REVIEW

CrossMark

Potassium and its role in cesium transport in plants

Dharmendra K. Gupta [1] · Sarita Tiwari [2] · Soumya Chatterjee [3] · Clemens Walther [1]

Abstract

In plant cells, potassium (K^+) is abundantly present and is dominant cation plays a vital role in maintaining physiological and morphological characteristics of plants. Many membrane integrated channels and transporters specific to K^+ are involved in maintaining the potassium concentration within plants via membrane electrical activities. Elemental homologues to K^+ compete with it for entry inside plants; among those, cesium is very common radionuclide. Once cesium enters into the plant cell, it can cause phytotoxicity. Therefore, it is desirable to understand complete pathway and mechanisms of cesium uptake in the plants, in order to assess consequences from accidental release of radioactive substance. This review focuses on mechanism of K^+ ion uptake through channels/transporter and involvement of these channels/transporter in cesium uptake in plant cells.

Keywords Ion channels · Potassium · Radionuclides · Cesium

Introduction

Radioactive materials may enter the environment accidentally or by different human activities. Various industrial, mining, nuclear wastes may create further hazards to the environment due to the use of several artificial radioactive isotopes. These isotopes have been having adverse impact, when activity concentrations and related dose rates strongly exceed those of naturally occurring radioactive compounds (Nikitin et al. 2012; Foulkes et al. 2017; Kovler 2017). Among radioactive elements, cesium (^{137}Cs; T1/2 = 30.17 years), is a common radionuclide, used in various activities (Zhu and Smolders 2000; TermiziRamli et al. 2005; Hu et al. 2010; Chen et al. 2016). Further, ^{137}Cs is the chemical homologue of the essential elements K (potassium) which is usually taken up by the plants from soil and getting entry into the food chain (Chen et al. 2005a; Gupta et al.

2017; Stuenkel 2017). The mechanism of entering radionuclides inside plants varies on several edaphic and genetic factors, like, plant species, interaction with the element, chemistry, soil conditions, concentration and mobility of radioactive compounds in the contaminated matrix etc. (Gupta and Walther 2014; Gupta et al. 2016, 2017; Walther and Gupta 2015).

Plant cells are having a diverse group of channels and transporters for flow of different ions across the membranes. In respond to stimulations like, change in light intensity, temperature, specific chemicals (like hormones) or depolarising agents (like potassium, glutamate etc.), plasma membrane shows modified activities in their ion channels/transporters (Cuin et al. 2018). Ion channels are common to different cell types of plants that represents differentially polarized plasma membrane (−110 to −150 mV) and vacuole membrane (weakly polarized- 0 to −30 mV) interdependent on trans cytoplasmic potential of approximately −100 mV (Hedrich 2012; Wang et al. 2016) (Fig. 1).

In turgor-driven processes, potassium (K^+) ion is the major cationic osmoticum that play a pivotal role in many metabolic activities and plant survival (e.g. phototropism, stomatal movement, gravitropism and cell elongation etc.), Dreyer and Uozumi 2011; Dreyer et al. 2017; Hafsi et al. 2017. The concentration of potassium in normal soil is 10–100 μM, which is much less (about 3–4 orders of magnitude) than plants (Dreyer and Uozumi 2011). The plant uptake potassium inside through endothermal process by lowering entropy where, biological membranes are selectively permeable to ion transport through electrochemical potential generation,

✉ Dharmendra K. Gupta
guptadk1971@gmail.com; gupta@irs.uni-hannover.de

1 Institut für Radioökologie und Strahlenschutz (IRS), Leibniz Universität Hannover, Herrenhäuser Str. 2, 30419 Hannover, Germany

2 Environmental Biotechnology Division, National Environmental Engineering Research Institute (CSIR-NEERI), Nehru Marg, Nagpur 440020, India

3 Defence Research Laboratory, Defence Research and Development Organization (DRDO), Ministry of Defence, Post Bag No. 2, Tezpur, Assam 784001, India

Fig. 1 Elucidating common ion transporters, channels and pumps those are involved with Na and other ion transportations from root to shoot (NHX. vacuolar Na^+/H^+ antiporter; HAK. high affinity K^+ transporter; HKT. high affinity K^+ uptake transporter) (After Hedrich 2012; Sassi et al. 2012)
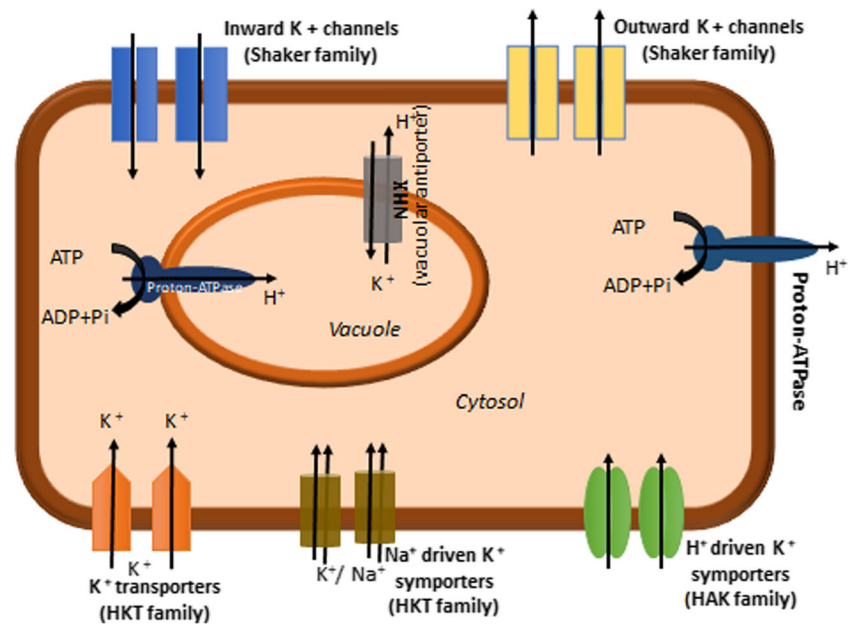
Singh and Reddy (2017). Approximately 100 mM potassium concentrations are required for enzyme activation and protein synthesis within cellular compartments (like cytosol, nucleus, stroma of the choloroplast, mitochondria matrix) Dreyer and Uozumi (2011). Epstein et al. (1963), studying on K^+-starved barley plant roots (*Hordeum vulgare*) initially reported that potassium uptake mechanisms can be differentiated into high-affinity (at low concentrations) and low-affinity (at high concentrations) transports. Later, it was revealed that, a family of transporters (namely, transporters of KUP/HAK/KT family) is primarily involved with high-affinity K^+ uptake (Santa-María et al. 1997). Chen et al. (2005b) studied K^+/Na^+ fluxes using radioactive chemical homologue to understand the mechanism of radionuclide uptake in plants. Depending on applied voltages or interaction between ligands and regulators (also by stress or hormones) causing transformation in protein structure, helps the essential ions to move in or out of the cell (Almeida et al. 2017; Wang and Wu 2017). The minimum K^+ concentration required for channel activation termed as critical concentration varies between different channels (Geiger et al. 2009). The high affinity K^+(HAK) transporters involved in co-transportation of K^+/H^+ ion and is responsible for uptake of K^+ at −180 mV membrane potential (Grabov 2007; Nieves-Cordones et al. 2016a). The specificity of ion channel and ion passing turnover in unit time depends on size of pore and amino acids at active site (Nieves-Cordones et al. 2016a).

It is important aspects for researchers working in this field to understand the pathways of uptake mechanisms of radioactive element, in order to evaluate significances for release of radioactive substances inadvertently. This review focuses on K^+ ion uptake in plants through channels/transporter and connection of these channels/transporter in cesium uptake.

Potassium transporters and channels

The activity of ion channels is followed by the ionic currents mediated through membrane voltage, where, on the basis of gating mechanism, these channels can be grouped into: ligand-gated, voltage-gated, stretch-activated and light-activated (Riedelsberger et al. 2015). The voltage-gated channels exhibit electrical signal transmission via membrane depolarization and also transmit signal during changes in membrane potential. All these channels simultaneously play an important role in maintaining membrane voltage, which is required for ionic balance and nutritional ion fluxes (Basu and Haswell 2017). In plants, on the basis of K^+ conductance, K^+ channels were described as inward (KIRC) and outward (KORC) rectifying potassium channels (Hirsch et al. 1998; Riedelsberger et al. 2015). The outward rectifying potassium channels control turgor regulation, cation release into xylem etc. (Roberts and Tester 1995; Liu and Luan 1998), while KIRC channels pull K^+ ions during cell expansion, growth processes, organ movements and stomatal openings (Maathuis and Sanders 1996; Maathuis et al. 1997). Schroeder et al. (1984) first reported K^+ channels in guard cell protoplast through Patch-Clamp method. Later more K^+ channels were discovered such as Shaker channels, two-pore K (TPK) channels and a single IRK-like K channel (Hedrich 2012). Also, K^+ channels determinants AKT1 & KAT1 were first reported in model plant *Arabidopsis thaliana* at molecular level (Anderson et al. 1992; Sentenac et al. 1992) which was structurally analogous to *Drosophila* Shaker channel (Jan and Jan 1997). Among various transmembrane transport components of potassium, HKT/Ktr/Trk and KT/HAK/KUP transporters are most popular, along with potassium channels. HKT (high affinity K^+ uptake transporter, HKT/Ktr/Trk)

which share both structural likenesses and differences at key positions with K$^+$ channels in plants (Hanelt et al. 2010; Corratge-Faillie et al. 2010; Uozumi and Dreyer 2011). Reports suggest that, HKT/Ktr/Trk gene (AtHKT1;1) in *A. thaliana* helps in enhancing salt tolerance by extracting sodium ions from xylem vessels (Uozumi and Schroeder 2010; Dreyer and Uozumi 2011).

