

Review

Potassium transport to increase abiotic stress tolerance

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Modulation of potassium transport to increase abiotic stress tolerance in plants

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Highlight

This review summarizes the latest knowledge regarding potassium homeostasis in plants and how it has been used to develop novel crops with improved abiotic stress tolerance.

Abstract

Potassium is the major cation responsible for the maintenance of the correct ionic environment in plant cells. Stable potassium homeostasis is indispensable for virtually all cellular functions, and, concomitantly, viability. Plants must cope with environmental changes such as salt or drought that can alter ionic homeostasis. Potassium fluxes are required to regulate the essential process of transpiration, so a constraint on potassium transport may also affect the plant's response to heat, cold, or oxidative stress. Sequencing data and functional analyses have defined the potassium channels and transporters present in the genomes of different species, so we know most of the proteins directly participating in potassium homeostasis. The still unanswered questions are how these proteins are

regulated and the potential cross-talk with other signaling pathways controlling growth, development, and stress responses. As we gain knowledge regarding the molecular mechanisms underlying regulation of potassium homeostasis in plants, we can take advantage of this information to increase the efficiency of potassium transport and generate plants with enhanced tolerance to abiotic stress through genetic engineering or new breeding techniques. Here, we review the published information on how modifying genes related to potassium homeostasis in plants affects abiotic stress tolerance at the whole plant level.

Keywords: Crop plants, drought tolerance, ion homeostasis, potassium channels, salt tolerance, stomatal opening.

Introduction

Potassium is the main monovalent cation in plant nutrition. It is a macronutrient that can represent about 2–5% of the plant dry weight ([Marschner, 1995](#)). In most plant cells, potassium accumulates against its concentration gradient in relatively high amounts, while other cations, such as sodium, must be excluded to avoid toxicity. It is not clear from an evolutive point of view why potassium has this pivotal role in biology. The paradox is that potassium is much less abundant than sodium in the sea, where life likely originated. In favor of a positive selection for potassium is the fact that its hydration shell has considerable structural flexibility and may lead to a reduced disruption of water molecules close to proteins ([Carrillo-Tripp *et al.*, 2003](#); [Mancinelli *et al.*, 2007](#)). Potassium gradients could have been used to energize membranes in ancient organisms, but during evolution, this may have diverged to use mainly protons (plants, fungi) or sodium (animals) ([Benito *et al.*, 2014](#)). In addition, potassium is required for proper functioning of the translational machinery, as well as for ameliorating the toxicity of methylglyoxal. This chemical is a toxic molecule produced by many ancestral metabolic

pathways such as the glycolysis. Many potassium efflux systems are activated by a rise in methylglyoxal concentration, which induces potassium efflux and a concomitant proton uptake. This decrease in cytoplasmic pH decreases methylglyoxal toxicity, and could be the most ancient role of potassium as a signaling molecule that is present even in bacteria ([Ferguson *et al.*, 1993](#)). This could also explain the current role of methylglyoxal as a signaling molecule for abiotic stress in plants ([Hoque *et al.*, 2016](#)). The alternative scenario, the accident hypothesis, would contend that potassium prevalence is the consequence of life emerging in some potassium-rich continental aqueous environment and its current role in biology is a result of the earth's geological history and has been maintained throughout the evolution of land plants. None of these possibilities can be discarded ([Danchin and Nikel, 2019](#)).

Potassium has many roles in plant physiology. Within plants, this cation is present as an unbound, highly mobile osmolyte required to maintain turgor pressure, cell volume, and membrane potential and to equilibrate the intracellular pH. Potassium is also essential for the chemical potential required for many enzymes to be functional and, among other enzymatic processes, for correct protein synthesis and folding. These parameters may be disturbed by the presence of sodium in the medium, so keeping a high cytosolic K^+/Na^+ ratio is essential to prevent the deleterious effects of salt stress ([Serrano *et al.*, 1999](#)). In nature, plants must deal with sodium-rich environments. The assimilation of potassium by the plant is affected by its availability in soils and by the presence of sodium. The response of plants to salt stress is complex, and energetically expensive, diverting metabolic energy from growth, with a concomitant decrease in yield. Therefore, fine-tuning potassium nutrition seems vital for the ability of plants to cope with salinity stress ([Bromham *et al.*, 2020](#)).

In plants, in addition to the basic functions at the cellular level described above, potassium has a fundamental role in plant physiology as it is involved in important processes such as stomatal movement, which controls water loss by transpiration and desiccation ([Anschütz *et al.*, 2014](#); [Véry *et al.*, 2014](#)). This process is fundamental for tolerance to drought stress since changes in the dynamics of stomatal aperture and closure can affect water use efficiency (WUE) ([Bertolino *et al.*, 2019](#)), which is defined as the amount of dry matter produced per unit of transpired water. WUE is a key character in determining crop yield and efficiency ([Lawson and Blatt, 2014](#)), and it is a major limiting factor under abiotic stress. In this sense, it is important to define the response of plants to the components of different kinds of abiotic stress and to identify the mechanisms of regulation of potassium channels at different levels under these stress conditions, as these may be important parameters influencing crop production. Therefore, generation of this knowledge will be useful in developing crop varieties more tolerant to abiotic stress ([Wu *et al.*, 2018](#)) and also for environmental applications, such as to increase forest mass in response to climate change ([Talbi *et al.*, 2015](#)). In this review, we will discuss the advances made in recent years regarding targets to improve potassium transport to increase plant resistance and/or tolerance to abiotic stress, including addition of potassium-rich biostimulants and genetic modification of potassium transport proteins ([Fig. 1](#)).

Modulating root potassium uptake to prevent abiotic stress

Potassium enters the plant via the root. Below, we will discuss the agronomical strategies based on increasing potassium concentration in the soil, supplementing with potassium-rich extracts, and the use of natural extracts to stimulate potassium uptake. Based on these practices, it is clear that increasing potassium uptake at the root level may counteract sodium toxicity or take advantage of the effect of potassium to retain

water to cope with drought stress. Molecular and genetic strategies to increase root potassium uptake are based on increasing, through genetic engineering, the efficiency of potassium transporters via their direct modification or modification of their regulators ([Kumari et al., 2021](#)). [Table 1](#) summarizes the results of this type of approach carried out in recent years by numerous investigators using transporters from different species.

Studies of plant genome sequences reveal three families of genes encoding plasma membrane potassium transporters: the HKT family ([Corratgé-Faillie et al., 2010](#)), the HAK/KUP/KT potassium transporter family ([Gierth and Misser, 2007](#)), and the channel family initially called Shaker but, renamed as voltage-gated (VG) based on structural and phylogenetic studies ([Véry et al., 2003](#); [Jegla et al., 2018](#)). The better characterized channels are the ones present in the Arabidopsis genome. The main players contributing to potassium nutrition, through assimilation from the soil, are HAK5, AKT1, and non-selective CYCLIC NUCLEOTIDE-GATED CHANNELs (CNGCs) acting in different ranges of substrate availability, from low to high, respectively ([Ragel et al., 2019](#)). Among the potassium uptake channels, only AKT1 and AtKC1 are highly expressed in root tissues ([Reintanz et al., 2002](#)). HAK5 has low levels of expression in roots under standard growth conditions, but is strongly induced upon potassium deprivation, with the function of maintaining potassium supply and potassium/sodium homeostasis (Li et al., 2018).

