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Genomic Identification of HKT, AKT and KEA Gene Families Involved in Potassium Transport

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Abstract

Potassium is considered a key nutrient for plants and plays a vital role in the growth of plants by affecting various metabolic processes. Further, potassium can be used as a supplement and helps to protect plants from numerous diseases. Various genes have been reported for their involvement in the potassium transportation of plants. However, potassium transportation mechanisms are still unclear. Plants have an organized and complex potassium distribution system (channels and transporters). These channels and transporters are responsible for the uptake of K^+ from the soil and its distribution among different parts of the plant. In the present studies, the potassium transportation system of wheat (*Triticum aestivum*) was identified along with the characterization of 25 genes (11 K^+ channels and 14 K^+ transporters). Protein structure predictions were performed, and 3D structures of the identified genes were reported, including their domains and motifs. Gene structural analyses showed that the introns and exons have similarities with the known sequences of rice and *Arabidopsis thaliana*. The identifications and characterization of potassium transportation genes may help to introduce new varieties of wheat with higher content of potassium.

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Introduction

Potassium (K^+) ions are the basic nutrient and essential component of plants. Potassium plays a key role, and its deficiency causes metabolic changes that lead to serious malfunctions in growth [1]. The abundance of K^+ in plants is up to 10 grams per kilogram (plant dry weight). K^+ is also a key player in terms of its importance regarding several plant processes like regulation of plant water level, biosynthesis, and photosynthesis [2]. Potassium also maintains the hormonal secretions and potassium content of cells under several conditions [3].

Potassium channels play an essential role in the potassium transportation system (PTS) and are involved in the conduction of K^+ ions to maintain various phenomena like cell turgidity and osmotic level. There are three families of potassium translators to defend against low K^+ ion situations [4]. High-affinity potassium transporters (HKTs) are from the Trk family having several MPM blocks as motifs. Potassium efflux anti-porters (KEA) are involved in the stabilization of K^+ ions across the membrane as it works electro-neutrally without affecting the charges across the membrane. It also involves maintaining the pH of cytosol [5].

Potassium transport channels have numerous functions, which urge the classification of potassium transport channel genes to differentiate their functions. Moreover, the classification is based on the molecular switch for the transportation of K^+ ions. The objectives of the current effort were to identify the potassium transporting genes in wheat and to locate their conserved regions by comparing those with known sequences of different plants.

Material and Methods

K^+ transporters and K^+ channels retrieval

The sequences of K^+ channel genes and K^+ transporter genes were retrieved along with the known sequences of rice and *Arabidopsis thaliana* as control. The similarity search was performed against the K^+ channel genes and K^+ transporter genes of wheat [6]. The genomic database of Rosacea (GDR) (https://www.rosaceae.org/) and Gen-Bank (a database provided and maintained by NCBI) (https://www.ncbi.nlm.nih.gov/) was utilized for the retrieval of gene sequences [7]. The sequences of K^+ transporting channels and transporters were retrieved and compared with the gene sequences of rice and *A. thaliana* [8]. The sequences were subjected to BLASTp for protein identification of the selected genes. In addition, BLASTn and tBLASTn were used to verify the generated results. The obtained data were manually curated to reduce the redundancy and to eliminate the false-positive results. The sequences with a high similarity of >60% against the known sequences were selected for further analyses. The selected sequences were further screened by identifying the channel and transporter-specific motifs. The sequences were observed in all six reading frames to explore the G-Y-G motif by utilizing the tBLASTx (https://www.ncbi.nlm.nih.gov/). Gomez and Porras approach was utilized to verify the selected genes. The selected transporting genes were further screened by searching against Pfam, CDD, and SMART. The selected genes were analyzed to validate the authenticity and phylogeny was generated by utilizing Pfam database (http://pfam.janelia.org/), NCBI conserved domain database (http: //www.ncbi.nlm.nih.gov/ Structure/cdd/wrpsb.cgi), and SMART database (http:// smart.embl-heidelberg.de/). The highly conserved sequences having high similarities were selected for further analyses [9].

Domain prediction and identification

The selected genes were further analyzed to identify functional domains and transmembrane domains. Gene and THMM (http://www.cbs.dtu.dk/services/TMHMM/) were utilized for the identification of domains and transmembrane domains [10], respectively. Gene databases were used to locate the chromosomal locations of the selected genes [10].