Santa-María et al. (1997) demonstrated that, cDNA of high-affinity K$^+$ uptake system of barley root (HvHAK1, that belongs to a multigene family) showed sequence homology to K$^+$ transporters of *Schwanniomyces occidentalis* and *Escherichia coli*. Pyo et al. (2010), working with high-affinity K$^+$ uptake into roots of *Arabidopsis thaliana* by two transmembrane proteins high-affinity AtHAK5 and inward-rectifier, showed that, these two transporters are very important for plant growth after germination and establishment of seedling. Rubio et al. (2010) showed that, AKT1 participates in the low-affinity K$^+$ range, while, both AtHAK5 and AKT1 are involved with the high-affinity K$^+$ transportation and, AtHAK5 facilitating K$^+$ uptake at concentrations less than 0.01 mM. Ruiz-Lau et al. (2016) cloned High-affinity K$^+$ (HAK) transporter of *Capsicum chinense* Jacq (CcHAK1), reporting its close relation with *Capsicum annuum* CaHAK1 and *Solanum lycopersicum* LeHAK5. Membrane voltage regulates (proton driven) the process of opening and closing of most K$^+$ channels (termed gating) (Papazian et al. 1987; Gierth et al. 2005). Electrical gradient and/or the proton motive forces established by H + ATPases play critical role in the high-affinity K$^+$ uptake, that maintain cytosolic concentration of potassium by the movement of ion from low level to high level (Dreyer and Uozumi 2011). These K$^+$ channel maintain balance of specific ion i.e. K$^+$/Na$^+$(sodium) and it is not only selective for the ions but differ over other potential competing ions (Nakamura and Gaber 2009; Assaha et al. 2017). Although, AtHAK5 gene regulation related to K$^+$ uptake is a complex phenomenon, however, it was evident that, K$^+$ deprivation upregulates the AtHAK5 gene, and repressed by presence of Na$^+$ &/or NH$^+_4$ (Rubio et al. 2008; Aleman et al. 2009). However, Xu et al. (2006) pointed out that, LKS1 gene overexpression helped in greater K$^+$ uptake and tolerance to low K$^+$ concentrations, that acted through its encoded protein kinase CIPK23 (also activated by calcineurin B-like CBL1 and CBL9), which directly phosphorylated K$^+$ transporter AKT1. Li et al. (2006) demonstrated that, Ca components contribute in signalling response for regulating turgor pressure and low-K. Ca^{2+} not only augment K$^+$ uptake through K$^+$ channel activation, but also, the orchestrated functions of Ca^{2+}-CBL-CIPK pathway helps in plants the K$^+$ transportation as per the external availability of the element (Li et al. 2006).

Low K$^+$ upregulates expression of K$^+$/Na$^+$ transporter HvHKT2;1 enhancing translocation of Na$^+$ to barley leaves, which suggests that HKT contributes towards Na$^+$ transport as

well (Mian et al. 2011). HAK/KUP/KT type transporters (as for example, AtHAK5) belongs to the amino acid-polyamineorganocation (APC) superfamily and linked with K transportation from bacteria, fungi, to plants (Li et al. 2018). These transporters are having assorted role in K uptake and translocation, regulation of osmotic potential and salt tolerance, controlling root morphology and shoot phenotype (Li et al. 2018). Responding to external K$^+$ concentrations, gene expression of HAK/KUP/KT are regulated by at least six positive or negative regulators, and phosphorylation through CIPK-CBL complex (Li et al. 2006, 2018). Shaker-like K$^+$ channels and associates are recognized voltage sensitive transporter in plants (Dreyer and Blatt 2009). KT/KUP/HAK transporters along with shaker-type K$^+$ channels, involved in both high- and low-affinity K$^+$ uptake, play a crucial role in K$^+$ homeostasis in plant cells (Vallejo et al. 2005). Depending on the structural prediction, HKT transporters could function as ion channels forming a specific ion-selective pore, having different properties (Cao et al. 2011; Yamaguchi et al. 2013; Benito et al. 2014). It means that transporters can electrically (from the point of ion electric current-voltage IV curve) behave in a way similar to ion channels and the reversal potential of ion current mediated by transporters can shift following ion concentrations inside and outside the cell. K$^+$ transport activity is also facilitated by the family of cation/H$^+$ antiporters (CHXs) and Na$^+$/H$^+$ antiporters (NHXs) (Chanroj et al. 2011; Dreyer and Uozumi 2011; Lu et al. 2011). Although it's difficult to distinguish clearly, however, transporters contribute to the high affinity K$^+$ uptake, while K$^+$ channels are involved with transporting the low affinity components (Dreyer and Uozumi 2011).

The inward and outward flows of K$^+$ are based on hyperpolarization and depolarization respectively. Based on voltage, selectivity and sensitivity to mediators, transport components facilitate most of the K$^+$ currents defined in the plasma membrane of plant cells (Very and Sentenac 2002; Cherel 2004). On the basis of functional level, K$^+$ channels are distributed into four groups: (a) inward-rectifying (Kin) channels (b) silent (K silent) channel subunits (c) weakly rectifying (Kweak) channels and (d) outward-rectifying (Kout) channel subunits (Sentenac et al. 1992; Ache et al. 2000; Reintanz et al. 2002; Hedrich 2012). The lower level of extracellular K$^+$ influence channel modifications to inactivate the system of transportation. Upon K$^+$ reduction, channel-mediated K$^+$ efflux, i.e. K$^+$ leakage from the cell, is reduced in the case of (Inward rectifying K$^+$ channels) AKT1. The AKT1 of *Arabidopsis* root cells also showed an enhanced sensitivity in preventing K$^+$ loss when outward environment was having less K$^+$ (Geiger et al. 2009). These processes allow root epidermal cells to uptake K$^+$ through AKT1/AtKC1 complexes, extremely reducing loss of cytosolic K$^+$ toward potassium-depleted soils. Besides K$^+$ uptake channels, K$^+$ releasing channels also make use of a pore-intrinsic K$^+$ sensor

(Gajdanowicz et al. 2009). Because of its involvement in gating machinery of these channels, the K^+ sensor property is more evident (Gajdanowicz et al. 2009). The key feature of the K^+ sensitivity in these channels, increase K^+ at outside environment acts to suppress channel opening in a voltage-dependent manner. As a result, the channels only open at voltage positive to the K^+ equilibrium voltage and so ensure K^+ efflux regardless of the extracellular K^+ concentration (Szczerba et al. 2009; Hedrich 2012). This ability to adapt channel gating to the prevailing K^+ concentration guarantees that the channels open only when the driving force for net K^+ flux is directed outward, thus ensuring stomatal closure through the K^+ efflux (Zhang et al. 2014). K^+ uptake and translocation also depend upon other essential macronutrients present in the environment. Ródenas et al. (2017) working on Arabidopsis and tomato, found that, deprivation PO_4^{3-}, NO_3^-, and SO_4^{2-} leads to less low-affinity K^+ uptake and translocation, which is controlled at gene level by downregulating obtaining of other nutrients. The genes, namely AKT1 and SKOR in Arabidopsis and LKT1 and SlSKOR in tomato, which are liable for low-affinity K^+ uptake and translocation respectively, play important roles in the process of transcriptional repression and regulation (Ródenas et al. 2017).

Cesium uptake and accumulation: possible mechanisms

Cesium (Cs) belongs to group I alkali metal and is available in only one stable isotope (^{133}Cs) (Davis 1963), its concentration naturally ranging up to 25 μg^{-1} in dry soil. And, radiocesium (commonly occurring ^{137}Cs, ^{134}Cs and the long lived ^{135}Cs), which are produced during nuclear fission (135, 137) and neutron activation (134) in atomic reactors is the second heaviest alkali metal of groups I metals. However, there is no identified physiological role of Cs in plants but when exceeds the limit it hampers the plant development (Kanter et al. 2010; Olondo et al. 2017). Furthermore, only a certain fraction of Cs^+ is available for plant uptake and this fraction decreases with time due to immobilization effects of clay particles in soil. Radiocesium paved way inside human food chain through the pathway of plants nutrient uptake from the soil (Shaw et al. 1992). Cesium enters through roots and is transported to shoots and upper parts of the plants. Cesium has higher degree of resemblance with other alkali metals and especially with K^+ which belongs to the same alkali I metal group (Pacheco-Arjona et al. 2011). Thus, Cs^+ acts as a K^+ analogue and exerts phytotoxicity (White and Broadley 2000; Chatterjee et al. 2017). In a detailed review on Cs translocation in plants from environment, Burger and Lichtscheidl (2018) demonstrated that, like K, Cs uptake by plants also differs in presence of different elements, which may be

explored for the Cs bioremediation potential of plants. Studies suggests that the K^+ transporter not only transports K but also other ions in the order $K > Cs > Rb > Na > NH_4$ (Schachtman and Schroeder 1994; Sanches et al. 2008).

For the maintenance of K^+ homeostasis, K^+ movement across the plasma membrane and utilization of vacuolar K^+ reserve is the regulatory step (Gupta and Walther 2016). Unlike other radioactive elements like Rb^+ and Th^+, Cs^+ has weaker correlation with K^+ because of which the probability of Cs^+ uptake is somewhat different from K^+ (Kanter et al. 2010). It is established that the functioning of K^+ transporters are governed by the K^+ level and pH, and the relation between K^+ and Na^+ uptake is also well known. In terrestrial plants, it has been discovered that calcium (Ca^{2+}) act as stimulant in K^+ and Cs^+ uptake. There is a competitive interaction between K^+ and Cs^+ uptake which was observed in some grasses and agricultural plants having increased K^+ concentration with declined Cs uptake (Gupta and Walther 2016; Voronina et al. 2018). Waegeneers et al. (2009) observed decreased Cs uptake in the dominancy of K^+ concentration in soil. Application of K rich fertilizer reduced Cs entry up to 80% with respect to control inside barley grain and straw (Rosén and Vinichuk 2014). Root cells are laced with different mechanisms for transportation of K^+ across the plasma membrane. Initial physiological studies demonstrated competition between K^+ and Cs^+ for intake inside excised roots, which gave clue of similar molecular mechanism for influx of these cations to root cells. Molecular studies showed that some transporters demonstrated poor differentiation between K^+, Cs^+ and Na^+ has decreased K^+ uptake through them. It also seems that these transporters could carry K^+ coupled with the entrance of protons, which has been generally considered the mechanism for the high-affinity of K^+ transports in plants (Gupta and Walther 2016). A recent study showed that SNARE proteins Sec22p specifically involved in Cs^+ accumulation in yeast and plants (Draxl et al. 2013). Ishikawa et al. (2017) working with the low-cesium rice mutant 1 (lcs1), reported that a mutation in serine/threonine-protein kinase encoding gene OsSOS2 was responsible for reduced Cs level, even in low K^+ conditions. The transcript levels of several K^+ and Na^+ transporter genes, such as OsHAK1, OsHAK5, OsHKT2;1, OsAKT1, were down-regulated considerably in lcs1 grown at low K^+/Na^+, which was the cause of low Cs uptake in lcs1 (Ishikawa et al. 2017).