Studies in the model plant Arabidopsis have determined that AtHAK5 participates in high affinity (below 0.01 mM) potassium uptake ([Nieves-Cordones et al., 2010](#); [Pyo et al., 2010](#)), and also in the 0.01–0.05 mM range, together with AKT1 ([Rubio et al., 2010](#)). At higher concentrations, AtAKT1 participates together with CNGCs ([Caballero et al., 2012](#)). Therefore, HAK5 is mainly responsible for potassium uptake under limiting potassium conditions and this knowledge has agronomical implications. For instance, it

has been shown that HAK5 is a limiting factor for grafted cucumbers under salt stress ([Peng et al., 2023](#)).

A straightforward strategy would be to increase *HAK5* expression via direct overexpression or by the overexpression of a positive regulator. The use of transgenic *HAK5promoter::luciferase* plants has identified transcription factors responsible for the transcriptional regulation of *HAK5*, such as RAP2.11, DDF2, JLO, bHLH121, and IL_A ([Kim et al., 2012](#); [Hong et al., 2013](#)). The type III peroxidase RARE COLD INDUCIBLE GENE3 (RCI3) is also able to up-regulate *HAK5* expression ([Kim et al., 2010](#)). More recently, the R2R3-type MYB transcription factor MYB77 has been described as another *HAK5* transcriptional regulator and proposed as a target to increase plant tolerance to low potassium ([C. Z. Feng et al., 2021](#)). There are several reports of negative regulators of *HAK5* in the literature. Auxin response factor 2 (ARF2) is a negative regulator of *HAK5* expression. Under normal potassium conditions, ARF2 is bound to the *HAK5* promoter and inhibits the expression. Under starvation conditions, ARF2 is phosphorylated, and this phosphorylation compromises the ability of ARF2 to bind DNA, releasing it from the *HAK5* promoter and enabling expression of the transporter ([Zhao et al., 2016](#)).

AKT1 transport activity is important at higher potassium concentrations in soil. AKT1 mediates ammonium (NH₄⁺)-insensitive K⁺ transport ([Hirsch et al., 1998](#)). In the *akt1* mutant, the level of *HAK5* expression has been shown to be higher than the wild type, possibly due to reduced K⁺ uptake in the absence of AKT1 ([Spalding et al., 1999](#)). The activity of AKT1 is negatively regulated by CPK3 ([Huimin et al., 2021](#)) and by AtHELPS, a DexD/H box RNA helicase ([Xu et al., 2011](#)). Plants overexpressing *AKT1* have improved capability for proton efflux and are less sensitive to ABA inhibition. This mechanism may differ in roots and in guard cells ([Planes et al., 2015](#)). Positive regulation of AKT1 and HAK5 depends on the protein kinase CIPK23 ([Xu et al., 2006](#); [Ragel et al.,](#)

[2015](#)). In fact, CIPK23 has a central role in regulating root nutrient transporters, so its function is not specific to potassium homeostasis ([Ródenas and Vert, 2021](#)). Mutations in *CIPK23* result in deficient growth in low potassium, but drought tolerance ([Cheong et al., 2007](#)).

AKT1 has been used as a target to design transgenic plants with increased abiotic stress tolerance. Overexpression of *HvAKT1* increases drought stress and potassium uptake in barley, and also regulate reactive oxygen species and nitric oxide signaling (X. Feng et al., 2021). Another attempt was based on the use of AKT1 from the salt grass *Puccinellia tenuiflora*. Its overexpression increased salt tolerance in Arabidopsis ([Ardie et al., 2010](#)). It also enhanced growth under potassium starvation conditions and diminished the sodium/potassium ratio when co-expressed with the β -subunit of the rice orthologue (KOB1) ([Ardie et al., 2011](#)). In addition, rice AKT1 increases drought tolerance and osmotic stress when overexpressed ([Ahmad et al., 2016b](#)).

CNGCs are one of the largest channel families in plants ([Kühler et al., 1999](#); [Talke et al., 2003](#)). The functions of several members of this family have been related to stress responses ([Demidchik et al., 2002](#)). In Arabidopsis, CNGC1, CNGC2, CNGC4, and CNGC10 are bona fide inward-rectifying K^+ channels. In addition, CNGC2 shows higher selectivity for K^+ over Na^+ , while CNGC4 does not discriminate between K^+ and Na^+ ([Leng et al., 1999](#)). In the absence of AtAKT1 and AtHAK5, there is a hyperpolarization, which drives potassium uptake, mainly through AtCNGC3 and AtCNGC10. However, upon potassium deprivation no up-regulation of these channels is observed, suggesting that potassium transport may not be their main role in plant physiology ([Caballero et al., 2012](#)). Members of the CNGC family also contribute to heavy metal ion uptake in Arabidopsis ([Moon et al., 2019](#)).

Given their versatility, attempts have been made to use CNGCs to increase tolerance of crop plants to stress conditions. The problem is that in some cases a gain-of-function mutation of these channels has been shown to be deleterious for cell development. For instance, in *Arabidopsis*, the mutation of *AtCNGC10* confers salt tolerance, while overexpression confers sensitivity, indicating that when sodium is present in the medium, this channel may be the preferential entry path for this toxic cation ([Jin et al., 2015](#)). In *Lotus japonicus*, a gain-of-function CNGC mutation (*brush*) was also deleterious, probably because in this genetic background there is a competition between subunits for the formation of tetramers and there was a dominant-negative effect ([Chiasson et al., 2017](#)). However, there are some reports of successful overexpression of CNGCs to increase stress tolerance. Overexpression of a CNGC in orange Ruby Red tress increased cold tolerance, but other transformed orange tree cultivars were not more resistant to lethal freezing temperatures ([Kunta et al., 2019](#)). The overexpression of *GsCNGC20-f* from *Glycine soja* confers submergence tolerance to *Glycine max* by enhancing anaerobic respiration ([Li et al., 2022](#)). In a different study, a differential transcriptomic analysis between salt-sensitive and salt-tolerant soybean plants identified the *GsCNGC20-d* allele as being differentially expressed. Its overexpression confers salt stress tolerance in *Arabidopsis* and soy plants ([Pi et al., 2023](#)).

Potassium from roots to shoots

Once potassium has been absorbed by the roots, it must be loaded into the xylem for translocation to the shoots. The channel mainly responsible for this translocation is SKOR, a Shaker-like outward-rectifying K⁺ channel. SKOR mediates K⁺ transport from the stelar cells to the xylem in the roots, which is a key step for long-distance K⁺ distribution to the aerial part of the plant. Studies in the model plant *Arabidopsis* have found that abscisic acid (ABA) inhibits SKOR expression, suggesting that decreased K⁺

transport to the shoots may be part of the whole plant drought response ([Gaymard et al., 1998](#)). Further studies in the same model determined that the hydrophilic C-terminal region of SKOR is required for the intracellular K⁺ sensing process ([Liu et al., 2006](#)). Interestingly, in a comparative transcriptomic expression among salt-tolerant and salt-sensitive soybean cultivars, SKOR expression correlated with salt tolerance and the overexpression of SKOR in soybean root hairs enhanced the salt tolerance of soybean composite plants ([Qiang et al., 2017](#)). Overexpression of *CmSKOR* (*Cucumis melo* L.) improved tolerance to salt stress in Arabidopsis, measured as higher fresh and dry weight, and accumulation of K⁺ in shoots. These plants also presented increased root length in MS plates and displayed higher maximum photochemical efficiency of PSII (F_v/F_m) ([Long-Tang et al., 2018](#)). Overexpression of *ERF96*, a small ethylene response factor gene, enhances salt tolerance in Arabidopsis. Among the genes that were up-regulated in these plants in response to NaCl stress were *SKOR* and the potassium transporter 2/3 (*AKT2/3*) ([Wang et al., 2017](#)). There are several transcription factors whose overexpression confers salt tolerance and *SKOR* is among their described targets. Specifically, overexpression of the transcription factor HbWRKY82 increases abiotic stress tolerance, and this tolerance correlates with *SKOR* up-regulation ([Kang et al., 2021](#)). *SKOR* is also downregulated by ABF4, an ABRE-binding bZIP factor, an essential component of ABA signaling ([Kang et al., 2002](#)).

