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GENOMIC EXPLORATION OF THE MST(-like) GENE FAMILY IN *Mangifera indica*: INSIGHTS INTO DEVELOPMENT AND STRESS RESPONSE

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ABSTRACT

Mangifera indica (*M. indica*) is a widely consumed fruit in tropical and subtropical regions. The Monosaccharide Transporter (MST) gene family plays a crucial role in sugar transport and stress response. This study investigates the MST(-like) gene family in *M. indica* to understand its genomic characteristics and role in fruit development and stress response. Comparative analysis with *Arabidopsis thaliana* identified 28 MST(-like) genes in *M. indica*. Phylogenetic analysis and promoter region analysis were conducted. Gene expression was evaluated using Next Generation Sequencing (NGS) data, and qRT-PCR was used to validate responses to drought stress. MiSTP5 exhibited the highest up-regulation, while MiINT3 showed significant down-regulation. Promoter analysis revealed involvement in drought, salicylic acid signaling, and light responsiveness. Following drought stress, MiPLT5 and MiPLT6 gene expressions increased, while MiSTP5 and MiINT3 decreased over seven days. The identified MST(-like) genes are key to understanding the developmental processes and stress response in *M. indica*. These genes may serve as valuable markers for detecting stress, with potential applications in agriculture.

Keywords: Genomics Analysis, *Mangifera indica*, NGS, Phylogenetic Analysis

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INTRODUCTION

M. indica is a perennial plant belonging to the Anacardiaceae family and native to tropical regions (Lora and Hormaza 2018). The *M. indica* plant has received special attention in recent years due to important pharmacological applications in cancer chemotherapy (Akkewar *et al.,* 2024), rheumatoid arthritis (Akkewar *et al.,* 2024), in vitro activity against lung cancer cells (Alshwyeh *et al.,* 2024), breast cancer (Yap *et al.,* 2021), colorectal cancer (Lozano-Casabianca *et al.,* 2022), antibacterial (Alshwyeh *et al.,* 2024) and anti-inflammatory activities (Kim *et al.,* 2020).

There was extensive work to understand the genomics and proteomics of *M. indica* with emphasis on gene expression of several gene families and their implications. Among these studies are the dof gene family (Alghanem *et al.,* 2024), Mi14-3-3 gene family (Xia *et al.,* 2022), gene families in fruit ripening (Dautt-Castro *et al.,* 2015), MYB transcription factor gene family (Zhang *et al.,* 2022), polygalacturonases (Dautt-Castro *et al.,* 2019), TCS gene family (Sadaqat *et al.,* 2024), potassium transport-related gene families (Tan *et al.,* 2023), eIF genes (Li *et al.,* 2019) and cyclic nucleotide-gated channel gene family (Zhang *et al.,* 2023). Yet, the MST(-like) gene family is still to be investigated.

The monosaccharide transporter (-like) gene family is believed to be present in higher plants (Büttner and Sauer 2000). Catalyzing the transport of hexoses, polyols, and, in one instance, pentoses and tetroses, the 53 members of the monosaccharide transporter(-like) gene family in Arabidopsis contribute to sugar partitioning or subcellular sugar distribution (Büttner 2007). This family has received the attention to understand the biology, development and resistance to abiotic stress in several plants (Cheng *et al.,* 2018; Liu *et al.,* 2018; Wu *et al.,* 2021).

The 14-member monosaccharide -H^+ symporter family is the largest and best-characterized family of the MST(-like) gene family, with the first member involved in transporting hexoses (Schofield *et al.,* 2009). While many plants are known to leach sugars and polyols during freeze-thaw events in freezing temperature environments, members of the Arabidopsis subfamily of polyol transporters subfamily of MST transporters are known to act as osmoprotectants when under stress (Johnson *et al.,* 2006).

Despite *M. indica* being a globally important fruit crop, particularly in tropical and subtropical regions, the molecular mechanisms underlying its development and response to environmental stress remain poorly

understood. Specifically, the role of the MST gene family, which is known to regulate sugar transport and stress responses in other plants, has not been comprehensively studied in *M. indica*. This knowledge gap limits our understanding of how these genes influence critical processes such as fruit development, sugar accumulation, and the plant's ability to cope with environmental stressors like drought. The objectives of this study are: (1) to identify and characterize the MST(-like) gene family in *M. indica* at the genomic level, (2) to analyze the expression patterns of these genes during key stages of fruit development and under stress conditions, and (3) to explore the regulatory elements and interactions that govern their response to environmental stress. This research aims to provide novel insights into the genetic regulation of *M. indica* development and stress resilience.

MATERIALS AND METHODS

Identification and sequence analysis of MST(-like) gene family in *M. indica*: Members of MST(-like) gene family from *A. thaliana* were retrieved from the TAIR database (TAIR - Home Page (arabidopsis.org) (Swarbreck *et al.,* 2007), and NCBI (https://www.ncbi.nlm.nih.gov/). After retrieving protein sequences, BLASTp was used to identify homologs of MST(-like) gene family from *M. indica* plant. The database was searched using the settings of an E-value threshold of 0.001 to ensure a high level of homology, with a minimum identity cutoff of 50%. The BLOSUM62 matrix was used for alignment, and standard gap cost of 11 (existence) and 1 (extension) were applied.

Phylogenetic analysis of MST(-like) gene family in *M. indica*: MST(-like) gene family protein sequences from *M. indica* and *A. thaliana* were used to construct the phylogenetic tree. The maximum likelihood tree was constructed using the IQ tree (http://iqtree.cibiv.univie.ac.at/)(Nguyen *et al.,* 2015). IQ-TREE v1.6.12 was used, applying the JTT+G model, determined through ModelFinder analysis, to optimize for the protein sequence data. Bootstrap replicates of 1000 were applied and SH-aLRT testing with 1000 replicates to ensure robust branch support. Furthermore, a tree was modified and generated by using the software iTOL (https://itol.embl.de/)(Letunic and Bork 2007).

Gene sequence analysis of monosaccharide transporter(-like) gene family in *M. indica*: Introns and Exons structures of MST(-like) gene family were predicted using an online tool Gene Structure Display Server 2.0 (GSDS) (http://gsds.gao-lab.org/)(Hu *et al.,* 2015).

