

# Potassium Transport Systems and Their Role in Stress Response, Plant Growth, and Development

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**Abstract**—In this review, the K<sup>+</sup> transport systems were selected and characterized. Detailed literature analysis and data summarizing regarding main members of K<sup>+</sup> transport systems, their biological roles in plant growth and developments, and mechanisms of abiotic stress tolerance were conducted. The processes of K<sup>+</sup> uptake, transport in tissues, and cellular distribution were described. Structure characteristic and topology of K<sup>+</sup> transport proteins and their role in function specificity were analyzed. The role of these membrane transport proteins in signaling, drought, and salt tolerance or K<sup>+</sup> deficiency were critically evaluated. New perspective directions for further research of K<sup>+</sup> transport proteins were suggested.

**Keywords:** potassium transport, two-pore TPK channels, *Shaker*-like channels, Kir-like channels, nonselective cation channels NCCC, KUP/HAK/KT transporters, Trk/HKT transporters, CPA transporters

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## INTRODUCTION

Potassium (K<sup>+</sup>) is one of the most important mineral elements necessary for the growth and development of plants. The use of mineral fertilizers, including potassium fertilizer, made the first “green revolution” in agriculture and significantly raised yield and productivity. Approximately 25 million t of potassium fertilizers are used by world agriculture annually. K<sup>+</sup> is one of the most common elements in plant tissues and it can compose from 1 to 10% of dry matter (Gierth et al., 2007). This element is important for plant growth and development, and the consumption of food high in K<sup>+</sup> reduces the risk of cardiovascular disease and has a positive effect on blood pressure. This element is involved in many important processes of plant life, namely in osmoregulation, the maintenance of electrical membrane potential, generation of turgor pressure and stretching of cells, plant movements, pollen development, respiratory cell function, and signaling processes. In addition, K<sup>+</sup> is involved in the activation of many enzymes and the transport of nitrates and sucrose over long distances, and it is an important component of photosynthesis (Amtmann et al., 2008; Ahmad et al., 2013; Sharma et al., 2013). It should be noted that K<sup>+</sup> is a key element of resistance to salinity and drought (Sharma et al., 2013). While Na<sup>+</sup> is a cytotoxic ion and the ionic imbalance is realized in case of water and salt stresses due to Na<sup>+</sup>, K<sup>+</sup> acts as an osmoprotector (Isayenkov, 2012; Isayenkov et al.,

2019; Llopis-Torregrosa et al., 2016). Concentrations of this element in the soil can vary depending on geological features and other natural factors; therefore plants acquired different ways of absorbing and maintaining the intracellular concentration of K<sup>+</sup> ions during evolutionary development (Grabov, 2007). The process of absorption and transport of this element requires the passage of K<sup>+</sup> through the plasma membrane by membrane transport proteins or transport through the apoplast during its absorption from the soil and release into the lumen of the xylem, the passage through the tonoplast during accumulation, or leakage in or out of the vacuole. Active and passive transport are performed by transport proteins and are characterized by their high or low affinity for potassium (Amtmann et al., 2008; Epstein et al., 1961).

The *Arabidopsis thaliana* genome contains approximately 77 genes potentially belonging to potassium-selective transport systems (Demidchik, 2014). K<sup>+</sup> transport systems can be divided into seven different families, four of which are channels (two-pore TPK channels, *Shaker* and K<sub>ir</sub>-like channels, nonselective cationic channels NCCC) belonging to the low-affinity potassium channels and others are transporters (KUP/HAK/KT, Trk/HKT, CPA), which, in turn, are characterized by high-affinity to potassium (Sharma et al., 2013; Osakabe et al., 2013). The process of absorption, transport, and tissue redistribution of this element occurs due to the operation of ion channels or transporters in root epidermal cells and

then it is transported to shoots and leaves by xylem elements, promoting plant growth and development (Zhao et al., 2015).

The purpose of this review was to analyze the literature and data summarizing the main representatives of the  $K^+$  transport systems in the plant, their biological roles, and physiological functions in the growth and development of the plant organism and mechanisms of resistance to abiotic stress.

**Systems of passive  $K^+$  transport.** Passive transport systems are potassium membrane channels that provide transport of this element across the membrane due to the electrochemical gradient without the involvement of energy (Fig. 1). In addition,  $K^+$  can be absorbed and transported by the plant through the apoplastic pathway without the involvement of membrane transport protein systems (Isayenkov, 2012). Usually, potassium channels are multimeric proteins, which are characterized by the presence of  $\alpha$ -subunits (transmembrane subunit), forming one or two pore domains. Potassium channels are activated by high concentrations of  $K^+$  ions ( $>0.5$  mM) and, therefore, they belong to the high-affinity transport systems (Cheng et al., 2018). GYGD motif (glycine-tyrosine-glycine), present in the pore domains of members of the seven transport channel families (Lebaudy et al., 2007), make these channels highly selective for potassium. Three families of  $\alpha$ -subunits that form potassium-selective channels have been identified in plants. The  $\alpha$ -subunits of the *Shaker*-like channel family consist of six transmembrane segments and one pore domain located between the last pair of transmembrane segments. In the TPK family,  $\alpha$ -subunits have a hydrophobic nucleus consisting of four transmembrane segments and two pore domains. Representatives of  $K_{ir}$ -like channels have two transmembrane segments and one pore domain (Lebaudy et al., 2007; Very et al., 2003). All potassium channels have a pore-loop that binds  $K^+$  ions and interacts with the oxygen of the carbonyl group of the GYGD filter located in the pore domain (Ward et al., 2009).

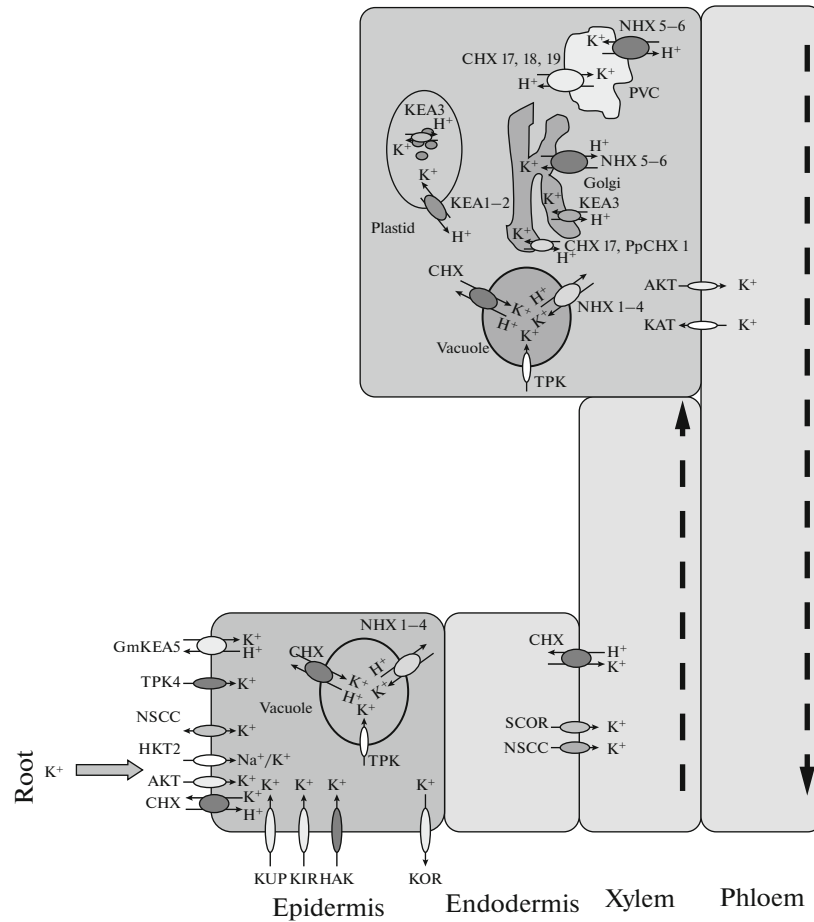
In addition to “classical” membrane channels with GYGD pores, the family of nonselective cationic channels (NCCC) can mediate  $K^+$  transport.

