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REVIEW ARTICLE

Recent Advances in Genome-wide Analyses of Plant Potassium Transporter Families

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Abstract: Plants require potassium (K^+) as a macronutrient to support numerous physiological processes. Understanding how this nutrient is transported, stored, and utilized within plants is crucial for breeding crops with high K^+ use efficiency. As K^+ is not metabolized, cross-membrane transport becomes a rate-limiting step for efficient distribution and utilization in plants. Several K^+ transporter families, such as KUP/HAK/KT and KEA transporters and *Shaker*-like and TPK channels, play dominant roles in plant K^+ transport processes. In this review, we provide a comprehensive contemporary overview of our knowledge about these K^+ transporter families in angiosperms, with a major focus on the genome-wide identification of K^+ transporter families, subcellular localization, spatial expression, function and regulation. We also expanded the genome-wide search for the K^+ transporter genes and examined their tissue-specific expression in *Camelina sativa*, a polyploid oil-seed crop with a potential to adapt to marginal lands for biofuel purposes and contribution to sustainable agriculture. In addition, we present new insights and emphasis on the study of K^+ transporters in polyploids in an effort to generate crops with high K^+ Utilization Efficiency (KUE).

Keywords: KUP/HAK/KT transporters, *shaker*-like channels, TPK channels, KEA transporters, subcellular localization, gene expression, function, *Camelina sativa*.

1. INTRODUCTION

Potassium (K^+) is the most abundant mineral nutrient in plants, contributing up to 10% of dry biomass [1-3]. Plants require 100-200 mM K^+ in the cytoplasm [1, 4, 5] to carry out many fundamental processes involving membrane transport, protein synthesis, carbohydrate metabolism, enzyme activation, anion neutralization, osmoregulation, stomatal movement and photosynthesis [6-8]. However, the availability of K^+ is limited in soil (> 1mM) [9, 10], thus requiring fertilizer application to meet the nutritional demands for plant growth and productivity. The reliance on fertilizers is clearly not a long-term solution as both production and application of fertilizers cause pollution and threaten the sustainability of our environment. Further, K^+ fertilizer comes from potash, a natural resource that will be depleted in the near future [11, 12]. Thus, there is an urgent need to identify new methods to ensure sustainable mineral nutrition for optimal crop production by minimizing or removing fertilizer inputs. An effective strategy to achieve these goals is to breed crops with high K^+ use efficiency (KUE), which requires a better understanding of the K^+ transport systems within plants.

In plants, K^+ transport is mediated by four families of typical K^+ transport systems, which include KUP/HAK/KT (K^+ Uptake/High-Affinity K^+/ K^+ Transporter) transporters, *Shaker*-like channels, TPK/KCO (Tandem Pore K^+/K_{ir}-like K^+) channels, and KEA (K^+ Efflux Antiporter) transporters. These K^+ transporters and channels are required to cross the barriers presented by plasma membrane (PM) at the root epidermis for K^+ acquisition and membranes of the subcellular compartments for K^+ storage and distribution. Our current knowledge of these K^+ transport systems mainly stems from the model plant Arabidopsis. It is time for us to apply this knowledge to crop research to engineer high KUE crops. For this purpose, we need to first identify and understand the physiological role of these K^+ transporters and channels in various crop species as their diverse genetic backgrounds allow them to respond to the changing nutrient status differently. Through sequence homology, homologs of some of the key K^+ transporters found in Arabidopsis are identified and functionally characterized in several other plant species. With growing publications on plant genome sequences [13], we need to put more efforts into genome-wide search for K^+ transporter families in crop plants to initiate comparative genomic analysis and deduce how K^+ transporters evolve throughout domestication.

Polyploid crops are important groups in crop breeding, and yet little is known about these plant species. The previous work on multiple Arabidopsis accessions confirmed the beneficial effect of the polyploid nature in enhancing K^+ acquisition and salt tolerance [14]. Therefore, extending our

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studies to polyploid crops might reveal the underlying genes and regulatory mechanism that allow these crops to adapt to various environmental stresses. Oil-producing crops are important polyploids that support various commodities such as food, feeds and fuels. However, little effort has been made to understand how these polyploids might adapt to low-K^+ stress at the genomic level. To establish such a knowledge base, we first provide a comprehensive review of the four major K^+ transporter family genes in various model and crop species, with reference to other reviews that cover similar topics. We then extend our genome-wide search of the K^+ transporter family genes in *Camelina sativa* (false flax or gold-of-pleasure), an allohexaploid oilseed crop with a great potential for biofuel production on marginal lands to support sustainable agriculture [15-19]. In addition, we evaluated the tissue-specific expression of these K^+ transporter genes in Camelina using the publicly available transcriptomic data [16], and compared their expression profiles with other plant species to deduce functional conservation or divergence. Since the Camelina genome closely resembles Arabidopsis as members of the same Brassicaceae family [15], it provides a comparable polyploid model to study KUE.

2. KUP/HAK/KT TRANSPORTERS

2.1. Identification of KUP/HAK/KT Family in Plants

KUP/HAK/KT members are K^+ transporters present in fungi, plants and bacteria [20]. In plants, these K^+ transporters contain 10-14 transmembrane segments consisting of MFS (Major Facilitator Superfamily) domains [21-23]. The plant KUP/HAK/KT transporters are first identified in barley [24] and Arabidopsis [25-27], from their homology to bacterial KUP and fungal HAK transporters [28, 29]. Since then, KUP/HAK/KT transporters have been cloned from many other plant species, especially after genome sequence became available [30-40]. Genome-wide search by sequence homology has resulted in the identification of KUP/HAK/KT transporter family in several diploid and polyploid species, as shown in Table **1**. This K^+ transporter family is further identified in 46 angiosperm plant species, consisting of monocots and dicots [41]. So far, the genomes of more than 400 plant species [13], including ~50 polyploid plants [42] have been sequenced. However, the identification of K^+ transporter families is limited to a relatively small number of species. To facilitate understanding of gene duplication events among the K^+ transporters, we examined the Camelina genome and identified 38 KUP/HAK/KT transporters that are divided into five major clades (Fig. **1**). These include AtKUP1/2/6/8 and their close homoeologs in one large clade; and AtKUP3/4, AtKUP9/10/11, AtKUP5/7/12 and AtHAK5, and their corresponding Camelina homoeologs in four separate clades. Genome triplication of Camelina has resulted in maintaining triplet homoeologs for the majority of Arabidopsis KUP/HAK/KT orthologs, while further gene duplication resulted in an additional member for AtKUP9 ortholog. Two Camelina homoeologs are identified for AtKUP3 and AtKUP11 orthologs. Interestingly, both diploid and polyploids have evolved a large number of KUP/HAK/KT transporters through whole-genome multiplication or gene duplication events, signifying the importance of these K^+ transporters for plant productivity.