Physical properties of MST(-like) in *M. indica*: Physiochemical characteristics of MST(-like) proteins including molecular weight, theoretical pI, number of amino acids, and aliphatic index were predicted using ProtParam (https://web.expasy.org/protparam/) (Garg *et al.,* 2016). The sub-cellular localization of the proteins was forecasted using another online tool called Cello2.0 (http://cello.life.nctu.edu.tw/cello2go/).

MST(-like) motif analysis in *M. indica*: Conserved motifs and their locations were detected through protein sequences of MST(-like) gene family using MEME (https://meme-suite.org/meme/tools/meme) (Bailey *et al.,* 2015). Specifically, the maximum number of motifs was set at 10, with motif widths ranging from 6 to 50 residues. The motif distribution model allowed for zero or one occurrence per sequence. Motifs were retrieved for all 28 present members of MST(-like) gene family.

MST(-like) domain analysis: To identify the conserved domains for MST(-like) genes, we used the NCBI's integrated database CDD (Conserved Domain Database) (https://www.ncbi.nlm.nih.gov/Structure/cdd/cdd.shtml) then all protein sequences were searched against Pfam database two crosses verify predicted conserved domains. Afterward, results were visualized through TBtools (Chen *et al.,* 2020). The E-value cutoff of 1x 10^{-5} and validated against the Pfam database using HMMER3 with the default gathering threshold and all member databases were selected.

Identification of Cis-acting regulatory elements MST(-like) genes: For the identification of cis-acting regulatory elements in *M. indica* mainly up to 2kb was retrieved manually from the NCBI gene database (https://www.ncbi.nlm.nih.gov/gene) by considering the upstream regions of genes. Afterward, the PlantCare database (https://bioinformatics.psb.ugent.be/webtools/plantcare/html/)(Lescot *et al.,* 2002) was used to identify and visualize the cis-acting regulatory elements which after extraction from the database are displayed on an Excel sheet.

Gene expression analysis based on RNA-seq data: Transcriptomic data for drought stress was retrieved from the NCBI's SRA database (https://www.ncbi.nlm.nih.gov/sra). This data was used for mapping the reads against reference *M. indica* genome to identify MST(-like) gene family expression by using Galaxy Bowtie2 (https://usegalaxy.org/)(Afgan *et al.,* 2018). The data retrieved and organized from the RNA-seq tool i.e., Galaxy was used, and the gene expression levels of MST(-like) gene family were evaluated using a fragments mapping tool called Cufflinks (specialized for transcription, estimation and testing of DEGs in the RNA sample). For the identification of the genes of *M. indica* the petitioned IDs were retrieved from the NCBI. Moreover, this data was

mapped as generic heat maps using another tool called TBtools.

RNA Extraction, qRT-PCR, and cDNA synthesis of MST(-like) in *M. indica*: qRT-PCR was performed to track the expression pattern of four *MST(-like)* genes from *M. indica*. These genes comprise MiPLT5, MiPLT6, MiSTP5 and MiINT3. The plants were exposed to drought stress for seven days. Samples were extracted for gene expression evaluation after 2, and 7 days following the drought stress initiation. Trizol technique was followed to extract RNA from *M. indica* leaves sample utilizing a Thermo Nanodrop 2000 kit. cDNA was synthesized and qRT-PCR was performed using an iTaq Universal SYBR Green Super-Mix (Bio-Rad Labs, Hercules, CA, USA) in a qRT-PCR detection system (CFX96 Touch-TM RT PCR Detection System). An algorithm NCBI Primer-BLAST "(https://www.ncbi.nlm.nih.gov/tools/primer-blast/ was used to predict gene-specific primers for MST(-like) genes which were further verified through Oligo Calculator "(http://mcb.berkeley.edu/labs/krantz/tools/oligocalc.html/)".

Statistical Analysis: Descriptive statistics, including means and standard deviations (SD), were computed for all quantitative variables. For comparisons between multiple groups, a one-way analysis of variance (ANOVA) was performed, followed by Tukey's post-hoc test to identify specific group differences.

RESULTS

Identification of MST(-like) family in *M. indica*: The biological sequence recognition process involves several steps. The reference sequences of the monosaccharide transporter (-like) gene family were first retrieved and used as a query to perform a BLAST against plant sequences. The results were then filtered to identify the homologs in the target plant, *M. indica*, by investigating specific domains in the retrieved sequences. Before retrieving the MST(-like) genes in *M. indica*, the sequences were first collected from *A. thaliana*, a related species, using the TAIR database. The collected sequences were then used to identify homologs in *M. indica* through NCBI BLAST. After filtering to obtain the most likely matches, 28 members of the monosaccharide transporter (-like) gene family were retrieved from NCBI, showing homology with *M. indica*. The retrieved transporter family homologs were named based on the BLAST results and renamed from *A. thaliana* to *M. indica* according to the sub-family name.

Sequence alignment and phylogenetic analysis: To demonstrate the evolutionary relationship between the MST(-like) gene family from *M. indica*, the sub-families were aligned using the MEGA7.0.26 software (https://www.megasoftware.net/)(Kumar *et al.,* 2016). The maximum likelihood tree was generated using the online software IQ-Tree, which produced a phylogenetic tree based on the aligned sequences. The algorithm also assigned distinct identifications to each sub-family. All recognized monosaccharide transporters from *M. indica* were assigned to their family members based on their classification and functions, as referred by *A. thaliana*. The xylose transporter and the putative monosaccharide transporter ERD families were not characterized as no protein was predicted, and the plastid localized gene pGlcT has not been identified.

The circular phylogenetic tree illustrates the evolutionary relationships of the MST(-like) gene family in *M. indica* and their homologs in *A. thaliana*, divided into five distinct sub-families: PLT, INT, TMT, SFP, and STP (Figure 1). Each sub-family is color-coded for clarity, with purple representing PLT, green for INT, yellow for TMT, orange for SFP, and red for STP. The tree highlights the evolutionary divergence between these genes, with branching points representing common ancestors and numerical values indicating bootstrap support for each branch.