The inward-rectifying K^+ (KIR), outward-rectifying K^+ (KOR) and voltage-insensitive cation (VIC) channels can penetrate Cs^+. Entry of cation through KIR channels is possibly inhibited by extracellular Cs^+ under particular ionic conditions in the soil. Mattsson and Lidén (1975) observed large difference of concentration between ^{137}Cs and K^+ in the forest moss *Pleurozium schreberi* in which Cs^+ concentration was found higher even in senescence parts. Broadley et al. (2001) also confirmed that KIR channel in root does not contribute

significantly in Cs^+ uptake. A permeation model highlighted that Cs^+ enters through plant roots via voltage insensitive cation (VIC) channel in plasma membrane and K1 uptake permeases (KUPs) (White and Broadley 2000). In *A. thaliana*, the members of the KUP family have high affinity K1 transporter (HAK5) and KUP9 are highlighted to be engaged in Cs^+ uptake (Qi et al. 2008; Kobayashi et al. 2010). This indicated the ability of plants to absorb and accumulate high levels of Cs1, high enough to hinder normal growth (Turekian and Wedepohl 1961). Smolders and Shaw (1995) observed that wheat grown in Cs^+ spiked nutrient solution showed ten times more Cs^+ in plant tissue than in nutrient solution. At lower K^+ concentration, Cs^+ is taken up by K^+ uptake system of the root (Zhu and Shaw 2000). A recent study indicated HKT1 as Na^+/ K^+ cotransporter (Suzuki et al. 2016). Collander (1941) observed that the pace of Cs^+ uptake was quick as that of K^+ or Rb^+ (Rubidium) when these cations were supplemented in nutrient medium at a concentration of 0.1 mM. Ayub et al. (2008) experimentally found out that the increase of K^+ level in the experimental medium reduced Cs^+ uptake in *Cynodon* sp., which affirm the fact of dual transportation of both cations by the similar transport systems. In environmental matrix, Cs^+ detection in plants is low where Cs^+ concentration is smaller than K^+ in soil. However, the studied plants can add Cs inside if its range in soil matrix increases. If the Cs^+ concentration exceeds than K^+, Cs inhibits K^+ uptake through various K^+ channels and transporters (Fu and Luan 1998; Hille 2001). In K^+ deprivation condition Cs^+ influx raised, indicating the significance of inside and outside K^+ status (Zhu and Smolders 2000). The uptake of K^+ through AtKUP was inhibited by the inhibitors of K^+ channel blockers such as TEA, Cs^+, and Ba^{2+} (Fu and Luan 1998; Straltsova et al. 2015). While, KORC (K outward rectifying conductance) channels show a substantial conductance for Na^+ but little permeability for Li^+ and Cs^+. This indicates that KORC channels can also act as a `barrier' protecting the shoot from harmful Cs^+ or Li^+ ions (Maathuis et al. 1997). Prorok et al. (2016), studying on radish (*Raphanus sativus* L.) grown in Chernobyl area and reported that, Cs and K uptake was positively correlated and ^{137}Cs uptake against K selectivity amplified significantly with decreasing Cs and K, whereby, plants ^{137}Cs concentration increased rapidly. When plants become K deficient, it manages by augmenting abundance of constitutively expressed, inward rectifying K^+ channels (KIRC) and K^+/H^+-symporters at the root cells, while Cs is presumed to get entry into the root cells via cation channel like, NSCC (non-specific cation channels) and importantly, K^+/H^+-symporters (where plants lacking adequate K inside) abundance significantly regulate K deficiency (Prorok et al. 2016). Again, studying on transfer of ^{137}Cs to plants after the accident of Fukushima Dai-ichi Nuclear Power Plant, Sugiura et al. (2016) reported that woody plants exhibited high values of concentration ratios at stems and/or leaves as ^{137}Cs tends to get deposited in the fresh developing tissues. Further, plants of Amaranthaceae, Polygonaceae, and Chenopodiaceae taxa, known for Cs accumulation, did not show any significant ability, while, deciduous trees *Chengiopanax sciadophylloides* and *Acer crataegifolium* and perennial plant *Houttuynia cordata* showed potentiality for phytoremediation of Cs (Sugiura et al. 2016).

However, the concern of uptake of radiocesium in food items is enormous. Due to their inherent ability, plants take up Cs^+ from low concentrations. Rice (*Oryza sativa* L.) plants are vulnerable in this issue, where, production of rice is also being affected. Among several strategies, biotechnological approaches to reduce accumulation of Cs^+ in rice continue to provide interesting studies. Nieves-Cordones et al. (2017) working on the Cs^+ permeable K^+ transporter OsHAK1 in rice, developed CRISPR-Cas system that considerably help in reducing Cs^+ uptake in rice plants grown in ^{137}Cs contaminated Fukushima soil. OsHAK1 is less competent to distinguish among Cs^+ and K^+ and active transport mechanism is followed for Cs^+ transportation from very low external concentrations (Nieves-Cordones et al. 2017). Similar observations were also reported by Rai et al. (2017), who were working with transporter OsHAK1 transport systems. These authors described that knockout OsHAK1 reduces the Cs uptake without hampering the plants growth, recommending new lines of rice for cultivating in Cs^+ contaminated areas (Rai et al. 2017). Genies et al. (2017), in similar observations, suggested that, nonselective cation channels may be involved both in Cs uptake under K-sufficient and insufficient concentrations and AtHAK5 did not show effects on Cs uptake, where, external Cs concentration was more than 100 μM. Mohamed et al. (2018) reported that even micromolar concentrations of Cs affects root elongation in rice plant advocating Cs triggered root modification. Transportation of Cs^+ into plants body may cause K^+ deficiency. In tomato (*Solanum lycopersicum* L.), Ródenas et al. (2018) recently reported that, K^+ deficit in the plants' body may happen due to high concentrations of Cs^+, however, that does not affect any induction of either high-affinity K^+ transporter SlHAK5gene or high-affinity K^+ uptake. At higher concentrations, Cs^+ uptake may take place using a non-selective cation channel through Ca^{2+} mediated pathway; however, at lower concentrations, high-affinity uptake, resembling K^+ uptake is evident having insensitivity to Ca^{2+} and Ba^{2+} and sensitivity to NH_4^+ (Ródenas et al. 2018).

Ion channels and cell signaling

It is apparent that regulation of many ion channels and transporters are dependent on cell signalling through G-proteins, second messengers and phosphorylation/dephosphorylation processes (Carraretto et al. 2016). The anchoring of ligand with its specific receptors results into conformational changes

in channel proteins. During signal transduction cascades the second messengers regulates the metabolism of the cell with respect to environmental conditions. The commonly reported ligands for K^+ channels are calcium (Ca^{2+}), hydrogen ion (H^+), nucleotides, proteins and plant hormones (Unwin 1989). Both inward and outward membrane bound K^+ channels act by direct binding of ligands like H^+, Ca^{2+} or indirectly via membrane-bound regulators (Blatt et al. 1999; Czempinski et al. 1999). During abiotic stressors induced phytotoxicity, generation of ROS (reactive oxygen species) is involved in regulation of ion channels in plant membrane. For example, K_{out} (Outward rectifying K channel) channel is the direct target of generated ROS. One of the K_{out} channels i.e. SKOR (Stellar K^+ outward rectifier) protein contain sites specific to H_2O_2 which act depending on membrane depolarization (Dreyer and Uozumi 2011). In active SKOR channels, hydrogen peroxide involves in positive feedback mechanism (Dreyer and Uozumi 2011). Similarly, Gated Outwardly rectifying K^+ channels i.e. GORK (K_{out} channel) expressed in guard cells resemble that of SKOR. Guard cells regulate stomatal opening by osmotic swelling and wince due to different environmental factors. This is controlled by fluxes of ions and organic compounds across the membrane, where, K^+ acts as prior solutes. Voltage-gated K^+ channels directly influence guard cell volume regulation. The mechanism of stomatal opening or closure in guard cells is operated by signal transduction pathways comprising various protein phosphatases and kinases (Kim et al. 2010). A study by Sano et al. (2007) found that that K^+ is essential for proper functioning of cell cycle progression during the transition from G1 to S phase. Jan and Jan (1997) reported receptor for hormones and transmitters involved in regulating ion channels such as G protein-gated and cGMP-gated K^+ Channels, voltage- gated K^+ in animal tissue.