2.2. Subcellular Localization and Expression Pattern of KUP/HAK/KT Transporters

The in-depth reviews on the KUP/HAK/KT transporters in terrestrial photosynthetic organisms [57], and their function and regulation [23] are recently published. Several KUP/HAK/KT transporters are localized to the PM based on experiments using transgenic plants or protoplasts. Other members of this family also localize to various subcellular compartments, including AtKUP4 in endomembrane [58]; AtKUP12 in chloroplast [59, 60]; OsHAK10 and potentially AtKUP5/7/12 transporters in vacuole [44, 61, 62]; and AtKUP9 in endoplasmic reticulum (ER) [63]. This suggests the potential roles of these K^+ transporters in not only K^+ acquisition, but also in K^+ distribution *via* sequestration into or remobilization from various subcellular compartments to maintain K^+ homeostasis.

Table 1. The genome-wide identification of KUP/HAK/KT family in plants.

Plant Species	Common Name	Ploidy Level	KUP/HAK/KT Members	References
Arabidopsis thaliana	Arabidopsis	Diploid	13	[43]
Oryza sativa L.	Rice	Diploid	27	[2, 44, 45]
Zea mays L.	Maize	Diploid	27	[45]
Populus trichocarpa	Poplar	Diploid	31	[46]
Solanum lycopersicum L.	Tomato	Diploid	19	[47]
Pyrus bretschneideri	Pear	Diploid	20-21	[48, 49]
Setaria italica	Foxtail millet	Diploid	29	[50]
Arabidopsis lyrata	Arabidopsis	tetraploid	15	[41]
Glycine max	Soybean	Allotetraploid	29-32	[41, 51]
Manihot esculenta Crantz	Cassava	Diploid, autotetraploid	21	[52]
Nicotiana tabacum	Tobacco	Allotetraploid	41	[53]
Saccharum spontaneum	Sugarcane	Autotetraploid	30	[54]
Brassica napus	Rapeseed	Allohexaploid	40	[55]
Triticum aestivum L.	Wheat	Allohexaploid	56	[56]

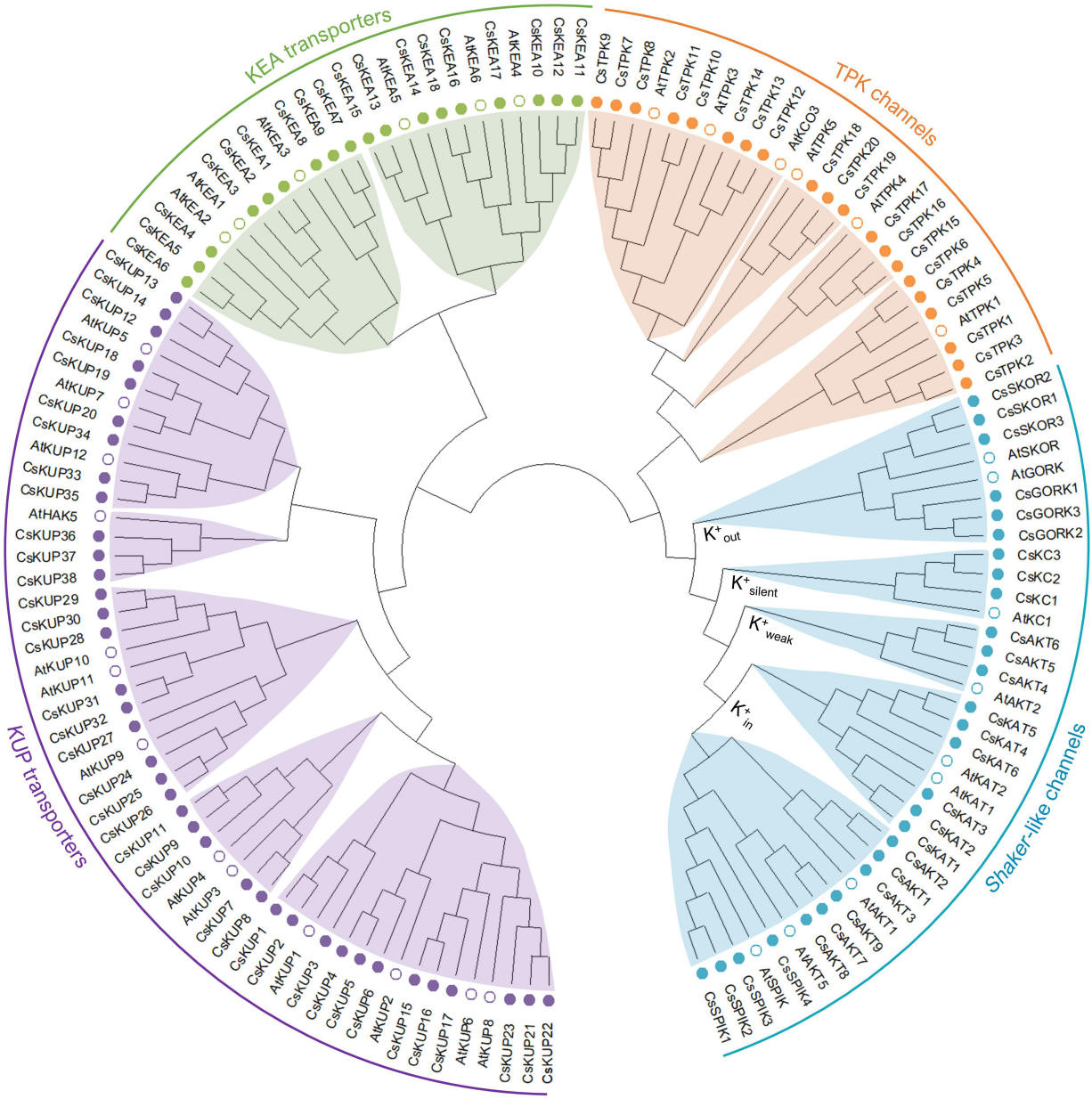

Fig. (1). Evolutionary relationship between Camelina and Arabidopsis K^+ transporters. The four major K^+ transporter family proteins are color-coded, with distinct clades. The Camelina K^+ transporters are represented in closed circles, and Arabidopsis in open circles. The gene IDs are presented in Table **S1**. (*A higher resolution / colour version of this figure is available in the electronic copy of the article*).

