Plant Physiology and Biochemistry 216 (2024) 109095

Contents lists available at ScienceDirect

Plant Physiology and Biochemistry

journal homepage: www.elsevier.com/locate/plaphy

Comprehensive identification and expression analyses of sugar transporter genes reveal the role of *GmSTP22* in salt stress resistance in soybean

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ARTICLE INFO

Keywords:
Monosaccharide transporter
Sucrose transporter
Sugar transporter protein
Phylogenetic analysis
Evolution
Expression pattern
Stress response
Cis-acting element

ABSTRACT

The transport, compartmentation and allocation of sugar are critical for plant growth and development, as well as for stress resistance, but sugar transporter genes have not been comprehensively characterized in soybean. Here, we performed a genome-wide identification and expression analyses of sugar transporter genes in soybean in order to reveal their putative functions. A total of 122 genes encoding sucrose transporters (SUTs) and monosaccharide transporters (MSTs) were identified in soybean. They were classified into 8 subfamilies according to their phylogenetic relationships and their conserved motifs. Comparative genomics analysis indicated that whole genome duplication/segmental duplication and tandem duplication contributed to the expansion of sugar transporter genes in soybean. Expression analysis by retrieving transcriptome datasets suggested that most of these sugar transporter genes were expressed in various tissues, and a number of genes exhibited tissue-specific expression patterns. Several genes including *GmSTP21*, *GmSFP8*, and *GmPLT5/6/7/8/9* were predominantly expressed in nodules, and *GmPLT8* was significantly induced by rhizobia inoculation in root hairs. Transcript profiling and qRT-PCR analyses suggested that half of these sugar transporter genes were significantly induced or repressed under stresses like salt, drought, and cold. In addition, GmSTP22 was found to be localized in the plasma membrane, and its overexpression promoted plant growth and salt tolerance in transgenic *Arabidopsis* under the supplement with glucose or sucrose. This study provides insights into the evolutionary expansion, expression pattern and functional divergence of sugar transporter gene family, and will enable further understanding of their biological functions in the regulation of growth, yield formation and stress resistance of soybean.

1. Introduction

Sugars (including sucrose, monosaccharides, polyols) are main products of photosynthesis in plants, and play crucial roles in plant growth and development, as well as in responses to various biotic and abiotic stresses by acting as metabolites, nutrients, osmotic molecules, and signal molecules (Mishra et al., 2022; Ruan, 2014). Sugars are mainly synthesized in source organs (leaves) and translocated via the phloem over long distance into sink organs (roots, stems, and fruits) to supply the carbon substrate for plant growth and/or storage. Sucrose and monosaccharides including glucose, fructose, mannose, ribose, and galactose, are the main sugar forms providing energy and metabolites in plants (Ruan, 2014). Sugar alcohols (also called polyols, e.g., mannitol, sorbitol, inositol) and organic acids (e.g., citrate and malate), also play irreplaceable roles in plant growth and development as well as in stress responses (Dumschott et al., 2017). In most plant species, sucrose is the preferred long-distance transport form of sugars in the phloem (Li et al., 2017). Both the loading and the unloading of sugars from phloem vessels or from companion cells require transmembrane transportation of sugars (Braun, 2022). Sugars are also transported between different compartments intracellularly. The vacuole serves as a storage organelle for various carbohydrates (Hedrich et al., 2015). The transportation and allocation of sugars either at the whole plant level or at the intercellular and subcellular levels is essential for plant productivity, yield formation and fruit quality (Ren et al., 2023; Wingenter et al., 2010; Braun et al., 2014). Therefore, understanding the mechanism of sugar transportations and the physiological functions of sugar transporters is vital to ensure crop yield and fruit quality for the growing human population

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https://doi.org/10.1016/j.plaphy.2024.109095
Received 23 April 2024; Received in revised form 2 August 2024; Accepted 3 September 2024
Available online 4 September 2024

under global climate change.

Sugar transporters that facilitate sugar transport are required for the loading and unloading of sugars, and also for sugar compartmentation at the cellular and whole-plant levels (Kühn and Grof, 2010; Büttner, 2007). Sugar transporters can be divided into three major types, i.e., sucrose transporters (SUTs) (also named sucrose carriers, SUCs), monosaccharide transporters (MSTs), and sugars will eventually be exported transporters (SWEETs) in plants (Doidy et al., 2012; Xue et al., 2022). SWEET is a relatively newly identified sugar transporter family (Xu et al., 2023). SWEET family members can be divided into four phylogenetic clades based on their protein sequences and they have different substrates, such as sucrose, glucose, or fructose. SWEETs have been known to be involved in phloem loading, nectary secretion, pollen development, seed filling, and fruit development (Wang et al., 2022; Xue et al., 2022). SUTs and MSTs belong to the major facilitator superfamily (MFS), which is characterized by 12 transmembrane domains (Slewinski, 2011; Büttner, 2007). SUTs in plants are ubiquitous transmembrane proteins that are divided into two transmembrane regions separated by a hydrophilic cytoplasmic loop (Lalonde et al., 2004). SUT family can be grouped into five subfamilies, including one dicot-specific (SUT1), two monocot-specific (SUT3 and SUT5), and two subfamilies existing in both monocot and dicot plants (SUT2 and SUT4)(Kühn and Grof, 2010). SUTs are located in the plasma membrane (PM) or tonoplast and contribute to H^+/sucrose symport in both source and sink organs (Riesmeier et al., 1994; Durand et al., 2018). SUTs play important roles in the loading and unloading of phloem sucrose (Kühn and Grof, 2010).