Ion transporters in different plant species

The HKT transporter was first reported in wheat through cDNA library construction (Schachtman and Schroeder 1994). In barley and *Arabidopsis,* the presence of K^+ transporter gene i.e. *HvHAK1* and *AtKUP3* respectively in root was identified indicating enhanced uptake of K^+ in the plants (Santa-María et al. 1997; Kim et al. 1998). In wheat roots, genes *HKT1* and *LCT1* mediate K^+ uptake in root part (Chrispeels et al. 1999). In barley, gene for K^+/Na^+ transporter is HvHKT2;1 which is upregulated at lower K^+. The overexpression of HvHKT2 increases Na^+ uptake in the xylem sap which directly leads to enhanced uptake of Na^+ by leaves, also related to barley potential for salt tolerance (Mian et al. 2011). From this, it can be concluded that high affinity K^+ transporters HKT type are also having Na^+ transport ability and thus add to general cation homeostasis in plants (Fig. 2). Recent study by Zhang et al. (2011) reported a KAT1-like channel in melon having extraordinary property of K^+/Na^+ permeation blocking. The two main systems for K uptake by root in different species are mostly described in high affinity HAK5- like transporter and inward-rectifier AKT1 like channel (Nieves-Cordones et al. 2016b). Han et al. (2016) demonstrated significance of KT/HAK/KUP transporter KUP7 in K^+ uptake and translocation in *A. thaliana*.

Ion transport components in plants and cellular transport mechanism

Potassium channels are mostly studied in plasma membranes and vacuole membranes of various plant cell types (Schroeder and Hedrich 1989; Hedrich and Becker 1994). The K^+ channel KAT1 is expressed in guard cells are sensitive to external

Fig. 2 K^+/Na^+ transport is facilitated by K-Na ion pump, where Na is transported from cytoplasm to extracellular fluid using ATP as energy source and in turn, K is transported inward towards the cytoplasm. **a** Showing attachment of Na to the transporter and in (**b**) Na is being delivered to the extracellular fluid; where in (**c**) K is inwardly transported
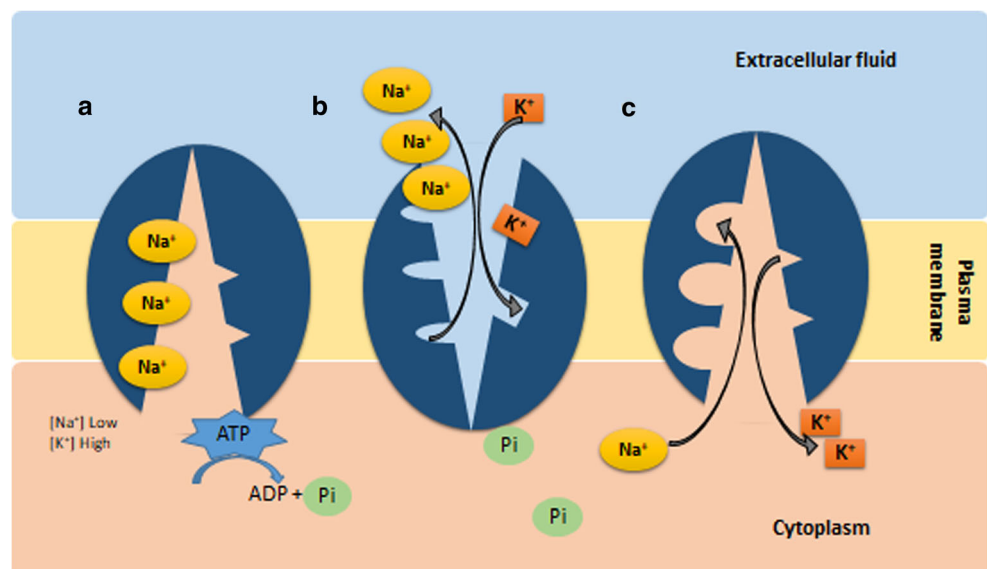
K^+ in the millimolar level, on the other hand AKT1 which is expressed in root epidermis cells is affected by lower potassium concentrations. The compartmentalization of K^+ in vacuoles represents the largest K^+ rich zone in plant cells; however, the concentration of vacuolar K^+ varies in the range between 10 and 200 mM depending on the K^+ availability and tissue type (Walker et al. 1996; Wang and Wu 2013). In an experiment related to K^+ uptake in a solution with initial concentration of about 50 μM K^+ observed decline in the K^+ concentration in the solution, from which it was concluded that the plantlet roots were capable of absorbing external K^+; which also depend on K^+ starvation time of that part. The location of K^+ transporter are predicted to be present on plasma membrane which was recently confirmed by Dreyer and Uozumi (2011) who found genes of K^+ transporter, expressed on plasma membrane of xylem parenchyma, which is found to involve in removing sodium ion from xylem vessels. In the tonoplast of higher plants there are three distinct kinds of voltage-sensitive potassium channels (FV, fast activating; SV, slow activating; and VK, strongly K selective). The plasma membrane accommodates all Shaker-like channels (Hedrich et al. 2012). SKOR and GORK protein are having shaker-like voltage- dependent gating (Ache et al. 2000). GORK is found in guard cells and root hairs and SKOR is localized in the xylem parenchyma cells, where it is involved in solute loading with the xylem network (Ivashikina et al. 2001; Hosy et al. 2003).

The onset of plant K_{in} channels, such as KAT1, KAT2, or AKT1, occur at hyperpolarized membrane potentials (around 80 to 100 mV), and gating of these channels is not influenced by potassium concentrations at both sides of the membrane. In contrary, K_{out} channels, such as GORK and SKOR, turn on at depolarized membrane potentials, and gating is dependent on extracellular concentration, allowing channel opening positive of the equilibrium potential of K. K in channels are activated by hyperpolarizing potentials while K out are activated by membrane depolarization. Both K_{in} and K_{out} channels serve in keeping balance in membrane voltage to avoid them from becoming too negative or positive, respectively. Such a role of voltage-gated K^+ channels in stabilizing membrane voltages is universal among all eukaryotes (Maathuis et al. 1997).

High affinity K^+ uptake

Detailed study at molecular level differentiated K^+ transporting proteins into high and low affinity uptake components which were also confirmed practically in plants. Based on the K^+ uptake ability, transporters underlie within high affinity K^+ uptake component, while K^+ channels usually belongs to low affinity component. However, in exceptions, the channels also contribute in high affinity K^+ uptake. A study in pepper (*Capsicum annum*) roots has affirmed the

belonging of HAK1 transporters to high-affinity K^+ uptake component (Martínez-Cordero et al. 2004, 2005). When there is K^+ deprivation, the pepper plants expresses high-affinity K^+ uptake through transporter CaHAK1 in their roots. Another feature of high affinity K^+ uptake is its sensitivity to NH_4^+ which was observed in *Arabidopsis* (Spalding et al. 1999), barley (Santa-María et al. 2000) and pepper (Martínez-Cordero et al. 2005). However, the NH_4^+ insensitive K^+ transport component has also been reported in *Arabidopsis* which is carried out by inward-rectifier K^+ channel AtAKT1, describing the probability of involvement of channels in high-affinity K^+ uptake in a range of K^+ concentrations (Hirsch et al. 1998; Spalding et al. 1999; Gierth and Maser 2007). In some plants like rice and tomato (LeHAK5), NH_4^+ are responsible for promoting gene expression of high-affinity K^+ transporters (Nieves-Cordones et al. 2007, 2014). In 1994, the first high affinity K^+ uptake transporter i.e. HKT was discovered through wheat cDNA library (Schachtman and Schroeder 1994). Other genes for high-affinity K^+ transporters that are found in roots are reported in *A. thaliana* (*AtKUP1*, *AtKUP2*, *AtKUP3* and *AtKUP*4) and barley (*HvHAK1*). They belong to large gene families. Within above gene, AtKUP1 and HvHAK1 transporters are mainly expressed in root part (Santa-María et al. 1997; Fu and Luan 1998; Nieves-Cordones et al. 2014; Véry et al. 2014), and its localization is assumed to be on plasma membrane. The opening of KIR channels depends upon membrane hyperpolarization which in open state allows K^+ influx to root cells. The KIR channel has been well studied in the roots of different plant species. Various form of KIR channel have been identified, many of them differ minutely in conductance, gating kinetics and pharmacology. HKT (high affinity K^+ transporters) are equivocally involved in Na^+ transport across membrane (Nieves-Cordones et al. 2016b). AtHAK5 was identifies as efficient high affinity transporter which functions even at lower K^+ concentrations below 10 μM (Aleman et al. 2011).

Genes involved in K^+ transport

The first identified genes encoding K^+ channels KAT1 in plants was functionally an inward rectifying K^+ channel (Schachtman et al. 1992). Successively, other genes encoding inward K- rectifiers were reported for Shaker-type channels, KAT1 from the *A. thaliana* and its homolog KST1 from the *Solanum tuberosum* (Hedrich 2012; Muller et al. 1995; Nakamura et al. 1995). The first gene related to potassium channels i.e. KAT1 and AKT1 (*Arabidopsis* K- transporter 1) was cloned in yeast cell deprived of K^+ system (Anderson et al. 1992; Sentenac et al. 1992). Later, complete genome sequencing of *Arabidopsis*, poplar and rice give a breakthrough in vivid understanding of molecular diversity of plant potassium channel genes (Ward et al. 2009). In *A. thaliana*,

nine genes coding for shaker-like K$^+$ channels and six genes related with structurally separate potassium channel sub-groups were discovered (Ward et al. 2009). The study of Buschmann et al. (2000) in wheat confirmed the importance of K$^+$ channels in K$^+$ uptake. During experimentation, he observed that absence of K$^+$ leads to an increase in the *AKT1* gene transcript in wheat plants, which support the facts that AKT1 inward-rectifier K$^+$ channel could be involved in K$^+$ transport into *Arabidopsis* from low K$^+$ concentration environment (Buschmann et al. 2000). Several genes related to KIR channels have been cloned and expressed in root parts are *AKT1* gene (*A. thaliana)* and its homologues in *Brassica napus* (Lagarde et al. 1996), and *SKT1 (*potato) (Zimmermann et al. 1998), *AtKC1* (Dreyer et al. 1997) and *KAT1* (Kochian and Lucas 1993; Nakamura et al. 1995). Ammonia also affect the activity of K$^+$ transporter, as its presence may reduce the expression of HAK/KUP/KT transporters in rice, as also observed in *Arabidopsis* and pepper plants (Martínez-Cordero et al. 2005). The genome of *A. thaliana* comprise of a single copy of an HKT/Ktr/rk gene (AtHKT1;1) which is expressed in the plasma membrane of xylem parenchyma cells that functions in removing Na$^+$ from xylem vessels a tolerance strategy against salt stress (Uozumi et al. 2000; SunarpiHorie et al. 2005; Horie et al. 2007; Uozumi and Schroeder 2010).