The diverse roles of KUP/HAK/KT transporters are also implicated by their tissue-specific expression. Generally, *KUP/HAK/KT* genes are expressed in multiple tissues throughout various developmental stages (roots, leaves, flowers, seeds and so forth) in Arabidopsis [43], rice [36], maize [45], wheat [56], pear [49], and sugarcane [54]. This is also evident in Camelina, where *CsKUP* genes are expressed in 12 different tissues covering four developmental stages (Fig. **2A**). In terms of tissue-specific expression, *AtKUP8*-like genes in Camelina are predominantly expressed in leaves; *AtKUP9*- and *AtHAK5*-like genes in roots; *AtKUP1*-like genes in reproductive organs; and *AtKUP6*- and *AtKUP11*-like genes in seeds. While some of their functions are confirmed in these tissues in Arabidopsis such as AtHAK5 in root K^+ uptake [64, 65] and AtKUP9 [63] in maintaining root meristem activity under low-K^+ stress, the physiological roles of other AtKUP transporters in various tissues remain unresolved.

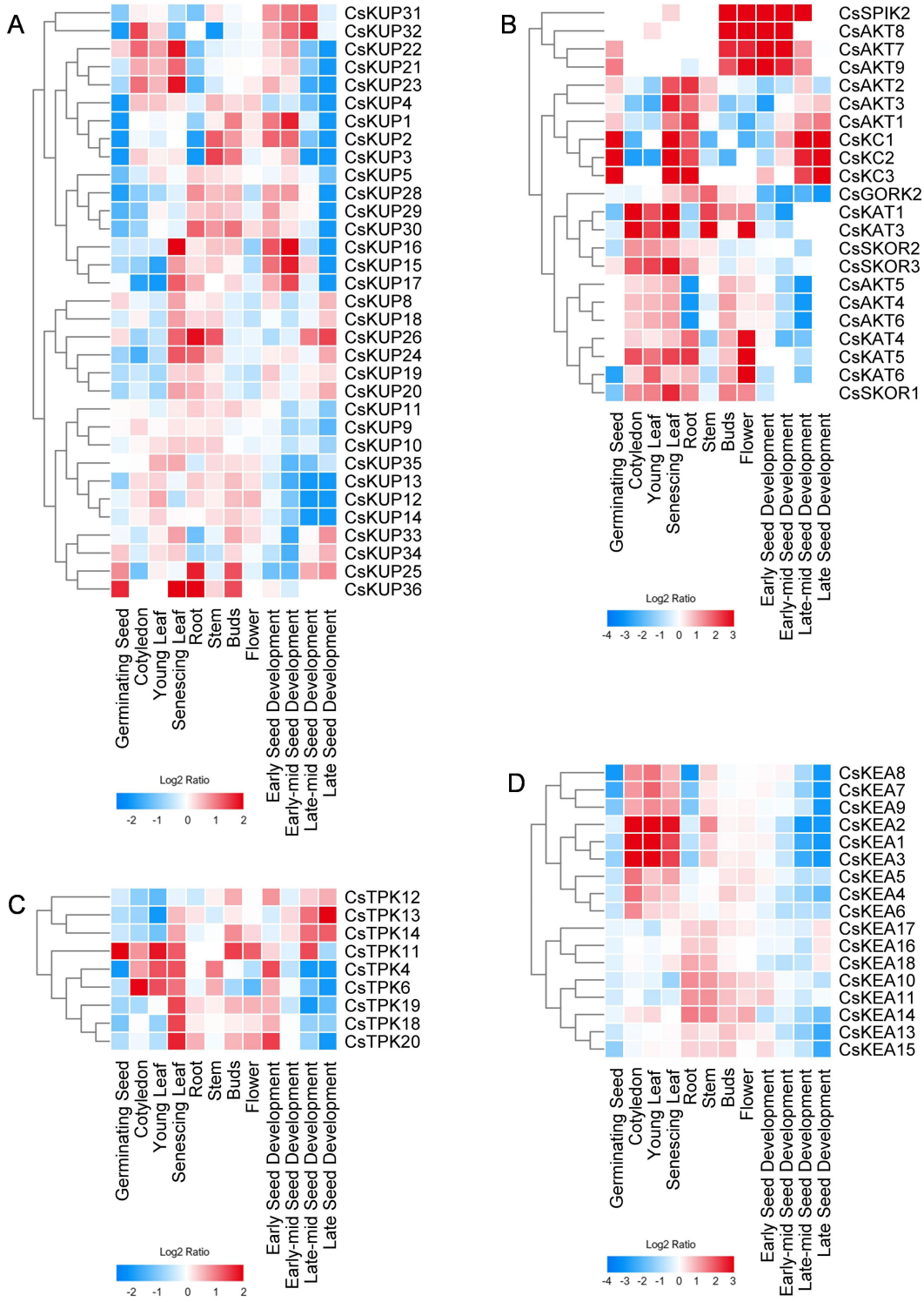

Fig. (2). Spatial expressions of the Camelina **(A)** *KUP,* **(B)** *Shaker-like,* **(C)** *TPK* and **(D)** *KEA* transporter family genes in twelve different tissues covering the whole life cycle. The transcriptomic data are extracted from Camelina eFP browser (http://bar.utoronto.ca/efp_camelina/cgi-bin/efpWeb.cgi) [16]. Genes without available data or no expression are excluded. (*A higher resolution / colour version of this figure is available in the electronic copy of the article*).