The regulation of this process may be multifactorial and dependent on different substrates and different pools of potassium. [Shabala et al. \(2010\)](#) observed that salt-tolerant barley varieties were loading more sodium into the phloem sap than salt-sensitive ones, but this high sodium concentration is compensated by an increase in the potassium uploaded to the phloem, which is dependent not only on the SKOR channel. They demonstrated the participation of K⁺-permeable voltage-sensitive channels in xylem

loading and the regulation depended on a feedback circuit to maintain a constant K^+/Na^+ ratio in the xylem sap. The sodium uptake to the xylem sap may be mediated by cation-chloride co-transporters (CCC), which are expressed at the symplast/xylem interphase (reviewed in Zhao *et al.*, 2020). Finally, overexpression of the quiescin sulfhydryl oxidase QSO2 increases potassium loading to the xylem and positively abiotic stress tolerance, but in a SKOR-independent manner, pointing to the existence of additional systems yet to be identified that may contribute to potassium translocation from root to shoot (Alejandro *et al.*, 2007). In fact, HAK5 could be, at least in part, responsible for this phenotype. In a recent report, Kanno *et al.* (2023) using Arabidopsis *skor* mutants, i.e. mutants deficient in root-to-shoot K^+ translocation, determined that the internal K^+ status affects the expression of HAK5. Therefore, the high-affinity potassium transporter HAK5 is not only regulated by external K^+ conditions, but also by internal levels. The authors propose that HAK5 plays a role in xylem K^+ loading and distribution under K^+ -limiting conditions. In rice, a CRISPR/Cas9-mediated mutagenesis of *HAK8* impaired not only potassium uptake, but also root-to-shoot translocation, stressing the role of HAK proteins in this process, together with SKOR (X. Wang *et al.*, 2021). In rice, it has been shown that OsHAK12 mediates sodium exclusion from the shoots, indicating that some potassium transporters have specialized in sodium extrusion (Zhang *et al.*, 2021).

HKT1-like proteins are determinant in the interplay between sodium and potassium homeostasis. HKT proteins have eight transmembrane domains. There are two classes of HKT proteins: class I transporters have a serine residue in the pore loop domain A that confers sodium specificity and they act as uniporters, for instance, Arabidopsis AtHKT1;1, while class II proteins have a glycine at the same position and act as sodium/potassium symporters (Ali *et al.*, 2021). In cereals, there is a multiplicity of orthologues and they have been related both to shoot sodium exclusion and accumulation.

This apparently contradictory role may be explained by a complex interplay between HKT transporters and candidate transporters involved in xylem loading, such as SOS1 and chloride/cation exchangers ([Venkataraman et al., 2021](#)). From the evolutionary perspective, the fact that HKT could have low selectivity for Na⁺ and K⁺ or even be Na⁺ transporters could be explained by the difference in the hydration shells. Concomitantly, Na⁺ and K⁺ could enter through the same transporter, but with different permeation mechanisms among the same channels, and the selection pressure would have led some HKT channels to stabilize mutations causing specificity for sodium or potassium transport (Benito *et al.*, 2014). Recent evidence suggest that this complex regulatory network may not be evolutionarily conserved ([Nieves-Cordones et al., 2023](#)).

What other transporters may be responsible for the root-xylem potassium loading? K⁺ EFFLUX ANTIPTORTERS (KEAs) are considered to be H⁺/K⁺ antiporters ([Tsuji et al., 2019](#)) and have been proposed to play a role in K⁺ efflux into the xylem sap ([Adams and Shin, 2014](#)), although most of the characterized members in Arabidopsis are located in plastids or endomembranes ([Zheng et al., 2022](#)). Some of the plasma membrane-localized members of the family are up-regulated by salt stress, like the soybean KEA gene *Glyma16g32821* and the *NHX* gene *Glyma09g02130* ([Chen et al., 2015](#)). However, other family members have been ascribed other functions and subcellular locations (as discussed below). Overexpression of a Phosphatidylinositol-Specific Phospholipase C Gene from *Populus simonii* × *P. nigra* improves salt tolerance in transgenic tobacco, and interestingly, in these lines, the expression level of *KUP2*, *KUP6*, and *KEA4* potassium transporter genes was significantly lower than in the control plants ([Sun et al., 2022](#)).

Once in the xylem, the main potassium transporter in the parenchyma is HKT1 ([Davenport et al., 2007](#)). Although it is considered to be a sodium transporter in the model plant Arabidopsis, this appears not to be a general trait and the sodium/potassium

discrimination and preference of this class of transporters may differ even in closely related species. For instance, TsHKT1;2, a HKT1 homolog from the extremophile *Theleungiella salsuginea*, an Arabidopsis relative, shows K⁺ specificity in the presence of NaCl ([Ali et al., 2012](#)). This channel is crucial for salt tolerance in monocots ([Shohan et al., 2019](#)); in dicots like Arabidopsis there is only one copy and its role is not pivotal. In the halophytic grass *Puccinellia tenuiflora*, the ability to grow in sodium-rich and potassium-deprived soils is attained by a joint activity of PutHKT1;5 and the plasma membrane Na⁺/H⁺ antiporter SOS1 (Shi et al., 2000) and by other ion transporters/channels, such as PutHKT1;4, PutHKT2;1, and PutAKT1. This indicates that halophytic plants present a complex radial network of Na⁺ and K⁺ transport processes, coordinating their loading to the xylem, Na⁺ retrieval and extrusion under conditions of mild salinity and/or K⁺ deprivation ([Han et al., 2022](#)). The expression of *HmHKT2;1* is also a differential trait between salt-tolerant and salt-sensitive ecotypes of the halophyte *Hordeum maritimum* ([Hmidi et al., 2019](#)).

Several regulators of HKT transporters have been identified and characterized at the molecular level. In rice, *OsHKT1;1* is regulated by the transcription factor OsMYBc, which in turn is regulated by the E3 ubiquitin ligase OsMSRFP. A knockout of this latter gene induced salt tolerance in rice ([Xiao et al., 2022](#)). Also, in rice the Really Interesting New Gene (RING) H2-type E3 ligase, OsSIRH2-14 (previously named OsRFP2-14), plays a positive role in salinity tolerance by regulating *OsHKT2;1*. *OsSIRH2-14* overexpressing rice plants showed significantly enhanced salinity tolerance and reduced Na⁺ accumulation in the aerial shoot and root tissues ([Park et al., 2019](#)). In a similar manner, overexpression of poplar *PalERF109*, a transcription factor belonging to the B4 group of ethylene response factors, enhanced salt tolerance of transgenic poplars, and up-regulated the HKT gene *PalHKT1;2*, which at least partially explains the

phenotype ([Chen et al., 2021](#)). In alfalfa (*Medicago sativa*), overexpression of two Rare Cold Inducible Genes (*MsRCI2D* and *MsRCI2E*) enhanced salt tolerance and, *MsHKT2* was among the up-regulated genes (Zhang *et al.*, 2022). Finally, overexpression of a date palm Metallothionein 2A (*PdMT2A*) in Arabidopsis enhanced salt tolerance and the *AtHKT1* gene was found to be up-regulated in these transgenic plants ([Patankar et al., 2019](#)).