Conclusions and future prospects

The diverse form of K$^+$ transporters and channels play an important role in maintaining K and ionic concentration within cells. K$^+$ channels are controlled by many post-translational processes and still studies are going on in determining the regulatory steps involved in the pathway. One of the most characterized K$^+$ channels in plants is Shaker-type transport proteins. However, Cs is structurally identical to essential element like K, and therefore, enters into the plants body through the K$^+$ channels/transporter. This radioactive element exerts adverse impact by ceasing normal functioning of plants which may lead to death. The uptake of radionuclide is positively correlated with K, where K concentration is low. Although plants try to augment K deficiency through constitutively expressing K$^+$/H$^+$-symporters and inward rectifying K$^+$ channels (KIRC) at the root cells, the fact that can further be utilised in research and development by application of appropriate K rich fertilizer. This also further be extended to develop strategies to reduce radionuclide entry into the food chain. Thus, multi-disciplinary studies on radioactive compounds related to its behaviour in environment and translocation pathways inside plants may throw light on anthropogenic utilities, waste management and natural remediation (phytoremediation) practices appropriately.

Compliance with ethical standards

Conflicts of interest and contributions statement All the authors listed have approved this manuscript and worked equally and there is no conflict of interest to publish this MS.

References

Ache P, Becker D, Ivashikina N, Dietrich P, Roelfsema MR, Hedrich R (2000) GORK, a delayed outward rectifier expressed in guard cells of *Arabidopsis thaliana*, is a K$^+$-selective, K$^+$-sensing ion channel. FEBS Lett 486:93–98. https://doi.org/10.1016/S0014-5793(00)02248-1

Aleman F, Nieves-Cordones M, Martinez Rubio F (2009) Differential regulation of the HAK5 genes encoding the high-affinity K+ transporters of *Thellungiella halophila* and *Arabidopsis thaliana*. Environ Exp Bot 65:263–269. https://doi.org/10.1016/j.envexpbot.2008.09.011

Aleman F, Nieves-Cordones M, Martinez V, Rubio F (2011) Root K$^+$ acquisition in plants: the *Arabidopsis thaliana* model. Plant Cell Physiol 52:1603–1612. https://doi.org/10.1093/pcp/pcr096

Almeida DM, Oliveira MM, Saibo NJM (2017) Regulation of Na$^+$ and K$^+$ homeostasis in plants: towards improved salt stress tolerance in crop plants. Genet Mol Biol 40:326–345. https://doi.org/10.1590/1678-4685-GMB-2016-0106

Anderson JA, Huprikar SS, Kochian LV, Lucas WJ, Gaber RF (1992) Functional expression of a probable *Arabidopsis thaliana* potassium channel in *Saccharomyces cerevisiae*. Pro Natl Acad Sci USA 89: 3736–3740

Assaha DVM, Ueda A, Saneoka H, Al-Yahyai R, Yaish MW (2017) The role of Na$^+$ and K$^+$ transporters in salt stress adaptation in glycophytes. Front Physiol 8:509. https://doi.org/10.3389/fphys.2017.00509

Ayub J, Juri L, Valverde R, Garcia-Sanchez MJ, Fernández JA, Velasco RH (2008) Kinetics of caesium and potassium absorption by roots of three grass pastures and competitive effects of potassium on caesium uptake in *Cynodon* sp. In: The Natural Radiation Environment: 8th International Symposium (NRE VIII). AIP Publishing 1034:269–272. https://doi.org/10.1063/1.2991224

Basu D, Haswell ES (2017) Plant mechanosensitive ion channels: an ocean of possibilities. Curr Opin Plant Biol 40:43–48. https://doi.org/10.1016/j.pbi.2017.07.002

Benito B, Haro R, Amtmann A, Cuin TA, Dreyer I (2014) The twins K$^+$ and Na$^+$ in plants. J Plant Physiol 171:723–731. https://doi.org/10.1016/j.jplph.2013.10.014

Blatt MR, Grabov A, Brearley J, Kosack KH, Jones JDG (1999) K$^+$ channels of Cf-9 transgenic tobacco guard cells as targets for *Cladosporium fulvum* Avr9 elicitor-dependent signal transduction. Plant J 19:453–462

Broadley MR, Escobar-Guttierrez AJ, Bowen HC, Willey NJ, White PJ (2001) Influx and accumulation of Cs$^+$ by the akt1 mutant of *Arabidopsis thaliana* (L.) Heynh. lacking a dominant K$^+$ transport system. J Exp Bot 52:839–844

Burger A, Lichtscheidl I (2018) Stable and radioactive cesium: a review about distribution in the environment, uptake and translocation in plants, plant reactions and plants' potential for bioremediation. Sci Total Environ 618:1459–1485. https://doi.org/10.1016/j.scitotenv.2017.09.298

Buschmann PH, Vaidyanathan R, Gassmann W, Schroeder JI (2000) Enhancement of Na^+ uptake currents, time-dependent inward-rectifying K^+ channel currents, and K^+ channel transcripts by K^+ starvation in wheat root cells. Plant Physiol 122:1387–1398. https://doi.org/10.1104/pp.122.4.1387

Cao Y, Jin X, Huang H, Derebe MG, Levin EJ, Kabaleeswaran V, Pan Y, Punta M, Love J, Weng J, Quick M, Ye S, Kloss B, Bruni R, Martinez-Hackert E, Hendrickson WA, Rost B, Javitch JA, Rajashankar KR, Jiang Y, Zhou M (2011) Crystal structure of a potassium ion transporter, TrkH. Nature 471:336–340. https://doi.org/10.1038/nature09731

Carraretto L, Teardo E, Checchetto V, Finazzi G, Uozumi N, Szabo I (2016) Ion channels in plant bioenergetic organelles, chloroplasts and mitochondria: from molecular identification to function. Mol Plant 9:371–395. https://doi.org/10.1016/j.molp.2015.12.004

Chanroj S, Lu Y, Padmanaban S, Nanatani K, Uozumi N, Rao R, Sze H (2011) Plant-specific cation/H+ exchanger 17 and its homologs are endomembrane K^+ transporters with roles in protein sorting. J Biol Chem 286:33931–33941. https://doi.org/10.1074/jbc.M111.252650

Chatterjee S, Sarma MK, Deb U, Steinhauser G, Walther C, Gupta DK (2017) Mushrooms: from nutrition to mycoremediation. Environ Sci Pollut Res 24:19480–19493. https://doi.org/10.1007/s11356-017-9826-3

Chen SB, Zhu YG, Hu QH (2005a) Soil to plant transfer of ^{238}U, ^{226}Ra and ^{232}Th on a uranium mining-impacted soil from south eastern China. J Environ Radioact 82:223–236. https://doi.org/10.1016/j.jenvrad.2005.01.009

Chen Z, Newman I, Zhou M, Mendham N, Zhang G, Shabala S (2005b) Screening plants for salt tolerance by measuring K^+ flux: a case study for barley. Plant Cell Environ 28:1230–1246. https://doi.org/10.1111/j.1365-3040.2005.01364.x

Chen J, Rennie MD, Sadi B, Zhang W, St-Amant N (2016) A study on the levels of radioactivity in fish samples from the experimental lakes area in Ontario, Canada. J Environ Radioact 153:222–230. https://doi.org/10.1016/j.jenvrad.2016.01.005

Cherel I (2004) Regulation of K^+ channel activities in plants: from physiological to molecular aspects. J Exp Bot 55:337–351. https://doi.org/10.1093/jxb/erh028

Chrispeels MJ, Crawford NM, Schroeder JI (1999) Proteins for transport of water and mineral nutrients across the membranes of plant cells. Plant Cell 11:661–675. https://doi.org/10.1105/tpc.11.4.661

Collander R (1941) Selective absorption of cations by higher plants. Plant Physiol 16:691

Corratge-Faillie C, Jabnoune M, Zimmermann S, Very AA, Fizames C, Sentenac H (2010) Potassium and sodium transport in non-animal cells: the Trk/Ktr/HKT transporter family. Cell Mol Life Sci 67:2511–2532. https://doi.org/10.1007/s00018-010-0317-7

Cuin TA, Dreyer I, Michard E (2018) The role of potassium channels in *Arabidopsis thaliana* long distance electrical signalling: AKT2 modulates tissue excitability while GORK shapes action potentials. Int J Mol Sci 19:926. https://doi.org/10.3390/ijms19040926

Czempinski K, Gaedeke N, Zimmermann S, Muller RB (1999) Molecular mechanisms and regulation of plant ion channels. J Exp Bot 50:955–966. https://doi.org/10.1093/jxb/50.Special_Issue.955

Davis JJ (1963) Cesium and its relationship to potassium in ecology. In: Schultz V, Klement AW (eds) Radioecology. Reinhold, New York, pp 539–556

Draxl S, Muller J, Li WB, Michalke B, Scherb H, Hense BA, Tschiersch J, Kanter U, Schäffner AR (2013) Caesium accumulation in yeast and plants is selectively repressed by loss of the SNARE Sec22p/SEC22. Nat Commun 4:2092. https://doi.org/10.1038/ncomms3092

Dreyer I, Blatt MR (2009) What makes a gate? The ins and outs of Kv-like K^+ channels in plants. Trend Plant Sci 14:383–390. https://doi.org/10.1016/j.tplants.2009.04.001

Dreyer I, Uozumi N (2011) Potassium channels in plant cells. FEBS Lett 278:4293–4303. https://doi.org/10.1111/j.1742-4658.2011.08371.x

Dreyer I, Antunes S, Hoshi T, Müller RB, Palme K, Pongs O, Reintanz B, Hedrich R (1997) Plant K^+ channel alpha-subunits assemble indiscriminately. Biophys J 72:2143. https://doi.org/10.1016/S0006-3495(97)78857-X