2.3. Function and Regulation of KUP/HAK/KT Transporters

The transport activities of several KUP/HAK/KT transporters have been studied in heterologous systems. AtKUP1 is the first plant KUP/HAK/KT member to be identified using a yeast system [26]. The *in planta* function of some of these transporters have been examined using genetic mutants. The Arabidopsis *AtHAK5*, and its close homologs in barley (*HvHAK1*) [24], rice (*OsHAK1*) [37, 44], tomato (*LeHAK5*) [30, 66], pepper (*CaHAK5*) [32], salt cress (*ThHAK5*) [67], wheat (*TaHAK1*) [56], foxtail millet (*SiHAK1*) [50], pear (*PbHAK12*) [49], and maize (*ZmHAK1*) [68] are highly expressed in roots and serve as PM-localized K^+-uptake transporters under low-K^+ stress. The other KUP/HAK/KT transporters that mediate K^+ transport in Arabidopsis include AtKUP2/6/8 in K^+ efflux from root stele [69], and AtKUP7 in K^+ uptake from roots and translocation to shoots under low-K^+ stress [70]. Several KUP/HAK/KT transporters in other plant species are also found to function in K^+ uptake under K^+ deficiency, which include lotus *LjKUP* [33], rice *OsHAK5/16/19/20/21/27* [37, 71-73], cotton *GhKT2* [39], maize *ZmHAK5* [68], Goji *LrKUP8* [40], and sugarcane *SsHAK1/21* [54]. In rice, OsHAK5 and OsHAK21 might also be involved in long-distance K^+ transport between roots and shoots as they are highly expressed in root vasculature [37, 71]. Some KUP/HAK/KT family transporters also appear to promote K^+ uptake when symbiotically associated with *Arbuscular mycorrhizal* (AM) fungi. For instance, mutation of tomato *SlHAK10* led to reduced mycorrhizal-mediated K^+ uptake and lower AM colonization rate under low-K^+ stress [74].

Beyond K^+ acquisition, KUP/HAK/KT transporters are also involved in plant development and in response to various abiotic stresses. For instance, AtKUP4/TRH1 contributes to the polar auxin transport in root apex to generate auxin gradients for gravitropic responses and root hair growth [58, 75, 76]. AtKUP9 has been shown to control primary root growth and meristematic activity by mediating K^+ and auxin efflux from the ER lumen to the cytoplasm in quiescent center cells under low-K^+ conditions [63]. AtKUP2 (SHY3) [77], GhKT1 [78], and VvKUP1/2 [35] are involved in cell expansion in Arabidopsis, cotton and grape, respectively. AtKUP2/6/8 negatively affect lateral root formation, but play a positive role in drought response by modulating turgor and hormone signaling in roots and guard cells [69]. Several KUP/HAK/KT transporters in other plant species are shown to be involved in drought tolerance [79, 80] and salt tolerance [37, 40, 64, 65, 71, 81, 82].

While the functional studies are gradually expanding in Arabidopsis and other plant species, our understanding of the regulation of these KUP/HAK/KT transporters is still in its infancy. At the transcriptional level, studies have shown that *AtHAK5* expression is controlled by several transcriptional factors, including RAP2.11 (AP2/ERF), DDF2 (Dwarf and Delayed Flowering 2), JLO (Jagged Lateral Organs), TFII_A (Transcription initiation Factor II-A gamma chain), bHLH121 (basic Helix-Loop-Helix 121) and ARF2 (Auxin Response Factor 2) [23, 57, 83]. The post-translational regulation of KUP/HAK/KT transporters by several protein kinases has been reported, such as phosphorylation-dependent activation of AtHAK5 and its close homologs in other plant species by the CBL-CIPK (Calcineurin B-Like sensor and CBL-Interacting Protein Kinase) signaling networks [7, 23, 57, 83]. The other potential candidate kinases include SRK2E (SNF1-Related protein Kinase 2E) and ILK1 (INTERGRIN_LINKED KINASE1) that physically interact with AtKUP6 and AtHAK5 in Arabidopsis, respectively, and CrRLK1L receptor kinase with OsHAK1/19/20 in rice [23, 57].

3. *SHAKER*-LIKE CHANNELS

3.1. Identification of *Shaker*-like Family in Plants

Shaker-like channels are K^+-selective voltage-gated channels that are found in both prokaryotes and eukaryotes. Arabidopsis has nine *Shaker*-like channels categorized into several subfamilies based on their differential voltage responses [84]. These include inward-rectifying (K^+_{in}) channels such as AtAKT1, AtAKT5, AtSPIK, AtKAT1 and AtKAT2 that are activated by hyperpolarization and mainly mediate K^+ uptake [84-88]. Contrarily, the outward-rectifying (K^+_{out}) channels, such as AtSKOR and AtGORK, are activated by depolarization and mediate K^+ efflux [89, 90]. The weakly rectifying (K^+_{weak}) channels, such as AtAKT2, could be activated by hyperpolarization and may mediate both K^+ uptake and release depending on the membrane potentials [91-94]. AtKC1 is considered an electrically silent (K^+_{silent}) channel but can form heteromeric complexes with K^+_{in} channels to regulate their activities in response to changing environmental conditions [95-98]. These *Shaker*-like channels share a similar hydrophobic core consisting of six transmembrane segments with voltage-sensor and pore loop modules [2, 84]. These channels in plants typically contain a long cytoplasmic C-terminal region featuring a putative cyclic nucleotide-binding domain and, in some, an ankyrin repeat domain [2, 84].

The first insight in the molecular analysis of membrane K^+ transport in plants comes from the identification of *Shaker*-like channels, AtAKT1 and AtKAT1, in Arabidopsis by functional complementation of yeast strains defective in K^+ uptake [99-101]. Later, many genes encoding *Shaker*-like channels have been functionally characterized in Arabidopsis and other plant species, discussed in the following section. However, only a few plant species were examined using genome-wide analysis to identify the complete set of *Shaker*-like channels. These studies revealed 9 members in Arabidopsis [84] and grapevine [102], 11 in rice [2, 84] and poplar [103], 8 in pear, 10 in apple, 6 in peach, strawberry and Chinese plum [104]. To extend this effort, here we identified 28 *Shaker*-like channels in Camelina, with three homoeologs for each Arabidopsis ortholog except AtSPIK1 with an additional member (Fig. **1**). Similar to Arabidopsis,

these channels in Camelina are classified into five groups based on functional diversifications [84].