MSTs are integral membrane proteins that participate in the transportation of various monosaccharides. According to sequence features and substrate specificities, MSTs can be divided into seven subfamilies, i.e., sugar transporter protein (STP) (also named hexose transporter, HT), sugar facilitator protein (SFP) (also named early-response to dehydration 6-like protein, ERDL/ESL), polyol/monosaccharide transporter (PLT/PMT), tonoplast monosaccharide transporters (TMT) (also named tonoplast sugar transporter, TST), vacuolar glucose transporter (VGT), inositol transporter (INT), and plastidic glucose transporter (pGlcT) family (Slewinski, 2011; Büttner, 2007; Doidy et al., 2012). STPs act as H^+/sugar symporters of monosaccharides, such as glucose, fructose, pentose and galactose (Rottmann et al., 2018). PLTs function as symporters localized in the PM for monosaccharides and polyols (Juchaux-Cachau et al., 2007; Klepek et al., 2009). SFPs form a distinct family that includes genes encoding vacuolar hexose exporters functioning in osmotic regulation (Poschet et al., 2011; Yamada et al., 2010; Klemens et al., 2014). INTs are characterized as H^+/inositol symporters that transport inositols into the cytoplasm (Sambe et al., 2014; Schneider et al., 2008). TMT and VGT are two subfamilies involved in sugar uptake in vacuoles (Aluri and Büttner, 2007; Wormit et al., 2006; Cheng et al. 2018a, 2018b). pGlcT has been known to export sugars (e.g., maltose and glucose) derived from starch degradation into the cytosol in plants (Cho et al., 2011; Weber et al., 2000). Based on the evolutionary analysis, these seven subfamilies of MSTs have been found to be existed across the plant kingdom including mosses (Johnson et al., 2006). Since the first report of hexose transporter (Sauer and Tanner, 1989) in unicellular *Chlorella*, sucrose transporter in spinach (Riesmeier et al., 1992), and polyol transporter in celery (Noiraud et al., 2001), many sugar transporters in the families of MST, SUT, and SWEET have been identified in numerous plants, such as *Arabidopsis* (Buettner, 2007; Chen et al., 2010), rice (Deng et al., 2019; Hu et al., 2021), pear (Li et al., 2015), grape (Afoufa-Bastien et al., 2010), apple (Wei et al., 2014), woodland strawberry (Jiu et al., 2018), tomato (Reuscher et al., 2014), longan (Fang et al., 2020), and pineapple (Fakher et al., 2022). For example, a total of 53 MST genes, 9 SUT genes, and 17 SWEET genes have been identified in *Arabidopsis* (Buettner, 2007; Chen et al., 2010). A total of 64 MST genes, 5 SUT genes, and 21 SWEET genes have been identified in rice (Deng et al., 2019; Sosso et al., 2015).

Soybean is an important crop providing oil- and protein-rich food. The genome of a cultivated soybean (*Glycine* max L. var. Williams 82) has been sequenced and annotated for more than a decade (Schmutz et al., 2010). However, the entire sugar transporter families in the whole genome of soybean have not been comprehensively identified, and their roles in growth regulation, seed yield formation, and stress tolerance are unclear. Because the SWEET gene family of soybean has been identified (Patil et al., 2015), it will not be included in this study. Here, we genome-widely identified all the other putative sugar transporter genes in soybean, and analyzed their tissue expression patterns and their responses to stresses. We further selected the stress-responsive *GmSTP22* for functional analysis by genetic transformation in *Arabidopsis*. Transgenic plants overexpressing *GmSTP22* showed higher biomass under growth media supplemented with glucose or sucrose, and exhibited more resistance to salt stress in the presence of sugar. These results provide useful information for further functional studies of sugar transporters and also for future exploitation of their functions for developing soybean cultivars with improved seed yield and stress resistance.

2. Materials and methods

2.1. Identification of sugar transporter genes

Genes encoding putative sugar transporters in soybean were retrieved by using BLAST tool in the Soybase (https://www.soybase.org/). Protein sequences of sugar transporter members from *Arabidopsis* were used for searching. The nucleotide sequences and protein sequences of candidate sugar transporters in soybean were obtained from the SoyBase. Protein domains were analyzed by using the InterPro database (http://www.ebi.ac.uk/interpro/) and the HMMScan (https://www.ebi.ac.uk/Tools/hmmer/search/hmmscan). The TMHMM2.0 program (http://www.cbs.dtu.dk/services/TMHMM/) was used for transmembrane helix prediction. The WoLF PSORT program (http://wolfpsort.hgc.jp) was used for the prediction of subcellular localization. Protein sequences were analyzed by the MEME program (https://meme-suite.org/meme/tools/meme) to analyze the conserved motifs.

2.2. Phylogenetic analysis of sugar transporter family

Protein sequences of sugar transporters from soybean, *Arabidopsis*, and rice were obtained from the SoyBase (https://www.soybase.org/), TAIR (http://www.arabidopsis.org/), and RGAP (http://rice.uga.edu/), respectively. The protein sequences were aligned using ClustalW or Muscle, and the phylogenetic trees were constructed using MEGA6.0 (Tamura et al., 2013).

2.3. Analyses of chromosome distribution, gene structure, and promoter cis-acting regulatory elements

Gene structures of soybean sugar transporters were analyzed with TBtools by using the gff date downloaded from Ensembl Plants (https://plants.ensembl.org/index.html). The chromosome distribution information of sugar transporter genes was obtained from genome annotation file and chromosome distribution figure was generated by TBtools (Chen et al., 2020). Two kb promoter sequences upstream the transcription start sites were obtained from the SoyBase for analysis of the location of *cis*-acting regulatory elements.

2.4. Gene duplication, Ka/Ks value, and collinearity analysis

Two neighboring paralogous genes were considered to be tandemly duplicated if the distance of them was less than 100 kb and was separated by five or less genes (Zhao et al., 2021). To analyze the duplication and synteny of sugar transporter genes in soybean, genomic files and genome annotation files were retrieved and analyzed by the program of One Step MCScanX in TBtools. The duplications and the synteny block

were visualized by using the Circos program of TBtools (Chen et al., 2020). The synonymous substitution rate (Ks), and nonsynonymous substitution rate (Ka) of gene pairs was determined using TBtools (Chen et al., 2020). The divergence time (T) was calculated by the formula: $T = Ks/(2 \times 6.1 \times 10^{-9}) \times 10^{-6}$ million years ago (MYA) (Lynch and Conery, 2000).

2.5. In silico expression analysis of sugar transporter genes

To investigate the expression of sugar transporter genes, we retrieved the expression levels of sugar transporter genes in different tissues of soybean from Soybean Expressio Atlas (https://venanciogroup.uenf.br/cgi-bin/gmax_atlas/index.cgi) (Machado et al., 2020). Expression values of each gene were log2-transformed and visualized using the heatmap. Microarray or RNA-sequencing datasets of salt stress (1 h, 6 h, and 12 h) in soybean root, dehydration stress (1 h, 6 h, and 12 h) in soybean root, cold stress (24 h) and drought stress (6 days) in soybean leaves were retrieved from previous datasets (Dung Tien et al., 2012; Maruyama et al., 2012; Belamkar et al., 2014). Previous dataset of transcriptomic response to rhizobia (*Bradyrhizobium japonicum*) in soybean root hairs was obtained and analyzed (Libault et al., 2010).

