WORLD JOURNAL OF PHARMACEUTICAL RESEARCH
SJIF Impact Factor 5.045
Volume 4, Issue 2, 1640-1652. Research Article ISSN 2277– 7105

COMPARATIVE ANALYSIS AND IDENTIFICATION OF GENES RELATED TO POTASSIUM TRANSPORTER FAMILIES IN *SORGHUM BICOLOR*

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Article Received on
09 Dec 2014,

Revised on 03 Jan 2015,
Accepted on 28 Jan 2015

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ABSTRACT

The molecular basis of K+ channel function is universally conserved. The various functions of plant potassium transporter genes range from mineral nutrition to the regulation of cell growth and development K+ channels allow K+ flux and are essential for the generation of electric current across excitable membranes. K+ channels are also the targets of various intracellular control mechanisms, such that the suboptimal regulation of channel function might be related to pathological conditions. In the present study, an analysis of the genomic sequences related to K+ transporter families in *Sorghum bicolor* was carried out by searching genome in public databanks. Comparative analysis of sorghum genome against rice as a model plant has identified a total of 60 genes. Phylogenetic analyses of selected potassium transporter families have been analyzed. These analyses show the number of genes, the number and constellation of sub groups, as well as the complexity of each of these gene families in the sorghum genome. Furthermore, results from each of the analyzed gene families are described. In this study, a total of 60 genes are possibly involved with K+ transport in *Sorghum bicolour*. Among the 60 genes 31 genes related to HAK family, 11 genes to shaker family (1P\6TM), , four sequences to KCO family (2P\4TM ORK Type), eight genes to CNGC, 4 genes to Trk family and two putative K+ /H+ antiporter genes were analyzed. The HAK family forms the tightest and most distinct branch in the phylogenetic tree of sorghum K+ transporters. All putative SbHAK transporters exhibited more than 30% identity with rice OsHAK1.

KEYWORDS: Phylogenetic analyses, K+ channels, *Sorghum bicolour*, shaker family, *Oryza sativa*.

1. INTRODUCTION

The alkali metal potassium (K+) is a major plant macronutrient. Potassium stimulates early growth, increases protein production, and improves the efficiency of water use. Potassium plays an important role in the activation of enzymes which are fundamental to metabolic processes, especially the production of proteins and sugars. The potassium status of plant determines the profile and distribution of primary metabolites in plant tissues. K nutrition is closely related to sugar allocation, nitrogen assimilation and amino acid levels.

Potassium is required for every major step of protein synthesis. The “reading” of the genetic code in plant cells to produce proteins and enzymes that regulate all growth processes would be impossible without adequate K. When plants are deficient in K, proteins are not synthesized despite an abundance of available nitrogen. The enzyme responsible for synthesis of starch (starch synthetase) is activated by K. The level of starch declines while soluble carbohydrates and N compounds accumulate in inadequate potassium levels.[1]

A growing body of evidence suggests that potassium channel dysregulation is associated with key aspects of cancer, and targeting potassium channel is a viable therapeutic approach. Rational design of therapeutic targeting of potassium channels for cancer treatment will be based on our better understanding of their functions from mechanistic study.[2]

In plants, potassium transporters are required for the accumulation of potassium ions (K+) from soil and for their distribution throughout diverse plant tissues, root and shoot growth, tropisms, cell expansion, enzyme homeostasis, salinity stress, stomatal movements, osmo regulation and salt tolerance. [3][4] Recent completion of rice genome sequencing project offered the opportunity to make an inventory of all putative K^+ transporter proteins. More than 5% of the rice genome appears to encode membrane transport proteins.

Plant potassium transporters are classified into the following families

1) Potassium transporters belonging to the KT/KUP/HAK family are important for various aspects of plant life including mineral nutrition and the regulation of development. It includes bacterial K + uptake permeases named KUPs and fungal high-affinity K^+ transporters named HAKs.[5]

2) Potassium channels are the most widely distributed type of ion channel and are found in virtually all living organisms. Potassium channels have a tetrameric structure which includes shaker type, TPK and Kir-like channels.[6]
3) Trk/HKT transporters are reminiscent of K+ channels in that they possess in a single polypeptide chain four domains resembling P-loops.[7]
4) Cation / proton anti porters extrude cations from the cytosol to the predicted proteins in general have 10-14 transmembrane domains with about 400 to <900 residues with proton pumps at the PM and endomembranes of plant cells. $^{K+}/^{H+}$ antiporters are suggested to be responsible for the active accumulation of $^{K+}$ inside vacuoles, essential to maintain turgor and drive cell expansion.[8]
5) Genes encoding members of the NRAMP family of integral membrane proteins have been identified in bacteria, fungi, plants and animals. The proteins encoded by AtNRAMP genes cluster in two subfamilies.[9]