3.2. Subcellular Localization, Expression, Function and Regulation of *Shaker*-like Channels in Arabidopsis

In Arabidopsis, the *Shaker*-like family is the most intensively studied among all the K^+ transport systems. The expression pattern of *Shaker*-like genes at tissue and cell-type levels, their functions and regulations have been characterized and previously reviewed [7, 12, 20, 83, 105-108]. To briefly summarize, the *Shaker*-like channels are usually localized at the plasma membrane of plant cells and dominate the membrane conductance in most cell types [20]. *AtAKT1* is highly expressed in root hairs, epidermis and cortex to absorb K^+ from soil under varying K^+ concentrations [34, 85, 109]. *AtKC1* is expressed in similar tissues where it interacts and inhibits the activities of the K^+_{in} channels such as AKT1, AKT2, KAT1 and KAT2 by forming heteromeric complexes [95-98]. After K^+ enters the root cells, *AtSKOR*, highly expressed in root stele (pericycle and xylem parenchyma cells), loads K^+ into the xylem and initiates long-distance transport of K^+ from root to the aerial parts of the plants [89, 110]. In parallel, the recycling of K^+ from shoot to root may be mediated by AtAKT2 *via* phloem loading [91, 111, 112]. *AtGORK* is expressed in guard cells where it contributes to K^+ efflux to control stomatal closure in response to environmental changes [90, 113-115]. *AtKAT1* and *AtKAT2* are also expressed in guard cells where they form heteromeric channels that mediate K^+ influx to promote stomatal opening [86, 100, 116, 117]. The roles of *Shaker*-like channels in stomatal movement and the associated signaling networks are comprehensively reviewed elsewhere [106, 118, 119]. Among the *Shaker*-like channels, *AtAKT5 and AtSPIK* display flower-specific expression, with the confirmed role of AtSPIK in K^+ influx into germinating pollen to promote pollen tube growth and development [87, 88, 91]. However, the physiological role of AtAKT5 has yet to be evaluated. The regulation of *Shaker*-like channels in Arabidopsis by transcriptional factors, hormones, pH, calcium-dependent protein kinases, phosphatases, 14-3-3 proteins and so forth are discussed in detail in recent reviews [7, 12, 83, 120].

3.3. Expression and Function of *Shaker*-like Channels in Other Plant Species

The comparison of tissue-specific expression of the *Shaker*-like channels between Arabidopsis and other plant species is reviewed [20]. Many *Shaker*-like channels have been functionally characterized in various plant species using patch-clamp systems (Table **2**). These channels display overlapping expression and conserved K^+ transport properties as their Arabidopsis counterparts. However, divergence is also observed between and within dicots and monocots because of variations in plant architectures and cell types. For instance, rice OsAKT1.2, another close homolog of AtAKT1, is shown to be involved in reproduction as it is highly expressed in pollen and the knockout lines display reduced pollen germination rates [121]. In maize, ZMK1 (AtAKT1-like) is an inward-rectifying K^+ channel whose expression is auxin-induced and implicated in coleoptile growth and gravitropism [122-124].

While Arabidopsis possesses two AtKAT channels, four AtKAT1-like members are found in maize (KZM1-4) [125] and three in rice (OsKAT1-3) [126, 127]. KZM1/ZmK2.1 functions as a K^+_{in} channel in leaf epidermis and vascular strands, however it cannot mediate K^+ influx in the submillimolar concentration range, unlike its Arabidopsis orthologs [128, 129]. *KZM2* and *KZM3* display *AtKAT*-like expression in guard cells and promote K^+ influx in HEK293 cells, but KZM2 did not mediate K^+-inward currents in oocytes, instead inhibited the activity of KZM3 as a heteromeric channel [125]. In rice, OsKAT2 plays a major role in K^+ influx into guard cells; however, its activity is inhibited by OsKAT3 when coexpressed in CHO cells [126, 127].

The GORK function is conserved in both monocots and dicots (Table **2**). However, GORK channels in monocots are additionally expressed in subsidiary cells that form stomatal complexes along with guard cells. Moreover, OsK5.2/OsGORK is found to perform dual function in stomatal movement and K^+ loading into xylem sap, which requires the action of both AtGORK and AtSKOR in dicots [130]. A similar situation might happen in poplar in which *PTORK* is expressed in both vascular tissues and guard cells [131, 132]. Interestingly, single amino acid mutations in AtSKOR and AmGORK can convert these outward-rectifying channels into an inward-rectifying and leak-like channel (AtAKT2/3-like), respectively [133, 134], implying a common ancestor of inward and outward channels in the *Shaker*-like family.

The AtAKT2/3-like channels are found in four other plant species, which display similar phloem-specific expressions and conserved functions as weak-rectifying K^+ channels (Table **2**). However, *VvK3.1* is additionally expressed in the pulvinus (a motor organ) that is involved in paraheliotropic leaf movement [135, 136]. Barley HvAKT2 is also a weakly-rectifying K^+ channel, but, unlike Arabidopsis, it is more expressed in leaves than roots [137, 138]. Moreover, maize *ZMK2* is expressed in vascular-enriched coleoptile sections, *e.g.,* the mesocotyl and primary leaves, where it mediates voltage-independent K^+ currents [122, 123]. Currently, the physiological roles of many of these *Shaker*-like channels in different plant tissues and organs are unknown.

We also examined the expression of *Shaker*-like genes in Camelina and have found that they follow a similar pattern as in Arabidopsis (Fig. **2B**). For instance, *AtAKT1*- and *AtKC1*-like genes in Camelina are highly expressed in roots in which they might control K^+ acquisition from the soil. The *AtKAT*- and *AtSKOR*-like genes are highly expressed in leaves with a potential role in regulating stomatal movement. The *AtAKT5*- and *AtSPIK*-like genes are expressed in reproductive organs. However, *AtAKT2*-like genes in Camelina are not expressed in roots, unlike Arabidopsis. In addition, the *AtGORK*-like gene is not expressed in green leaves, but more in root and stem. These differences may suggest divergence in functions between diploid Arabidop-

Table 2. The conserved roles of *Shaker*-like channels in plants.