Gene structure analysis

The gene structures of K^+ ion transporting genes were generated by utilizing NCBI [11]. The sequences were classified according to respective genes and GSDS (Gene Structure Display Server) http://gsds.cbi.pku.edu.cn/ was utilized [11].

Multiple sequence alignment, molecular clock analysis, and phylogenetic analysis

MEGA-X was utilized for multiple sequence alignment and adaptive evolutionary analyses along with the phylogenetic analyses. WebLogo3 (http://weblogo.threeplusone. com/) was utilized to identify the conserved regions [12]. The neighbor-

joining method along with the maximum likely hood method having 1000 bootstrap values was utilized to generate the phylogenetic tree of K^+ transporting genes [13].

Protein structure prediction

Potassium transporter protein structures were predicted by using the SWISS-MODEL homology-modeling server. Protein sequences were submitted in FASTA format by using the default parameters [13].

Protein-protein partner identification analysis

The protein-protein partner identification analyses were done by STRING (https://string-db.org/) and all the sequences of potassium transporting proteins were subjected one by one for identification [14].

Results

Identification of potassium transportation system in wheat

The struggle was initiated from extensive literature review leads to exploring the potassium transportation system of wheat. The identified genes and mechanism through computational means were utilized to characterize the K^+ ion transporting channels and K^+ ion transporting transporters. The characterization was done on the basis of their binding domains, motifs, phylogenetic analyses, and gene structures. Through extensive literature review, it was observed that 25 genes are involved in PTS as 11 potassium ion K^+ transporting channels, and 29 were observed as K^+ transporting transporters. The selected families were classified according to the nomenclature rules provided by Pandey and Mahiwal [14] (Table 1).

Structural insights of potassium transporting genes

The conserved regions from all the selected gene families were observed based on their introns and exons. The overall genetic structural integrity of potassium ion transporters and channels in wheat were analyzed through introns and exons configuration, their abundance and localization. In wheat shaker family channels, *TaAKT1.1*, *TaAKT1.2*, and *TaAKT1.3* showed a similar pattern of structures, introns, exons and locations; however, TaAKT1.1 have long introns with unique features. It was also observed and characterized that the selected gene families showed a close relationship. It was observed that the selected 25 genes were involved in PTS of wheat and have similar features in comparison with different PTS