In this study, Rice is considered as a model plant because of its high degree of co-linearity with other cereals and used to compare and identify potassium transporter families in *Sorghum bicolor*. Sorghum is the fifth most important cereal crop in the world. It has a genome of about 760 Mb with 2n = 20 chromosomes. Its genome falls between the genome of rice and other crops. The whole Sorghum genome has been sequenced and is available. This makes sorghum a good model for structural genomic analysis. Minimal level of gene duplication makes sorghum, like rice, an attractive system for many approaches to determining gene function. Many plant genomes are complex in the sense that they have much repetitive DNA and a high degree of duplication even in genic regions. This complexity poses a challenge of genomic analysis among them. As a model for the tropical grasses sorghum is a logical complement to *Oryza sativa*.

2. METHODS

In this study comparative genomics principles are used to evaluate sorghum genome for potassium transporter families. Rice is taken as model plant and the analysis is carried out in *Sorghum bicolor* to establish Sequence similarity searching using BLAST tool, Identification of putative genes prediction programmes, confirmation of protein domain, multiple sequence alignment using Clustal Omega and phylogenetic analysis.[10]

Oryza sativa (variety, japonica) is taken as standard plant for the analysis of potassium transporter families in sorghum bicolour. Reference proteins taken are OsHAK1

(6VVA6.2, GI: 62900231), OsAKT1 (Q0JKV1.1, GI: 122241153), CNGC1 Plants Protein (217969CNGC1-cyclicnucleotide-regulated ion channel,), OsKEA1 (CAE03437.2) and OsHKT1 (A2YGP9.2).[11] The above proteins were used as query sequences and searches were made in sorghum bicolor to identify translated nucleotide sequences using the TBLASTN tool against GenBank database non-redundant (NR) and Universal Protein resource Uniprot (http://www.ebi.uniprot.org/uniprot-srv/protein/ uniProtView).[12] TBLASTN searches were made using genomic blast against sorghum genome to examine the intro-exon structure across species. Putative genes contained within them were predicted using abinitio gene prediction algorithms of genomic sequence alignments. The prediction algorithms were GenScan, FGENESH GeneMark.hmm and GrailEXP. Prediction of homology and signature sequences for the putative K+ transporter proteins were carried out with PROSITE database and Pfam databases. Sequences were included into families based on homology and presence of signature sequences. Related protein sequences were identified the algorithm of choice for the multiple alignments of protein sequences was Clustal Omega. Protein alignments obtained with Clustal Omega were used for phylogenetic analysis. Phylogenetic trees for each family were prepared using MEGA Unrooted trees were prepared by the neighbor-joining method.

3. RESULTS

Sorghum bicolor genome data in NCBI is used to construct an overview of K+ transporter genes. As a starting point, the protein families HAK, AKT, KCO, HKT/Trk and K+/H+ that have positive molecular implications on K+ uptake and transport in rice were chosen for analysis. For CNGC sequences, reference proteins from Arabidopsis were taken for analysis. Specific members of these families are taken as query sequences, searches were carried out for orthologous sequences in GenBank, and Uniprot current databases using TBLASTN. After searching the databanks with TBLASTN sequences, genomic sequences related to the respective families were taken and putative genes were predicted using gene prediction programmes. Repeated sequences were removed using Clustal Omega. In each family, similar sequences were removed and the sequences were subjected to PROSITE and Pfam databases to see the presence of signature sequences for the corresponding families. Potassium transporter domain is confirmed for sequences identified in *sorghum bicolor* using Inter Pro scan (Fig. 1). After subjecting the sequences to PROSITE, 34sequences related to HAK, 19 to the shaker type to , 5 to KCO, 12 to CNGC,9 to HKT and 5 to K+/H+ antiporter families were obtained. The percent identity for all the sequences was calculated in each family with the corresponding query sequence using GENEDOC (Fig. 2). Proteins that are showing more than 30% identity were taken for the construction of phylogenetic tree. In case of AKT family, proteins having more than 25% identity with the query sequence were taken. In this study, a total of 60 genes are possibly involved with K+ transport in *Sorghum bicolor*. Among the 60 genes 31 genes related to HAK family (Table 1), 11 genes to shaker family (1P\6TM), four sequences to KCO family (2P\4TM ORK Type), eight genes to CNGC (Table 2), 4 genes to Trk family (Table 3) and two putative K+ /H+ antiporter genes were analyzed (Table 4). The HAK family forms the tightest and most distinct branch in the phylogenetic tree of sorghum K+ transporters. All putative SbHAK transporters exhibited more than 30% identity with rice OsHAK1. Systematic searching in public databanks with Rice sequences OsKT1 and OsKCO1 as query sequences resulted in identification of total of 15 orthologous genes containing conserved K+ channel P-loops. A non-rooted phylogenetic tree of all 15 genes revealed two major branches: 1P/6TM K+ channels and 2P/4TM K+ channels. Thus, the channels are segregated according to the number of their P-loops. Within the shaker type channels SbKT10 and SbKT11 sequences were found to contain GORK (Gated outward rectifying potassium channel) domain. Among the HKT transporters SbHKT2 has shown 43% similarity with query protein. Only one k+\H+ Transporter from KEA family, SbKEA1 has 82% similarity with rice sequences. Phylogenetic trees for all potassium transporters were prepared using MEGA Unrooted trees were prepared by the neighbor-joining method (Fig.3).