Arabidopsis Orthologs	Channel Names	Plant Species	References
AtAKT1	SKT1	*Solanum tuberosum*	[139, 140]
	LKT1	*Solanum lycopersicum*	[141]
	NKT1	*Nicotiana tabacum*	[142]
	HvAKT1	*Hordeum vulgare*	[138]
	VvK1.1	*Vitis vinifera*	[143]
	GhAKT1	*Gossypium hirsutum*	[144]
	OsAKT1 (OsK1;1)	*Oryza sativa*	[145]
AtKAT1/2	KST1	*Solanum tuberosum*	[139]
	SIRK (VvK2.1)	*Vitis vinifera*	[146]
	KPT1	*Populus tremula*	[147]
	AmKAT1	*Ammopiptanthus mongolicus*	[148]
	PbrKAT1	*Pyrus bretschneideri*	[104]
	KZM2	*Zea mays*	[125]
	OsKAT2	*Oryza sativa*	[126, 127]
AtGORK	NTORK	*Nicotiana tabacum*	[142]
	AmGORK	*Ammopiptanthus mongolicus*	[134]
	MtGORK	*Medicago truncatula*	[149]
	OsK5.2 (OsGORK)	*Oryza sativa*	[130]
	ZORK	*Zea mays*	[150]
AtSKOR	CmSKOR	*Cucumis melo* L.	[151]
	Vv5.1	*Vitis vinifera*	[136]
AtAKT2	VFK1	*Vicia faba*	[152]
	PTK2	*Populus tremula*	[131]
	VvK3.1	*Vitis vinifera*	[135, 136]
	OsAKT2	*Oryza sativa*	[153]
AtKC1	KDC1	*Daucus carota*	[154]

sis and hexaploid Camelina over the course of evolution. Interestingly, *AtKC1*-like genes in Camelina share overlapping expression patterns with *AtAKT5*-like genes in germinating seeds, *AtAKT1*- and *AtKAT*-like genes in senescing leaves and many in roots. This implies that AtKC1-like silent channels may form heteromeric channels with a broad spectrum of K^+_{in} channels in Camelina to fine-tune plant response to the changing K^+ availability and other environmental conditions.

4. TPK CHANNELS

4.1. Identification of TPK Family in Plants

TPK/KCO family proteins are voltage-independent K^+ channels that consist of six members in Arabidopsis. These include five tandem-pore channels, AtTPK1-5, and a single K_{ir}-like channel, *AtKCO3*. These AtTPK channels possess four transmembrane segments and two pore-loop domains in tandem, whereas *AtKCO3* has two transmembrane segments and a single pore-loop domain [105, 155-157]. Members of the TPK/KCO family contain Ca^{2+}-binding EF-hands in the cytosolic C-terminal region and 14-3-3 protein binding sites in the cytosolic N-terminal region [105, 157]. AtTPK1 is the first plant TPK channel to be identified *via* an Arabidopsis EST database search for the conserved K^+ channel pore domain motif TXGYGD [106, 158]. Later, its homologs are found and characterized in tobacco (NtTPK1) [159] and in strawberry (FaTPK1) [160]. Only limited effort has been made to survey the TPK/KCO channels in other plant species using genome-wide analysis, which identified 3 TPK family members in rice [2, 103], 10 in poplar [103], and 9 in soybean [51]. We additionally identified 20 CsTPK channels in Camelina, with triplet homoeologs for AtTPK3/4/5 orthologs and no homoeolog for *AtKCO3* ortholog (Fig. **1**). Moreover, the Camelina genome underwent further expansion in AtTPK1- and AtTPK2-like channels, with 6 and 5 homoeologs, respectively. These TPK/KCO channels in Camelina are phylogenetically divided into four major clades, with AtTPK1 and its close homoeologs in one clade, AtTPK2/3 and their close homoeologs in another large clade along with *AtKCO3*, and AtTPK4 and AtTPK5 with their corresponding homoeologs into two separate clades.

4.2. Subcellular Localization and Expression of TPK Channels

All the Arabidopsis TPK/KCO channels are localized to tonoplast except AtTPK4, which is localized to PM [161-165]. Tonoplast localization is also observed for strawberry FaTPK1 [160], tobacco NtTPK1 [159], and rice OsTPKa (lytic vacuoles) and OsTPKb (protein storage vacuoles)

[166]. The expression patterns of *AtTPK* and *AtKCO3* genes are assessed in-depth using qRT-PCR and promoter-reporter gene (GUS) fusions [157, 167]. The overlapping expression is observed for *AtTPK1/5* and *AtKCO3* genes in vascular tissues, *AtTPK1/3* in root tips, and *AtTPK1/2/3/4* in pollen [157, 167]. Tobacco *NtTPK1*, and rice *OsTPKa* and *OsTPKb* are ubiquitously expressed, similar to *AtTPK1* [159, 166]. Soybean *GmKCO1* (Glyma02g46930.1) and *GmKCO2* (Glyma19g40890.1) genes are differentially expressed in nodulated root hairs, implying their roles in nodulation [51]. In Camelina, almost all *CsTPK* genes are expressed in senescing leaves, with *AtTPK1*- and *AtTPK2*-like genes displaying the predominant expression in leaves throughout the vegetative growth (Fig. **2C**). This suggests the potential roles of these CsTPKs in K^+ remobilization from vacuoles of the source to sink during the aging process. In addition, many *CsTPK* genes are expressed in early-seed development, suggesting these genes might be involved in seed maturation. Interestingly, *AtTPK3*-like genes in Camelina are expressed predominantly in late-seed development, implying their possible roles in K^+ storage into seed vacuoles to support the next growth cycle.

4.3. Function and Regulation of TPK Channels

The physiological roles of a few AtTPK channels have been examined in Arabidopsis. AtTPK1 mediates K^+ release from vacuoles under low-K^+ stress to maintain K^+ homeostasis, and plays a role in stomatal closure and seed germination [161, 164, 167-170]. The tonoplast-localized AtTPK2 and AtTPK5 channels are shown to form functional K^+ transport systems in *E. coli* [171], but their physiological roles in plants are yet to be elucidated. AtTPK3 is also present in the vacuole and may function in K^+ remobilization [165, 167, 172]. On the other hand, AtTPK4 is an open rectifier that contributes to the K^+ conductance across the PM of pollen tubes [163].

Aside from studies in Arabidopsis, TPK homologues have also been analyzed in other plants. For example, tobacco NtTPK1 complimented K^+ uptake-deficient *E. coli* and exhibited high selectivity for K^+ over Na^+ in patch-clamp studies [159]. In rice, the transgenic lines overexpressing *OsTPKb* display higher K^+ content and better growth under low-K^+ and drought stress [173]. In addition, vacuolar TPKs have been shown to be mechanosensitive and osmosensitive when examined using patch-clamp experiments [174]. In strawberry, vacuolar FaTPK1 is associated with fruit ripening, linking K^+ homeostasis to fruit quality and commercial value [160].