2.6. Soybean growth and stress treatment

Soybean seeds (*Glycine* max var. Williams 82) were germinated at room temperature for 4 days, then seedlings were transferred to hydroponic culture system containing half-strength modified Hoagland nutrient solution (Zeng et al., 2019). Soybean were grown in a growth chamber under conditions: photoperiod 12-h-light/12-h-dark at 28/25 °C, light intensity 250 μmol m^{-2} s^{-1}. Twelve-day old seedlings were treated with stresses. For salt stress, the roots of seedlings were immersed in nutrient solution containing 100 mM NaCl. For dehydration treatment, plants were removed from the hydroponic culture system and left in air (Belamkar et al., 2014). After treatments for 6 h, roots of the stress-treated and non-treated plants were harvested.

2.7. Quantitative RT-PCR analysis

Total RNA was isolated using an Ultrapure RNA Kit (CWBIO, Beijing) according to the manufacturer's instructions. One μg purified RNA was reverse transcribed into cDNA using a kit (HiScript III All-in-one RT SuperMix Perfect for qPCR, Vazyme, Nanjing). qRT-PCR was conducted on a CFX96 Real-Time PCR Systems (Bio-Rad) by using Taq Pro Universal SYBR qPCR Master Mix (Vazyme, Nanjing) as described previously (Zeng et al., 2017). Gene expression levels were normalized to *GmACTIN11* (Glyma.18G290800) and *GmEF1b* (Glyma.02G276600) in soybean, or to *AtACTIN2* (AT3G18780) and *AtTUBULIN2* (AT5G62690) in *Arabidopsis*. Primer sequences used for qRT-PCR analysis were listed in Supplementary Table S1.

2.8. Subcellular localization analysis

The coding sequence (CDS) without stop codon of *GmSTP22* was amplified, and inserted into pCAMBIA1300-GFP vector to generate 35S: GmSTP22-GFP expression construct. The agrobacterium cells (*Agrobacterium tumefaciens* GV3101) transformed with plasmids were added to LB liquid media and oscillated at 28 °C and 200 rpm for 24 h until the OD_{600} was 0.5–0.6. The *A. tumefaciens* was then collected and suspended with the infection solution (10 mM MES, 10 mM $MgCl_2$, 150 μM acetosyringone, pH = 5.6). The leaves of tobacco (*N. benthamiana*) with the same growth period were used for injection of agrobacteria using a syringe. Empty vector pCAMBIA1300-GFP was used as a positive control. After injection for 12 h, the injected tobacco leaves were collected and used for subcellular localization observation by using a fluorescence confocal microscope (NiKon, Japan). The plasmid vectors of 35S: GmSTP22-GFP and the PM marker were cotransformed into rice protoplasts by PEG-mediated transformation. After the transformation, protoplasts were incubated in the dark at 28 °C for 12–16 h. Fluorescence was observed with a confocal laser scanning microscope (Zeiss, Germany).

2.9. Arabidopsis transformation and phenotypic analyses

The coding sequence (CDS) without stop codon of *GmSTP22* was inserted into pCAMBIA1300-3flag plasmid through the homologous recombination method by using pEASY®-Basic Seamless Cloning and Assembly Kit (TransGen Biotech, Beijing). The overlapping fragments were assembled with the linearized expression vector pCAMBIA1300-3flag digested with the restriction enzyme *Sac*I to generate Pro35S: GmSTP22-3flag expression construct. The recombinant plasmid was transformed into agrobacterium GV1301 and genetically transformed wild-type *Arabidopsis* (Col-0) by the floral dip method (Clough and Bent, 1998). The T1 seeds were screened against 50 mg L^{-1} hygromycin and the T2 seeds showing 3:1 segregation with hygromycin resistance were harvested and used for further homozygous line screening. Homozygous lines with *GmSTP22* overexpression were used for phenotypic analyses. Arabidopsis seeds were surface-sterilized using 33% bleach for 10 min and placed in sterile water at 4 °C for 2 days for stratification, followed by grown for 7 days at 22 °C in 1/2 Murashige and Skoog (MS) growth medium (pH 5.7, 1% sucrose and 0.7% (w/v) agar) under 16 h light/8 h dark growth conditions. For sugar treatment, *Arabidopsis* seeds were sowed and grown on 1/2 MS growth media containing 30 mM sucrose or 50 mM glucose according to previous studies (Schofield et al., 2009). For seed germination and cotyledon greening rate assay to analyze salt stress tolerance, seeds were surface sterilized and plated on 1/2 MS medium with or without 1.5% sucrose in the presence or absence of 140 mM NaCl. The dishes were incubated for 2 days at 4 °C to break seed dormancy, and then transferred to 22 °C under a 16 h light/8 h dark regime. The number of germinated seeds and seedlings with green cotyledons was counted at the indicated time. For salt stress tolerance of seedlings, four-day old seedlings were transferred to 1/2 MS growth media containing 120 mM NaCl, and fresh weight and root length were calculated after treatment for 8 days.

3. Results

3.1. Identification and phylogenetic analyses of sugar transporters in soybean

To investigate the sugar transporter family genes in soybean, the BLAST algorithm was used to search the soybean genome database using protein sequences of *Arabidopsis* sugar transporters as the query. In total, 122 genes were identified to putatively encode sugar transporter proteins (Supplementary Table S2). Phylogenetic analysis of the 122 sugar transporters reveals that these proteins could be classified into eight subfamilies, including STP, PLT, TMT, INT, pGlcT, VGT, SFP, and SUT (Fig. 1 and Supplementary Figs. S1–S3). The first seven subfamilies belong to the MST superfamily. These sugar transporters identified here included 32 *STP* genes, 22 *PLT* genes, 9 *TMT* genes, 15 *INT* genes, 9 *pGlcT* genes, 4 *VGT* genes, 20 *SFP* genes, and 11 *SUT* genes (Supplementary Fig. S4). To investigate the evolutionary relationships, unrooted phylogenetic trees were constructed for individual sugar transporter subfamily in soybean, *Arabidopsis* and rice. The topology of phylogenetic trees indicated that sugar transporters of each subfamily in soybean have a close evolutionary relationship with those in *Arabidopsis* and rice (Supplementary Figs. S1–S3). The sugar transporter genes identified here were named according to the phylogenetic analyses and their homologous genes in *Arabidopsis*. The amino acid number of these sugar transporters was ranged from 166 to 738, and their predicted molecular weight was ranged from 18.1 to 79.3 kDa (Supplementary Table S2). The theoretical isoelectric point (pI) of the sugar transporters was ranged from 4.86 to 9.76. Furthermore, most of these soybean sugar