***Shaker*-like potassium channels.** For the first time, channels of the *Shaker*-like family were identified in *Drosophila* (Papazian et al., 1987). Representatives of this family are divided into three functional types, namely, outward-rectifying channels, inward-rectifying channels, and weakly-rectifying channels, which play an important role in the homeostasis of  $K^+$  (Fig. 1) (Gambale et al., 2006). It is known that *Shaker*-like channels play a particularly important role in the loading and unloading of conductive tissues with  $K^+$  ions (Britto et al., 2008). Nine genes in the *Shaker*-like family have been identified in *Arabidopsis*. These channels are of great importance for many physiolog-

ical processes. In particular, they are responsible for the constant entry or removal of  $K^+$  from plant tissues (Jeanguenin et al., 2011). The inward-rectifying  $K^+$  channels include KAT1, KAT2, AKT1, AKT5, and AKT6 (SPIK), which are activated during membrane hyperpolarization and mediating the influx of  $K^+$  ions (Fig. 2). Potential-dependent stellar  $K^+$  outward rectifier channels (SKOR), mediating the entry of  $K^+$  into the xylem sap and guarding cell outward-rectifying  $K^+$  channels (GORK) localized in stomatal cells, are activated by membrane depolarization and mediate the outflow of  $K^+$  (Fig. 2) (Kleeff et al., 2018; Forster et al., 2019).

An interesting fact is that the weakly-rectifying channel AKT2 can mediate both the inflow and outflow of  $K^+$  (Kleeff et al., 2018). It is also believed that AKT2 is responsible for the circulation (or recirculation) of  $K^+$  ions for controlling the level of potassium in the phloem and regulating the polarization of the cell membrane (Gajdanowicz et al., 2011). In addition, KAT3 (*AtKCI*) itself is not a functional potassium channel, but it regulates the activity of AKT1 and KAT1 channels, forming hetero-tetramers (Kleeff et al., 2018). Transport of  $K^+$  through the phloem elements is carried out by AKT2/3 channels mediating both uptake and outflow of  $K^+$  (Ahmad et al., 2013). Also, the inward-rectifying *Shaker*-like channels KAT1 and KAT2 are responsible for the movements of the stomata (Jeanguenin et al., 2011; Cuin et al., 2018).

GORK channels are also known to mediate the release of  $K^+$  from stomatal cells and play an important role in the outflow of  $K^+$  from *Arabidopsis* root cells mediated by cell depolarization (Kleeff et al., 2018). GORK activity can be enhanced by phosphorylation and promote the outflow of  $K^+$  from respiratory cells (Forster et al., 2019). It is assumed that the main physiological function of the GORK channel is to control the opening and closing of the stomata by releasing  $K^+$  (Cuin et al., 2018; Hosy et al., 2003). Recent data suggest that the loss of  $K^+$  by plant roots induced by various types of stress is mediated by the operation of GORK channels (Isayenkov, 2012; Demidchik et al., 2018). The SKOR channel (Fig. 2) has a hydrophobic nucleus, contains six transmembrane domains, and a pore loop motif characteristic for GYGD potassium channels. In addition, this channel has a cyclic nucleotide binding domain, an ankyrin domain, and an acid domain (Demidchik et al., 2014; Gaymard et al., 1998). In *Arabidopsis*, SKOR is expressed in endodermal root cells and participates in the loading of xylems with  $K^+$ , ensuring the transport of this element from the roots to the upper organs of the plant (Fig. 1) (Liu et al., 2008). It was noted that SKOR channels are regulated by several physiological signals, including pH level on the inside and outside of the membrane and the extracellular potassium level. Both intra- and external cellular acid-

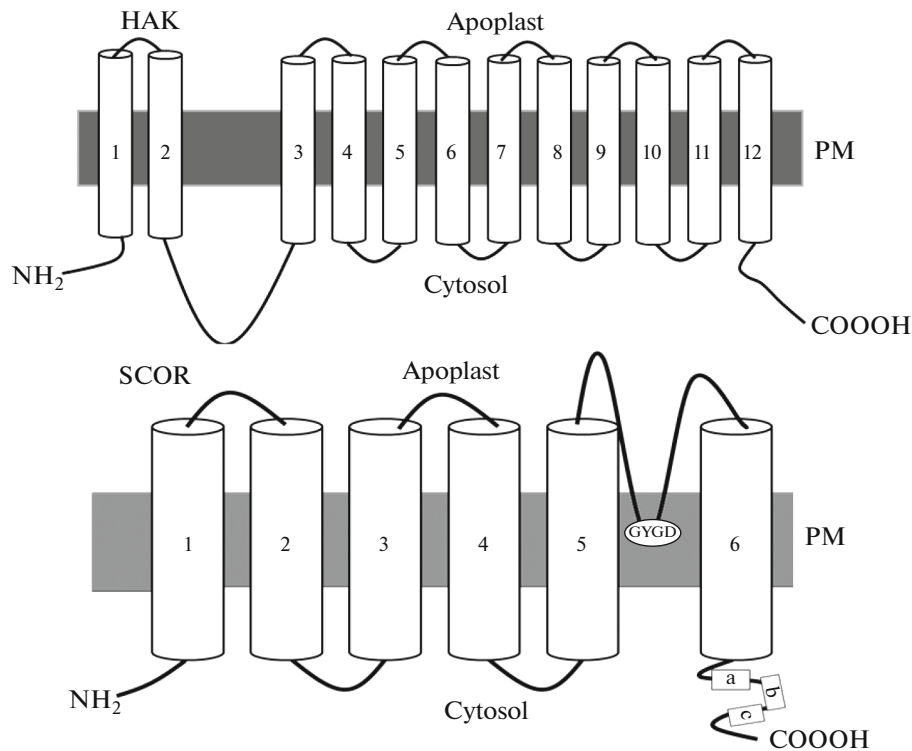


**Fig. 1.** Schematic description of the main transport routes of absorption and redistribution of  $K^+$  in plants. Various types of channels and transporters (AKT, HKT2, NSCC, HAK, CHX, TPK4, NSCC, HAK, KIR, KUP, GmKEA5) can be involved in the process of absorption and transport of this element across the plasma membrane. The process of compartmentalization of  $K^+$  in the vacuole is mediated by the operation of TRK channels, NHX 1–4 exchangers, and some representatives of the antiporters of the CHX subfamily. Transport and storage of  $K^+$  in plastids are provided by specialized KEA 1–2 and 3 transporters. Compartmentalization of  $K^+$  in membrane systems of the Golgi apparatus and prevacuolar compartments (PVC) are mediated by the operation of representatives of KEA 4–6 transporters, CHX17 or PpCHX1 antiporters from *Physcomitrella patens*, and NHX 5–6 exchangers. In addition, some CHX antiporters, namely CHX 16, 20, 23, and OsCHX17 from rice, are localized on endoplasmic reticulum (ER) membranes and may potentially participate in the compartmentalization of  $K^+$  in the inner lumen of the ER. Further transport and tissue redistribution of  $K^+$  in plants is mediated by the operation of representatives of several families of membrane transporters, namely SCOR, CHX, and NSCC. It is believed that the Shaker-like SCOR channel is the main supplier of potassium to the xylem. Some ACT potassium channels may be responsible for phloem loading and phloem enrichment. Instead, KAT potassium channels can mediate the removal of  $K^+$  from phloem elements and its transport to cells of tissues with active photosynthesis. The loss of  $K^+$  by the plant at the level of the root system is mediated by the operation of another member of this family of channels, namely GORK. It is also suggested that leakage of this element from root tissues may be caused by the operation of some nonselective cation channels (NSCC). Note: AKT, Arabidopsis  $K^+$  transport system (shaker inward potassium channel); KAT,  $K^+$  AKTlike channel (shaker inward potassium channel); HKT, High-affinity  $K^+$  transporter Type; NSCC, Non-selective cation channels; CHX, cation/ $H^+$  exchanger; NHX,  $Na^+$ / $H^+$  exchanger; KEA,  $K^+$  efflux antiporter; TPK, two-pore potassium channel; KUP,  $K^+$  uptake permease; KIR,  $K^+$  inward rectifier; HAK, High-affinity  $K^+$  uptake transporter; SCOR, stellar  $K^+$  outward rectifying channel; GORK, guard cells outward rectifying channel.

ification inhibits the activity of SKOR (Johansson et al., 2006). It is known that the activation of SKOR channels is carried out in response to fluctuations in the concentration of potassium in the xylem and its permeability by a potential-independent mechanism (Liu et al., 2008). The expression of the gene encoding SKOR in *Arabidopsis* was significantly increased in the root pericycle and xylem parenchymal cells in

response to low extracellular  $K^+$  levels (Zhao et al., 2015). Thus, SKOR is an important component of the regulation of  $K^+$  homeostasis, the recirculation of this element, and resistance to abiotic stresses.