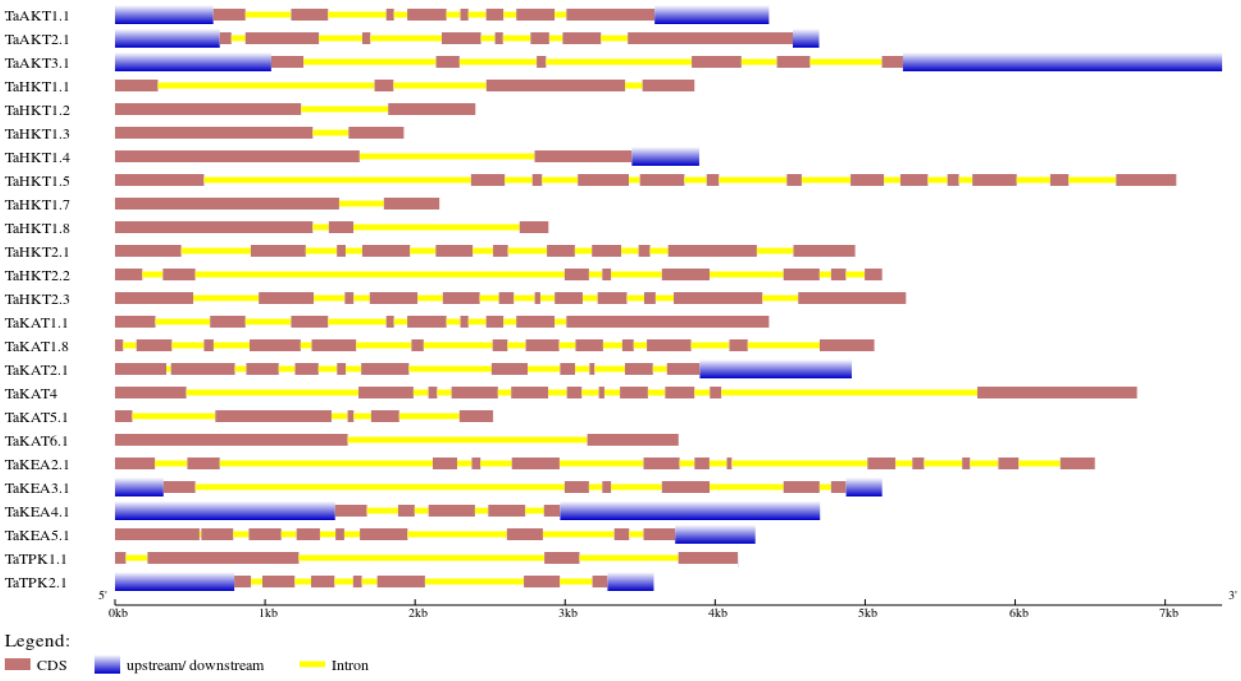

Fig. 1 Introns and exons along with untranslated regions (UTRs) for the selected potassium transporting genes.

Table 1 Important genomic and proteomic features associated with potassium transporting genes/proteins.

Genes	Length	Molecular weight	Exons	Introns	Domains	TMHs	Theoretical PI	Subcellular localization	Gravy
TaHKT1.1	552	62024.62	4	3	TrkH; Cation transport protein	8	6.04	Nuclear	-0.428
TaHKT1.2	532	59904.02	2	1	PotE; K_trans;	8	7.53	Nuclear	-0.694
TaHKT1.3	563	62218.00	2	1	PotE; K_trans;	9	6.39	Nuclear	-1.480
TaHKT1.4	578	63310.58	2	1	K_trans; K^+ potassium transporter	9	9.40	Nuclear	-1.256
TaHKT1.5	516	57295.00	13	12	K_trans; K^+ potassium transporter	7	7.58	Nuclear	-0.617
TaHKT1.7	563	62401.96	2	1	PotE; K_trans	9	6.36	Nuclear	-0.293
TaHKT1.8	518	57460.30	3	2	potassium transporter; Provisional	7	8.86	Nuclear	-0.797
TaHKT2.1	533	58932.44	11	10	PotE; Amino acid transporter	8	6.32	Nuclear	-0.751
TaHKT2.2	699	75196.55	8	7	PLN00151; potassium transporter;	10	8.88	Nuclear	-0.650
TaHKT2.3	609	64991.43	12	11	potassium transporter;	10	8.29	Nuclear	-0.531
TaKEA2.1	582	62527.41	13	12	potassium transporter;	9	8.86	Nuclear	-0.469
TaKEA3.1	349	39448.93	6	5	PotE; Amino acid transporter	6	6.32	Nuclear	-0.428
AtKEA4.1	366	39123.58	5	4	K_trans; K^+ potassium transporter	4	8.88	Nuclear	-0.694
TaKEA5.1	894	100617.51	9	8	K_trans; K^+ potassium transporter	12	8.29	Nuclear	-1.480
TaTPK1.1	812	91312.17	4	3	PotE;K_trans;	11	9.45	Nuclear	-0.428
TaTPK2.1	911	101116.73	7	6	K_trans; K^+ potassium transporter	14	8.86	Nuclear	-0.694
TaAKT1.1	726	83643.01	8	7	PLN00151; potassium transporter;	10	6.32	Nuclear	-1.480
TaAKT2.1	530	61519.22	8	7	K_trans; K^+ potassium transporter	7	8.87	Nuclear	-1.256
TaAKT3.1	595	66917.71	6	5	K_trans; K^+ potassium transporter	8	8.23	Nuclear	-0.617
TaKAT1.1	500	57208.24	9	8	K_trans; K^+ potassium transporter	5	9.41	Nuclear	-0.296
TaKAT2.1	572	64805.38	8	7	ERM; Ezrin/radixin/moesin;MttA_Hc f106	6	8.87	Nuclear	-0.727
TaKAT6.1	532	59946.06	2	1	Na_H_Exchanger; Sodium/hydrogen exchanger family	5	6.33	Nuclear	-0.721
TaKAT4	394	43588.07	11	10	Na_H_Exchanger; Sodium/hydrogen exchanger family	3	8.89	Nuclear	-0.610
TaKAT5.1	582	64571.46	5	4	Glutathione-regulated potassium-efflux system	5	8.25	Nuclear	-0.561
TaKAT1.8	504	56182.86	14	13	Protein KefB; KefB; Kef-type K^+ transport system,TrkA_N	4	9.43	Nuclear	-0.489