HKT transporters have been extensively used to increase salt tolerance by means of transgenic plants. *AtHKT1* has been expressed in potato, where it was shown to reduce Na^+ accumulation in leaves, effectively promoting the K^+/Na^+ homeostasis that minimizes osmotic imbalance, maintains photosynthesis and stomatal conductance, and increases plant productivity (Zhang *et al.*, 2019). Overexpression of the soybean *GmHKT1* increases salt tolerance of transgenic tobacco plants ([Chen et al., 2011](#)). A gene similar to *HKT*, *IbHKT-like*, leads to enhanced low potassium tolerance in transgenic roots of sweet potato (*Ipomoea batatas* (L.) Lam.) ([Jiang et al., 2022](#)). This strategy has also been used in woody trees. Overexpression of *PeHKT1;1*, a gene from hybrid poplar based on the sequences of the *Populus trichocarpa* genome, improves salt tolerance in poplar (Xu *et al.*, 2018). However, the use of HKT transporters may not be a straightforward strategy to increase salt tolerance in all plants. Arabidopsis expressing *HKT2s* from barley or from the halophytic turf grass *Sporobolus virginicus* showed reduced salt tolerance ([Tada and Ohnuma, 2020](#)), while overexpression of *HvHKT2;1* in barley showed enhanced salt tolerance ([Mian et al., 2011](#)). In this case, the phenotype was due to the low selectivity for sodium or potassium of this channel. More specifically, *HvHKT2;1* expression leads to Na^+ accumulation in the shoots, reinforcing the salt-accumulating behavior of barley, while this same strategy was deleterious for Arabidopsis. It has been proposed that a coordinated enhancement of Na^+ accumulation

and sequestration mechanisms in shoots could be a promising strategy to confer salt tolerance to glycophytes ([Tada and Ohnuma, 2020](#)). However, it has been proposed that this should be combined with enhanced potassium transport to keep the K^+/Na^+ ratio high. Overexpression of rice *OsHKT1;4* also increases salt sensitivity in rice ([Oda et al., 2018](#)). A similar phenotype is found in Arabidopsis upon the overexpression of the *Sorghum bicolor* *SbHKT1;4* gene. In this case, the sodium hypersensitivity of transgenic plants could be alleviated by potassium supplementation (T. T. Wang et al., 2014). This problem could be due to the low selectivity of HKT channels. For instance, the rice *OsHKT2;4* mediates Mg^{2+} homeostasis under high Mg^{2+} conditions in transgenic Arabidopsis plants (C. Zhang et al., 2017).

The natural variation of the HKT channels has also been studied in crop plants. Two HKT1;5 (HKT8) genes, *Nax2* and *Kna1*, have been identified in wheat by means of microsatellite and linkage analysis as being responsible for sodium extrusion in this species ([Byrt et al., 2007](#)). Importantly, this knowledge has been used to improve wheat yield in saline soils ([Munns et al., 2012](#)). The durum wheat genes *Nax1* and *Nax2*, identified as Na^+ transporters TmHKT1;4-A2 and TmHKT1;5-A, have also been transferred to bread wheat, resulting in decreased sodium accumulation in leaves under saline and waterlogged conditions ([James et al., 2011](#)). In maize, the association between sequence variations in ZmHKT1;5 and salt tolerance was evaluated in 54 different cultivars. Two SNPs (A134G and A511G) were associated with increased salt tolerance, and overexpression of the allele containing these two SNPs conferred salt tolerance to transgenic tobacco plants ([Jiang et al., 2018](#)).

The guard cell as a paradigm

A strategy to increase abiotic stress tolerance in plants is to optimize WUE by improving the ability to close stomata upon an environmental constraint. The

coordination of proton pumps, potassium, chloride, and malate transporters is crucial in controlling stomatal movements in plants. During stomatal opening, proton pumps actively transport protons out of the guard cells, and this causes K^+ ions to move into the guard cells, along with chloride Cl^- ions moving out. Simultaneously, malate ions are taken up into the guard cells. The accumulation of K^+ , Cl^- , and malate ions leads to an increase in osmotic potential, causing water to enter the guard cells, making them turgid. For stomatal closure, proton pumps stop actively transporting protons out of the guard cells, K^+ moves out of the guard cells, Cl^- moves back in, and malate ions are released from the guard cells. The loss of K^+ , Cl^- , and malate ions leads to a decrease in osmotic potential, causing water to move out of the guard cells. Flaccid guard cells lose their bowing shape, and the stomatal pore closes, preventing excessive water loss (transpiration) in adverse conditions.

The coordination between these proton pumps, potassium, chloride, and malate transporters ensures that stomata respond appropriately to environmental factors such as light, humidity, and CO_2 levels, optimizing gas exchange and water balance in the plant. Therefore, modulating the potassium flux in the guard cells may constitute a strategy to improve abiotic stress tolerance in plants ([Sirichandra *et al.*, 2009](#)).

Given this pivotal role, guard cells represent the best characterized plant cell type with respect to ion transport and signal transduction ([Jezek and Blatt, 2017](#)). Drought stress induces stomatal closure and inhibits stomatal opening simultaneously. Stomatal opening is driven by the plasma membrane H^+ -ATPase, which is activated by auxin and light ([Shimazaki *et al.*, 1986](#); [Lohse and Hedrich, 1992](#)). Recent studies showed that the transcription factors PHYTOCHROME INTERACTING FACTORS (PIFs) are required for blue light stomatal aperture ([Rovira *et al.*, 2023, Preprint](#)). Activation of the signaling leading to stomatal aperture results in membrane hyperpolarization, driving the uptake of

K⁺ via inward-rectifying potassium channels ([Schroeder *et al.*, 1987](#); [Thiel *et al.*, 1992](#)). Stomatal closure can be triggered by raising the cytosolic Ca²⁺ concentration to approximately 1 μm or by drought stress-induced ABA production ([MacRobbie, 1981](#); [Schroeder and Hagiwara, 1989](#); [Assmann, 1993](#); [Lemtiri-Chlieh and MacRobbie, 1994](#); [Schroeder *et al.*, 2001](#)). In *Arabidopsis* guard cells, the inward-rectifying channels KAT1 and KAT2 and the outward-rectifying channel GORK have been shown to mediate the major potassium currents. The activity of these channels is critical in regulating stomatal movements in response to different environmental cues ([Kwak *et al.*, 2001](#); [Hosy *et al.*, 2003](#); [Lebaudy *et al.*, 2008](#); [Blatt *et al.*, 2014](#)). Among them, KAT1 is the main potassium channel in guard cells. Its function is essential for light-induced stomatal opening ([Ichida *et al.*, 1997](#)) and this opening is energized by the plasma membrane proton gradient. In fact, the overexpression of an H⁺-ATPase in guard cells promotes light-induced stomatal opening and enhances plant growth (Y. Wang *et al.*, 2014).