Table 1: kup/hak/kt family found in the *Sorghum bicolor*

Sequence name	Reference sequences	Related nucleotide accession	Related protein accession	Gene name	Chr no	%identity with query
SbHAK1	XM_002446325.1 XP_002446370.1	CM000765.1	EES10698.1	Sb06g014930	6	81
SbHAK2	XM_002452131.1 XP_002452176.1	CM000763.1	EES05152.1	Sb04g021210	4	69
SbHAK3	XM_002446334.1 XP_002446379.1	CM000765.1	EES10707.1	Sb06g014960	6	69
SbHAK4	XM_002446333.1 XP_002446378.1	CM000765.1	EES10706.1	Sb06g014950	6	56
SbHAK5	XM_002456848.1 XP_002456893.1	CM000762.1	EES02013.1	Sb03g044780	3	54
SbHAK6	XM_002456849.1 XP_002456894.1	CM000762.1	EES02014.1	Sb03g044790	3	52
SbHAK7	XM_002464267.1 XP_002464312.1	CM000760.1	EER91310.1	Sb01g015990	1	49
SbHAK8	XM_002464269.1 XP_002464314.1	CM000760.1	EER91312.1	Sb01g016010	1	48

SbHAK9	XM_002464265.1 XP_002464310.1	CM000760.1	EER91308.1	Sb01g015970	1	48
SbHAK10	XM_002459151.1 XP_002459196.1	CM000761.1	EER95717.1	Sb02g000340	2	43
SbHAK11	XM_002462261.1 XP_002462306.1	CM000761.1	EER98827.1	Sb02g023620	2	38
SbHAK12	XM_002456859.1 XP_002456904.1	CM000762.1	EES02024.1	Sb03g045180	3	36
SbHAK13	XM_002448479.1 XP_002448524.1	CM000765.1	EES12852.1	Sb06g028380	6	37
SbHAK14	XM_002461917.1 XP_002461962.1	CM000761.1	EER98483.1	Sb02g011240	2	37
SbHAK15	XM_002463320.1 XP_002463365.1	CM000761.1	EER99886.1	Sb02g042430	2	35
SbHAK16	XM_002438656.1 XP_002438701.1	CM000769.1	EER90068.1	Sb10g024660	10	33
SbHAK17	XM_002443974.1 XP_002444019.1	CM000766.1	EES13514.1	Sb07g006000	7	34
SbHAK18	XM_002462869.1 XP_002462914.1	CM000761.1	EER99435.1	Sb02g034330	2	33
SbHAK19	XM_002467852.1 XP_002467897.1	CM000760.1	EER94895.1	Sb01g036050	1	33
SbHAK20	XM_002463342.1 XP_002463387.1	CM000761.1	EER99908.1	Sb02g042930	2	34
SbHAK21	XM_002437386.1 XP_002437431.1	CM000769.1	EER88798.1	Sb10g026960	10	33
SbHAK22	XM_002464268.1 XP_002464313.1	CM000760.1	EER91311.1	Sb01g016000	1	40
SbHAK23	XM_002438175.1 XP_002438220.1	CM000769.1	EER89587.1	Sb10g009770	10	32
SbHAK24	XM_002454294.1 XP_002454339.1	CM000763.1	EES07315.1	Sb04g029030	4	31
SbHAK25	XM_002448462.1 XP_002448507.1	CM000765.1	EES12835.1	Sb06g02813	6	33
SbHAK26	XM_002457794.1 XP_002457839.1	CM000762.1	EES02959.1	Sb03g015030	3	34
SbHAK27	XM_002445855.1 XP_002445900.1	CM000766.1	EES15395.1	Sb07g027710	7	32
SbHAK28	XM_002460252.1 XP_002460297.1	CM000761.1	EER96818.1	Sb02g026170	2	31
SbHAK29	-	EU871661.1	ACJ66609	HAK1		21
SbHAK30	XM_002456849.1 XP_002456894.1.	CM000762	EES02014.1.	Sb03g044790		53
SbHAK31	XM_002459151.1 XP_002459196.1	CM000761	EER95717.1.	Sb02g000340		43