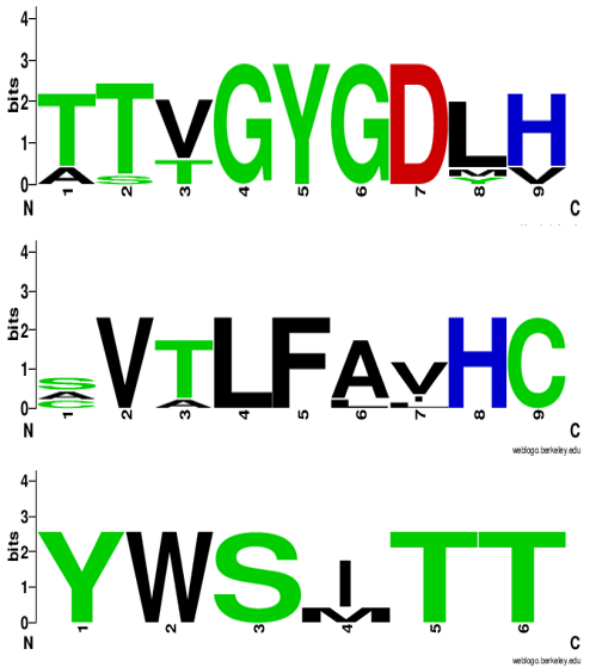

Fig. 2 Three highly conserved motifs predicted by multiple sequence alignment of potassium transporting genes.

of plants (Fig. 1). The reported K^+ ion transporting channels and K^+ ion transporters were specific to their activities according to their locations and structure. They also have a key role to transport and distribute the K^+ ions from the roots to other parts of the plant.

Multiple sequence alignment, molecular clock analysis, and phylogenetic analyses

Multiple sequence alignment was performed against potassium transporting genes from different species, and it was observed that the selected genes are highly conserved in the selected species (rice, Arabidopsis, glycine max. and chickpea plant). Three motifs were observed highly conserved in channels and transporters (Fig. 2). The observed results of multiple sequence alignment were considered reliable based on the conserved region (Fig. 3). Phylogenetic analyses and molecular clock analyses were performed to analyze the relationships between different species having potassium transporting networks as well as potassium transportation genes homology in wheat. Comparative phylogenetic analyses of rice, wheat, chickpea, and *Arabidopsis* were performed to reveal the relationship of potassium transporting genes related to each other (Fig. 4), and a phylogenetic tree was observed to specify the potassium transporting genes (Fig. 5). A molecular clock analysis was performed [15], and it was observed that the phyletic lineage relation between ancestors and descendants (Fig. 5) was conserved.

Protein structure prediction analyses

The protein structure predictions were performed for the selected 25 genes having >60 similarities against the selected templates for all the proteins. The predicted models were evaluated based on overall quality factors and the best models were selected for further analysis. The predicted structures were visualized and analyzed for conserved domains against potassium transporters (Fig. 6) and potassium channels (Fig. 7).

Protein interacting partner prediction of potassium transporting proteins

Protein interacting partner prediction was done to observe the interacting partners of concerned proteins (Fig. 8). The observed partners were specific, and proteins were jointly contributing to a common function. It was observed that the potassium transporting proteins linked to each other in order to complete the primary functions, including transport of potassium in the plant.

Discussion

In this study, PTS in wheat was analyzed along with the gene families [16]. K^+ transportation in wheat comprises 25 genes (14 transporters genes as, 10 HKTs, and 4 KEAs) and K^+ channels (11 genes as 3 AKT, 6 KAT-Shakers, and 2 TPKs). Seven members of this family have been observed in wheat; however *A. thaliana* has transporters [17]. The characterization was made according to their close relations with *Arabidopsis*. In wheat, the selected family has a protein length of 574 to 1198 amino acids [18]. The genomic analyses concluded that 12-15 exons in every gene transporter family of wheat were present. The observed channels were initially identified in *A. thaliana* (9-members) at the molecular level [19]. There were 6 shaker channels in wheat and protein ranges from 618 to 892 amino acids and has exons in genes ranging from 9-14 [20]. Eight TPKs and five Kir-like channels in the genome of wheat were identified. TPKs have 3 transmembrane domains having one hydrophobic core and Kir-like channels have one domain and one hydrophobic core [21]. It has been observed that the sequence RSXpSXpx was observed highly conserved among all TPKs in