KAT1 has a complex regulation at different levels. For instance, the protein accumulation at the plasma membrane is regulated by endocytosis and membrane trafficking. It has been reported that ABA promotes the selective endocytosis of KAT1 in endosomal vesicles ([Sutter *et al.*, 2007](#)). This KAT1 trafficking regulation is thought to contribute to the ABA-mediated changes in ion fluxes required for stomatal movements. Two types of SNARE (soluble *N*-ethylmaleimide-sensitive factor protein attachment protein receptor) proteins, the Qa-SNARE SYP121 and the R-SNARE VAMP721, have been shown to physically interact with KAT1 and to modulate channel activity by controlling their gating at the plasma membrane ([Sutter *et al.*, 2006](#); [Sokolovski *et al.*, 2008](#); [Honsbein *et al.*, 2009](#); [Grefen *et al.*, 2010](#); Zhang *et al.*, 2020). There is a second subset of SNAREs that interact to control these K⁺ channels, but with opposing actions on gating to SYP121. Vesicle-associated membrane proteins (VAMPs),

which target vesicles to the plasma membrane, also interact with and suppress the activities of KAT1 and KC1 (Zhang *et al.*, 2015). In the case of SYP121, it also participates in recycling of the channel to the plasma membrane after ABA-mediated internalization ([Eisenach *et al.*, 2012](#)). The BCL2-ASSOCIATED ATHANOGENE4 protein (BAG4) contributes to the trafficking of the KAT1 channel and its accumulation in the guard cell plasma membrane. BAG4 regulates stomatal aperture in a KAT1-dependent manner ([Locascio *et al.*, 2019](#)). KAT1 is also regulated at the level of phosphorylation. It is known that the Thr306 is a phosphorylation site and essential for its activity ([Sato *et al.*, 2009](#)). Some proteins able to phosphorylate KAT1 have been identified. KAT1 is phosphorylated by the ABA-responsive Open Stomata 1 (OST1) kinase and the non-canonical Ca²⁺-dependent protein kinase CPK13 (Zhang *et al.*, 1999; [Acharya *et al.*, 2013](#)). The S-type anion channels SLAC1 and SLAH3 are negative regulators of KAT1 by protein–protein interaction, and thus prevent stomatal opening. In addition, SLAC1 is negatively regulated by CBL-interacting protein kinase 23 (CIPK23), indicating that during standard growth it is important to maintain potassium channels active, and thus stomata open, but under stress conditions a fast closure is important ([Huang *et al.*, 2023](#)). Finally, functional analyses have demonstrated that miRNAs are essential for the ability of plants to resist environmental stress ([Jover-Gil *et al.*, 2005](#)). In this sense, in *Phaseolus vulgaris*, the miR398 is down-regulated under drought conditions ([Formey *et al.*, 2015](#)), and it was suggested that this miRNA may regulate *KATI* expression in *Paulownia fortunei* under drought stress (Zhao *et al.*, 2018).

There have been several attempts to engineer the complex regulatory network governing guard cells ion fluxes to enhance plant stress tolerance. Overexpression of *KATI* increases salt tolerance in yeast cells and rice cells ([Obata *et al.*, 2007](#)). Overexpression of *KATI* also rescued the phenotype of the double mutant *aks1 aks2-1*,

with mutations in two bHLH transcription factors that facilitate K⁺ uptake during stomatal opening. In wild type plants, AKSs facilitate stomatal opening through the transcription of genes encoding inward-rectifying K⁺ channels, such as KAT1. Both transcription factors are repressed by abscisic acid through phosphorylation ([Takahashi et al., 2013](#)). OST1 has also been proposed as an alternative to generate drought-resistant crops, as it blocks stomatal opening by inhibiting potassium currents ([Acharya et al., 2013](#)). CPK13 inhibits KAT1 and KAT2 in oocytes and its overexpression was shown to reduce light-induced stomatal opening ([Ronzier et al., 2014](#)). Overexpression of truncated forms of the magnesium-chelatase H subunit and OST1 increased KAT1 phosphorylation and drought stress tolerance in Arabidopsis ([Liang et al., 2015](#)).

GORK genes encode outward-rectifying potassium channels located in guard cells and several other plant tissues. GORK channels possess the binding motifs and domains that may enable them to operate as ligand-gated channels. It has been proposed that the activity of GORK channels may be modulated by cyclic nucleotides, γ -aminobutyric acid, G-proteins, protein phosphatases, inositol, and ATP (reviewed in [Adem et al., 2020](#)). GORK is also the target of the antibiotic peptaibol and is required for the formation of the auxin gradient ([Shi et al., 2016](#)). The triple mutant *kup6 kup8 gork* has impaired tolerance to drought stress ([Osakabe et al., 2013](#)). GORK channels are up-regulated under abiotic stress conditions, suggesting a pivotal role in this response. Electrophysiological measurements in root epidermal cells indicated that ABA, acting through the PYR/PYL/RCAR receptors ([Rodriguez et al., 2014](#)), induced membrane hyperpolarization due to K⁺ efflux through the GORK channel ([Planes et al., 2015](#)). On the other hand, GORK is also regulated by jasmonate and wounding signaling via the Ca²⁺ sensor-kinase CBL1–CIPK5 complex. GORK activity is required for wounding-

induced stomatal closure, and this is antagonized by the ABA receptor ABI2, so GORK also participates in ABA–jasmonate crosstalk ([Forster et al., 2019](#)).

The abiotic stress tolerance of several reported transgenic plants may be explained by GORK activation. Overexpression of the wheat NAC transcription factor *TaSNAC4-3A* gene confers drought tolerance in transgenic Arabidopsis, and GORK was up-regulated in these transgenic plants, exhibiting a 3.65-fold change ([Mei et al., 2021](#)). The overexpression of the Arabidopsis transcription factor, *AtLOS5* induced the expression of ABA biosynthetic genes leading to ABA accumulation. This, in turn, activates ion transporters and PIP aquaporin gene expression to regulate root ion fluxes and water uptake, thus maintaining high cytosolic K^+ and Na^+ homeostasis and better water status in maize exposed to salt stress. It has been proposed that this overexpression also induced GORK activity ([Zhang et al., 2016](#)). The regulation of the interplay of this channel may be very complicated, and some strategies could have an effect contrary to what is expected. For instance, the overexpression of a salt-induced HAK/KUP/KT transporter (*PvHAK16*) from the halophyte seashore paspalum (*Paspalum vaginatum* O. Swartz) in Arabidopsis had a deleterious effect under salt stress, as Na^+ levels increased and K^+ decreased, thus increasing toxicity. The ectopic expression of the *PvHAK16* transgene altered transcript levels of ion homeostasis genes *K⁺-Uptake Permease 7 (KUP7)*, *AKT2*, *Salt Overly Sensitive 1 (SOS1)*, and *GORK* ([Dai et al., 2022](#)). Finally, it is worth mentioning that CNGCs also mediate ABA-induced stomatal closure, but in contrast to root CNGCs, in guard cells CNGCs are mainly responsible for Ca^{2+} transport ([Tan et al., 2023](#)). Also, CNGC18 controls directional pollen tube growth, localizes at the plasma membrane of the pollen tube, and regulates K^+ , but probably not Na^+ , homeostasis ([Frietsch et al., 2007](#)).

Phloem: from leaves to the roots

Potassium is also present in the phloem, indicating that there is also a downward circulation of potassium. KAT2 is orthologous to KAT1. It is expressed in guard cells, but in addition, it is phloem-associated and also localized to the cotyledons and the apical part of the hypocotyl ([Philippar et al., 2004](#)). KZM1, the maize orthologue of KAT1 and KAT2, is expressed in guard cells and phloem ([Philippar et al., 2003](#)). A recent report indicated that the overexpression of the potato NAC transcription factor *StNACo53* increased salt tolerance in Arabidopsis. The NAC (NAM, ATAF1/2, and CUC2) transcription factors comprise one of the largest transcription factor families in plants and play important roles in stress responses. The authors suggested that the observed tolerance phenotype could be explained by the genes up-regulated in the overexpressing lines, among them *KAT2* (Q. Wang *et al.*, 2021).