Gene structure and motif analysis of MST(-like) in *M. indica*: Figure 2 presents a comprehensive analysis of the MST(-like) gene family in *M. indica*, combining phylogenetic relationships, gene structure, and motif composition. Panel A shows a phylogenetic tree that organizes the genes based on their evolutionary relationships, grouping them into distinct clades. Panel B illustrates the gene structure, where red boxes represent exons and black lines indicate introns, highlighting the variation in exon-intron arrangements among the genes. Intron phases (0, 1, 2) are also noted, showing further diversity in gene architecture. Panel C focuses on the motif composition of these genes, where different colored boxes represent the identified motifs (1-10) across the gene family, indicating the conservation and variability of these functional regions. Panel D provides the consensus sequences for each of the motifs, showcasing the conserved functional domains that play a critical role in the proteins encoded by these genes.

Physical characteristics of MST(-like) in *M. indica*: Table 1 summarizes the characteristics of MST(-like) proteins in *M. indica*, including molecular weights ranging from 52022.34 to 79,435.31 Da and theoretical pI values between 4.9 and 9.55. These proteins, consisting of 479 to 739 amino acids, are localized in the plasma membrane. The aliphatic index, which suggests protein thermostability, varies from 101.16 to 117.53, showing considerable diversity in protein stability among the family members. The hydropathicity average, or GRAVY, of all the MST(-like) proteins is below 0, indicating they are hydrophilic or water-loving.

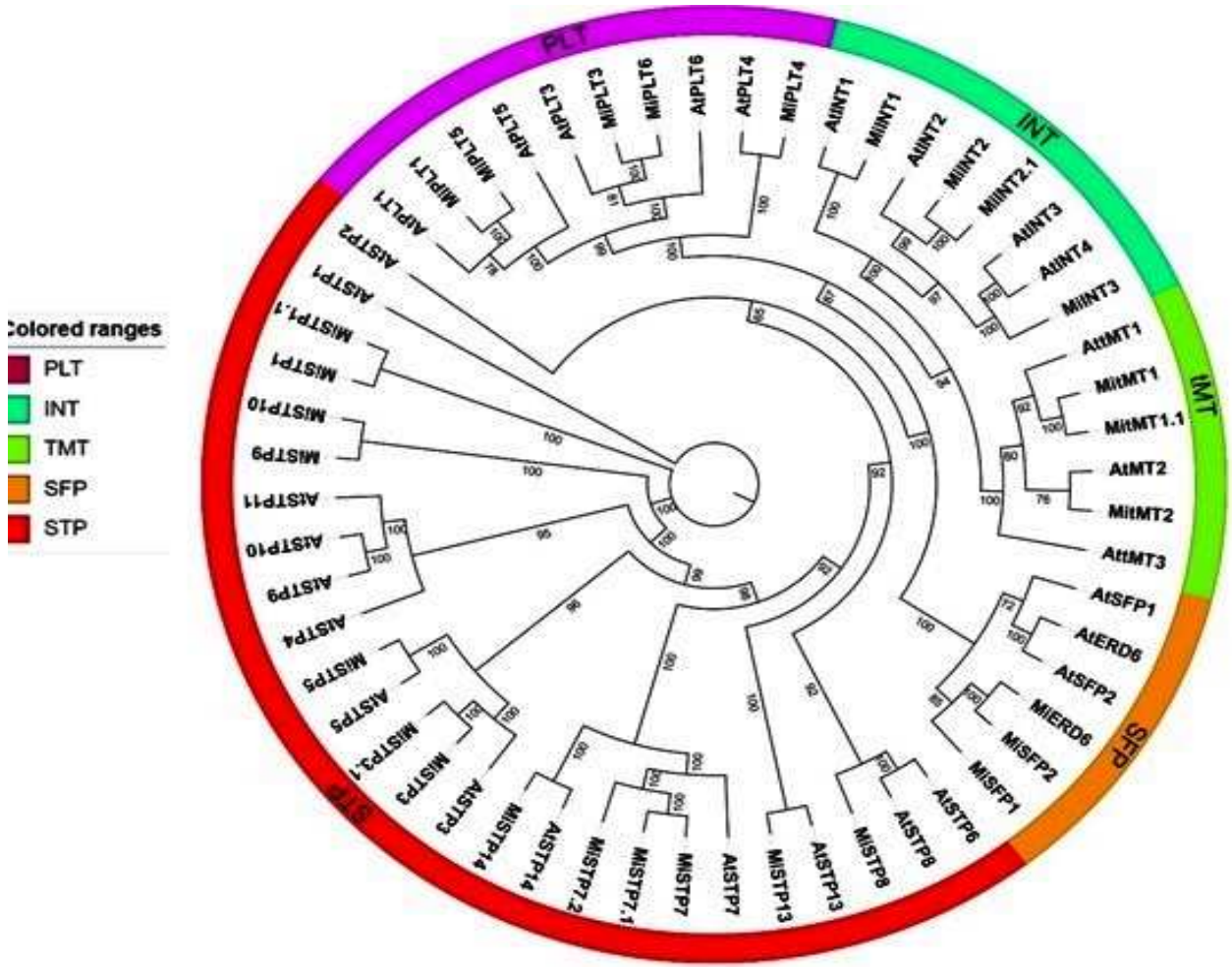

Figure 1. Phylogenetic tree of MST(-like) sub-families from *A.thaliana* and *M.indica*. Five out of seven sub-families and a maximum likelihood tree were created using IQ-Tree. The colors in the tree demonstrate and distinguish the sub-families.

Domain analysis and visualization of MST(-like) family in *M. indica*: The conserved domains of MST(-like) sequences in *M. indica* were analyzed using NCBI CDD and Tbtools program (Figure 3). Different domains are represented by color-coded bars: MFS superfamily (green), MFS_PLT (yellow), MFS_HMIT_like (pink), MFS_STP (blue), and MFS_GLUT6_8_Class3_like (red). Each bar represents the length of the protein sequence, with corresponding domains located across the sequence. The most conserved domain was the Sugar_tr domain, which was present in 23 members, followed by the least conserved domain, the MFS superfamily, which included the MitMT family and two members of the SFP family. The less conserved domains indicate that they have a distinct function in comparison to other protein families.