Table 2: K+ channels found in the *Sorghum bicolor*

Sequence name	Reference sequences	Related nucleotide	Related protein	Gene name	Chr no	%identity with query
SbKT1	XM_002458189.1 XP_002458234.1	CM000762.1	EES03354.1	Sb03g02950	3	77
SbKT2	XM_002459361.1 XP_002459406.1	CM000761.1	EER95927.1	Sb02g00410	2	55
SbKT3	XM_002441100.1 XP_002441145.1	CM000768.1	EES19575.1	Sb09g02120	9	34
SbKT4	XM_002441096.1 XP_002441141.1	CM000768.1	EES19571.1	Sb09g02110	9	34
SbKT5	XM_002441098.1 XP_002441143.1	CM000768.1	EES19573.1	Sb09g02110	9	33
SbKT6	XM_002453555.1 XP_002453600.1	CM000763.1	EES06576.1	Sb04g00870	4	34
SbKT7	XM_002456331.1 XP_002456376.1	CM000762.1	EES01496.1	Sb03g03490	3	29
SbKT8	XM_002456209.1 XP_002456254.1	CM000762.1	EES01374.1	Sb03g033010	3	52KAT3
SbKT9	XM_002454023.1 XP_002454068.1	CM000763.1	EES07044.1	Sb04g024100	4	43KAT3
SbKT10	XM_002447865.1 XP_002447910.1	CM000765.1	EES12238.1	Sb06g017830	6	81 GORK
SbKT11	XM_002438114.1 XP_002438159.1	CM000769.1	EER89526.1	Sb10g008960	10	49 GORK
SbKCO1	XM_002462110.1 XP_002462155.1	CM000761.1	EER98676.1	Sb02g020740	2	81
SbKCO2	XM_002458315.1 XP_002458360.1	CM000762.1	EES03480.1	Sb03g032020	3	31
SbKCO3	XM_002449420.1 XP_002449465.1	CM000764.1	EES08453.1	Sb05g015110	5	25
SbKCO4	XM_002463820.1 XP_002463865.1	CM000760.1	EER90863.1	Sb01g007830	1	23
SbCNGC1	XM_002453583.1 XP_002453628.1	CM000763.1	EES06604.1	Sb04g009250	4	53
SbCNGC2	XM_002447160.1 XP_002447205.1	CM000765.1	EES11533.1	Sb06g030420	6	45
SbCNGC3	XM_002437019.1 XP_002437064.1	CM000769.1	EER88431.1	Sb10g020550	10	50
SbCNGC4	XM_002466707.1 XP_002466752.1	CM000760.1	EER93750.1	Sb01g013500	1	45
SbCNGC5	XM_002442510.1 XP_002442555.1	CM000767.1	EES16393.1	Sb08g021830	8	44
SbCNGC6	XM_002454637.1 XP_002454682.1	CM000763.1	EES07658.1	Sb04g035530	4	42
SbCNGC7	XM_002436576.1 XP_002436621.1	CM000769.1	EER87988.1	Sb10g005970	10	41
SbCNGC8	XM_002452435.1 XP_002452480.1	CM000763.1	EES05456.1	Sb04g026580	4	42