AKT2/3 potassium channels are members of the plant voltage-gated (formerly Shaker) channel family, which mediate dual-directional K⁺ transport with weak voltage-dependency, although the rice *OsAKT2* functions mainly as an inward-rectifier with strong voltage dependency and acutely suppresses outward activity ([Huang et al., 2021](#)). *AKT2* has been shown to be regulated by extracellular protons and Ca²⁺ and to function as the photosynthate-induced phloem K⁺ channel ([Hoth et al., 2001](#); [Ivashikina et al., 2005](#)). *AKT2* can form heterotetramers with *KAT2* ([Xicluna et al., 2007](#); [Sharma et al., 2013](#)). In guard cells, *AKT2/3* is responsible for the Ca²⁺ sensitivity of the K⁺ uptake channel. An Arabidopsis mutant, *akt2/3-1*, has reduced potassium content ([Deeken et al., 2002](#)), but overexpression of *OsAKT2* increases salt tolerance in Arabidopsis wild type plants ([Huang et al., 2021](#)). Co-expression of *HvAKT2* and *HvHAK1* confers drought tolerance in barley, likely due to enhanced leaf mesophyll H⁺ homeostasis. In addition, the co-expression of these two channels altered the K⁺, H⁺, and Ca²⁺ fluxes across the plasma membrane and also the production of nitric oxide and hydrogen peroxide in leaves

([Feng et al., 2020](#)). Interestingly there is an observation that an increase in potassium fertilization diminishes the incidence of soybean mosaic virus. *GmAKT2* is highly induced upon inoculation with the virus, and engineered soybean plants overexpressing *GmAKT2* present increased resistance to the virus ([Zhou et al., 2014](#)). The overexpression of the cotton CBL-interacting protein kinase gene *GhCIPK6* in Arabidopsis significantly enhanced the tolerance to salt, drought, and ABA stresses, and also increased the expression of several genes, among them *AtAKT2*, whose increase was higher than *AtKAT1*, while in these transgenic plants, *AtSKOR* expression decreased ([He et al., 2013](#)).

Intracellular potassium homeostasis

Sodium must be excluded from the cytoplasm and the potassium concentration must be kept high. One strategy to attain this objective is to accumulate sodium in vacuoles or increase potassium compartmentation. For instance, the *AtNHX1* exchanger mediates potassium compartmentation in vacuoles of transgenic tomato ([Leidi et al., 2010](#)), but in the long term, some of the effects of this potassium compartmentation may be deleterious for the plant (De Luca *et al.*, 2018). The K^+/H^+ antiporter from *Lycopersicon esculentum* (tomato), *LeNHX2*, increases salt tolerance by improving K^+ homeostasis in transgenic tomato plants ([Huertas et al., 2012](#)). It has been reported that co-expression of the vacuolar Na^+/H^+ antiporter *TnHXS1* and H^+ -pyrophosphatase with an IRES-mediated bicistronic vector improves salinity tolerance and enhances potassium biofortification of tomato ([Gouiaa and Khoudi, 2015](#)). Another cation exchanger from tomato (*LeNHX4*) increases salt tolerance in transgenic tomato plants upon application of gibberellic and indole acetic acid ([Baghour et al., 2023](#)). Overexpression of the potassium channel *OsTPKb*, mainly expressed in tonoplasts of small vacuoles, confers osmotic and drought tolerance in rice ([Ahmad et al., 2016a](#)).

The K^+/H^+ antiporter AhNHX1 from *Arachis hypogaea* improved tobacco tolerance to NaCl stress by enhancing K^+ retention (W. W. Zhang *et al.*, 2017).

As mentioned above, some KEA family members are thought to participate in root-xylem potassium loading. Another member of this family, KEA2, has been shown to be a functional H^+/K^+ antiporter and to modulate monovalent cation and pH homeostasis in chloroplasts or plastids ([Aranda-Sicilia *et al.*, 2012](#)). K^+ Efflux Antiporters 4, 5, and 6 mediate pH and K^+ homeostasis in endomembrane compartments, such as the Golgi, the *trans*-Golgi network and the pre-vacuolar compartment ([Zhu *et al.*, 2018](#)).

In recent years there has been an increase in interest in the role of potassium as a signaling molecule, especially during salt stress. Halophytism, the ability of plants to withstand salinity at a level at which most plants die, is an unusual trait in nature ([Flowers and Colmer, 2008](#)). It has emerged in at least 100 different angiosperm families, even though less than 2% of flowering plants are halophytic ([Santos *et al.*, 2016](#)). Salt tolerance in plants, from the macroevolutionary perspective, is considered a self-destructive trait. It can be obtained often, but once there is no selective pressure it is rapidly lost by reversal or extinction ([Bromham *et al.*, 2020](#)). The explanation behind this complex phenomenon is that from the bioenergetic point of view, maintaining potassium homeostasis in saline (sodium-rich) soils is extremely costly, and the energy to maintain a proper ion homeostasis must be diverted from essential processes for the plant. In this context, there is growing evidence that potassium can act as a signaling molecule during salt stress to participate in the modulation of energetic metabolism ([Rubio *et al.*, 2020](#)). During salt stress there is a decline in ATP production, but when the sodium concentration is over 40 mM there is a potassium efflux from the cells that causes that plant to redirect the available ATP to the defense reactions. This potassium efflux is a 'metabolic switch' that

diverts a large pool of ATP towards the salt stress response ([Demidchik, 2014](#); [Shabala, 2017](#)).

In yeast, a standard model to study potassium homeostasis in plants ([Locascio *et al.*, 2019](#)), it has been shown that K⁺ and H⁺ efflux systems participate in programmed cell death (PCD) ([Hoeberichts *et al.*, 2010](#)). A similar process has been described in plants. During stress, there is an increase in the production of reactive oxygen species. These molecules activate potassium efflux channels in the plasma membrane. This activation has been related to PCD. This efflux and subsequent PCD is very slow in *gork1-1* mutants, pointing to a pivotal role of this channel in the process ([Demidchik *et al.*, 2010](#)).

Potassium salts in the soil: fertilizers and biostimulants

To finish this review, we would like to mention that another strategy to modulate potassium transport as a means to increase abiotic stress tolerance is the use of potassium and potassium salts as agricultural inputs. Potassium, as a major plant nutrient, is an essential component of nitrogen–phosphate–potassium fertilizers. Increasing the potassium concentration in soil can be a way to prevent abiotic stress and salt toxicity, as it competes with sodium for entry using the low affinity potassium transporters and entry through non-specific plasma membrane transporters or channels ([Tittal *et al.*, 2021](#)).

In recent years, there is increased interest in the use of biological inputs of natural origin. Biostimulants have been proposed as useful tools to achieve this objective and represent an emerging category of agricultural inputs that can improve crop yield under normal and abiotic stress conditions. These products have been gaining more attention in recent years due to their natural origin and their integration among the environmentally friendly tools that can assist in securing high crop yields ([Colla and Rouphael, 2015](#);

[Bhupenchandra et al., 2022](#)). In addition, they can be used both in conventional and organic farming ([Benito et al., 2022](#)). The European Biostimulants Industry Council (EBIC), which fosters the role of the biostimulant sector in sustainable agricultural production, defines biostimulants as ‘substance(s) and/or micro-organisms whose function when applied to crops or the rhizosphere is to stimulate natural processes to enhance/benefit nutrient uptake, nutrient efficiency, tolerance to abiotic stress, and crop quality’ (EBIC, 2019). Commercially available biostimulants can be classified into eight different categories: (i) humic substances, (ii) complex organic materials, (iii) beneficial chemical elements, (iv) inorganic salts, (v) seaweed extracts and botanicals, (vi) chitin and chitosan derivatives, (vii) anti-transpirants, and (viii) free amino acids and other nitrogen-containing substances. Products containing beneficial rhizosphere microorganisms, such as plant growth-promoting bacteria (PGPBs) and mycorrhizal fungi, are considered to be a ninth category ([Traon et al., 2014](#)). Biostimulants are not considered agrochemicals because they only influence the vigor of plants and do not have a direct action against pests or diseases, and nor do they provide nutrients directly to plants (du Jardin, 2015).