Dreyer I, Gomez-Porras JL, Riedelsberger J (2017) The potassium battery: a mobile energy source for transport processes in plant vascular tissues. New Phytol 216:1049–1053. https://doi.org/10.1111/nph.14667

Epstein E, Rains DW, Elzam OE (1963) Resolution of dual mechanisms of potassium absorption by barley roots. Proc Natl Acad Sci U S A 49:684–692

Foulkes M, Millward G, Henderson S, Blake W (2017) Bioaccessibility of U, Th and Pb in solid wastes and soils from an abandoned uranium mine. J Environ Radioact 173:85–96. https://doi.org/10.1016/j.jenvrad.2016.11.030

Fu HH, Luan S (1998) AtKUP1: a dual-affinity K^+ transporter from Arabidopsis. Plant Cell 10:63–73

Gajdanowicz P, Garcia-Mata C, Gonzalez W, Morales-Navarro SE, Sharma T, Gonzalez-Nilo FD, Gutowicz J, Mueller-Roeber B, Blatt MR, Dreyer I (2009) Distinct roles of the last transmembrane domain in controlling *Arabidopsis* K^+ channel activity. New Phytol 182:380–391. https://doi.org/10.1111/j.1469-8137.2008.02749.x

Geiger D, Becker D, Vosloh D, Gambale F, Palme K, Rehers M, Anschuetz U, Dreyer I, Kudla J, Hedrich R (2009) Heteromeric AtKC1/AKT1 channels in *Arabidopsis* roots facilitate growth under K^+-limiting conditions. J Biol Chem 284:21288–21295. https://doi.org/10.1074/jbc.M109.017574

Genies L, Orjollet D, Carasco L, Camilleri V, Frelon S, Vavasseur A, Leonhardt N, Henner P (2017) Uptake and translocation of cesium by *Arabidopsis thaliana* in hydroponics conditions: links between kinetics and molecular mechanisms. Environ Exp Bot 138:164–172. https://doi.org/10.1016/j.envexpbot.2017.03.013

Gierth M, Maser P (2007) Potassium transporters in plants involvement in K^+ acquisition, redistribution and homeostasis. FEBS Lett 581:2348–2356. https://doi.org/10.1016/j.febslet.2007.03.035

Gierth M, Maser P, Schroeder JI (2005) The potassium transporter AtHAK5 functions in K(+) deprivation-induced high-affinity K(+) uptake and AKT1 K(+) channel contribution to K(+) uptake kinetics in Arabidopsis roots. Plant Physiol 137:1105–1114. https://doi.org/10.1104/pp.104.057216

Grabov A (2007) Plant KT/KUP/HAK potassium transporters: single family–multiple functions. Ann Bot 99:1035–1041. https://doi.org/10.1093/aob/mcm066

Gupta DK, Walther C (2014) Radionuclide contamination and remediation through plants. Springer, Cham. https://doi.org/10.1007/978-3-319-07665-2

Gupta DK, Walther C (2016) Impact of cesium on plants and the environment. Springer, Cham. https://doi.org/10.1007/978-3-319-41525-3

Gupta DK, Chatterjee S, Dutta S, Voronina AV, Walther C (2016) Radionuclides: accumulation and transport in plants. Rev Environ Contam Toxicol 398:1–22. https://doi.org/10.1007/398_2016_7

Gupta DK, Tawussi F, Hölzer A, Hamann L, Walther C (2017) Investigation of low level ^{242}Pu contamination on nutrition disturbance and oxidative stress in *Solanum tuberosum* L. Environ Sci Pollut Res 24:16050–15061. https://doi.org/10.1007/s11356-017-9071-9

Hafsi C, Falleh H, Saada M, Ksouri R, Abdelly C (2017) Potassium deficiency alters growth, photosynthetic performance, secondary metabolites content, and related antioxidant capacity in *Sulla carnosa* grown under moderate salinity. Plant Physiol Biochem 118:609–617. https://doi.org/10.1016/j.plaphy.2017.08.002

Han M, Wu W, Wu WH, Wang Y (2016) Potassium transporter KUP7 is involved in K^+ acquisition and translocation in Arabidopsis root under K^+-limited conditions. Mol Plant 9:437–446. https://doi.org/10.1016/j.molp.2016.01.012

Hanelt I, Wunnicke D, Muller-Trimbusch M, Vor der BM, Kraus I, Bakker EP, Steinhoff HJ (2010) Membrane region M2C2 in subunit KtrB of the K$^+$ uptake system KtrAB from *Vibrio alginolyticus* forms a flexible gate controlling K$^+$ flux: an electron paramagnetic resonance study. J Biol Chem 285:28210–28219. https://doi.org/10.1074/jbc.M110.139311

Hedrich R (2012) Ion channels in plants. Physiol Rev 92:1777–1811. https://doi.org/10.1152/physrev.00038.2011

Hedrich R, Becker D (1994) Green circuits-the potential of plant specific ion channels. Plant Mol Biol 26:1637–1650

Hedrich R, Becker D, Geiger D, Marten I, Roelfsema M (2012) Role of ion channels in plants. In: Okada Y (ed) Patch clamp techniques. From beginning to advanced protocols. Springer, Cham, pp 295–232. https://doi.org/10.1007/978-4-431-53993-3

Hille B (2001) Ionic channels of excitable membranes. Sinauer, Sunderland

Hirsch RE, Lewis BD, Spalding EP, Sussman MR (1998) A role for the AKT1 potassium channel in plant nutrition. Science 280:918–921

Horie T, Costa A, Kim TH, Han MJ, Horie R, Leung HY, Miyao A, Hirochika H, An G, Schroeder JI (2007) Rice OsHKT2;1 transporter mediates large Na$^+$ influx component into K+−starved roots for growth. EMBO J 26:3003–3014. https://doi.org/10.1038/sj.emboj.7601732

Hosy E, Vavasseur A, Mouline K, Dreyer I, Gaymard F, Poree F, Boucherez J, Lebaudy A, Bouchez D, Very AA, Simonneau T, Thibaud JB, Sentenac H (2003) The *Arabidopsis* outward K- channel GORK is involved in regulation of stomatal movements and plant transpiration. Pro Natl Acad Sci USA 100:5549–5554. https://doi.org/10.1073/pnas.0733970100

Hu QH, Weng JQ, Wang JS (2010) Sources of anthropogenic radionuclides in the environment: a review. J Environ Radioact 101:426–437. https://doi.org/10.1016/j.jenvrad.2008.08.004

Ishikawa S, Hayashi S, Abe T, Igura M, Kuramata M, Tanikawa H, Iino M, Saito T, Ono Y, Ishikawa T, Fujimura S, Goto A, Takagi H (2017) Low-cesium rice: mutation in OsSOS2 reduces radiocesium in rice grains. Sci Report 7:2432. https://doi.org/10.1038/s41598-017-02243-9

Ivashikina N, Becker D, Ache P, Meyerhoff O, Felle HH, Hedrich R (2001) K channel profile and electrical properties of *Arabidopsis* root hairs. FEBS Lett 508:463–469. https://doi.org/10.1016/S0014-5793(01)03114-3

Jan LY, Jan YN (1997) Receptor-regulated ion channels. Curr Opin Cell Biol 9:155–160. https://doi.org/10.1016/S0955-0674(97)80057-9

Kanter U, Hauser A, Michalke B, Draxl S, Schaffner AR (2010) Cesium and strontium accumulation in shoots of *Arabidopsis thaliana*: genetic and physiological aspects. J Exp Bot 61:3995–4009. https://doi.org/10.1093/jxb/erq213

Kim EJ, Kwak JM, Uozumi N, Schroeder JI (1998) AtKUP1: an Arabidopsis gene encoding high-affinity potassium transport activity. Plant Cell 10:51–62

Kim TH, Bohmer M, Hu H, Nishimura N, Schroeder JI (2010) Guard cell signal transduction network: advances in understanding abscisic acid, CO_2, and Ca^{2+} signaling. Annu Rev Plant Biol 61:561–591. https://doi.org/10.1146/annurev-arplant-042809-112226

Kobayashi D, Uozumi N, Hisamatsu S, Yamagami M (2010) AtKUP/HAK/KT9, a K1 transporter from *Arabidopsis thaliana*, mediates Cs1 uptake in *Escherichia coli*. Biosci Biotechnol Biochem 74:203–205. https://doi.org/10.1271/bbb.90638

Kochian LV, Lucas WJ (1993) Can K$^+$ channels do it all? Plant Cell 5:720

Kovler K (2017) The national survey of natural radioactivity in concrete produced in Israel. J Environ Radioact 168:46–53. https://doi.org/10.1016/j.jenvrad.2016.03.002

Lagarde D, Basset M, Lepetit M, Conejero G, Gaymard F, Astruc S, Grignon C (1996)Tissue-specific expression of Arabidopsis AKT1 gene is consistent with a role in K nutrition. Plant J 9:195–203

Li L, Kim BG, Cheong YH, Pandey GK, Luan S (2006) A Ca^{2+} signaling pathway regulates a K$^+$ channel for low-K response in Arabidopsis. Proc Natl Acad Sci U S A 103:12625–12630. https://doi.org/10.1073/pnas.0605129103

Li W, Xu G, Alli A, Yu L (2018) Plant HAK/KUP/KT K transporters: function and regulation. Semin Cell Dev Biol 74:133–141. https://doi.org/10.1016/j.semcdb.2017.07.009

Liu K, Luan S (1998) Voltage-dependent K channels as targets of osmosensing in guard cells. Plant Cell 10:1957–1970

Lu Y, Chanroj S, Zulkifli L, Johnson MA, Uozumi N, Cheung A, Sze H (2011) Pollen tubes lacking a pair of K$^+$ transporters fail to target ovules in Arabidopsis. Plant Cell 23:81–93. https://doi.org/10.1105/tpc.110.080499