It was noted that *Shaker*-like channels could also be regulated by phosphorylation in the  $Ca^{2+}$ -dependent manner. It has been shown that CBL-interacting protein kinase (CIPK) is activated by specific calcin-

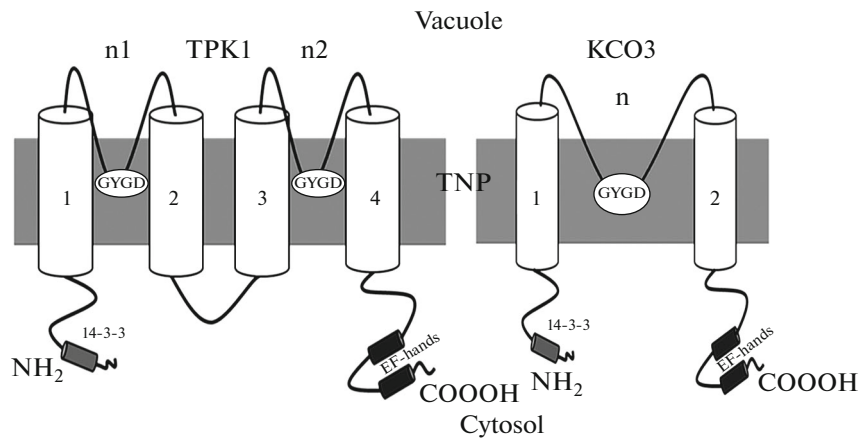


**Fig. 2.** Topology of HAK channel and *Shaker*-like SKOR channel. PM plasma membrane; 1–6 and 1–12 transmembrane domains; P, pore domain; GYGD, K<sup>+</sup> selective motif in the pore domain; (a) CNBD cyclic nucleotide binding domain; (b) ANK ankyrin domain (it is assumed that this type of domain is responsible for binding with cytoskeletal proteins or regulatory proteins (Sentenac et al., 1992); (c) KHA acid domain (responsible for interaction with K<sup>+</sup>).

erin-B-like protein (CBL) and regulates the uptake and distribution of K<sup>+</sup> in the plant. CBL1/9-CIPK23 and CBL4/CIPK6 complexes activate *Shaker*-like channels AKT1 and AKT2, respectively (Corratge-Faillie et al., 2017; Held et al., 2011). However, in a study of the effect of CPK13 on members of *Shaker*-like family KAT1 and KAT2, it was found that the inhibitory effect on the latter is Ca<sup>2+</sup>-independent (Corratge-Faillie et al., 2017). The expression of genes encoding representatives of *Shaker*-like channels can be regulated both at the transcriptional and at the posttranslational levels under the influence of K<sup>+</sup> deficiency or long-term salt or hormonal treatment (Kleeff et al., 2018; Maathuis et al., 2003). Thus, *Shaker*-like potassium channels are an important part of potassium transport and support of many physiological functions and protective processes of the plant.

**Two-pore potassium channels.** TPK channels consist of four transmembrane domains that form two pores (Fig. 3). Each pore contains a K<sup>+</sup> selective GYGD domain and the C end contains one or two EF-hands (Isaenkov et al., 2013) (Fig. 3). The genome of *Arabidopsis thaliana* encodes five different members of the TPK family channels in *Arabidopsis* (TPK1, TPK2, TPK3, TPK4, and TPK5) (Isaenkov et al., 2013; Voelker et al., 2006). One of the

most characterized representatives of TPK channels is AtTPK1 from *Arabidopsis*. It is known that the regulation of AtTPK1 can involve cytosolic Ca<sup>2+</sup> and phosphorylation by 14-3-3 proteins at the N-terminus and pH value in the cytosol (Gobert et al., 2007; Tang et al., 2020). AtTPK1 is responsible for K<sup>+</sup> homeostasis, the release of this ion during stomata closing, and seed germination. In addition, there are experimental data indicating the role of this channel and its homologues, namely HvTPK1 from barley and OsTPK1a from rice, in osmoregulation. These channels can be intracellular osmosensors that rapidly increase the activity of channels during hypersmotic shock to release vacuolar K<sup>+</sup> (Maathuis et al., 2011; Isayenkov et al., 2011). Almost all members of the TPK family of *Arabidopsis thaliana* are localized in the tonoplast of lytic vacuoles (Fig. 1). TPK3 is expressed in pollen and root tips, and TPK5 is expressed in vascular tissues, hydathodes, and flower organs (Isaenkov et al., 2013; Voelker et al., 2006). Unlike other members of the TPK4 family, it is localized in the plasma membrane of pollen (Becker et al., 2004; Marcel et al., 2010). Although it has been suggested that AtTPK3 is localized in the thylakoid membrane of chloroplast, where it is responsible for K<sup>+</sup> homeostasis, recent data indicate its tonoplast localization (Carraretto et al., 2013; Hohner et al.,



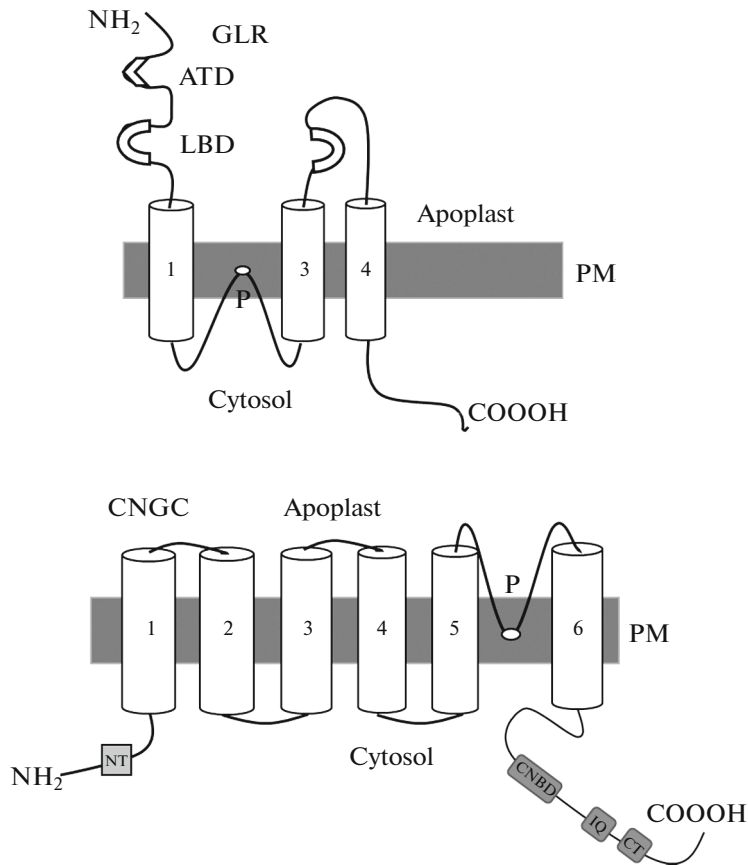
**Fig. 3.** Topology of TPK1 and KCO3 channels. TNP, tonoplast; P, pore domain; 1–4, transmembrane domains; GYGD, K<sup>+</sup> selective motif in the pore domain; 14-3-3, amino binding site; EF-hands, Ca<sup>2+</sup> binding domain at the carboxyl end.