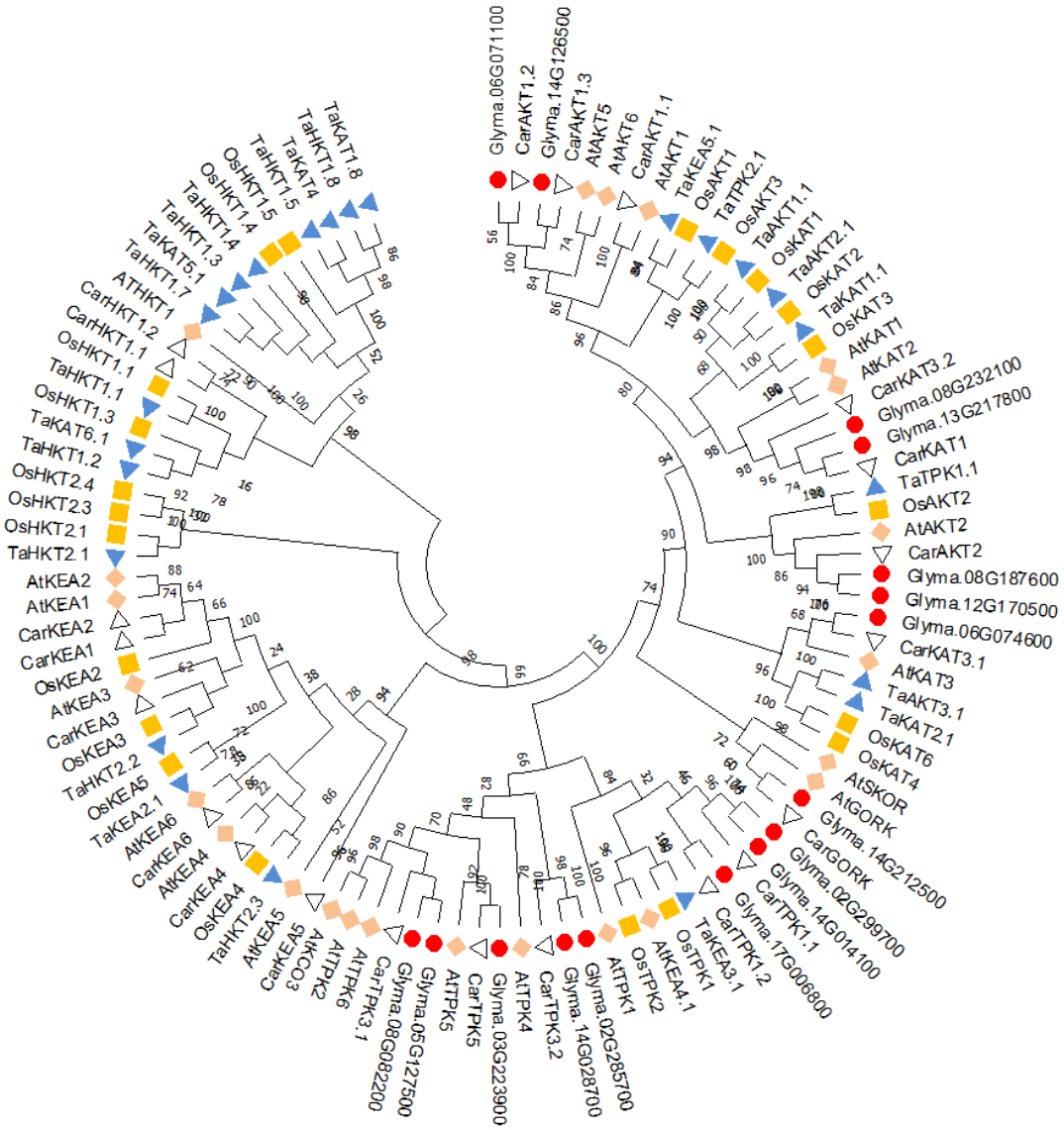

Fig. 3 Multiple sequence alignment of potassium transporting genes, performed using MEGA-X.