Maathuis FJM, Sanders D (1996) Mechanisms of potassium absorption by higher plant roots. Physiol Plant 96:158–168. https://doi.org/10.1111/j.1399-3054.1996.tb00197.x

Maathuis FJM, Ichida AM, Sanders D, Schroeder JI (1997) Roles of higher plant K channels. Plant Physiol 114:1141–1149

Martínez-Cordero MA, Martínez V, Rubio F (2004) Cloning and functional characterization of the high-affinity K$^+$ transporter HAK1 of pepper. Plant Mol Biol 56:413–421. https://doi.org/10.1007/s11103-004-3845-4

Martínez-Cordero MA, Martínez V, Rubio F (2005) High-affinity K$^+$ uptake in pepper plants. J Exp Bot 416:1553–1562. https://doi.org/10.1093/jxb/eri150

Mattsson S, Lidén K (1975) ^{137}Cs in carpets of the forest moss *Pleurozium schreberi* 1961-1973. Oikos 26:323–327

Mian A, Oomen RJ, Isayenkov S, Sentenac H, Maathuis FJM, Very AA (2011) Overexpression of a Na(+) and K(+) -permeable HKT transporter in barley improves salt tolerance. Plant J 68:468–479

Mohamed S, Sentenac H, Guiderdoni E, Véry AA, Nieves-Cordones M (2018) Internal Cs$^+$ inhibits root elongation in rice. Plant Signal Behav 13:e1428516. https://doi.org/10.1080/15592324.2018

Muller RB, Ellenberg J, Provart N, Willmitzer L, Busch H, Becker D, Dietrich P, Hoth S, Hedrich R (1995) Cloning and electrophysiological analysis of KST1, an inward rectifying K- channel expressed in potato guard cells. EMBO J 14:2409–2416

Nakamura RL, Gaber RF (2009) Ion selectivity of the Kat1 K+ channel pore. Mol Membr Biol 26:293–308. https://doi.org/10.1080/09687680903188332

Nakamura RL, McKendree Jr WL, Hirsch RE, Sedbrook JC, Gaber RF, Sussman MR (1995) Expression of an *Arabidopsis* potassium channel gene in guard cells. Plant Physiol 109:371–374. https://doi.org/10.1104/pp.109.2.371

Nieves-Cordones M, Martínez-Cordero MA, Martínez V, Rubio F (2007) An NH$_4$$^+$-sensitive component dominates high-affinity K$^+$ uptake in tomato plants. Plant Sci 172:273–280. https://doi.org/10.1016/j.plantsci.2006.09.003

Nieves-Cordones M, Alemán F, Martínez V, Rubio F (2014) K$^+$ uptake in plant roots. The systems involved their regulation and parallels in other organisms. J Plant Physiol 171:688–695. https://doi.org/10.1016/j.jplph.2013.09.021

Nieves-Cordones M, Al Shiblawi FR, Sentenac H (2016a) Roles and transport of sodium and potassium in plants. Met Ions Life Sci 16:291–324 https://doi.org/10.1007/978-3-319-21756-7_9

Nieves-Cordones M, Martínez V, Benito B, Rubio F (2016b) Comparison between Arabidopsis and Rice for main pathways of K(+) and Na(+) uptake by roots. Front Plant Sci 7:992. https://doi.org/10.3389/fpls.2016.00992

Nieves-Cordones M, Mohamed S, Tanoi K, Kobayashi NI, Takagi K, Vernet A, Guiderdoni E, Perin C, Sentenac H, Very AA (2017) Production of low-Cs$^+$ rice plants by inactivation of the K+ transporter OsHAK1 with the CRISPR-Cas system. Plant J 92:43–56. https://doi.org/10.1111/tpj.13632

Nikitin AI, Kryshev II, Bashkirov NI, Valetova NK, Dunaev GE, Kabanov AI, Katrich IY, Krutovsky AO, Nikitin VA, Petrenko GI,

Polukhina AM, Selivanova GV, Shkuro VN (2012) Up-to-date concentrations of long-lived artificial radionuclides in the tom and Ob rivers in the area influenced by discharges from Siberian chemical combine. J Environ Radioact 108:15–23. https://doi.org/10.1016/j.jenvrad.2011.11.013

Olondo C, Legarda F, Herranz M, Idoeta R (2017) Validating proposed migration equation and parameters' values as a tool to reproduce and predict ^{137}Cs vertical migration activity in Spanish soils. J Environ Radioact 169-170:40–47 https://doi.org/10.1016/j.jenvrad.2016.12.013

Pacheco-Arjona JR, Ruiz-Lau N, Medina-Lara F, Minero-Garcia Y, echevarria-Machado I, santos-Briones CDL, Martinez-Estevez M (2011) Effects of ammonium nitrate, cesium chloride and tetraethyl ammonium on high-affinity potassium uptake in habanero pepper plantlets (Capsicum chinense Jacq.). Afr J Biotechnol 10:13418–13429. https://doi.org/10.5897/AJB10.2097

Papazian DM, Schwarz TL, Tempel BL, Jan YN, Jan LY (1987) Cloning of genomic and complementary DNA from shaker, a putative potassium channel gene from Drosophila. Science 237:749–753

Prorok VV, Dacenko OI, Bulavin LA, Poperenko LV, White PJ (2016) Mechanistic interpretation of the varying selectivity of Cesium-137 and potassium uptake by radish (Raphanus sativus L.) under field conditions near Chernobyl. J Environ Radioact 152:85–91. https://doi.org/10.1016/j.jenvrad.2015.11.005

Pyo YJ, Gierth M, Schroeder JI, Cho MH (2010) High-affinity K+ transport in Arabidopsis: AtHAK5 and AKT1 are vital for seedling establishment and postgermination growth under low-potassium conditions. Plant Physiol 153:863–875. https://doi.org/10.1104/pp.110.154369

Qi Z, Hampton CR, Shin R, Barkla BJ, White PJ, Schachtman DP (2008) The high affinity K1 transporter AtHAK5 plays a physiological role in planta at very low K1 concentrations and provides a caesium uptake pathway in Arabidopsis. J Exp Bot 59:595–607. https://doi.org/10.1093/jxb/erm330

Rai H, Yokoyama S, Satoh-Nagasawa N, Furukawa J, Nomi T, Ito Y, Fujimura S, Takahashi H, Suzuki R, Yousra ELM, Goto A, Fuji S, Nakamura S, Shinano T, Nagasawa N, Wabiko H, Hattori H (2017) Cesium uptake by rice roots largely depends upon a single gene, HAK1, which encodes a potassium transporter. Plant Cell Physiol 58:1486–1493 https://doi.org/10.1093/pcp/pcx137

Reintanz B, Szyroki A, Ivashikina N, Ache P, Godde M, Becker D, Palme K, Hedrich R (2002) AtKC1, a silent Arabidopsis potassium channel α-subunit modulates root hair K+ influx. Pro Natl Acad Sci USA 99:4079–4084. https://doi.org/10.1073/pnas.052677799

Riedelsberger J, Dreyer I, Gonzalez W (2015) Outward rectification of voltage-gated K+ channels evolved at least twice in life history. PLoS One 10(9):e0137600. https://doi.org/10.1371/journal.pone.0137600

Roberts SK, Tester M (1995) Inward and outward K+-selective currents in the plasma membrane of protoplasts from maize root cortex and stele. Plant J 8:811–825. https://doi.org/10.1046/j.1365-313X.1995.8060811.x

Ródenas R, García-Legaz MF, López-Gómez E, Martínez V, Rubio F, Botellac MÁ (2017) NO_3^-, PO_4^{3-} and SO_4^{2-} deprivation reduced LKT1-mediatedlow-affinity K+ uptake and SKOR-mediated K+ translocation in tomato and Arabidopsis plants. Physiol Plant 160:410–424. https://doi.org/10.1111/ppl.12558

Ródenas R, Nieves-Cordones M, Rivero RM, Martinez V, Rubio F (2018) Pharmacological and gene regulation properties point to the SlHAK5 K+ transporter as a system for high-affinity Cs+ uptake in tomato plants. Physiol Plant 162:455–466. https://doi.org/10.1111/ppl.12652

Rosén K, Vinichuk M (2014) Potassium fertilization and (137) Cs transfer from soil to grass and barley in Sweden after the Chernobyl fallout. J Environ Radioact 130:22–32. https://doi.org/10.1016/j.jenvrad.2013.12.019

Rubio F, Nieves-Cordones M, Alem´an F, Martinez V (2008) Relative contribution of AtHAK5 and AtAKT1 to K+ uptake in the high-affinity range of concentrations. Physiol Planta 134:598–608. https://doi.org/10.1111/j.1399-3054.2008.01168.x

Rubio F, Aleman F, Nieves-Cordones M, Martinez V (2010) Studies on Arabidopsis athak5, atakt1 double mutants disclose the range of concentrations at which AtHAK5, AtAKT1 and unknown systems mediate K+ uptake. Physiol Plant 139:220–228. https://doi.org/10.1111/j.1399-3054.2010.01354.x

Ruiz-Lau N, Bojórquez-Quintal E, Benito B, Echevarría-Machado I, Sánchez-Cach LA, Medina-Lara MF, Martínez-Estévez M (2016) Molecular cloning and functional analysis of a Na+ −insensitive K+ transporter of Capsicum chinense Jacq. Front Plant Sci 7:1980. https://doi.org/10.3389/fpls.2016.01980

Sanches N, Anjos RM, Mosquera B (2008) ^{40}K/^{137}Cs discrimination ratios to the above ground organs of tropical plants. J Environ Radioact 99:1127–1135. https://doi.org/10.1016/j.jenvrad.2008.01.003

Sano T, Becker D, Ivashikina N, Wegner LH, Zimmermann U, Roelfsema MR, Nagata T, Hedrich R (2007) Plant cells must pass a K+ threshold to re-enter the cell cycle. Plant J 50:401–413. https://doi.org/10.1111/j.1365-313X.2007.03071.x