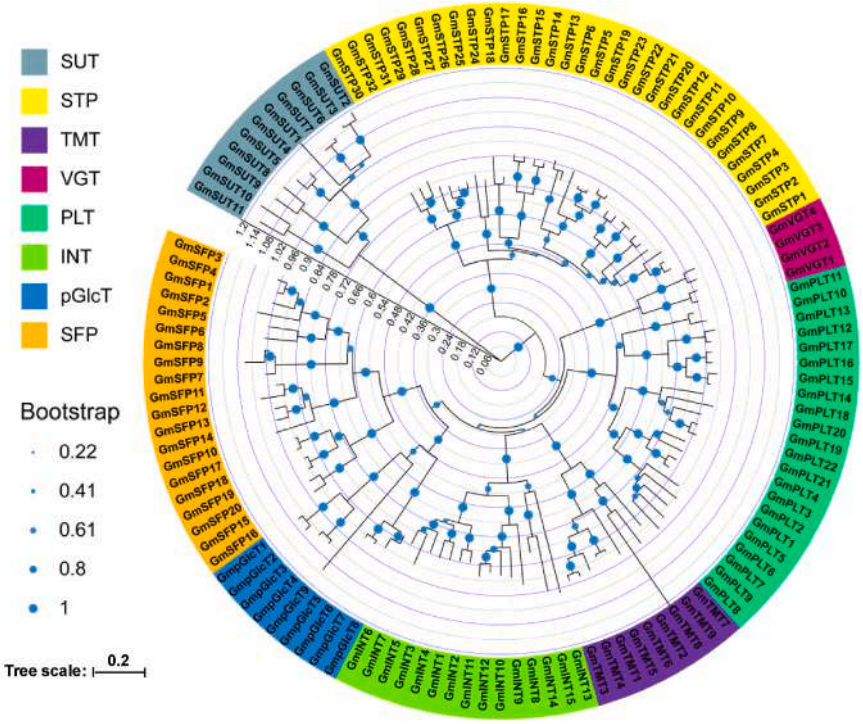

Fig. 1. Phylogenetic relationships of sugar transporters in soybean. The full-length amino acid sequences were used for alignment by ClustalW and the neighbor-joining phylogenetic tree was constructed by MEGA6 with 1000 bootstrap replications. The name of these proteins were designated according to their homologs in *Arabidopsis thaliana*. Proteins from eight different subfamilies are assigned with distinct colors for shading.

transporters harbored at 10–12 conserved transmembrane domains (TMDs), while several proteins such as GmSTP5, GmSTP6, GmPLT20, GmINT13, GmpGlcT9, and GmSFP2 contained less than 7 TMDs (Supplementary Table S2). The prediction of subcellular localization of these sugar transporters by the WoLF PSORT program suggested that 60.7% (74 out of 122) of them localized in the PM, and 18.0% (22 out of 122) of them localized in the tonoplast, which is followed by 10 proteins localized in Golgi, 9 proteins localized in the endoplasmic reticulum, 5 proteins localized in the cytosol, and 2 proteins localized in the chloroplast (Supplementary Table S3).

3.2. Gene structure, conserved motif, and protein domain of sugar transporters in soybean

The exon and intron boundaries, which are known to play crucial roles in the evolution of multiple gene families, were explored. Results showed that the intron number of these sugar transporter genes ranged from 1 to 18 (Supplementary Fig. S5). The number of exons and the gene length were relatively similar within the same subfamily. For instance, *GmVGT* subfamily genes have 12–13 introns, but the intron number of *GmPLT* subfamily genes was only 1 to 3. Each subfamily has a different number of exons, which may result in functional diversity in closely related genes encoding sugar transporters.

Conserved domains of these sugar transporters were predicted by using the InterPro database (http://www.ebi.ac.uk/interpro/). Sugar transporters within the same subfamily were found to have similar predicted protein domains (Fig. 2). All the MST superfamily (including 7 subfamilies) members were predicted to contain conserved MSF domains, while all the SUT subfamily transporters were predicted to contain a conserved Glycoside-Pentoside-Hexuronide (GPH) domain (Fig. 2). In order to investigate the characteristic regions of these sugar transporters, MEME software was used to analyze the conserved motifs. A total of 12 conserved motifs were identified in all these soybean sugar transporters (Supplementary Fig. S6). Motif 7 was identified in the functional domains of almost all sugar transporters (117/122), suggesting its importance for the sugar transporters in soybean. Furthermore, the comparison of motifs from sugar transporters revealed that there are differences in the number of conserved motifs between different subfamilies. In STP and PLT subfamilies, most proteins possessed at least 10 conserved motifs, while the motif number varied from 6 to 11 for other subfamilies, with the exception that several proteins contain less than 6 conserved motifs, such as GmINT13, GmpGlcT9, GmSFP2 and GmSFP9 (Supplementary Fig. S6). Only two to four conserved motifs (Motif 1, 9, 11 and 12) were contained in the SUT subfamily transporters. This discrepancy may be attributed to functional disparities between SUT transporters (responsible for sucrose transport) and MST transporters (responsible for monosaccharide transport). In addition, the three-dimensional structural models predicted by using the SWISS-MODEL showed that these sugar transporters were mainly composed by α-helices (Fig. 3). All these models were monomeric and they shared more than 59.5% sequence identity with their respective homologous templates, with GMQE (global model quality estimate) values ranged from 0.69 to 0.89 (Supplementary Table S4), suggesting a high reliability of three-dimensional model predictions.