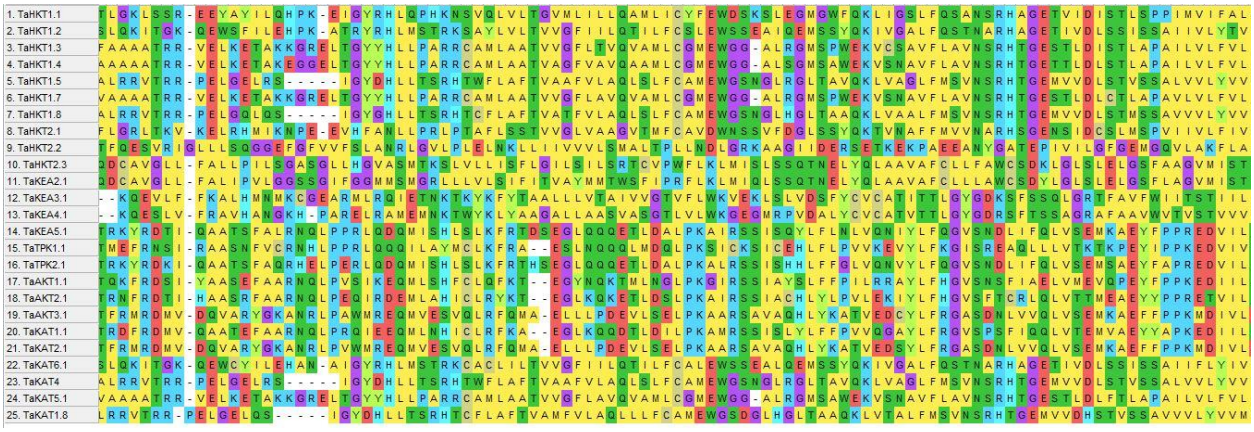

Fig. 4 Phylogenetic analysis among different species to evaluate the relationship between these genes from multiple species.

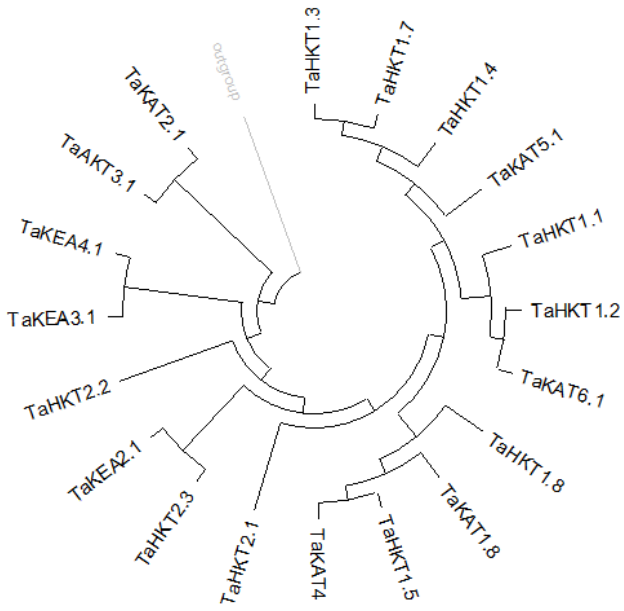

Fig. 5 Molecular clock analysis of potassium transporting genes to check evolutionary relations between these genes.

wheat. The protein length has 365 to 401 amino acids and several exons in 9 to 11 per sequence. The structural relativity of TPKs from wheat and other plants was also analyzed. The whole-genome analyses of *Triticum aestivum* showed that the wheat has 2 TPK channel transport genes [22]. *A. thaliana* has several TPKs of 5, and a total of 6 Kir channels of wheat were identified and named as a separate group. Plant Kir-like channels were initially considered as a separate group; however, TPKs in *A. thaliana* has similarities. The highly conserved motif G-Y-G has been reported as the signature of the selected channels in wheat [23]. KAT and AKT gene families were identified in numerous plants except for *A. thaliana*. In wheat, 5 transporter genes were characterized and the sequences of the selected genes have similarities to their variants from *A. thaliana* [24] and have similar domain patterns. 14 domains and one extra domain have been identified as the potassium transportation domain, which plays a crucial role in PTS.