Cis-acting regulatory elements monosaccharides transporter family in *M. indica*: Cis-acting regulatory elements share in controlling gene expression and their involvement in various biological processes. These elements, such as silencers, enhancers, insulators, and tethering elements, regulate the transcription of neighboring genes that impact development, morphogenesis, embryonic development, anatomy development, and stress response (Figure 4).

Gene expression analysis of monosaccharides transporter family in *M. indica*: The growth period in which cells divide and increase in size to enlarge the fruit is known as fruit development. It plays a critical role in regulating gene expression patterns. An ongoing study uses NGS to study gene expression during fruit development. Different stages of *M. indica* development were observed, from pre-mature to final. A total of six runs were taken in this genome project. The collected and analyzed data was uploaded to evaluate FPKM (Fragments per kilobase of exon per million mapped

fragments) values using a Galaxy server-based tool. After calculating the FPKM values of all MST(-like) genes, a heat map was generated using Tbtools (Figure 5). The rows represent the names of genes and the columns represent the experimental values. Highly expressed genes can be easily visualized by the color changing moderately from white to blue and blue to red, indicating downregulated and upregulated genes. The heat map shows gene regulation is scaled between 1.50 to 3.50. The most upregulated gene, MiPLT5, has the highest value at 3.50, and the most downregulated gene, MiINT3, has the lowest value at -1.50.

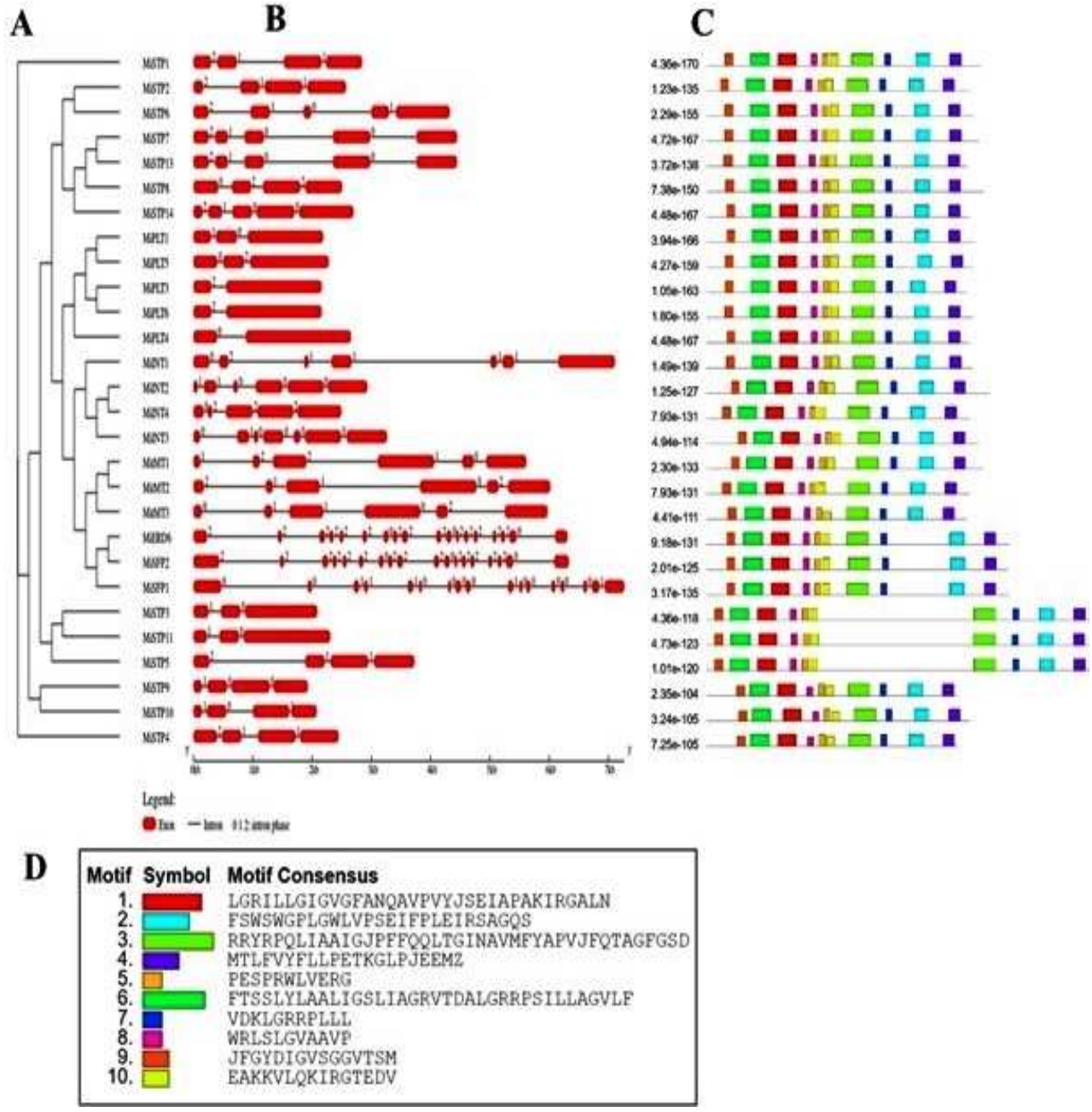

Figure 2. A) Using the GSD2.0 website, the exons and introns structures of MST(-like) were featured. Exons are shown in red rectangles while introns are demonstrated by grey lines. The introns phase is also shown by the number 0,1,2. B) Representation of Motifs involves the ten most conserved motifs in all the protein sequences along with their homologs. C) The distribution of the estimated motifs D) The colour and sequences of the motifs.

Table 1. The MST(-like) protein characteristics include Locus tag, Molecular weight, Theoretical pI (isoelectric point), Number of amino acids, Sub-cellular localization, GRAVY, and Aliphatic index.