2019). In addition, OsTPK1b from rice is localized exclusively on the membranes of protein vacuoles (Isayenkov et al., 2011; Isayenkov et al., 2011). TPKs can also play an important role in plant resistance to salinity and drought. It was shown that the expression of the TPK1a gene from tobacco increases more than two times under the action of osmotic shock and salt stress (Hamamoto et al., 2008). In addition, AtTPK1 undergoes phosphorylation by Ca<sup>2+</sup>-dependent protein kinase CDPK3 under salinity conditions (Latz et al., 2007) (Fig. 3). Rice plants with overexpression of OsTPK1b have better resistance to salinization and osmotic stress (Ahmad et al., 2016). Thus, further in-depth study of the group of these channels is important.

**K<sub>ir</sub>-like channels.** K<sub>ir</sub>-like channels localized in vacuoles were first detected in the genome of *Arabidopsis* (Lebaudy et al., 2007; Ward et al., 2009; Voelker et al., 2006). K<sub>ir</sub>-like channels consist of two transmembrane domains connected by a loop between them (MacKinnon et al., 2003). They are rudimentary potassium channels. K<sub>ir</sub>1 (also KCO3) was previously assigned to the TPK family (Ward et al., 2009) (Fig. 3). However, phylogenetic studies have shown that these channels were formed due to duplication of the TPK channel gene with a partial deletion, resulting in the loss of one pore domain. As a result, plant K<sub>ir</sub>-like channels have two transmembrane domains and one pore between them (Fig. 3) (Marcel et al., 2010). Now, representatives of K<sub>ir</sub>-like channels have been found only in members of the genus *Arabidopsis*; therefore, it is believed that this family emerged recently during the evolutionary process (Ward et al., 2009). A significant number of researchers consider K<sub>ir</sub>-like channels as a separate family. The *Arabidopsis* genome encodes only one member of the K<sub>ir</sub>-like channel family, KCO3 (Sharma et al., 2013; Ward et al., 2009). The expression of this gene can be observed in the vascular tissue of the leaf, the tissues of the flower, root and stem, as

well as in hydathodes, which is also characteristic for TPK5. KCO3 is probably involved in osmoregulation, since a plant with a knockout of the KCO3 gene shows reduced growth under osmotic stress (Voelker et al., 2006). However, this change in plant phenotype may be complemented by the expression of a mutant KCO3 gene with an inactive pore. These results show that the function of KCO3 under osmotic stress does not depend on its ability to transfer K<sup>+</sup> ions (Sharma et al., 2013).

**Nonselective cation channels (NCCC).** Nonselective cation channels (NSCCC) include two families of genes, namely glutamate receptor-like channels (GLRs) and cyclic nucleotide-gated channels (CNGC). GLR-channels consist of three transmembrane domains and one pore (Fig. 4). Unlike GLR, CNGC channels have six transmembrane domains and one pore (Fig. 4). It is assumed that these channels are the main gateway for Na<sup>+</sup> uptake by plants exposed to salt stress. However, these channel families also demonstrate conductivity for K<sup>+</sup> and Ca<sup>2+</sup> (Demidchik et al., 2014; Demidchik et al., 2018). NSCCs have been shown to be involved in the formation of plant resistance to abiotic and biotic stresses (Fig. 1) (Demidchik et al., 2018; Jha et al., 2016). The functioning of NSCCs is mainly associated with the transport and absorption of Na<sup>+</sup> during salinization and Ca<sup>2+</sup> for signaling functions. Among the NSCC, the group of CNGC channels was described in the most detail. Expression of a truncated version of AtCNGC1 without a calmodulin-binding domain (CaM binding domain) has been shown to increase intracellular K<sup>+</sup> concentrations in *trk1/trk2* yeast mutants with lost K<sup>+</sup> uptake systems (Ali et al., 2006). Analysis of plant mutants that lost the function of some members of the CNGC channels showed the ability of three members of this family to transport K<sup>+</sup>, namely AtCNGC1, AtCNGC3, and AtCNGC10. In particular, the *Arabidopsis Atcngcl*



**Fig. 4.** Topology of the nonselective cation channels NCCC family, namely glutamate-like receptors (GLR) and channels dependent on cyclic nucleotides (CNGC). PM, plasma membrane; P, pore domain; NT, the binding site for calmodulin at the amino terminus; CT, calmodulin binding site at the carboxyl end; IQ, isoleucin-glatamine domain with binding function to calmodulin; CNBD, cyclic nucleotide binding site; ATD, amino-terminal domain; LBD, ligand binding domain, 1–4 or 1–6, transmembrane domains.

mutant line that has lost *AtCNGC1* function has been shown to accumulate less  $\text{Ca}^{2+}$  in shoots and show less sensitivity to toxic  $\text{Na}^+$  concentrations (Hampton et al., 2004; Maathuis et al., 2006; Yuen et al., 2010). Plants of the mutant *Arabidopsis Atcngc3* line that have lost *AtCNGC3* function were less sensitive to high concentrations of  $\text{K}^+$ , which inhibit plant growth, and accumulated this element in their tissues in smaller quantities than the wild type (Gobert et al., 2006). Thus, NSCCs can play an important role in  $\text{K}^+$  transport, maintenance of ionic homeostasis and plant resistance to stress of various natures. Further disclosure of the transport properties and biological functions of this family of channels will provide a better understanding of the regulation of transport of the main cations of the plant, namely  $\text{Na}^+$ ,  $\text{K}^+$  and  $\text{Ca}^{2+}$ .

**Active  $\text{K}^+$  transport systems.** Active transport systems are divided into uniporters, symporters, and antiporters (Nieves-Cordones et al., 2010). The peculiarity of antiporters and symporters is the dependence of the activity of these transport proteins entirely on the

driving force of protons or cations, in particular,  $\text{Na}^+$  or  $\text{K}^+$  (Grabov, 2007). Due to these features, transporters are able to transport  $\text{K}^+$  against the concentration gradient (Cheng et al., 2018). In contrast to ion channels, whose transport properties are due to the presence of an electrochemical gradient (Busch, 2002), transporters are high-affinity systems and are able to provide  $\text{K}^+$  transport under conditions of the low external concentration of this element ( $<0.2$  mM) (Cheng et al., 2018).

#### **Potassium transporters of the KUP/HAK/KT family.**

The KUP/HAK/KT transporter family (K uptake permease, KUP; high affinity  $\text{K}^+$  transporter,  $\text{K}^+$  transporter) is the most numerous family of potassium transporters in plants. Representatives of this family have been found in many plant species (Cheng et al., 2018; Wang et al., 2018). The KUP/HAK/KT family transporters are involved in  $\text{K}^+$  uptake, cell stretching, root hair growth, auxin distribution, and the formation of a protective response to osmotic stress (Fig. 1) (Busch, 2002). KUP/HAK/KT transporters consist of 10–14 transmembrane domains (Fig. 5) (Wang et al.,

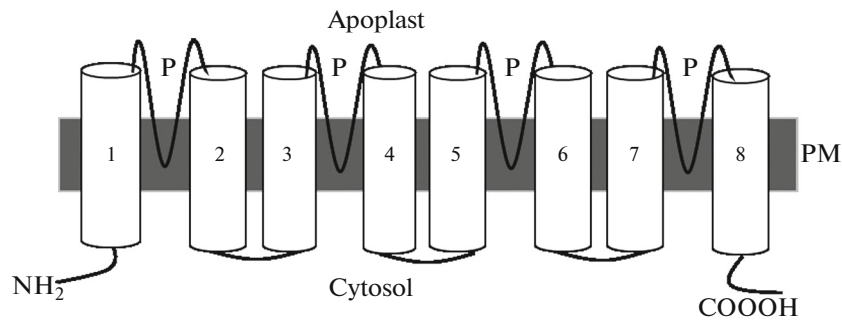


Fig. 5. Topology of HKT family transporters. PM, plasma membrane; P, pore loops; 1–8, transmembrane domains.