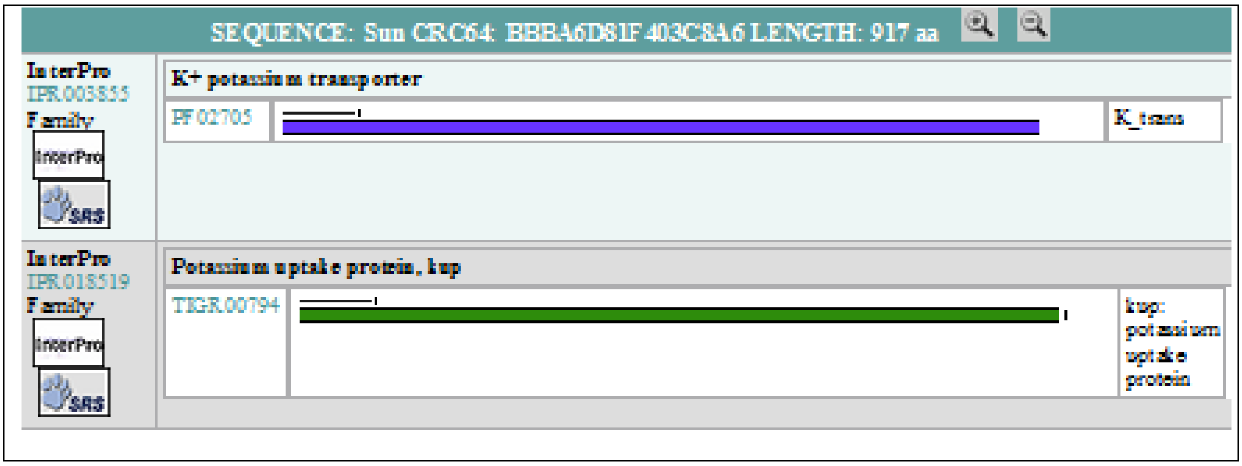
SbCNGC9	XM_002461239.1 XP_002461284.1	CM000761.1	EER97805.1	Sb02g000200	2	39
SbCNGC10	XM_002460609.1 XP_002460654.1	CM000761.1	EER97175.1	Sb02g032610	2	38

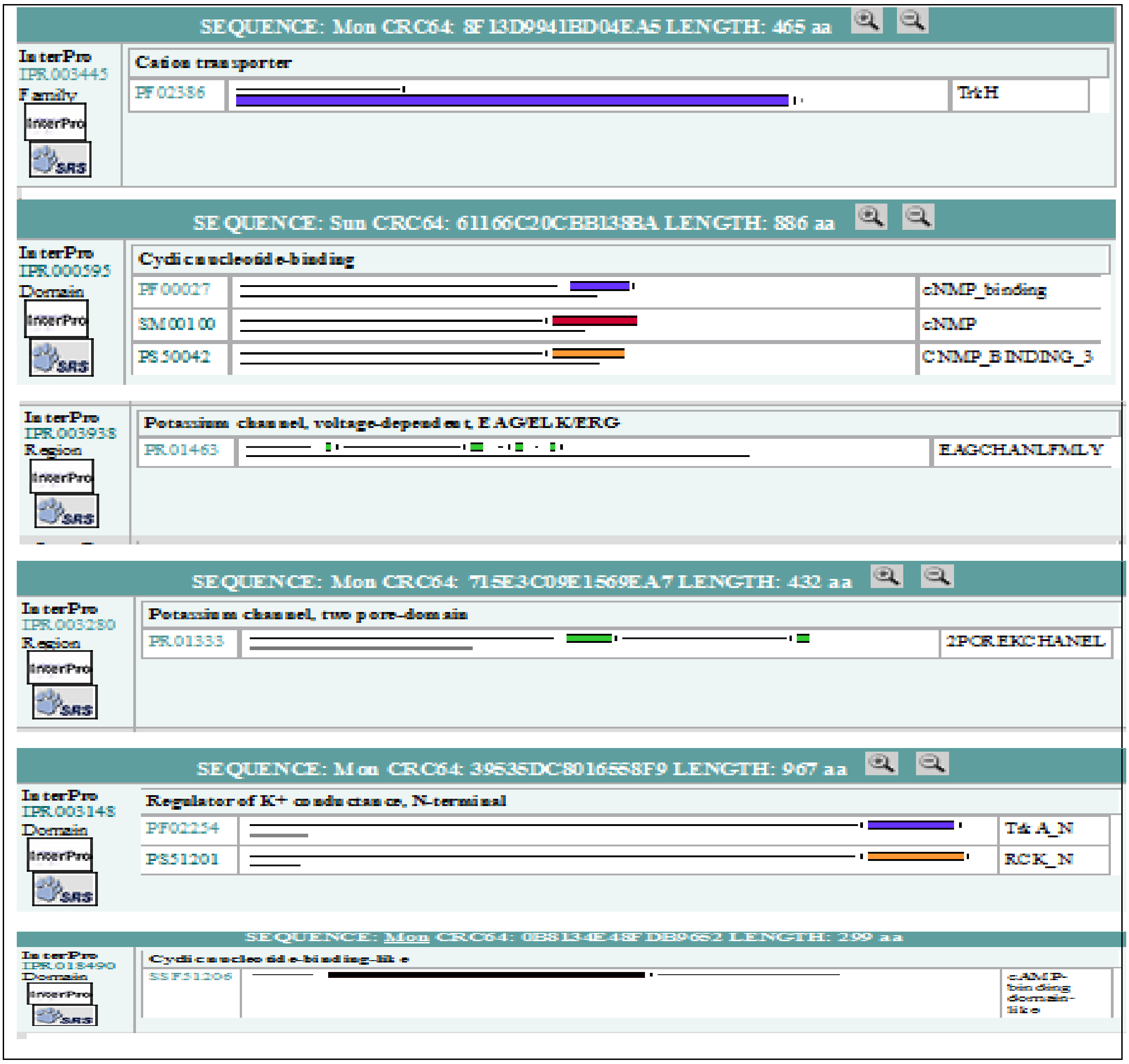
Table 3: HKT family found in the *Sorghum bicolor*