Santa-María GE, Rubio F, Dubcovsky J, Rodríguez-Navarro A (1997) The HAK1 gene of barley is a member of a large gene family and encodes a high-affinity potassium transporter. Plant Cell 9:2281–2289

Santa-María GE, Danna CH, Czibener C (2000) High-affinity potassium transport in barley roots. Ammonium-sensitive and -insensitive pathways. Plant Physiol 12:297–306. https://doi.org/10.1104/pp.123.1.297

Sassi A, Khan I, Véry AA, Sentenac H (2012) Molecular biology of K+ transport across the plant cell membrane: what do we learn from Arabidopsis and Rice model plants? Intl Potash Inst Anniversary Issue 32. https://www.ipipotash.org/udocs/e-ifc_no32_rf4-molecular-biology.pdf

Schachtman DP, Schroeder JI (1994) Structure and transport mechanism of a high-affinity potassium uptake transporter from higher plants. Nature 370:655–658

Schachtman DP, Schroeder JI, Lucas WJ, Anderson JA, Gaber RF (1992) Expression of an inward-rectifying potassium channel by the Arabidopsis KAT1 cDNA. Science 258:1654–1658

Schroeder JI, Hedrich R (1989) Involvement of ion channels and active transport in osmoregulation and signalling of higher plant cells.Trend Biochem Sci 14:187–192

Schroeder JI, Hedrich R, Fernandez JM (1984) Potassium-selective single channels in guard-cell protoplasts of Vicia faba. Nature 312:361–362

Sentenac H, Bonneaud N, Minet M, Lacroute F, Salmon JM, Gaymard F, Grignon C (1992) Cloning and expression in yeast of a plant potassium-ion transport-system. Science 256:663–665

Shaw G, Hewamanna R, Lillywhite J, Bell JNB (1992) Radiocaesium uptake and translocation in wheat with reference to the transfer factor concept and ion competition effects. J Environ Radioact 16:167–180

Singh SK, Reddy VR (2017) Potassium starvation limits soybean growth more than the photosynthetic processes across CO_2 levels. Front Plant Sci 8:991. https://doi.org/10.3389/fpls.2017.00991

Smolders E, Shaw G (1995) Changes in radioceasium uptake and distribution in wheat during plant development: a solution culture study. Plant Soil 176:1–6

Spalding EP, Hirsch RE, Lewis DR, Qi Z, Sussman MR, Lewis BD (1999) Potassium uptake supporting plant growth in the absence of AKT1 channel activity inhibition by ammonium and stimulation by sodium. J Gen Physiol 113:909–918

Straltsova D, Chykun P, Subramaniam S, Sosan A, Kolbanov D, Sokolik A, Demidchik V (2015) Cation channels are involved in

brassinosteroid signalling in higher plants. Steroids 97:98–106. https://doi.org/10.1016/j.steroids.2014.10.008

Stuenkel D (2017) Modeling considerations for ingestion pathway dose calculations using CAP88. Health Phys 112:343–351. https://doi.org/10.1097/HP.0000000000000636

Sugiura Y, Shibata M, Ogata Y, Ozawa H, Kanasashi T, Takenaka C (2016) Evaluation of radiocesium concentrations in new leaves of wild plants two years after the Fukushima Dai-ichi nuclear power plant accident. J Environ Radioact 160:8–24. https://doi.org/10.1016/j.jenvrad.2016.04.015

SunarpiHorie T, Motoda J, Kubo M, Yang H, Yoda K, Horie R, Chan WY, Leung HY, Hattori K, Konomi M, Osumi M, Yamagami M, Schroeder JI, Uozumi N (2005) Enhanced salt tolerance mediated by AtHKT1 transporter-induced Na unloading from xylem vessels to xylem parenchyma cells. Plant J 44:928–938. https://doi.org/10.1111/j.1365-313X.2005.02595.x

Suzuki K, Costa A, Nakayama H, Katsuhara M, Shinmyo A, Horie T (2016) OsHKT2; 2/1-mediated Na^+ influx over K^+ uptake in roots potentially increases toxic Na^+ accumulation in a salt-tolerant landrace of rice Nona Bokra upon salinity stress. J Plant Res 129:67–77. https://doi.org/10.1007/s10265-015-0764-1

Szczerba MW, Britto DT, Kronzucker HJ (2009) K^+ transport in plants: physiology and molecular biology. J Plant Physiol 166:447–466. https://doi.org/10.1016/j.jplph.2008.12.009

TermiziRamli A, Wahab A, Hussein MA, Khalik Wood A (2005) Environmental ^{238}U and ^{232}Th concentration measurements in an area of high level natural background radiation at Palong, Johor, Malaysia. J Environ Radioact 80:287–304. https://doi.org/10.1016/j.jenvrad.2004.06.008

Turekian KK, Wedepohl KH (1961) Distribution of the elements in some major units of the Earth's crust. Geol Soc Am Bull 72:175–191

Unwin N (1989) The structure of ion channels in membranes of excitable cells. Neuron 3:665–676

Uozumi N, Dreyer I (2011) Structure–function correlate in plant ion channels. In: Montal M (ed) Comprehensive biophysics, Vol. 6: channel proteins. Elsevier, Amsterdam

Uozumi N, Schroeder JI (2010) Ion channels and plant stress: past, present and future. In: Demidchik V, Maathuis FJ (eds) Ion channels and plant stress responses. Springer, Berlin, pp 1–22

Uozumi N, Kim EJ, Rubio F, Yamaguchi T, Muto S, Tsuboi A, Bakker EP, Nakamura T, Schroeder JI (2000) The Arabidopsis HKT1 gene homolog mediates inward Na^+ currents in Xenopuslaevis oocytes and Na^+ uptake in Saccharomyces cerevisiae. Plant Physiol 122:1249–1259. https://doi.org/10.1104/pp.122.4.1249

Vallejo AJ, Peralta ML, Santa-Maria GE (2005) Expression of potassium-transporter coding genes, and kinetics of rubidium uptake, along a longitudinal root axis. Plant Cell Environ 28:850–862. https://doi.org/10.1111/j.1365-3040.2005.01334.x

Very AA, Sentenac H (2002) Cation channels in the Arabidopsis plasma membrane. Trends Plant Sci 7:168–175

Véry AA, Nieves-Cordones M, Daly M, Khan I, Fizames C, Sentenac H (2014) Molecular biology of K^+ transport across the plant cell membrane: what do we learn from comparison between plant species? J Plant Physiol 171:748–769. https://doi.org/10.1016/j.jplph.2014.01.011

Voronina AV, Kulyaeva IO, Gupta DK (2018) Determination of the parameters of selective 137Cs sorption onto natural and Ferrocyanide-Modified glauconite and clinoptilolite. 60:35–41. https://doi.org/10.1134/S106636221801006X

Waegeneers N, Sauras-Yera T, Thiry Y, Vallejo VR, Smolders E, Madoz-Escande C (2009) Plant uptake of radiocesium from artificially contaminated soil monoliths covering major European soil types. J Environ Radioact 100:439–444. https://doi.org/10.1016/j.jenvrad.2008.08.011

Walker DJ, Leigh RA, Miller AJ (1996) Potassium homeostasis in vacuolate plant cells. Pro Natl Acad Sci USA 93:10510–10514

Walther C, Gupta DK (2015) Radionuclides in the environment: influence of chemical speciation and plant uptake on radionuclide migration. Springer, Cham. https://doi.org/10.1007/978-3-319-22171-7

Wang Y, Wu WH (2013) Potassium transport and signaling in higher plants. Annu Rev Plant Biol 64:451–476. https://doi.org/10.1146/annurev-arplant-050312-120153

Wang Y, Wu WH (2017) Regulation of potassium transport and signaling in plants. Curr Opin Plant Biol 39:123–128. https://doi.org/10.1016/j.pbi.2017.06.006

Wang XP, Chen LM, Liu WX, Shen LK, Wang FL, Zhou Y, Zhang Z, Wu WH, Wang Y (2016) AtKC1 and CIPK23 synergistically modulate AKT1-mediated low-potassium stress responses in Arabidopsis. Plant Physiol 170:2264–2277. https://doi.org/10.1104/pp.15.01493

Ward JM, Maser P, Schroeder JI (2009) Plant ion channels: gene families, physiology, and functional genomics analyses. Annu Rev Physiol 71:59–82. https://doi.org/10.1146/annurev.physiol.010908.163204

White PJ, Broadley MR (2000) Mechanisms of caesium uptake by plants. New Phytol 147:241–256

Xu J, Li HD, Chen LQ, Wang Y, Liu LL, He L, Wu WH (2006) A protein kinase, interacting with two calcineurin B-like proteins, regulates K^+ transporter AKT1 in Arabidopsis. Cell 125:1347–1360. https://doi.org/10.1016/j.cell.2006.06.011

Yamaguchi T, Hamamoto S, Uozumi N (2013) Sodium transport system in plant cells. Front Plant Sci 4:410. https://doi.org/10.3389/fpls.2013.00410

Zhang YD, Very AA, Wang LM, Deng YW, Sentenac H, Huang DF (2011) A K^+ channel from salt-tolerant melon inhibited by Na^+. New Phytol 189:856–868. https://doi.org/10.1111/j.1469-8137.2010.03526.x

Zhang T, Chen S, Harmon AC (2014) Protein phosphorylation in stomatal movement. Plant Signal Behav 9(11):e972845. https://doi.org/10.4161/15592316.2014.972845

Zhu YG, Shaw G (2000) Soil contamination with radionuclides and potential remediation. Chemosphere 41:121–128. https://doi.org/10.1016/S0045-6535(99)00398-7

Zhu YG, Smolders E (2000) Plant uptake of radiocaesium: a review of mechanisms, regulation and application. J Exp Bot 51:1635–1645

Zimmermann S, Talke I, Ehrhardt T, Nast G, Müller-Röber B (1998) Characterization of SKT1, an inward rectifying K channel from potato, by heterologous expression in insect cells. Plant Physiol 116:879–890