2018). KUP/HAK/KT family members are divided into four groups (I, II, III, IV) (Table 1, <http://cytgen.com/articles/5510075s.pdf>). Representatives of group I, for example, *HvHAK1* from barley, are responsible for the high-affinity uptake of  $K^+$  ions in the root. Members of group II, such as *AtHAK2*, *AtKUP4*, *AtHAK4*, and *OsHAK5*, participate in various processes of plant growth and development. Representatives of group III (*AtHAK2*, *AtKUP/KT5*, *AtHAK6*, *AtHAK7*, etc.) are responsible for maintaining  $K^+/Na^+$  homeostasis. Information on the biological functions of representatives of group IV is still very limited, but it is believed that they are responsible for the transport of  $Na^+$  in the plant (Ou et al., 2018; Li et al., 2018; Zhang et al., 2020).

In general, members of this family play an important role in various physiological processes of plants, namely the absorption and transport of  $K^+$  ions, regulation of growth and development, salt resistance, and regulation of osmotic potential (Li et al., 2018). In *Arabidopsis thaliana*, 13 members of the KT/HAK/KUP family were identified (Cheng et al., 2018). It is known that *AtHAK5* and *AtAKT1* are responsible for the uptake of potassium ions in *Arabidopsis* (Cheng et al., 2018; Li et al., 2018; Han et al., 2016). It was also found that *AtKUP7* is also involved in the absorption of  $K^+$  and may partially contribute to the saturation of the xylem with this element (Han et al., 2016). In rice, the homologues of *AtHAK1* and *AtAKT5* are *OsAKT1* and *OsHAK1*, respectively, which perform similar functions (Cheng et al., 2018). For example, *OsHAK1* provides salt resistance by regulating potassium uptake and maintaining an optimal  $K^+/Na^+$  ratio (Ou et al., 2018). Moreover, under drought conditions, plants with *OsHAK1* overexpression had a yield 35% higher than wild-type plants (Chen et al., 2017). The *OsHAK5* transporter gene also partially promotes high-affinity potassium uptake but at higher  $K^+$  concentrations than *OsHAK1*. High levels of *OsHAK5* expression have been observed in the parenchyma of xylem and phloem of root vascular tissues, especially under potassium deficiency conditions, suggesting that *OsHAK5* may be involved in the distribution of

potassium between root and shoot tissues (Yang et al., 2014). Another family member *OsHAK21* found in rice demonstrated potassium transporter activity but was not involved in the direct uptake of  $K^+$  ions. However, *OsHAK21* has been shown to be involved in the formation of the response to abiotic stress (Cheng et al., 2018; Ou et al., 2018).

Thus, according to the analyzed data, potassium transporters of the KUP/HAK/KT family play an important role in the uptake, transport, and tissue distribution of  $K^+$ ; they are responsible for the homeostasis of this element in the plant and formation of the adaptive responses.

**Transporters of the Trk/HKT family.** Transporters of the Trk/HKT family (High affinity  $K^+$  transporters, HKT) are representatives of  $K^+/Na^+$  transporters (Nawaz et al., 2019). This family provides transport of  $Na^+$  and  $K^+$  ions (Fig. 1). For example, *AtHKT1;1*, *TmHKT1;5* and *TmHKT1;4* mediate the uptake of  $Na^+$  by parenchymal cells from xylem juice, and the saturation of the phloem with  $Na^+$  (Su et al., 2015). *OsHKT1;5* is localized in parenchymal cells surrounding xylem vessels and is responsible for removing  $Na^+$  from xylem (Ren et al., 2005). A member of this family (*TaHKT2;1*, previously named *HKT1*) was first identified and isolated from the roots of wheat (*Triticum aestivum*) (Schachtman et al., 1994). Subsequently, members of the Trk/HKT family have been found in many other plant species (Su et al., 2015; Zhang et al., 2019).

Phylogenetic analysis revealed differences in the key amino acid of the first pore loop of the HKT family protein (Fig. 4), which led to the division of this group of proteins into two subfamilies (Table 2, <http://cytgen.com/articles/5510075s.pdf>) (Huang et al., 2008). Representatives of the subfamily 1 (HKT1) contain serine in the first pore loop, which enhances the specificity for the transport of  $Na^+$  ions. The subfamily 2 (HKT2) contains glycine, which is a co- or uni-transporter of  $K^+$  and  $Na^+$  ions (Fig. 5) (Zhang et al., 2019; Rodriguez-Navarro et al., 2006). It is known that monocotyledonous plants have more representa-

tives of HKT than dicotyledons. Also, HKT1 transporters are present in both monocotyledonous and dicotyledonous plants, and HKT2 is present exclusively in monocotyledons (Su et al., 2015). Interestingly, some researchers have identified subfamily III of the Trk/HKT family, into which they include transporters found in primitive higher plants *Selaginella moellendorffii* and *Physcomitrella patens* (Su et al., 2015). Currently, only eight representatives of subfamily III have been identified, and it is assumed that they perform the functions of  $K^+$ - $Na^+$ -transporters, but the limited information about them is available (Table 2) (Su et al., 2015).

Representatives of the subfamily HKT1 are  $Na^+$  transporters responsible for  $Na^+$  homeostasis and salt resistance in many plant species (Table 2) (Horie et al., 2009; Hauser et al., 2010; Mishra et al., 2016). They are mainly responsible for the removal of  $Na^+$  from xylem juice, which prevents the entry of this toxic ion into tissues with active photosynthesis (Almeida et al., 2013). Similar functions were demonstrated for AtHKT1;4 from *Arabidopsis*, OsHKT1;5 from rice, and TmHKT1;4 and TmHKT1;5 from wheat (Zhang et al., 2017). Interestingly, the EshKT1;2 transporter from the halophyte *Eutrema salsuginea* exhibited selectivity for  $K^+$ . EshKT1;2 has been shown to maintain  $K^+$  levels at the root under salinity conditions (Nawaz et al., 2019; Su et al., 2015). There are experimental data indicating the possibility of changing the selectivity for  $Na^+$  for HKT1 in halophytes (Isayenkov, 2012).

HKT2 transporters are  $K^+$ - $Na^+$  cotransporters (Table 2). HKT2 is able to absorb  $Na^+$  from the environment, especially under conditions of  $K^+$  deficiency (Mishra et al., 2016; Almeida et al., 2013; Horie et al., 2011). OsHKT2;4 from rice shows the most significant selectivity to both  $K^+$  and  $Na^+$  among HKT proteins. It provides  $K^+$  intake in the cell through the plasma membrane, which distinguishes it from other representatives of HKT type II transporters (Horie et al., 2011). *OsHKT2;4* is expressed predominantly in root hair cells and vascular parenchymal cells (Mishra et al., 2016). Because *OsHKT2;1* and *OsHKT2;4* are expressed in the root hairs and cells of the outer coverings of the roots, it is believed that they provide sodium transport from the soil to the roots (Mishra et al., 2016). The expression of *HvHKT2;1* from barley predominantly occurs in the root cortex, and its expression level increases in response to low  $K^+$  and high  $Na^+$  concentrations in the environment (Mian et al., 2011). Unlike *TaHKT2;1* from wheat, *HvHKT2;1* can support  $K^+$  transport even in the absence of  $Na^+$ , although the level of  $K^+$  absorption decreases under such conditions. For the proper functioning and transport of  $K^+$  by *TaHKT2;1*, the presence of  $Na^+$  is required (Almeida et al., 2013; Laurie et al., 2002). Transgenic barley plants with *HvHKT2;1* overexpression showed an increased concentration of  $Na^+$  in xylem sap, an

increased level of  $Na^+$  translocation to shoots, and an increase in the content of this element in the leaves. Overexpression of *HvHKT2;1* contributed to increased salt resistance due to enhanced plant ability to accumulate  $Na^+$  and minimize the negative effects of osmotic shock (Mian et al., 2011). It is assumed that *HvHKT2;1* provides  $K^+$  uptake by roots at its very low external concentrations (Almeida et al., 2013; Mian et al., 2011). *TaHKT2;1* from wheat and *OsHKT2;2* from rice are mainly  $Na^+$  transporters activated at low concentrations of  $Na^+$  ( $-0.1$  mM) and in the absence of  $K^+$  ions. Knockout of the *TaHKT2;1* gene revealed a decrease in the level of  $Na^+$  uptake by roots under high salinity conditions (Cao et al., 2018). OsHKT2;1-mediated  $Na^+$  uptake was able to promote plant growth under  $K^+$  deficiency (Horie et al., 2011). ZmHKT2 from maize is predominantly a potassium transporter with  $Na^+$  transport activity under conditions when the sodium concentration ( $-10$  mM) significantly exceeds the  $K^+$  concentration (Cao et al., 2018).