Sequence name	Reference sequences	Related nucleotide	Related protein	Gene name	Chr no	%identity with query
SbHKT1(1;1)	XM_002451593.1 XP_002451638.1	CM000763.1	EES04614.1	Sb04g005010	4	36
SbHKT2(1;2)	XM_002438915.1 XP_002438960.1	CM000769.1	EER90327.1	Sb10g029000	10	43
SbHKT3(1;3)	XM_002457691.1 XP_002457736.1	CM000762.1	EES02856.1	Sb03g012590	3	33
SbHKT4(1;4)	XM_002448447.1 XP_002448492.1	CM000765.1	EES12820.1	Sb06g027900	6	32

Table 4: K+/H+ Antiporters found in the *Sorghum bicolor*

Sequence name	Reference sequences	Related protein	Gene name	Chr no	%identity with query
SbKEA1	XM_002448749.1 XP_002448794.1	EES13122.1	Sb06g033310	6	85
SbKEA2	XM_002443531.1 XP_002443576.1	EES17414.1	Sb08g021840	8	19





SEQUENCE: Mon CRC64: 8F13D9941BD04EA5 LENGTH: 465 aa

InterPro IPR003445 Family — Cation transporter — PF02386 — TrkH

SEQUENCE: Sun CRC64: 61166C20CBB1388A LENGTH: 886 aa

InterPro IPR000595 Domain — Cyclic nucleotide-binding — PF00027 — cNMP_binding; SM00100 — cNMP; PS50042 — CNMP_BINDING_3

InterPro IPR003938 Region — Potassium channel, voltage-dependent, EAG/ELK/ERG — PR01463 — EAGCHANLFMLY

SEQUENCE: Mon CRC64: 715E3C09E1569EA7 LENGTH: 432 aa

InterPro IPR003280 Region — Potassium channel, two pore-domain — PR01333 — 2PORE KCHANEL

SEQUENCE: Mon CRC64: 39535DC8016558F9 LENGTH: 967 aa

InterPro IPR003148 Domain — Regulator of K+ conductance, N-terminal — PF02254 — TrkA_N; PS51201 — RCK_N

SEQUENCE: Mon CRC64: 0B8134E48FDB9652 LENGTH: 299 aa

InterPro IPR018490 Domain — Cyclic nucleotide-binding-like — SSF51206 — cAMP-binding domain-like