3.3. Chromosomal localization and collinearity analyses

The 122 sugar transporter genes identified here were mapped unevenly on all the 20 chromosomes in the soybean genome (Supplementary Fig. S7). The number of sugar transporter genes on these chromosomes ranged from 2 to 13. Twenty groups of genes showed tandem duplication (Supplementary Fig. S7). Among the 20 groups, 15 groups had two genes, each duplicated; the remaining groups had 3 to 6 genes duplicated. Seventy-one pairs of sugar transporter genes exhibited whole-genome duplication (WGD)/segmental duplication in soybean (Fig. 4), suggesting that WGD/segmental duplication plays an important role in the expansion of sugar transporter genes in soybean. To evaluate the driving force underlying the evolution of sugar transporter genes, Ks, Ka, and Ka/Ks ratio of 71 gene pairs of WGD/segmental duplication were calculated. The Ka/Ks of all the duplicated gene pairs

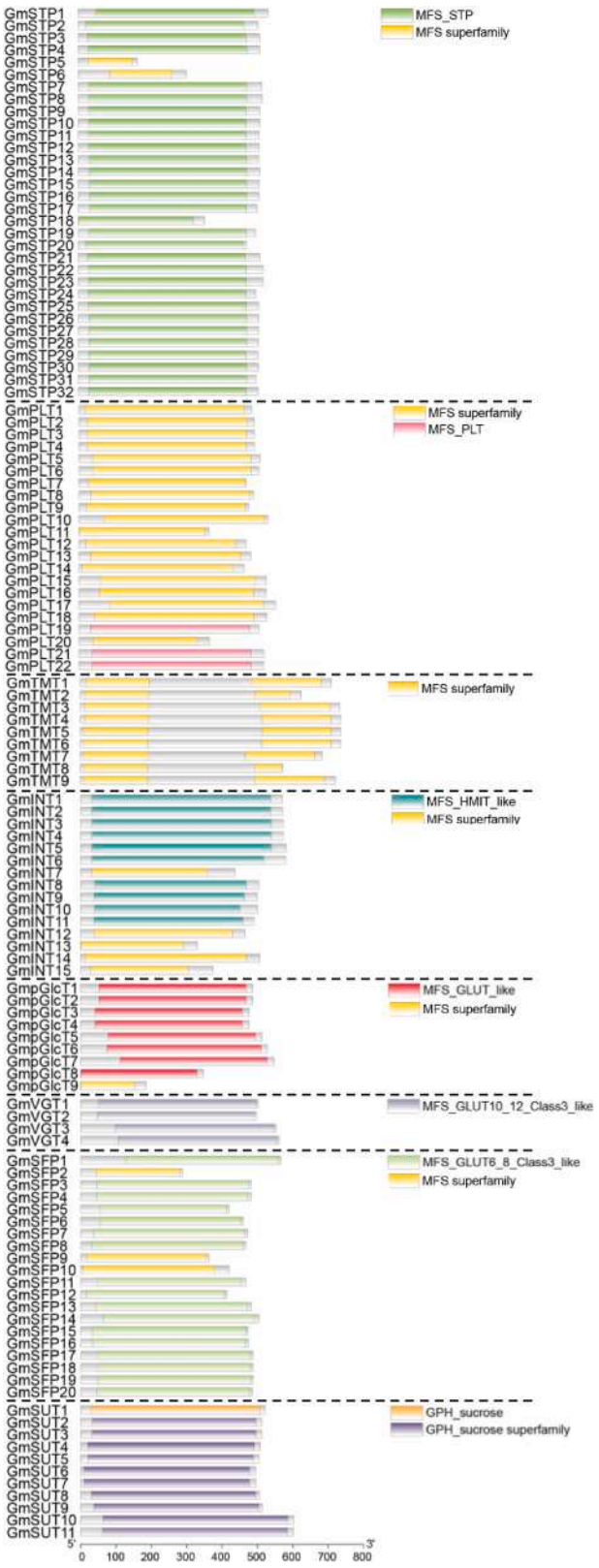

Fig. 2. Conserved domain of 122 sugar transporters identified in the annotated soybean genome.

was between 0.052 and 0.535 (Supplementary Table S5), indicating that MST and SUT families were subjected to purifying selection in soybean, because a pair of genes having Ka/Ks < 1 could indicate purifying selection during the evolution (Lynch and Conery, 2000). The divergence times of these duplication events ranged from 5.5 to 265.0 MYA, with an average time of 65.4 MYA (Supplementary Table S5).

3.4. Tissue expression patterns of sugar transporter genes in soybean

The tissue expression patterns of putative genes encoding sugar transporters in soybean were analyzed by RNA-seq datasets retrieved from the Soybean Expression Atlas (https://venanciogroup.uenf.br/cgi-bin/gmax_atlas/index.cgi). The dataset includes fifteen tissues, i.e., leaves, shoot, callus, hypocotyl, seedling, flower, green pods, root, root tip, nodules, seed coat, embryo, cotyledon, endosperm, and suspensor. Tissue expression patterns revealed that 106 of these sugar transporter genes were differentially expressed in various tissues. A number of genes were expressed ubiquitously in diverse tissues, such as *GmSTP6/8*, *GmINT9/10*, *GmpGlcT1/2/7*, *GmTMT3/4/6*, *GmPLT12/13/17*, *GmSUT8/10/11*, *GmSFP13/19/20*, and *GmVGT1*, whereas some genes showed tissue-specific expression pattern (Fig. 5; Supplementary Table S6). For example, *GmSUT6/7* and *GmSTP3/19/31* were predominantly expressed in flowers; *GmPLT5/6/7/8/9* were strongly expressed in nodules (Fig. 5).

3.5. Cis-acting elements in promoters of sugar transporter genes

We investigated the presence of 10 kinds of *cis*-acting elements associated with hormonal signaling and/or stress responses in the 2.0 kb promoter sequences of sugar transporters genes. *Cis*-acting elements including ABA responsive element (ABRE), auxin signaling component ARF1 binding site (AuxRE), salicylic acid (SA)-responsive promoter element (SARE), dehydration and cold response element (DRE/CRT), stress-related CAMTA transcription factor binding site (CG-box), environmental signal response element (G-box), WRKY binding site (W-box), light-regulated gene expression (Ibox) phosphate starvation signaling transcription factor PHR1 binding site (P1BS), and sulfur-responsive element (SURE), were analyzed (Supplementary Table S7). We found all the genes contained at least one of these *cis*-acting elements (Fig. 6; Supplementary Table S8). More than 71 sugar transporter genes contained more than 4 kinds of *cis*-acting elements in their promoters, among which *GmSTP16*, *GmSTP28*, *GmPLT13*, *GmPLT16*, and *GmINT5* contained at least 8 kinds of *cis*-acting elements. More than half of the sugar transporter genes contained SURE, W-box, SARE, and Ibox. Among these sugar transporters genes, most of them contain W-box, while most of them did not contain DRE/CRT, G-box and CG-box in their promoters (Supplementary Table S8). Moreover, the promoter regions of some sugar transporter genes contained multiple copies of *cis*-acting elements. For example, nine SARE elements were found in the promoter region of *GmPLT19*, six W-box elements were found in promoter regions of *GmSTP25*, *GmPLT6*, and *GmpGlcT6* (Fig. 6; Supplementary Table S8).