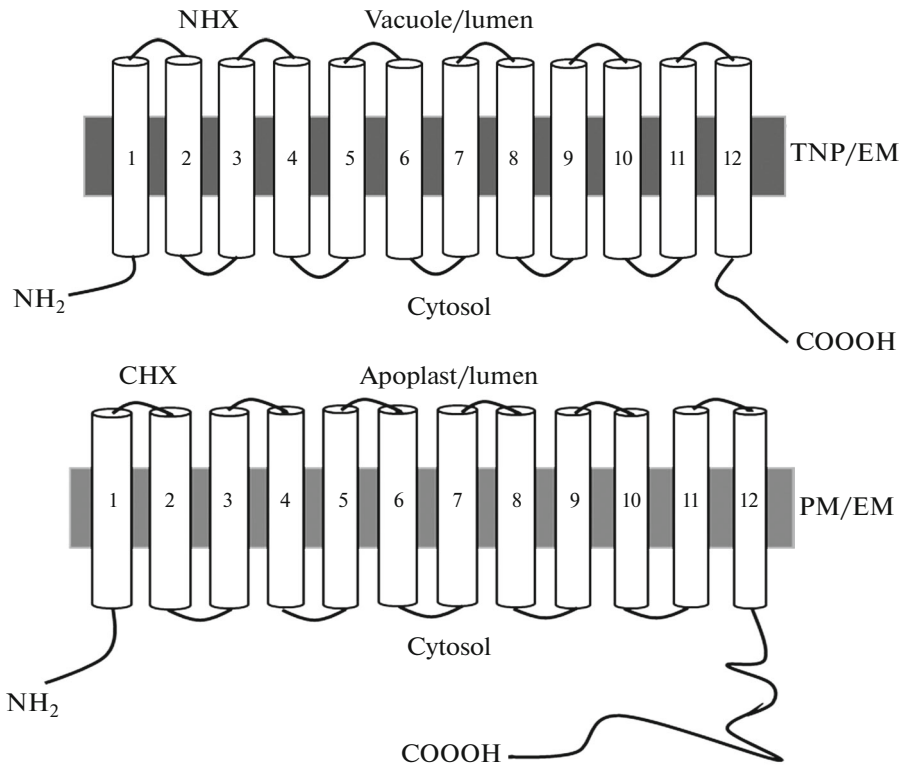
Thus, the operation of HKT transporters is extremely important during growth under conditions of potassium deficiency and osmotic compensation by sodium under osmotic stress and salinity.

**Group of CPA transporters.** The cation/proton antiporter (CPA) superfamily combines groups of proteins responsible for cation exchange in all living organisms. The main functions of these transport proteins are to control the level of pH and cationic homeostasis. The presence of a conservative  $Na^+/H^+$  exchange domain is a characteristic feature of the CPA superfamily (Jia et al., 2017). These proteins are localized in the vacuoles and membranes of organelles (Sharma et al., 2020). According to the Saier classification (Saier, 2000), this superfamily is divided into two functional groups: CPA1, which includes NHE-transporters or NHX- $Na^+/H^+$  exchangers and NhaP or SOS, and CPA2, which includes the KEA antiporter families and CHX exchangers (Sharma et al., 2020).

**NHX/NHE transporters.** Transporters of the NHX/NHE family ( $Na^+/H^+$  exchanger) (Fig. 6) mediate the exchange of cations for protons due to electrochemical gradients (Ayadi et al., 2019). NHX transporters are localized on the inner membranes of cells and are able to regulate cell pH, plant growth and development, and maintain potassium homeostasis and processes of tolerance to osmotic stress (Fig. 1) (Dong et al., 2018). Plant NHXs are widespread membrane  $Na^+/H^+$  antiporters that are responsible for the exchange of  $Na^+$  or  $K^+$  ions for  $H^+$  across the vacuolar or endosomal membrane maintaining ion homeostasis (Fig. 6) (Bassil et al., 2012). In general, among the known representatives of NHX, vacuolar and endosomal (Fig. 1) are distinguished (Bassil et al., 2019).

AtNHX1, the first plant representative which was identified in the *Arabidopsis* tonoplast, has been shown



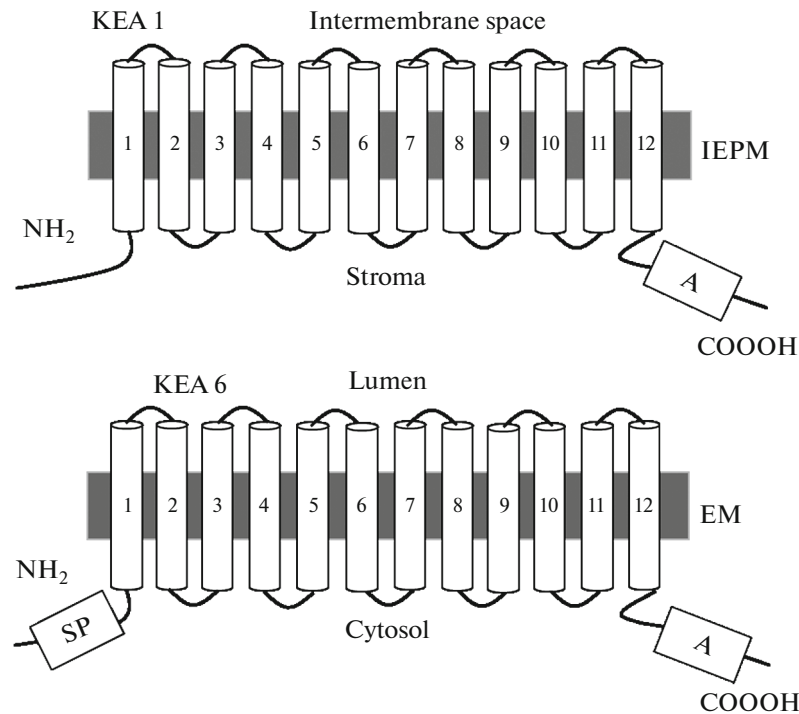


**Fig. 6.** Topology of NHX and CHX transporters. TNP, tonoplast; PM, plasma membrane; EM, endosome membranes; 1–12, transmembrane domains.

to exhibit Na<sup>+</sup>/H<sup>+</sup> metabolic activity in plant vacuoles (Apse et al., 1999). It was noted that the overexpression of *AtNHX1* increased the level of tissue Na<sup>+</sup> in transgenic tomatoes and *Arabidopsis* (Apse et al., 1999). However, further studies suggest that *AtNHX1* mediates the exchange of both Na<sup>+</sup> and K<sup>+</sup> for H<sup>+</sup> in the tonoplast of transgenic tomatoes. The knockout of the *AtNHX1* gene from *Arabidopsis* led to the disruption of Na<sup>+</sup>/H<sup>+</sup> and K<sup>+</sup>/H<sup>+</sup> metabolism in leaf vacuoles, changes in leaf development, and activation of high-affinity K<sup>+</sup> transporters (Jegadeeson et al., 2019). In total, six members of the NHE/NHX family were found in *Arabidopsis*, four of which are localized on the vacuolar membrane (*AtNHX1–4*) and two in endosomes (*AtNHX5* and *AtNHX6*) (Dragwidge et al., 2019). In *Arabidopsis*, the most common were *AtNHX1* and *AtNHX2*, which have been found in roots, shoots, and seeds. Interestingly, *AtNHX1* and *AtNHX2* are activated in response to salt stress and hyperosmotic shock in the seed, and activation of *AtNHX5* occurs exclusively in response to salt stress (Rodriguez-Rosales et al., 2009). Members of the NHX family are also able to transport K<sup>+</sup>. The overexpression of *AtNHX1* or *AtNHX2* led to increased content of intracellular K<sup>+</sup> and Na<sup>+</sup> in the presence of NaCl (Yokoi, 2002). Recent studies suggest that *AtNHX1* and *AtNHX2* are most likely responsible for maintaining