Protein Name	Locus tag	Molecular weight	Theoretical pI	No. of amino acids	GRAVY	Sub-cellular Localization	Aliphatic index
MiSTP1	LOC123192488	57587.83	9.44	524	0.519	Plasma membrane	105.69
MiSTP2	LOC123221291	55449.97	9.18	502	0.688	Plasma membrane	117.53
MiSTP3	LOC123225485	55313.18	9.43	509	0.516	Plasma membrane	103.63
MiSTP4	LOC123218049	57223.1	9.12	520	0.527	Plasma membrane	103.48
MiSTP5	LOC123229098	54000.5	9.49	498	0.621	Plasma membrane	106.55
MiSTP6	LOC123194838	57914.05	8.71	528	0.526	Plasma membrane	111.72
MiSTP7	LOC123201104	54457.56	9.44	501	0.558	Plasma membrane	111.36
MiSTP8	LOC123225113	56099.11	9.36	512	0.524	Plasma membrane	108.95
MiSTP9	LOC123226347	57062.34	9.3	509	0.506	Plasma membrane	101.16
MiSTP10	LOC123225211	55536.84	9.55	486	0.528	Plasma membrane	104.03
MiSTP11	LOC123194838	55372.28	9.31	509	0.516	Plasma membrane	103.24
MiSTP13	LOC123200430	54457.56	9.44	501	0.558	Plasma membrane	111.36
MiSTP14	LOC123215026	55644.7	8.56	508	0.602	Plasma membrane	115.57
MiPLT1	LOC123199542	58400.26	9	540	0.427	Plasma membrane	107.81
MiPLT3	LOC123196959	54521.46	9.2	503	0.608	Plasma membrane	112.7
MiPLT4	LOC123226902	56649.4	5.59	519	0.488	Plasma membrane	113.97
MiPLT5	LOC123199542	57475.52	9.26	528	0.456	Plasma membrane	109.7
MiPLT6	LOC123220278	54521.46	9.2	503	0.608	Plasma membrane	112.7
MiINT1	LOC123192455	53170.97	5	497	0.572	Plasma membrane	113.02
MiINT2	LOC123204437	63011.74	8.59	578	0.382	Plasma membrane	104.65
MiINT3	LOC123203251	62280.74	8.4	576	0.378	Plasma membrane	101.79
MiINT4	LOC123213541	62871.36	8.78	578	0.361	Plasma membrane	103.44
MitMT1	LOC123228943	78830.59	5.02	739	0.379	Plasma membrane	107.12
MitMT3	LOC123208916	79226.24	5.18	738	0.373	Plasma membrane	107.25
MitMT2	LOC123208910	79435.31	5.23	739	0.36	Plasma membrane	105.79
MiERD6	LOC123208915	52022.34	6.05	479	0.664	Plasma membrane	107.24
MiSFP1	LOC123200430	54349.26	4.9	501	0.588	Plasma membrane	106.27
MiSFP2	LOC123226902	52192.44	6.11	481	0.706	Plasma membrane	110.64

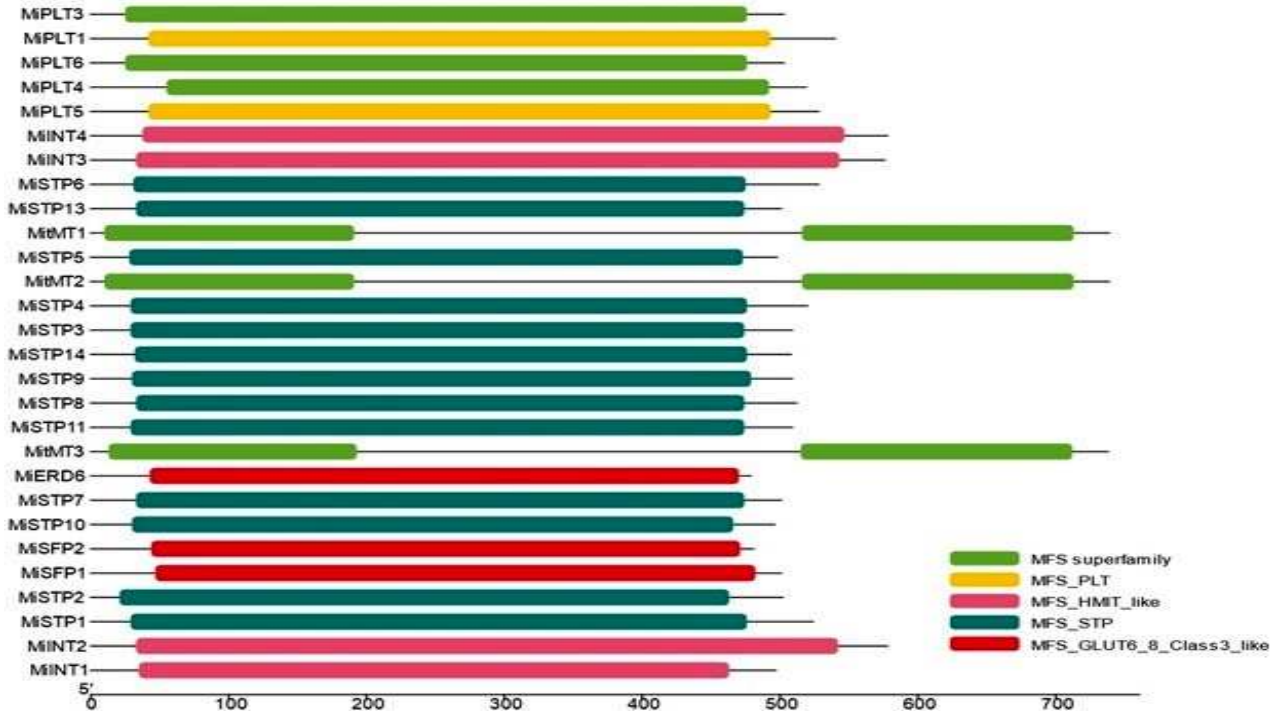

Figure 3. A) Protein domains retrieved from NCBI CDD. Members of the STP family show the most conserved domain.