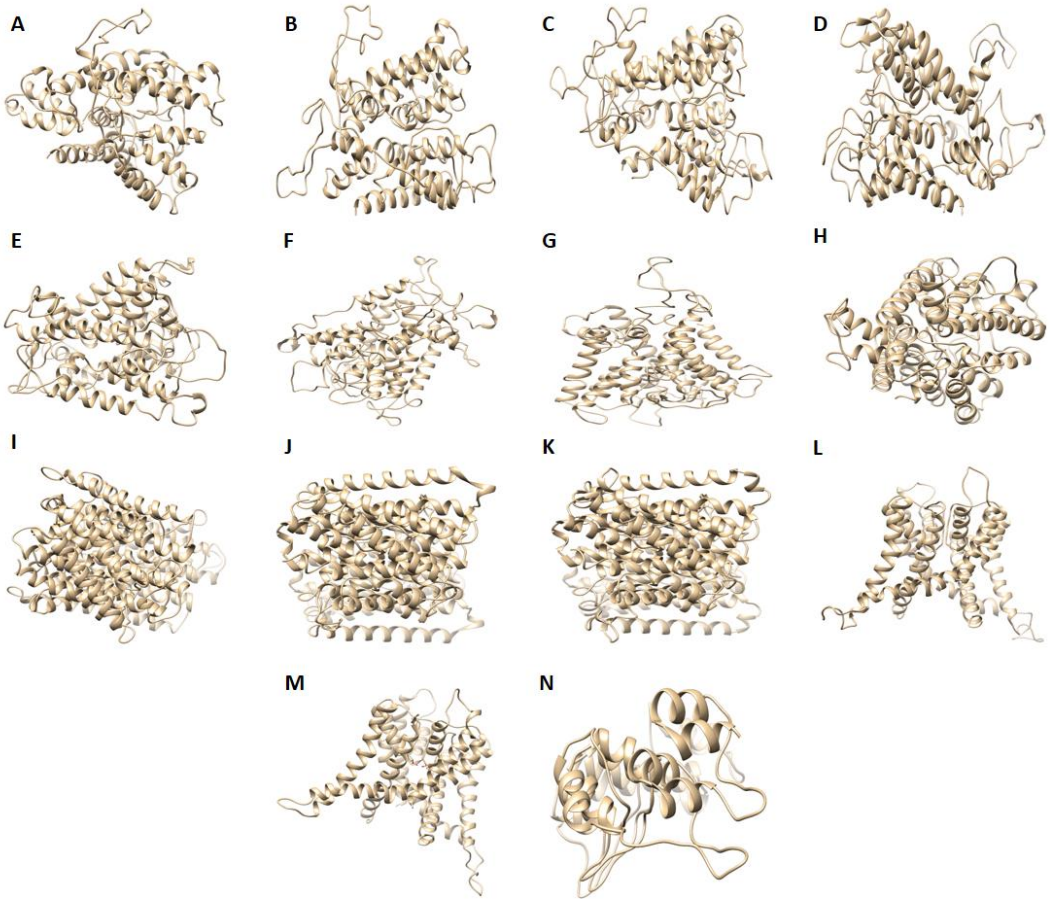

Fig. 6 Protein structures for all potassium transporting transporters as shown from A to N.

