, after discovering the essential signalling role of K^+ in plant adaptive responses to salinity (in addition to its merely rational role). However, in practical terms, K^+ -related traits have never been targeted in breeding programs, except at the whole-plant level. This is clearly not good enough, given the high specificity of tissue- and organelle-dependent regulation of K^+ transport and homeostasis. From this point of view, K^+ -related traits represent a previously untapped resource for breeders, and we are confident that the next decade will witness a major shift towards research on K^+ as a key determinant of plant salinity tissue tolerance. After all, salinity is not all about sodium.

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