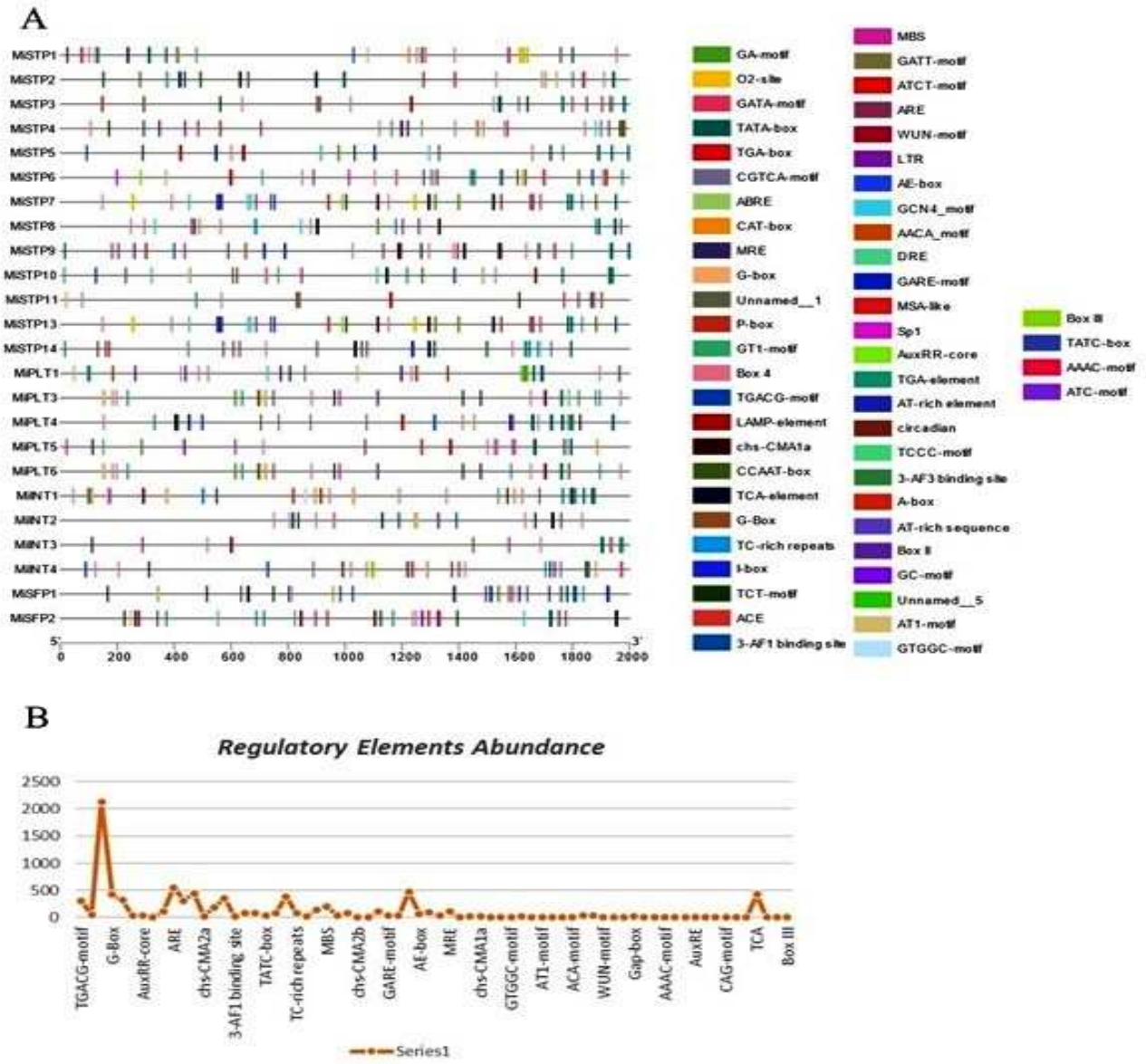

Figure 4 provides an analysis of the cis-regulatory elements in the promoter regions of the MST(-like) gene family in *M. indica*. Panel A shows the distribution of various regulatory elements such as the TATA-box, G-box, and ABRE, which play crucial roles in stress responses, hormone signaling, and light responsiveness. The elements are color-coded, revealing a complex regulatory architecture across different genes. Panel B displays a graph highlighting the abundance of these elements, with the TGACG motif being the most frequent, followed by other key elements like the ARE and MBS, which are important for regulating gene expression under stress conditions.

qRT-PCR expression analysis of MST(-like) genes: The transcript abundances of four MST(-like) genes from *M. indica* fruit were evaluated (Figure 6). The expression of these four genes showed varying levels of gene expression. The changes in gene expression were monitored and compared to control values. qRT-PCR was performed to determine the response of the fruit to regulation by the highly expressed genes. The treatment was given to *M. indica* for seven days. MiPLT5, the most highly expressed gene, was found to be significantly upregulated, while MiPLT6 was also shown to be significantly increased. On the other hand, MiSTP5, was found to be the gene that was most significantly downregulated. The expression of MiPLT5 and MiPLT6 increased significantly from day 4 to day 7, while the levels of MiSTP5 and MiINT3 decreased significantly over the same period, albeit MiSTP5 was also observed from day 2.