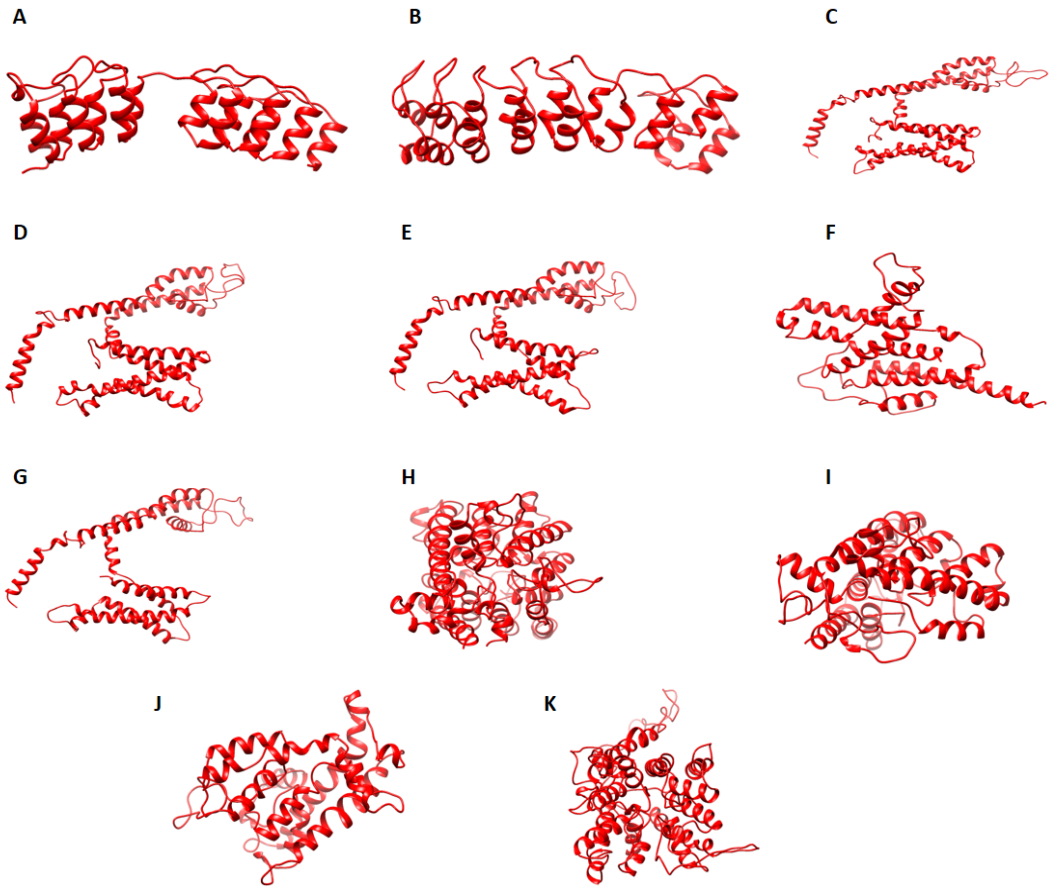

Fig. 7 Protein structures for all potassium transporting channels as shown from A to K.

TaKATs play a significant role in K^+ ion transport. Phylogenetic analyses of the selected family were classified into four subfamilies. Different plants showed diversity in their PTS and TaHAK4 has a low potassium influx of 70% in 0.2 mM solution [25].

TaHKT1.1 and TaHKT1.2 potassium transporters were observed in *Triticum aestivum*, and both genes were closely related to the members of the Trk channel family and were involved in PTS [26]. Multiple sequence analyses of selected families showed substitution mutation. K^+ transportation has been observed by the phylogenetic relationships of the selected genes with OsHKT1.4 and OsHKT1.5. Glycosylation affects membrane stability and shape were also reported and reconciled with the observed results. N-glycosylation has been reported in many plants as their casual property in membrane-linked proteins [27]. It is significant to have a K^+-rich diet while young in life. Girls with K^+-rich diet had a slower rate of increase in blood pressure [28]. It has been evidenced that the blood pressure-lowering advantage is due to physiological processes that are activated to eliminate K^+ eaten in a K^+-rich diet to keep plasma K^+ content within a limited range [29]. Increasing dietary K^+ may help to reduce the risk

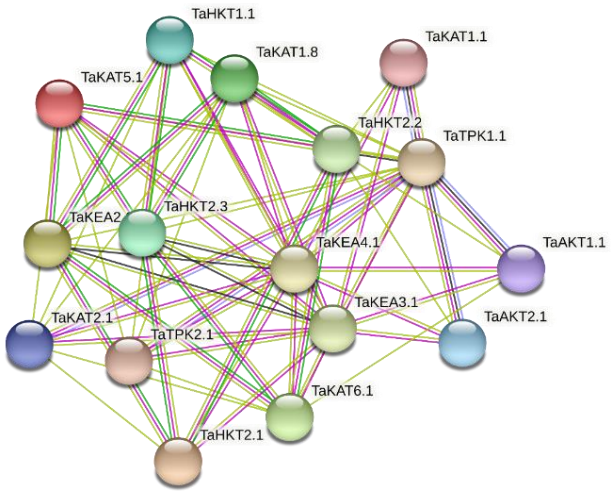

Fig. 8 Protein interacting partners of the potassium transporting gene family.

of hypertension, which is a key risk factor for stroke, coronary heart disease, heart failure, and end-stage renal disease [30]. Furthermore, proper K^+ consumption may play a significant role in glucose regulation and reducing the risk of diabetes. K^+ supplementation and fortification are less attractive than other vitamins and minerals to raise K^+ intake [31]. The amount of K^+ required to close the gap necessitates a high number of supplements. K^+ is a well-known modifiable factor for hypertension, the leading cause of some of the world's most common chronic diseases, and a greater understanding of its bioavailability in the diet will help researchers to improve overall human health [32].

Conclusions

Potassium (K^+) ion is a well-known nutrient of plants. A potassium transportation system has been reported in many plants. In this study, PTS was characterized in wheat (*Triticum aestivum*) and 25 genes were observed for the involvement in PTS in wheat. Among these 25 genes, 14 genes were observed in potassium (K^+) ion transporter genes, and the remaining 11 genes were potassium (K^+) ion transporting channel genes. Phylogenetic analyses, molecular clock analyses, and genetic structure identification of the selected genes revealed the close relationship and conserved domains.

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Conflict of Interest

The authors declare that they have no conflict of interest

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