K<sup>+</sup> homeostasis and pH level in vacuoles. An interesting fact is that *AtNHX3* maintains ionic homeostasis by removing K<sup>+</sup> from the plant (Ayadi et al., 2019). *AtNHX4* is also involved in the response to salt stress and maintains Na<sup>+</sup> homeostasis in the cell (Ayadi et al., 2019). However, the constitutive expression of *AtNHX5* and *LeNHX2* increases the content of intracellular K<sup>+</sup> but reduces the content of Na<sup>+</sup> (Yokoi 2002; Huerta et al., 2013). *AtNHX5* and *AtNHX6* are localized in the trans-Golgi network and play an important role in ion transport in it, but the mechanisms of such transport remain unexplored. It is assumed that the activity of *AtNHX5* and *AtNHX6* is aimed at maintaining the normal functioning of the Golgi apparatus (Dragwidge et al., 2017). In addition, it has been shown that the salt resistance of mulberry (*Morus notabilis*) is due to the operation of endosomal MnNHX6 [93].

The wheat genome encodes three known representatives of NHX (*TaNHX1*, *TaNHX2*, and *TaNHX3*). It was shown that the expression of *TaNHX1* and *TaNHX3* in transgenic tobacco plants increased salt resistance and *TaNHX2* contributed to the translocation of Na<sup>+</sup> from the cytosol to the vacuole and the formation of resistance to salinity (Mushke et al., 2019). Four vacuolar proteins (*OsNHX1–4*) and one endosomal (*OsNHX5*) protein were identified in the rice. It was



**Fig. 7.** Topology of KEA family transporters. IEPM, inner envelope of plastid membrane; EM, endosome membranes; 1–12, transmembrane domains; A, TrkA-N domain on the carboxyl ring (nucleotide-binding and K transport regulating domain); SP, signal peptide at the amino terminus.

demonstrated that all these transporters are involved in the formation of salt resistance (Isayenkov, 2012; Ayadi et al., 2019; Tester et al., 2003). Although the operation of NHX transporters has been associated with the vacuolar or endosomal utilization of  $\text{Na}^+$ , recent experimental data suggest an important role for these transport proteins in the transport and storage of  $\text{K}^+$  in vacuoles or endosomes (Yamaguchi et al., 2013).

**KEA antiporters.** Antiporters of the KEA family are phylogenetically derived from  $\text{K}^+$  *EcKefB* and *EcKefC* efflux transporters in *E. coli* (Zhu et al., 2018; Chanroj et al., 2012). Representatives of this family are  $\text{K}^+/\text{H}^+$  antiporters (Aranda-Sicilia et al., 2016). According to phylogenetic analysis, the KEA family is divided into two subgroups: KEA1–3 (similar to each other by 21.9–30.0%) and KEA4–6 (similar to 75.0–83.4%) (Fig. 7, Table 3, <http://cytgen.com/articles/5510075s.pdf>) (Zhu et al., 2018). KEA gene expression is activated in response to various environmental stressors. For example, the expression of *KEA1*, *KEA3*, and *KEA4* increases in response to stress at low concentrations of  $\text{K}^+$  in *Arabidopsis*. However, in *in vitro* studies, the activity of *KEA2* and *KEA5* was increased in the presence of sorbitol (osmotic stress) or abscisic acid. Thus, it was assumed that intracellular KEA 2–5 transporters play an important role in  $\text{K}^+$  homeostasis and osmotic regulation of plants (Zhu et al., 2018; Zheng et al., 2013).

KEA1–3 transporters have a chloroplast specialization (Fig. 1). KEA1 and KEA2 have been shown to be localized in the microdomains of the inner membrane near both poles of the chloroplast on the division site; they promote plastid division and thylakoid membrane biogenesis (Aranda-Sicilia et al., 2016). However, KEA3 (Fig. 1) is localized on the thylakoid membrane and minimizes pH-dependent energy loss under constant light conditions, which is necessary for photosynthetic activity and  $\text{CO}_2$  uptake (Zhu et al., 2018; Wang et al., 2017). KEA1–3 also play an important role in the development of chloroplasts, their integrity, and photosynthesis due to the mechanisms of control of  $\text{K}^+$  homeostasis and pH level (Dana et al., 2016).

KEA1–3 transporters have a characteristic TrkA-N (KTN) ( $\text{K}^+$  transport, nucleotide binding  $\text{K}^+$  transport) domain at the C-terminus. The minimum functional unit TrkA-N (Fig. 7) is a dimeric molecule connected by a flexible hinge section. The movement of these hinges is combined with transmembrane loops to control the flow of  $\text{K}^+$ , which provides a mechanism for opening the pore of the channel. Unlike KEA1–3, the TrkA-N domain is absent in KEA 4–6 (Fig. 7). It is assumed that the latter group phylogenetically originated from the descendants of cyanobacteria (Chanroj et al., 2012). Analysis of the transcription profiles of genes encoding KEA transporters revealed

that the highest level of expression for *KEA1* was observed in the rosette leaves, while that for *KEA2* and *KEA3* was in the middle leaves of the plant. It has been shown that the highest level of *KEA2* expression was observed in aging leaves. However, *KEA3* gene expression was observed in leaf tissues of any age (Dana et al., 2016).

AtKEA transporters 4–6 were detected in the Golgi apparatus, in the trans-Golgi network, in the prevacuolar compartments, and the multivesicular bodies. It was shown that AtKEA 4–6 are sensitive to low levels of  $K^+$  and high levels of  $Na^+$  and  $Li^+$  (Zhu et al., 2018). Interestingly, AtKEA 4–6 transport and accumulate more  $Na^+$  and fewer  $K^+$  in endosomes under salt stress (Zhu et al., 2018). Thus, this group of AtKEA 4–6 transporters may play an important role in the mechanisms of tissue salt resistance and endomembrane utilization of cytotoxic  $Na^+$ . The expression of *KEA4* and *KEA5* was detected in the surrounding vessels of primary and secondary root cells, and the expression of *KEA6* was observed in all types of root cells (Zhu et al., 2018). It was assumed that representatives of *KEA5* from soybeans can be localized on the plasma membrane and are responsible for potassium transport (Fig. 1) (Isayenkov, 2020).

There is very little direct evidence of the transport activity of KEA family transporters (Dana et al. 2016). *KEA1-6* is more selective for potassium than for sodium, which may indicate that these transporters are involved in the formation of the transmembrane potential of mitochondria (Tsujii et al., 2019). The analysis of the functional properties of *KEA1-6* did not reveal antiporter activity and confirmed their classification as being  $K^+$  transport systems (Tsujii et al., 2019). It is known that *KEA4-6* transporters are involved in the formation of resistance to salinity and respond to violations of potassium homeostasis; the translocation of  $K^+$  ions mediated by *KEA4-6* may indicate the ability of the latter to protect organelles from osmotic shock (Zhu et al., 2018; Tsujii et al., 2019). It was assumed that *AtKEA* transporters are able to maintain potassium homeostasis due to the outflow of  $K^+$  from the organelles in which they are localized (Zheng et al., 2013). Thus, KEA proteins play an important role in the formation and functioning of chloroplasts, the maintenance of  $K^+$  and  $H^+$  homeostasis in chloroplasts, and the formation of resistance to excessive salinity (Dana et al. 2016).