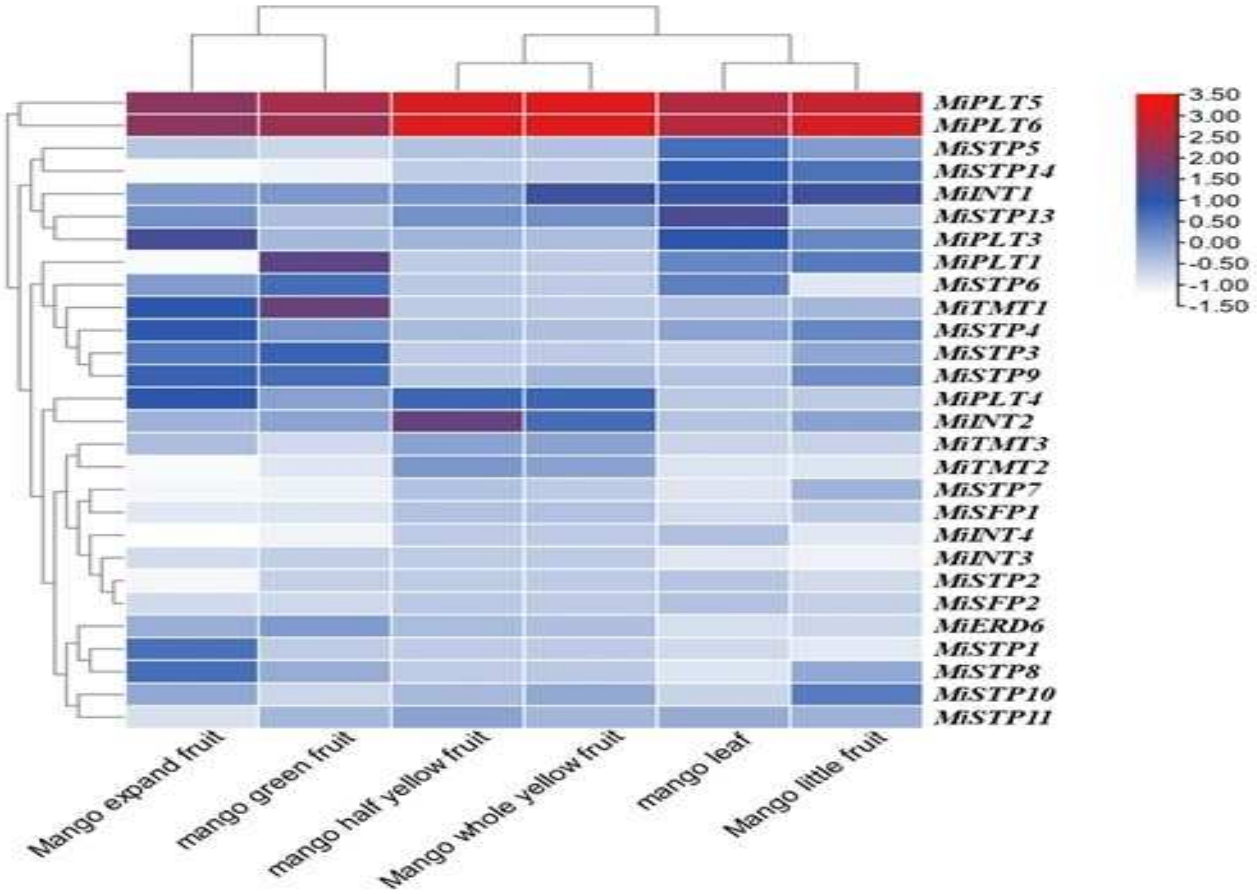

Figure 5. Gene Expression profiles of MiMSTs are presented under the fruit development responses and a heat map was created using the Tbtools and scaling was created between 1.50-3.50. Changes in gene expression are visualized by matching with the color of the scale.

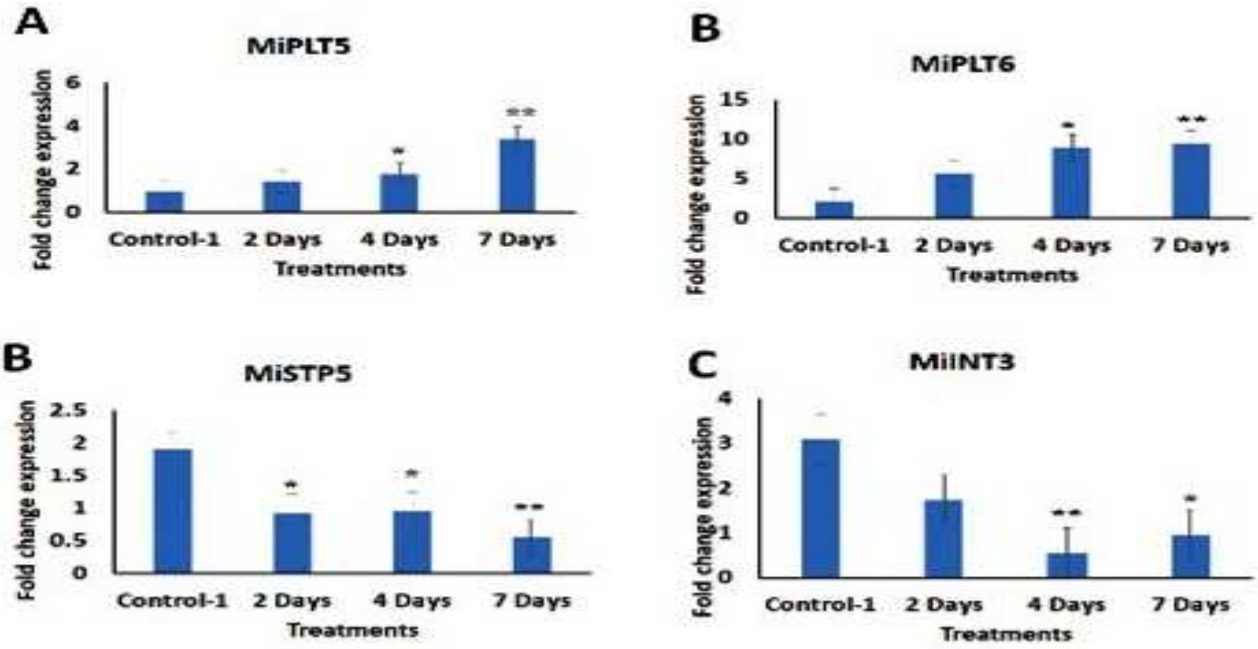

Figure 6. MiMSTs gene family relative qRT-PCR test in response to drought stress.

DISCUSSION

M. indica is an economically important tropical fruit that is known for its rich flavor and antioxidant properties, which helps in controlling various diseases like cancer (Akkewar *et al.,* 2024), heart disease (Minniti *et al.,* 2023), and diabetes (Yoopum *et al.,* 2023). The monosaccharides transporter (-like) gene family is a collection of 7 sub-families that play a role in various plant processes, such as light signaling, response to environmental elements, and plant development and synchronization (Büttner 2007; Slewinski 2011). However, there is a lack of comprehensive analysis of the MST(-like) genes in the fruit development of *M. indica*. Out of the 53 members of the monosaccharides sugar transporter family, 28 have been identified in *M. indica*. These members have also been identified in other plants such as rice (Deng *et al.,* 2019), maize (Zhu *et al.,* 2024), Arabidopsis (Johnson *et al.,* 2006), and peanuts (Wan *et al.,* 2020).