Figure 1: Interpro scan result for prediction of protein domain

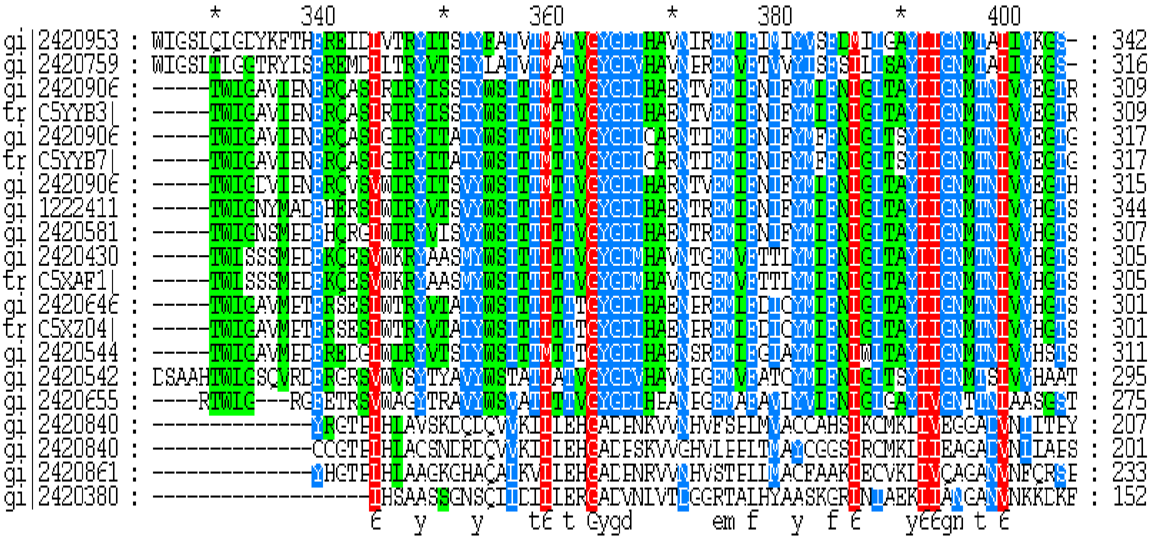


Figure 2: Sequence alignment of K$^+$CHANNEL family proteins in GeneDoc

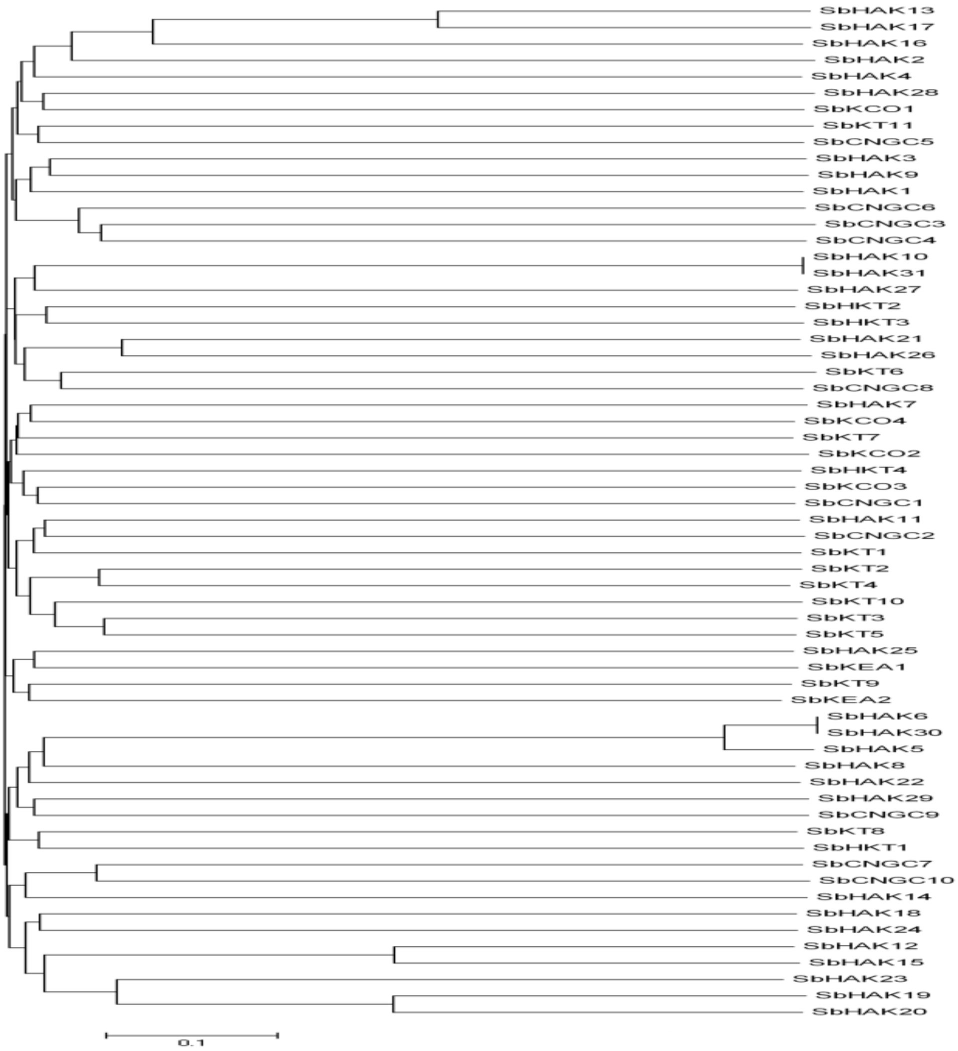


Figure 3: Phylogenetic tree of potassium transporter families in *Sorghum bicolor*