3.6. Sugar transporters in response to stresses

By retrieving previous microarray or RNA-seq datasets, we analyzed the expression profiles of sugar transporter genes in responses to stresses like salt, dehydration, and cold. Among these transporter genes, the expressions of 59 genes were found to be dramatically changed by at least one of these stresses (Fig. 7). *GmSTP2/7/16/17/22/23/24/25/28*, *GmPLT10*, *GmTMT9*, *GmINT4/7*, *GmVGT3*, *GmSFP13/14/18*, and *GmSUT4/5/8* were induced by salt stress, while *GmSTP26*, *GmPLT3/19*, *GmINT1/2/14* and *GmSFP3/4/8/10* were repressed by salt stress. *GmSTP22* was strongly induced by cold, salt, drought and dehydration. In addition, the expression profiles of sugar transporter genes in response to rhizobia (*Bradyrhizobium japonicum*) inoculation (12–48 h after inoculation (HAI)) in soybean root hairs was analyzed by retrieving published transcriptome data. Most of the sugar transporter genes (95 genes) could be detected in the root hairs with or without rhizobia inoculation (Supplementary Fig. S8; Supplementary Table S9). *GmPLT8* was remarkably affected by rhizobia inoculation; it was significantly

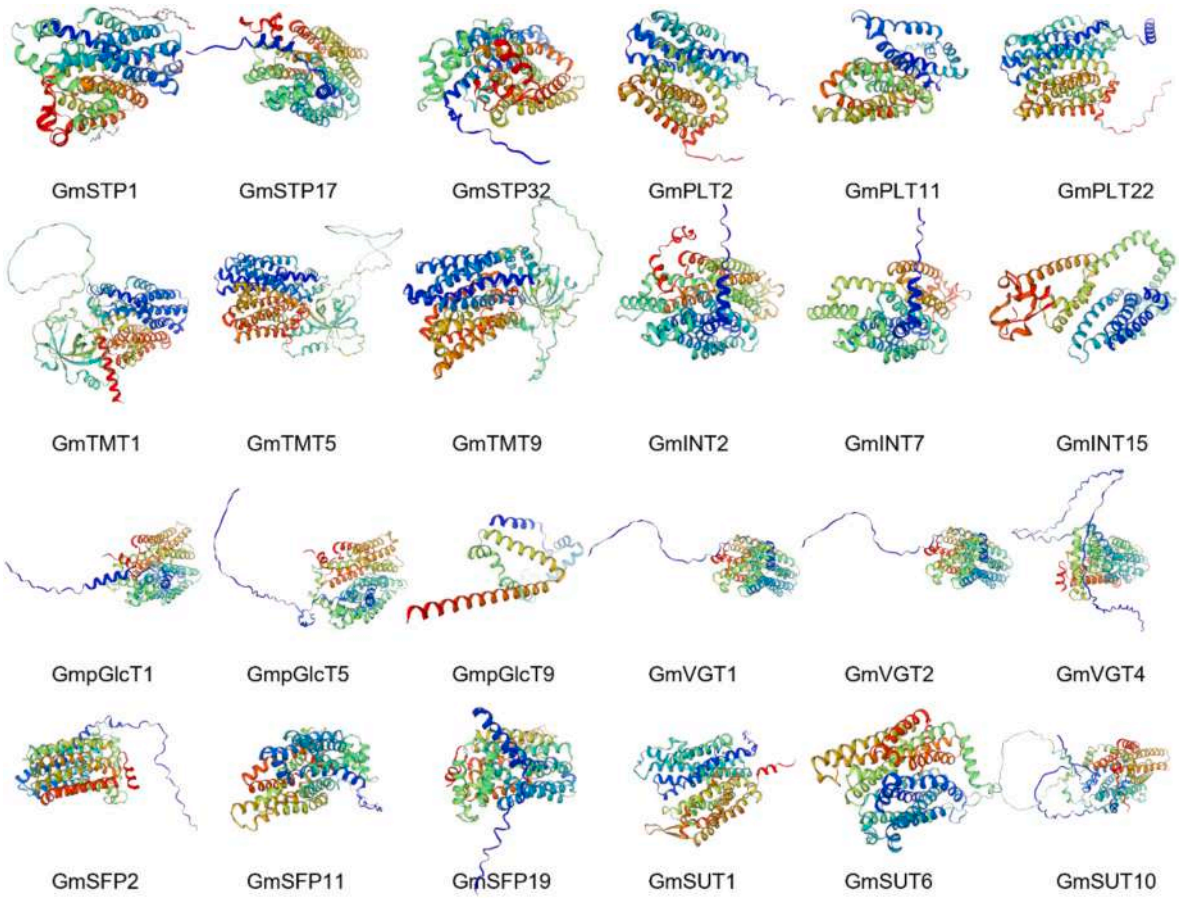

Fig. 3. Predicted three-dimensional structure of representative sugar transporters in soybean. Three representative proteins were shown for each subfamily. The predicted ribbon models of proteins were generated using the SWISS-MODEL (https://swissmodel.expasy.org/).

induced at 12 HAI, 24 HAI and 48 HAI (Supplementary Fig. S8).

We further selected 9 sugar transporter genes (*STP22*, *STP23*, *STP29*, *PLT3*, *PLT19*, *INT1*, *INT2*, *INT4* and *INT7*) to analyze their transcriptional responses to short-term salt and dehydration stresses. All these 9 sugar transporter genes were found to be significantly affected by salt and/or dehydration in a short time (6 h) (Fig. 9A), which are mainly consistent with the microarray/RNA-seq data (Fig. 7). For example, *GmSTP22*, *GmSTP23*, *GmPLT3*, and *GmINT4* were up-regulated by short-term salt/dehydration stress; *GmPLT19*, *GmINT2* and *GmINT7* were decreased by short-term salt/dehydration stress.