In terms of regulation, the activity of plant TPK channels is dependent on cytosolic factors such as calcium (Ca^{2+}), 14-3-3 proteins and pH [155, 163, 164, 168-170, 175, 176]. The maintenance of proper cytosolic pH has been shown to be critical for the channel activities of AtTPK1/4 in Arabidopsis [163, 164] and NtTPK1 in tobacco [159]. The interaction between 14-3-3 proteins and TPKs are confirmed in barley (HvTPK1) [177], rice (OsTPKb) [166] and Arabidopsis (AtTPK1 and AtTPK5) [157, 169]. Because TPKs harbor EF-hand motifs for Ca^{2+} binding, cytosolic Ca^{2+} elevation has been shown to activate AtTPK1 [155, 168, 169], AtTPK3 [176], OsTPKb [166], and NtTPK1 [159]. In addition, a Ca^{2+}-dependent protein kinase, CPK3, has been shown to phosphorylate and activate the AtTPK1 channel in response to salt stress [175]. Further, Ca^{2+}-dependent CBL2/3-CIPK3/9/23/26 complexes also promote AtTPK1 channel activity to maintain K^+ homeostasis under low-K^+ stress [170]. Because these vacuolar channels are essential for plant adaptation to multiple stresses, more in-depth analysis is required in order to fully understand the function of TPK channels (*e.g.,* AtTPK2/3/5 and *AtKCO3*) at the physiological and mechanistic levels in Arabidopsis and other plant species.

5. KEA TRANSPORTERS

5.1. Identification of KEA Family in Plants

The KEA transporter family is a subgroup of the large Cation/Proton Antiporter (CPA) superfamily. These transporters are highly homologous to the bacterial K^+/H^+ antiporters KefB and KefC [178, 179]. Six KEA members are encoded in the Arabidopsis genome, and phylogenetically, they diverge into two clades with AtKEA1/2/3 in clade I and AtKEA4/5/6 in clade II [178, 180]. Both clades contain an N-terminal Na^+/H^+ exchange domain, but only clade I contains C-terminal KTN (K^+ transport, nucleotide-binding) domain [178]. Sequence homology to Arabidopsis AtKEAs found 6 members in maize [181], 4 in rice [181], 12 in pear [182] and soybean [51], and 24 in wheat [183]. In Camelina, 18 CsKEA members are identified that form two major clades, with three homoeologs for each Arabidopsis ortholog (Fig. **1**).

5.2. Expression Patterns of KEA Transporter Genes

In Arabidopsis, the expression patterns of all six *AtKEA* genes are evaluated in detail [179]. The promoter-GUS fusions reveal overlapping expressions of *AtKEA2/4/5/6* in root steles, with *AtKEA4* additionally expressed in root tips [179]. In leaves, all *AtKEA* genes are expressed in guard cells except *AtKEA6* [179]. *AtKEA1/2/3* genes are also expressed in leaf vasculature and petioles, whereas *AtKEA4/5/6* in trichomes [172, 179, 184]. In flowers, all *AtKEA* genes are expressed in the sepals, but only *AtKEA1* in pollen grains [179]. In wheat, the majority of *AtKEA1/2/3*-like genes are expressed in leaves, whereas *AtKEA4/5/6*-like genes are more broadly expressed in the stem, spike, leaves and roots [183]. Similarly, *AtKEA1/2/3*-like genes in Camelina are also predominantly expressed in leaves, with *AtKEA1*-like genes displaying the highest levels (Fig. **2D**). On the other hand, *AtKEA4/5/6*-like genes in Camelina are all expressed in the roots and stems during vegetative growth, and several are expressed at a lower level in floral organs. These similar expression patterns in different plants suggest conserved functions of KEAs.

5.3. Subcellular Localization, Function and Regulation of KEA Transporters

AtKEA1 and AtKEA3 peptides are first detected in Arabidopsis chloroplast proteome [185]. AtKEA1 and AtKEA2 proteins are later found to localize to the inner envelope membrane of chloroplasts, whereas AtKEA3 is targeted to the thylakoid membrane [186]. The first functional study of the AtKEA transporter family came across by reconstituting AtKEA2 transporter in liposomes, which demonstrated cation/H^+ antiport activity with a preference for K^+ [184]. Later, clade I AtKEA1/2/3 transporters were found to be critical for photosynthesis, chloroplast structure, osmoregulation, and K^+/pH homeostasis [186]. These plastidial AtKEA transporters are also important for stress-induced Ca^{2+} elevation [187]. In addition, AtKEA3 transporter has been shown to increase photosynthetic efficiency under fluctuating light by reducing pH-dependent energy dissipation [172, 186, 188]. The role of KEA transporters in chloroplast development is also conserved in rice as the *Osam1* (*Atkea2*-like) mutants display similar phenotypes with impaired photosynthetic activity and abnormal plastid structure [189].

Clade II AtKEA4/5/6 transporters are found in Golgi, trans-Golgi network and prevacuolar compartment [190, 191]. These AtKEA transporters are crucial for maintaining K^+/H^+ homeostasis in the endomembrane networks to support plant growth and adapt to various abiotic stresses. The disruption of these genes in Arabidopsis (*Atkea4 Atkea5 Atkea6* triple mutants) resulted in a broad spectrum of defects in the mutant plants, including hypersensitivity to low-pH, low- and high-K^+, high-Na^+ and high Li^+ stresses [190, 191]. The mutants also show more acidic pH in the endomembranes and growth defects in skotomorphogenesis [190, 191]. However, the precise and specific physiological roles of AtKEA transporters and their underlying regulatory mechanisms in both chloroplast and endomembranes remain unexplored. In addition, there are minimal studies of KEA transporter in other plant species, which is worth further investigation.