**CHX transporters.** One of the most numerous transport families responsible for the transport of  $K^+$  in plants is CHX (Cation  $H^+$  exchangers). CHX antiporters are similar to bacterial cation/ $H^+$  exchangers and they participate in the absorption of  $K^+$ , transport of  $Na^+$ ,  $K^+$ , and  $H^+$  through endomembranes (Mottaleb et al., 2013) (Fig. 6). These functional characteristics of CHX are similar to the KEA, NHX, and HAK functions. Plants with a large number of CHX genes

have been shown to have fewer HAK genes, for example, 28 and 13 representatives were found in *Arabidopsis*, respectively, or vice versa, 17 CHX and 27 HAK genes were revealed in rice (Chanroj et al., 2012). Most CHX transporters are localized in Golgi membranes, the prevacuolar endomembrane, or the endoplasmic reticulum (Fig. 1) (Nieves-Cordones et al., 2016). PpCHX1 from moss *Physcomitrella patens* is localized in the Golgi apparatus (Mottaleb et al., 2013). It has been shown that the function of PpCHX1 can be replaced by another transporter and it does not change the growth and development of the plant (Mottaleb et al., 2013). For example, PpHAK3, which is also located in the Golgi apparatus and is responsible for  $K^+/H^+$  antiport, can function instead of PpCHX. Although most CPX transporters have endomembrane localization, some representatives, namely AtCHX13, AtCHX21, and PpCHX2, are localized in the plasma membrane (Chanroj et al., 2012; Mottaleb et al., 2013). Recent studies have found that CHX13 promotes the entry of  $K^+$  across the plasma membrane of root cells, and CHX14 mediates the removal and redistribution of  $K^+$  in root vessels (Zhao et al., 2015). Although CHX13 and CHX14 have different functions, the genes of both transporters are actively expressed during pollen development but do not affect pollen maturation. Also, *CHX13* is expressed in the roots of shoots, and CHX14 is localized in the root and leaf vascular tissues and in the root-shoot junctions (Zhao et al., 2015).

The *Arabidopsis thaliana* genome encodes 28 different members of the CHX family that are similar in size. The N-terminals of 28 representatives of AtCHX from *Arabidopsis* and 16 representatives of OsCHX from rice have ten to 12 transmembrane sites (approximately 430 amino acid residues) and a hydrophobic C-terminus (not more than 360 residues) (Sze et al., 2004). Recent phylogenetic studies of CHX transporters indicate the existence of seven different classes; representatives of CHX transporters from *Arabidopsis* belong to five different groups (Isayenkov, 2020; Jia et al., 2017; Jia et al., 2018). Group IV is the largest and has eight representatives: AtCHX15–21 and AtCHX23, among which AtCHX16–20 belong to endomembrane transporters (Jia et al., 2017; Chanroj et al., 2011). AtCHX 16–19 separate and overlap each other functions in the processes of seed reproduction and development. *AtCHX17* is expressed predominantly in roots under stress conditions (such as salinity, low soil pH, low soil  $K^+$  concentrations) and is involved in the maintenance of  $K^+$  homeostasis and regulation of pH under salt stress (Chanroj et al., 2011). AtCHX20 is involved in the processes of osmoregulation and movement of respiratory cells by controlling the movement of  $K^+$  ions and pH (Nieves-Cordones et al., 2016). AtCHX21 is probably responsible for regulating the  $Na^+$  balance in the xylem and its accumulation in the leaves. AtCHX23 regulates the pH of the cytosol (Sze

et al., 2004; Chanroj et al., 2011). *AtCHX21* and *AtCHX23* are also expressed in pollen, where they are presumably involved in the reception or transmission of female signals, targeting the pollen tube at the ovule (Nieves-Cordones et al., 2016). In soybean (*Glycine max*) plants, 34 CHX transporter genes characterized by the presence of the N-terminal  $\text{Na}^+/\text{H}^+$  exchange domain were identified. *GsCHX19.3* is responsible for the uptake of  $\text{K}^+$  and the formation of an adaptive response to salt and alkaline stress in plants (Jia et al., 2017). In vitro studies revealed high levels of expression of *AtCHX16-19* (group IV) in leaves, flowers, and roots and *GsCHX19.3* in leaves and flowers, which may indicate their role in the development of reproductive organs (Jia et al., 2017; 2018). It was also shown that incubation of plants at high salt concentrations increased *GsCHX19.3* expression, and the expression of this gene in transgenic *Arabidopsis* plants significantly increased their salt resistance (Jia et al., 2017). There is an assumption that the process of decrease of  $\text{Na}^+$  in transgenic *Arabidopsis* is a consequence of the *GsCHX19.3* activity and occurs similarly with the operation of the SOS1 pump (Jia et al., 2018; Gierth et al., 2007; Zhou et al., 2015).

Many CHX proteins exist as pairs of close homologues, such as *AtCHX13* and *AtCHX14*, *AtCHX21* and *AtCHX23*, which may indicate recent gene duplication processes. *AtCHX21* and *AtCHX13* are located on the second chromosome and their closest homologues are *AtCHX23* and *AtCHX14*, respectively, which are in turn located on the first chromosome. The situation is similar for the *AtCHX8* and *AtCHX7* genes, which are located next to each other on the second chromosome, and their closest homologues, *AtCHX6a* and *AtCHX5*, are also located next to each other on the first chromosome (Evans et al., 2011). Although the CHX family is considered one of the most numerous among cationic transporters, the functions of most of its members remain unknown and require further detailed study and characterization.

## CONCLUSIONS

Potassium transport systems are important elements of plant life, namely protective reactions, enzymatic processes, and regulation of physiological processes. Also, recent studies suggest that  $\text{K}^+$  can be an important signaling molecule in the response of plants to various types of stress in addition to these functions (Wu et al., 2018). Thus, in addition to the “classical” physiological functions, potassium transport systems are an important part of the signaling processes of the plant and the formation of adaptive responses to the various abiotic stresses. Adequate and coordinated operation of membrane transporters and channels responsible for membrane transport of this element is a key condition for maintaining ionic homeostasis, development of programmed cell death, mechanisms

of resistance and adaptation to stressors, reproduction, growth, and development of plants.

Advances in the study of major transport  $\text{K}^+$  proteins have clarified the main ways of intake, distribution, and utilization of this element. In addition, the main mechanisms of regulation of metabolism for this element and other related minerals were clarified. Maintenance of potassium homeostasis in plants occurs through the operation of potassium channels, namely TRK, SKOR, ACT, NSCC, and active transport systems CPA, HKT and KUP/HAK/KT. In particular, it was shown that plants with a high content of  $\text{K}^+$  are much better able to overcome salt stress and water deficiency. In addition to the well-known fact that the involvement of channels of the SKOR and ACT families improve  $\text{K}^+$  homeostasis and salt drought resistance, it would be worth paying attention to the functional characteristics of the channels of the TRK family. Recent data indicate the active participation of representatives of these channels in the mechanisms of drought and salinity resistance (Isayenkov, 2012). However, the detailed mechanism of participation of these channels in the regulation of these stresses remains unknown. The process of land colonization by plants, the acquisition of central vacuoles by cells, and a powerful evolutionary impulse for the development of flowering plants has led to a significant increase and structural complication of the transporters of the CPA superfamily. In particular, the vacuolar specialization NHX1-4 was recently acquired during evolutionary development. The significant increase in the number of members of the CHX subfamily is closely related to the development of flowering plants and the maintenance of flower functioning and pollen development (Jia et al., 2018). In our opinion, an important direction for further research of membrane systems of potassium transport is the intensification and deepening of research of active transport systems  $\text{K}^+$ , namely KEA and CHX transporters. Unfortunately, most of the functional characteristics and biological functions of these transporters remain unknown. Clarification of the peculiarities of transport of these transporters and the biological role of members of this subfamily will not only deepen our knowledge of the regulation and processes of flower and pollen formation, the activity of chloroplasts, and other cellular organelles but also will elucidate their role in adapting to abiotic stress and their further application in various areas of plant biotechnology, molecular selection, and implementation of modern agricultural techniques.

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## COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflict of interest. This article does not contain any studies involving animals or human participants performed by any of the authors.

## SUPPLEMENTARY MATERIALS

Supplementary materials are available for this article at <https://doi.org/10.3103/S0095452721010126> and are accessible for authorized users.

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