4. DISCUSSION

Comparative genomics is the study of the relationship of genome structure and function across different biological species or strains. Gene finding is an important application of comparative genomics, as is discovery of new, non-coding functional elements of the genome. Analysis of rice genome against Arabidopsis as a model plant has revealed around fifty one genes .comparative analysis of sorghum genome against rice as a model plant has identified a total of 60 genes. Around 52 genes present in sorghum were similar to that of rice in evolutionary relationship where as 8 genes belonging to the CNGC transporters resembles Arabidopsis genes. Hence the comparative analysis of *Sorghum bicolor* genome reveals that it is more closely related to the rice and other cereals and quite distinct from Arabidopsis. Most of the KUP/HAK transporters identified so far in sorghum, as like rice belong to the cluster of high-affinity transporters. The characteristic feature of HAK transporters is presence of consensus motif **GVVYGDLGTSPLY** (the amino acids conserved in all sequences are in bold) where all the HAK transporters vary very little from it. In plants, the homologues of KUP/HAK/KT transporters exist as multi gene families in both dicot and monocots. [13]By systematic BLAST searches in public databases, 13 members of this family were detected earlier in Arabidopsis, while at least 27 members are identified in rice. In this study, we identified 31 potential KT/HAK/KUP family genes in Sorghum (*sorghum bicolor*) by database searching. Most of the KUP/HAK transporters identified so far in sorghum, as like rice belong to the cluster of high-affinity transporters. They mediate high-affinity K+ transport in root cells. For all the HAK proteins of sorghum ,the functional domain of KUP family is confirmed through INTERROSCAN(IPR 018519).The characteristic feature of HAK transporters is presence of consensus motif **GVVYGDLGTSPLY** (the amino acids conserved in all sequences are in bold) where all the HAK transporters vary very little from it. Based on systematic sequencing programs and DNA based strategies, nine genes encoding Shaker-type K+ channels and six genes encoding 2P/4TM channels were identified in Arabidopsis. In rice, a total of 11 genes corresponding to shaker type K+ channel proteins and three genes to 2P/4TM KCO family were identified.[14]In *Sorghum bicolor,* 11genes belonging to shaker type K+ channel proteins, 4genes from 2P|4TM KCO family and 8 genes corresponding to CNGC family were identified. HKT transporters are proposed to contain 4 pore-forming regions enclosed by transmembrane segments.[15] Trk/Ktr/HKT transporters are involved in diverse functions, from K(+) or Na(+) uptake to membrane potential control, adaptation to osmotic or salt stress, or Na(+) recirculation from shoots to roots in plants.[16] Some members of the HKT protein family have been shown to be critical for salinity tolerance in commercially important crop species, particularly in grains, through exclusion of Na^+ ions from sensitive shoot tissues in plants.[17] Phylogenetic trees of publicly available full-length HKT coding sequences or HKT amino acid sequences show that the gene family splits into two major branches. The two HKT subfamilies can also be distinguished on the basis of gene organization. The division of the family into two major branches is associated with a glycine/serine substitution of a residue predicted to be in the first pore loop of the protein. All members of subfamily 1 have a serine at this position, whereas members of subfamily 2 (except for the likely revertant OsHKT2; 1) have a glycine. [18]In *Sorghum bicolor*, four genes corresponding to the sub family1 were identified. They are named as SbHKT1;1,SbHKT1;2,SbHKT1;3,SbHKT1;4. When rice protein from sub family 2 is taken as query, sequences with significant similarity were not found. An antiporter is an integral membrane protein which is involved in secondary active transport of two or more different molecules or ions (i.e. solutes) across a phospholipid membrane. They are named as

KEAs.[19] Only two sequences named as SbKEA1and SbKEA2 were identified. Among these two, SbKEA2 has shown 19% similarity with query protein.

5. CONCLUSION

In the present study, an analysis of the genomic sequences related to K+ transporter families in *Sorghum bicolor* was carried out by searching genome in public databanks. The purpose of this study is to contribute to the understanding of molecular mechanisms of K+ transport and functional characterization of identified new K+ transporter genes that play a major role in salt tolerance. Furthermore, results from each of the analyzed gene families are described. The presented analyses should lead to testing of hypotheses by the plant membrane transport community that can be derived from the presented phylogenetic relationships.

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