The genes *At3g03090* and *At5g17010* are localized in the vacuolar membrane (Büttner 2007), while *At5g59250* is believed to be present in the chloroplast membrane (TAIR). The largest sub-family, the STP family, has 14 members. *MiSTP1* is involved in the germination of seeds and is expressed in various parts of the plant, such as ovaries, stems, leaves, and sepals. *AtSTP2* and *MiSTP2* play a role in the uptake of glucose during pollen development (TAIR), while *STP13* is expressed in the parts of the plant undergoing programmed cell death (TAIR). The ABRE elements, GT1_motifs, and TCT-motifs of STPs plant response to drought and salinity stresses in strategic crops (Shariatipour and Heidari 2018). AtPLT5 of the subfamily plays a significant role in the transportation across plasma membranes and is widely expressed in the H+-symport of basic polyols and sugars (Reinders *et al.,* 2005). *AtINT4* of the tonoplast family is a highly specific transporter that synthesizes another symporter named raffinose, while *AtINT1* acts as a protein transporter in Arabidopsis (Schneider *et al*., 2006).

The results obtained from this study shed light on the identification and characterization of 28 members of the MST(-like) gene family in *M, indica*. These genes play crucial roles in the transport of sugars, which are vital for the plant's growth, fruit development, and response to environmental stressors such as drought (Shariatipour and Heidari 2018). Phylogenetic analysis revealed that these genes are grouped into five distinct subfamilies, with a close evolutionary relationship to homologs in *A. thaliana*. The gene structure analysis showed variation in exon-intron arrangements, which is indicative of the diverse functional roles of these genes. Motif analysis further supported this functional diversity, as conserved motifs were observed across the gene family, with some motifs being specific to certain subfamilies. These motifs may be responsible for the distinct roles of these genes in sugar transport and stress response. The identification of cis-acting regulatory elements associated with drought, salicylic acid signaling, and light responsiveness highlights the complex regulatory mechanisms governing these genes under different environmental conditions.

In terms of expression, MiSTP5 showed the highest up-regulation, while MiINT3 exhibited significant down-regulation during the fruit development process. Notably, the expression of MiPLT5 and MiPLT6 increased significantly in response to drought stress, whereas MiSTP5 and MiINT3 showed a decrease in expression over time. These findings suggest that the MST(-like) genes have both developmental and stress-responsive roles, which may have potential applications in improving crop resilience and productivity in agricultural settings. The study's use of NGS data and qRT-PCR validation further strengthens the relevance of these genes in stress signaling pathways.

Among the proteins of this gene family, the MFS_STP domain was the most conserved, while the least conserved domain was MFS_GLUT6_8_Class3_like in *M. indica*. Hexose transporters (STP1-STP14) are plant sugar transport proteins (STP). They actively absorb glucose, 3-O-methylglucose, fructose, xylose, mannose, galactose, fucose, 2-deoxyglucose, and arabinose via sugar/hydrogen symport (Deng *et al.,* 2015; MFS_STP). Many STP family transporters are tissue-specific or expressed at specific developmental stages. The highest expression of STP1 is seen in photosynthetic tissues including leaves and stems, while roots, siliques, and flowers have lesser expression. It is crucial to Arabidopsis seed and seedling sugar intake and response. The Major Facilitator Superfamily (MFS) membrane transport protein Glucose transporter-like (GLUT-like) family includes the STP subfamily (MFS_STP). This highlights the important role of these transporters in *M. indica*.

The real-time quantification (q-PCR) of highly expressed genes revealed that the control of plant growth affects the rate and fold change expression levels of genes such as MiPLT5, MiPLT6, MiSTP5, and MiINT3 in a 7-day analysis. The standard deviation of highly expressed genes increases over time, while the mean fold change expression in MiSTP5 and MiINT3 decreases with time, and vice versa for the other two expressed genes under treatment. This set of genes can be regarded as biomarkers for drought stress in *M. indica.*

The cis-acting regulatory elements initiate transportation and respond to various metabolic and biological pathways, and binding sites (Marand *et al.,* 2023). It can be concluded that the large number of STPs significantly affects the synchronization and development

of the plant, while some of the least responsive elements are modulated during the maturity of the plant.

This study provides a comprehensive exploration of the MST(-like) gene family in *M. indica* by integrating phylogenetic, structural, and functional analyses. The identification of 28 MST(-like) genes through comparative genomics offers new insights into their evolutionary relationships, particularly by comparing them to homologs in *A. thaliana*. The study's use of advanced bioinformatics tools, such as phylogenetic analysis, exon-intron structure prediction, motif identification, and promoter region analysis, provides a robust framework for understanding the gene family's role in both development and stress response. Furthermore, the identification of conserved and unique cis-regulatory elements across these genes highlights their involvement in crucial biological processes, offering potential molecular markers for stress resilience in mango crops. The inclusion of gene expression analysis based on transcriptomic data strengthens the functional relevance of these genes, particularly in response to drought, making this study valuable for agricultural applications.

Despite its strengths, the study has some limitations. One of the key limitations is the lack of experimental validation for the identified regulatory elements and gene expression patterns. While bioinformatics predictions and transcriptomic data provide valuable insights, experimental confirmation, such as gene knock-out or overexpression studies, would be essential to validate the predicted roles of these MST(-like) genes in *M. indica*. Additionally, the focus on drought stress, though important, limits the exploration of other abiotic and biotic stressors that could provide a more complete picture of the gene family's functions. Expanding the analysis to include more diverse environmental conditions and conducting experimental studies could further strengthen the conclusions drawn in this research.

Conclusions: Winding up this study all members of the monosaccharides transporters(-like) gene family were identified in *M. indica* and their phylogenetic correspondence, gene structure, conserved motifs, physiochemical characteristics, and protein-conserved domains were examined. Cis-acting regulatory elements were retrieved and investigated to check the functions and responses of the genes in the fruit development of the plant. Gene Expression Analysis was performed to probe the highly expressed genes of *MiMSTs*. *M. indica* fruit development response is mediated by *MiMSTs*. Providing information that will be useful in the future functional characterization of MiMSTs genes. This study provides information about how MST(-like) genes respond during fruit development and response to drought stress.

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