3.7. Overexpression of GmSTP22 improve plant growth and salt tolerance in transgenic arabidopsis

We further selected a stress-responsive sugar transporter gene *GmSTP22* for functional analyses. Recombinant construct 35S:GmSTP22-GFP and the empty vector 35S:GFP were transferred into tobacco leaves using the agrobacterium-mediated transient transformation. Subcellular localization analysis showed that the green fluorescence of GFP was dispersed over the whole cell, including the nucleus, cytosol, and the PM, while the green fluorescence signal of GmSTP22-GFP fusion protein was all exclusively observed in the PM (Fig. 8A). The construct of 35S:GmSTP22-GFP was co-transformed with the PM marker construct (35S:AtCBL1-mCherry) into rice protoplasts. The green fluorescence signal of GmSTP22-GFP overlapped with the red fluorescence signal generated by the PM marker-mCherry fusion protein (AtCBL1-mCherry) (Fig. 8B). These results indicated that GmSTP22 is localized in the PM. In addition, the protein-protein interaction (PPI) network of GmSTP22 was predicted by using the online STRING tool. The predicted PPI network contained 11 nodes, including four cytochrome P450 proteins and two alkaline/neutral invertases (Supplementary Fig. S9), suggesting their potential interaction with GmSTP22.

To analyze the physiological function of GmSTP22, we constructed an overexpression vector of 35S:GmSTP22 and transformed it into *Arabidopsis*, and generated three independent homozygous transgenic lines (OE#3, OE#6, and OE#8). qRT-PCR analysis confirmed the overexpression of *GmSTP22* in these transgenic lines. The biomass of *GmSTP22*-overexpression plants was similar to that of wild-type (WT, Col-0) when grown in the media without sugar, but it was significantly higher than that of WT when grown in the media supplemented with sucrose or glucose (Fig. 9).

We further test the salt tolerance of transgenic plants by analyzing the seed germination rate and cotyledon greening rate of *GmSTP22*-overexpressing lines under salt treatment in the half-strength MS media with or without sucrose. Under normal growth conditions with or without sucrose, the seed germination and cotyledon greening rates of *GmSTP22*-overexpressing plants were similar to that of WT (Supplementary Fig. S10). Under salt treatment supplemented with sucrose, the seed germination and cotyledon greening rates of *GmSTP22*-overexpressing plants were significantly higher than that of WT, but if sucrose was removed, there was no significant difference (Supplementary Fig. S10). These results suggested that overexpression of *GmSTP22* improves seed germination and early seedling development under salt stress in the presence of sugar. We also analyzed the salt stress tolerance of seedling by transferring 4-day-old seedlings to growth media containing 120 mM NaCl with or without sucrose. After treated with salt stress for 8 days, we found that the repression of root growth by salt stress was impaired in *GmSTP22*-overexpression plants in the presence of sucrose (Fig. 10A–C). But the root growth was not significantly

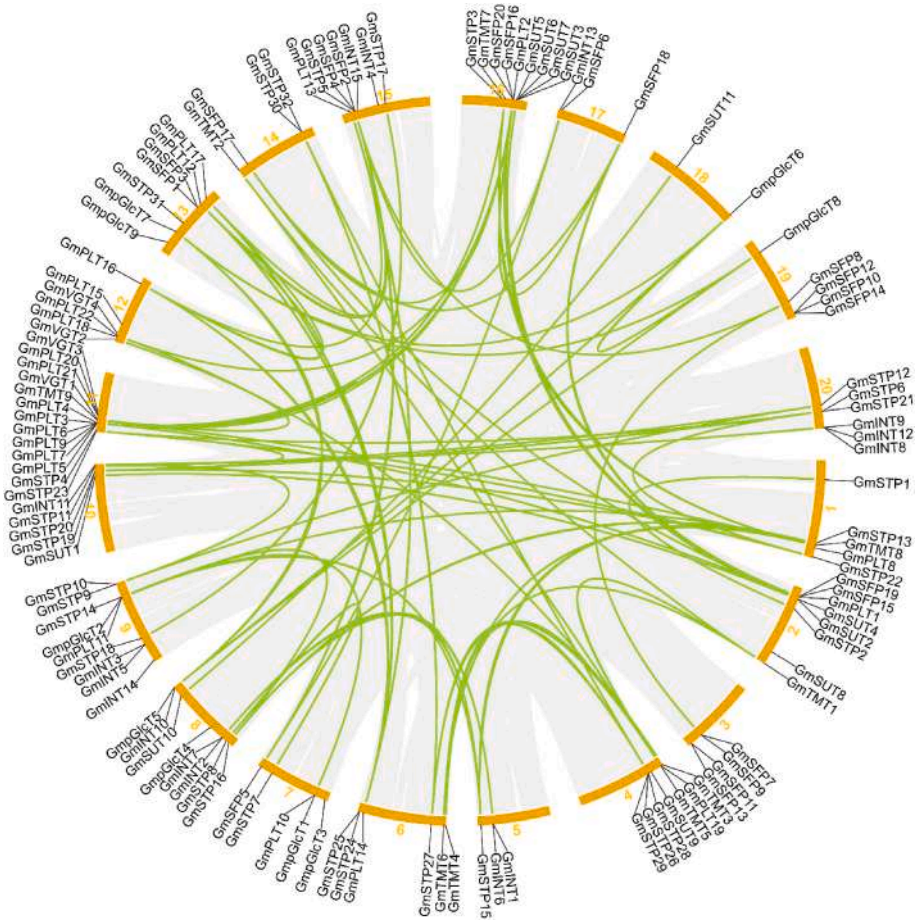

Fig. 4. Syntenic analysis of sugar transporter genes in soybean genome. The yellow circle represents the 20 chromosomes of soybean, each labeled with distinct Arabic numerals. The gene names on the chromosomes indicate the positions within the chromosomes. The syntenic relationships of sugar transporter genes are connected by the green lines.

affected by *GmSTP22*-overexpression under control or salt stress treatments when there was no sugar in the growth media (Fig. 10A–C). In addition, the fresh weight of *GmSTP22*-overexpression plants was significantly higher than that of WT under salt treatment in the presence of sucrose, but there was no difference in the absence of sucrose (Fig. 10D). These results suggested that overexpression of *GmSTP22* promotes salt stress tolerance possibly by facilitating sugar transport.