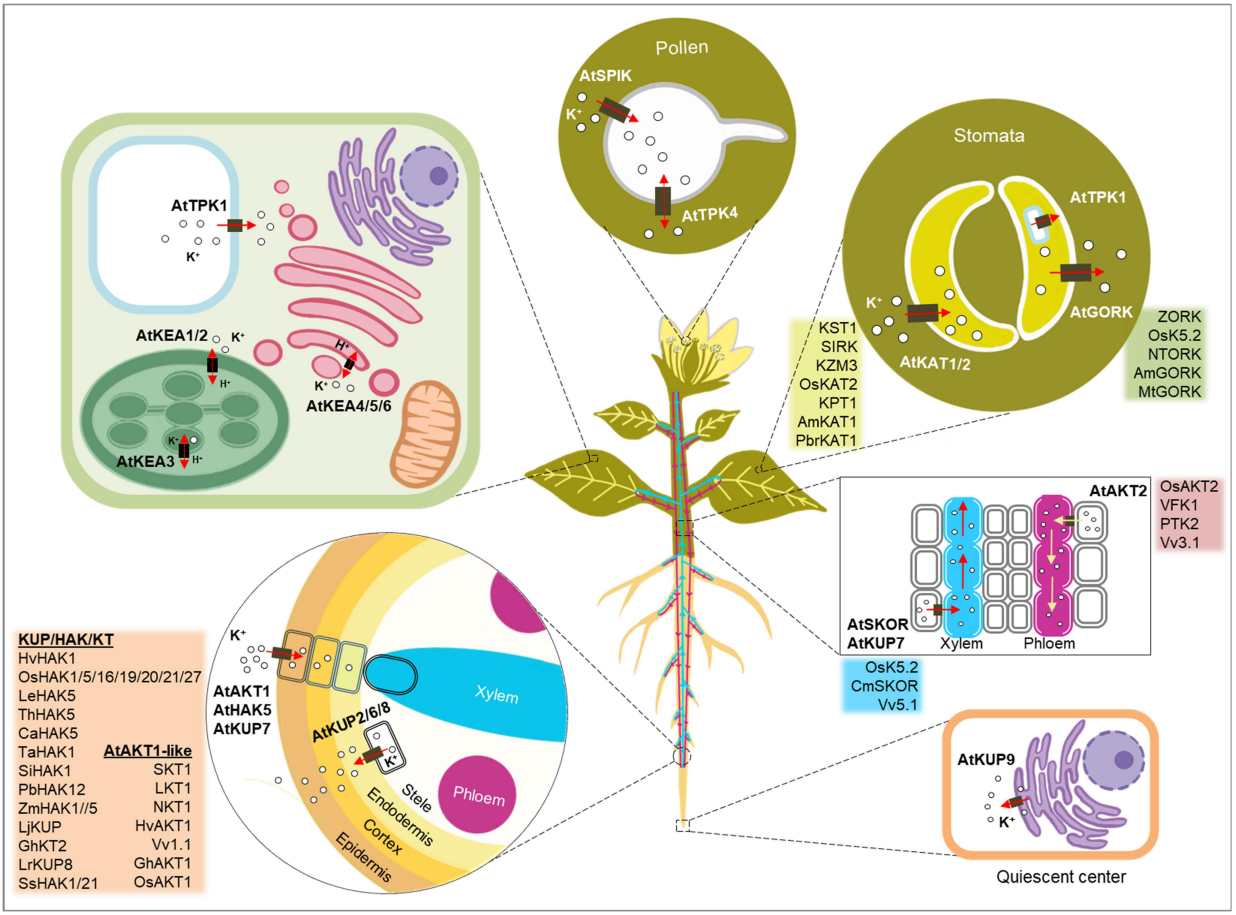

Fig. (3). Physiological roles of the K^+ transporters and channels in Arabidopsis and other plant species discussed in this review. For simplicity, the Arabidopsis genes are placed within the diagram and their closely-related genes from the other plant species are listed in the colored boxes. (*A higher resolution / colour version of this figure is available in the electronic copy of the article*).

CONCLUSION

In this review, we provide the current knowledge of K^+ transport systems in angiosperms. Fig. (**3**) summarizes the physiological roles of known K^+ transport systems in Arabidopsis and other plant species. Essentially, plants possess K^+ transport systems to facilitate K^+ uptake from the rhizosphere and further transport from roots to the aerial parts. At the cellular level, K^+ needs to be distributed into various cell types and subcellular compartments to support numerous physiological functions. While KUP/HAK/KT transporters and *Shaker*-like channels play major roles in K^+ uptake from soil and translocation to various tissues and organs, TPK channels and KEA transporters mediate K^+ transport in and out of different subcellular compartments. *Shaker*-like and TPK channels share complementary functions in stomatal movement and pollen tube growth.

Genome-wide query and transcriptomic analysis of the K^+ transporter genes can open a gateway for comparative genomic analysis and functional studies. In general, we find that the K^+ transporter family genes have expanded in both diploid and polyploid crops over the course of evolution, implicating the need to efficiently acquire and distribute K^+ to support plant growth under the changing nutrient status. Using Camelina as a potential polyploid model, we show how the polyploidization led to the expansion of specific K^+ transporter genes. For example, the copy numbers of *AtTPK1* and *AtTPK2*-like genes encoding vacuolar K-remobilizing transporters have doubled beyond its ploidy norm, which may contribute to enhanced K^+ remobilization in response to K^+-deficiency. In addition, the comparison of the expression profile of the K^+ transporter genes in Camelina with other plant species provides us with additional insights into the functional conservation and divergence in a specific tissue. Leveraging such publicly available datasets will initiate further functional studies in economically important crops.

While we find the functional conservation of several key K^+ transporters across multiple plant species, some variations exist due to the difference in genetic composition and plant architecture, as observed in monocots and dicots. Therefore, transitioning our studies to different crop species is critical to find novel K^+ transporters that evolved to function in a specific cell type, organ or tissue. However, the increased genetic complexity of crops imposes challenges in the functional analysis as the expanded genes resulting from genome or gene duplication events present high genetic redundancies. Genome-wide association studies and transcriptomic analyses may reveal natural genetic diversities present in a crop species under low-K^+ stress and will help identify important genetic loci and genes that contribute to high KUE. Further genetic analysis using the CRISPR-Cas9 system to generate single and higher-order mutants of these candidate K^+ transporters will be needed to study the dosage effect and the functional dominance among the closely related genes. Moreover, a great effort is required to dissect the regulatory mechanisms of the K^+ transporters and channels, even in Arabidopsis. Such studies will aid in unlocking the complexity of the K^+ transport in crops and ultimately lead to the genetic engineering of high KUE crops to support sustainable agriculture.

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CONFLICT OF INTEREST

The authors declare no conflict of interest, financial or otherwise.

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SUPPLEMENTARY MATERIALS

Supplementary material is available on the publisher's website along with the published article.

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