Although potassium cannot be considered as a biostimulant by itself since it is a nutrient, some commonly used biostimulants are presented in the form of potassium salts (mainly potassium humate and potassium fulvate), or as potassium-rich extracts ([Karthikeyan and Shanmugam, 2017](#)). Potassium humate is a well-known plant growth promoter obtained from the alkaline extraction of lignite. It is used mainly as a soil conditioner and to increase the efficiency of nitrogen and phosphate fertilizers ([Kumar et al., 2013](#)). The addition of potassium humate increases growth in wheat ([Ali and Elbordiny, 2009](#)), aromatic plants ([Said-Al Ahl et al., 2009](#)), and cotton plant fiber quality and productivity ([Ullah et al., 2020](#)). Under stress conditions, potassium humate has also

proven to be effective. It alleviates salt stress in common bean ([El-Beltagi et al., 2023](#)) and soybean ([Alharbi et al., 2022](#)), and arsenic toxicity in rice ([Ray et al., 2022](#)). Recent results from our laboratory have demonstrated that in the model plant *Arabidopsis* the effect on abiotic stress tolerance of potassium humate can be explained by alterations in starch accumulation ([Benito et al., 2023](#)).

Potassium fulvate is the result of the hydrophilic extraction of potassium humate, enriched in small molecular weight components and with a higher concentration of active groups. It has been described to increase nutrient uptake in maize, including potassium and other macro- and micronutrients ([Ngennoy et al., 2022](#)). A mixture of potassium silicate and fulvate, as well as betaine, improves potassium uptake in tomato (Xu *et al.*, 2022). Potassium fulvate also increases growth in squash (*Cucurbita pepo* L.) ([Omar et al., 2020](#)). In other cases, the use of biostimulants that do not contain potassium in their composition have also been reported to stimulate potassium uptake. For instance, it has been shown that an algal extract or the product of a bacterial fermentation can increase potassium uptake in almond trees ([Saa et al., 2015](#)), revealing a complex interplay between the regulation of different nutrients that has started to be elucidated in plants (Y. Wang *et al.*, 2021). Recently it has been shown that the anion channel SLAH3 interacts with potassium channels to regulate nitrogen–potassium homeostasis and membrane potential in *Arabidopsis* ([Liu et al., 2023](#)). Similar cross talks between potassium and other nutrients have also been observed previously in model organisms ([Perez-Valle et al., 2010](#); [Mahmoud et al., 2017](#)).

There is also growing interest in the use of symbiotic microorganisms. The traditional point of view is that symbiotic fungi, such as mycorrhiza, or plant growth promoting rhizobacteria increase the uptake of phosphate and nitrogen. However, there

is also evidence that root exudates and microorganisms may promote the uptake of additional macro- and micronutrients, among them, potassium ([Sardans *et al.*, 2023](#)).

Conclusions and future directions

Crops with enhanced abiotic stress tolerance, or those able to maintain yield with less water or with salinized water, are in major demand from farmers worldwide. Although there is a considerable amount known regarding ion homeostasis mechanisms, the genes and proteins participating in those mechanisms, and their complex regulatory networks, the transfer of this knowledge to practical applications has so far been severely limited.

To date, there are only two GMO traits that present abiotic stress tolerance, the DroughtGard maize, which overexpresses the bacterial cold shock protein B (CSPB) (Wang *et al.*, 2015) and, very recently, the drought-tolerant wheat IND-00412-7, which has been transformed with the sunflower transcription factor *HaHB4* ([Miranda *et al.*, 2022](#)). The *HaHB4* transgene previously was introduced in soy ([Ribichich *et al.*, 2020](#)).

Potassium homeostasis may be a good target for crop biotechnological improvement. Optimizing potassium uptake, translocation, compartmentalization, and/or potassium fluxes, which regulate stomatal closure, may be a strategy to increase plant nutrition and concomitantly yield, and at the same time improve abiotic stress tolerance. It should be noted that it may not be a straightforward strategy given that some constraints and limiting factors will surely come into play, such as ion imbalance, energetic costs or yield penalties. Although the challenge is complex, we should take advantage of all the available knowledge and the experience we have acquired in model plants, like *Arabidopsis*. It is time to apply these advances to non-model and crop plants to generate new varieties that can contribute to assuring food security worldwide in our changing climate. Farmers and society in general are demanding it. In our opinion, the most significant advances in the next few years are likely to derive from genome-editing

approaches applied to HAK and/or HKT transporters involved in root-to-shoot transport, including point mutations to change ion selectivity and alteration of expression levels by promoter modifications. Another promising approach is the employment of potassium salts as biostimulants that can improve yield under abiotic stress conditions, with the added advantage of being compatible with organic farming practices.

Author contributions

JMM and LY: conceptualization; JMM and RP: data curation; RP: visualization; JMM: writing—original draft; JMM, RP, and LY: writing—review and editing.

Conflict of interest

The authors declare no conflict of interest.

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Fig. 1. Selected targets to improve K⁺ homeostasis in plants. Schematic representation of sources of potassium and the major transport proteins in different plant tissues and cell types along with subcellular localization (see text for more details). Blue, potassium ions; orange, biostimulants and natural extracts in soil; green, voltage-gated potassium channels; red, HKT family transporters; grey, KUP/HAK/KT potassium channel family member, HAK5; black, K⁺/H⁺ and Na⁺/K⁺ antiporters; purple, ligand-gated channels. CNGC, cyclic nucleotide-gated channel; GLR, Glutamate Receptor-Like. See the text for more details.

Table 1. Genetic modifications employing potassium transport proteins or their regulators to improve abiotic stress tolerance

Gene	Source	Target	Phenotype	Reference
<i>AhNHX1</i>	<i>Arachis hypogaea</i> (peanut)	<i>Nicotiana tabacum</i> (tobacco)	Increased salt tolerance	W. W. Zhang <i>et al.</i> (2017)
<i>AKT1</i>	Arabidopsis	Arabidopsis	ABA insensitivity, increased H ⁺ efflux	Planes <i>et al.</i> (2015)
<i>AtCNGC10</i>	Arabidopsis	Arabidopsis	Increased sensitivity to salt stress	Jin <i>et al.</i> (2015)
<i>AtHKT1</i>	Arabidopsis	Arabidopsis	Increased salt tolerance	Ali <i>et al.</i> (2012)
<i>AtHKT1</i>	Arabidopsis	<i>Solanum tuberosum</i> (potato)	Increased plant productivity	Zhang <i>et al.</i> (2019)
<i>AtNHX1</i>	Arabidopsis	<i>Solanum lycopersicum</i> (tomato)	Increased potassium intracellular accumulation; increased salt tolerance	Leidi <i>et al.</i> (2010)
<i>AtNHX1</i>	Arabidopsis	<i>Solanum lycopersicum</i>	Altered cellular K homeostasis; loss of nutrient use efficiency	De Luca <i>et al.</i> (2018)
<i>CmSKOR</i>	<i>Cucumis melo</i> (melon)	Arabidopsis	Increased salt tolerance	Long-Tang <i>et al.</i> (2018)
<i>CNGCcit</i>	<i>Citrus sinensis</i> (sweet orange)	<i>Citrus sinensis</i>	Increased photosynthesis	Kunta <i>et al.</i> (2019)
<i>CNGCcit</i>	<i>Citrus sinensis</i>	<i>Citrus × paradisi</i> (grapefruit)	Increased cold tolerance	Kunta <i>et al.</i> (2019)
<i>ERF96</i>	Arabidopsis	Arabidopsis	Increased SKOR and AKT2/3 expression; increased salt tolerance	Wang <i>et al.</i> (2017)
<i>GhCIPK6</i>	<i>Gossypium hirsutum</i> (cotton)	Arabidopsis	Increased AKT2 expression; increased salt and drought tolerance	He <i>et al.</i> (2013)
<i>GmAKT2</i>	<i>Glycine max</i> (soybean)	<i>Glycine max</i>	Increased viral resistance	Zhou <i>et al.</i> (2014)
<i>GmHKT1</i>	<i>Glycine max</i>	<i>Nicotiana tabacum</i>	Increased salt tolerance	Chen <i>et al.</i> (2011)
<i>GsCNGC20-d</i>	<i>Glycine soja</i> (wild soybean)	<i>Glycine max</i>	Increased salt tolerance	Pi <i>et al.</i> (2023)
<i>GsCNGC20-d</i>	<i>Glycine soja</i>	Arabidopsis	Increased salt tolerance	Pi <i>et al.</i> (2023)

<i>GsCNGC20-f</i>	<i>Glycine soja</i>	<i>Glycine max</i>	Increased submergence tolerance	Li et al. (2022)
<i>HbWRKY82</i>	<i>Hevea brasiliensis</i> (rubber tree)	Arabidopsis	Increased SKOR and HKT1 expression; increased salt tolerance	Kang et al. (2021)
<i>HvAKT1</i>	<i>Hordeum vulgare</i> (barley)	<i>Hordeum vulgare</i>	Increased drought tolerance and K uptake	X. Feng et al. (2021)
<i>HvAKT2 and HvHAK1</i>	<i>Hordeum vulgare</i>	<i>Hordeum vulgare</i>	Increased drought tolerance	Feng et al. (2020)
<i>HvHKT2;1</i>	<i>Hordeum vulgare</i>	Arabidopsis	Decreased salt tolerance	Tada and Ohnuma (2020)
<i>HvHKT2;1</i>	<i>Hordeum vulgare</i>	<i>Hordeum vulgare</i>	Increased salt tolerance	Mian et al. (2011)
<i>IbHKT-like</i>	<i>Ipomea batatas</i> (sweet potato)	<i>Ipomea batatas</i>	Increased tolerance to low potassium	Jiang et al. (2022)
<i>KOB1</i>	<i>Oryza sativa</i> (rice)	Arabidopsis	Increased potassium shoot content	Ardie et al. (2011)
<i>KPutB1</i>	<i>Puccinellia tenuiflora</i>	Arabidopsis	Increased potassium shoot content	Ardie et al. (2011)
<i>LeNHX2</i>	<i>Solanum lycopersicum</i>	<i>Solanum lycopersicum</i>	Increased salt tolerance	Huertas et al. (2012)
<i>LeNHX4</i>	<i>Solanum lycopersicum</i>	<i>Solanum lycopersicum</i>	Increased salt tolerance (upon application of gibberellic and indole acetic acid)	Baghour et al. (2022)
<i>MsRCI2D,E</i>	<i>Medicago sativa</i> (alfalfa)	<i>Medicago sativa</i>	Increased MsHKT2 expression; increased salt tolerance	Zhang et al. (2022)
<i>MYB77</i>	Arabidopsis	Arabidopsis	Increased <i>AtHAK5</i> expression; tolerance to low K	C. Z. Feng et al. (2021)
<i>OsAKT1</i>	<i>Oryza sativa</i>	<i>Oryza sativa</i>	Increased drought and osmotic stress tolerance	Ahmad et al. (2016b)
<i>OsAKT2</i>	<i>Oryza sativa</i>	Arabidopsis	Increased salt tolerance	Huang et al. (2021)
<i>OsHKT1;4</i>	<i>Oryza sativa</i>	<i>Oryza sativa</i>	Decreased salt tolerance	Oda et al. (2018)
<i>OsSIRH2-14</i>	<i>Oryza sativa</i>	<i>Oryza sativa</i>	Increased OsHKT2;1 stability; increased salt tolerance	Park et al. (2019)
<i>OsTPKb</i>	<i>Oryza sativa</i>	<i>Oryza sativa</i>	Increased osmotic and drought tolerance	Ahmad et al. (2016a)
<i>PalERF109</i>	<i>Populus albus</i> (white poplar)	<i>Populus albus</i>	Increased PalHKT1	Chen et al. (2021)

			expression; increased salt tolerance	
<i>PdMT2A</i>	<i>Phoenix dactylifera</i> (date palm)	Arabidopsis	Increased AtHKT1 expression; increased salt tolerance	Patankar et al. (2019)
<i>PeHKT1;1</i>	<i>Populus thrichocarpa</i> (California poplar)	<i>Populus davidiana</i> ✘ <i>Populus bolleana</i> (poplar)	Increased salt tolerance	Xu et al. (2018)
<i>PsnPLC</i>	<i>Populus simonii</i> × <i>P. nigra</i> (poplar)	<i>Nicotiana tabacum</i> (tobacco)	Increased KUP2, KUP6, and KEA4 expression; increased salt tolerance	Sun et al. (2022)
<i>PtAKT1</i>	<i>Puccinellia tenuiflora</i>	Arabidopsis	Increased salt tolerance	Ardie et al. (2010)
<i>PvHAK16</i>	<i>Paspalum vaginatum</i> O. Swartz	Arabidopsis	Altered transcript levels of KUP7, AKT2, and GORK; decreased salt tolerance	Dai et al. (2022)
<i>RCI3</i>	Arabidopsis	Arabidopsis	Increased <i>AtHAK5</i> expression; Altered root response to K deficiency	Kim et al. (2010)
<i>SbHKT1;3</i>	<i>Sorghum bicolor</i> (sorghum)	Arabidopsis	Decreased salt tolerance	T. T. Wang et al. (2014)
<i>SKOR</i>	<i>Glycine max</i>	<i>Glycine max</i>	Increased salt tolerance	Qiang et al. (2017)
<i>StNACo53</i>	<i>Solanum tuberosum</i>	Arabidopsis	Increased KAT2 expression; increased salt tolerance	Q. Wang et al. (2021)
<i>SvHKT2;1</i>	<i>Sporobolus virginicus</i>	Arabidopsis	Decreased salt tolerance	Tada and Ohnuma (2020)
<i>SvHKT2;2</i>	<i>Sporobolus virginicus</i>	Arabidopsis	Decreased salt tolerance	Tada and Ohnuma (2020)
<i>TaSNAC4-3A</i>	<i>Triticum aestivum</i> (wheat)	Arabidopsis	Increased GORK expression; increased salt tolerance	Mei et al. (2021)
<i>TsHKT1;2</i>	<i>Thellungiella salsuginea</i>	Arabidopsis	Increased salt tolerance	Ali et al. (2012)
<i>ZmHKT1;5</i>	<i>Zea mays</i> (maize)	<i>Nicotiana tabacum</i>	Increased salt tolerance	Jiang et al. (2018)

This table summarizes studies expressing potassium transport proteins or their regulators in different target species to improve aspects of abiotic stress tolerance. The gene name and the species from which it was obtained (source), the species in which it was expressed (target), the resulting phenotype and the reference are included. See the text for more details.