4. Discussion

Sugar transporters are essential for carbohydrate allocation and yield formation in higher plants. Soybean is an important crop providing oil- and protein-rich food. The reference genome of soybean has opened the door for functional genomics. Here we genome-widely identified the MST and SUT sugar transporter family genes in soybean by performing homolog searches and analyzing the gene and protein structure, conserved protein domains, phylogenetic relationships, expression profiles, and *cis*-acting elements in promoters. A total of 122 sugar transporter genes were identified, which could be classified into eight subfamilies, i.e., SUT, STP, PLT, TMT, INT, pGlcT, VGT, and SFP (Fig. 1). This result is consistent with previous reports in *Arabidopsis* and other flowering plants (Buettner, 2007; Deng et al., 2019; Zhang et al., 2020). The conserved protein domains and motifs identified in these sugar transporter subfamilies of soybean were similar to those in other plant species, such as *Arabidopsis* (Buettner, 2007), pear (Li et al., 2015), grape (Afoufa-Bastien et al., 2010), and sugarcane (Zhang et al., 2020). In addition, subcellular localization prediction showed that most of the proteins were localized in the PM (74 proteins), followed by 22 proteins in the vacuole (Supplementary Table S3). Sugar transporters in other plants were also predicted to be mainly localized in the PM (Zhang et al., 2020). Here, GmSTP22 was confirmed to be localized in the PM (Fig. 8), which is consistent with the predicted result. Many sugar transporters have been found to be localized in the PM, such as AtSUC1 (Sivitz et al., 2008), AtPLT5 (Klepek et al., 2005), and AtSTP13 (Yamada et al., 2016). Different sugar transporter subfamilies could have different substrate specificity, subcellular localization and transport mechanisms, and therefore, they cooperatively participate in sugar transport and allocation in plants.

The total number of sugar transporter genes in soybean was about 1.97 times that in *Arabidopsis* and 1.77 times that in rice (Buettner, 2007; Deng et al., 2019)(Supplementary Fig. S4). It has been known that 75% of the genes in soybean present in multiple copies (Schmutz et al., 2010). The larger number of sugar transporter genes in soybean could be caused by the two events of whole-genome duplication that occurred about 59 and 13 MYA, respectively (Schmutz et al., 2010). By comparing of the number of sugar transporter subfamilies between dicotyledonous *Arabidopsis* and soybean, the number of PLT, TMT, and INT subfamily members in soybean was 3.0 times that in *Arabidopsis*, while the number of VGT, SFP, and SUT subfamily members in soybean was similar to that in *Arabidopsis* (Supplementary Fig. S4). The evolutionary expansion of different sugar transporter subfamilies that have different substrates could happen independently in plants. Different subfamilies of sugar transporters have also been known to have significant differences in size between vascular and non-vascular plants (Johnson et al., 2006). Gene duplication is a major driving force in gene expansion and neo-functionalization in plants, where tandem duplication, WGD, and

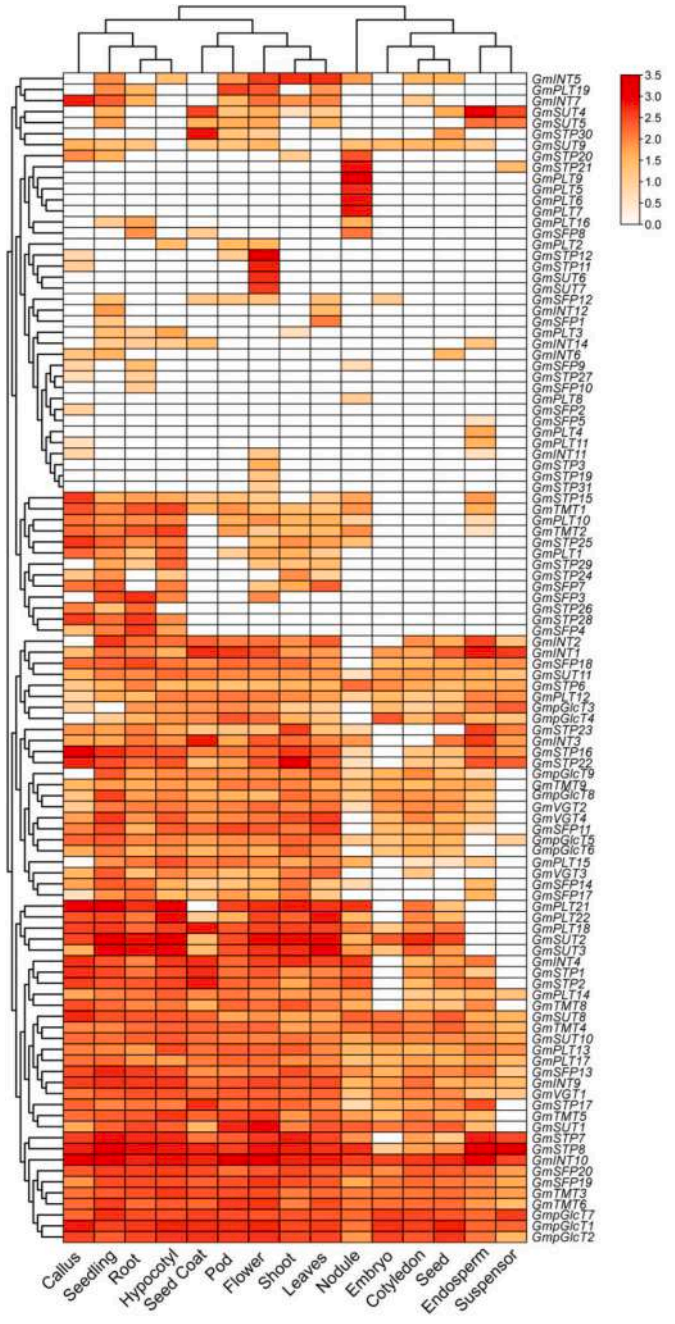

Fig. 5. Heatmap representation of the expression patterns of sugar transporter genes in different tissues of soybean according to the Illumina transcriptome data. The TPM (transcript per million mapped reads) transformed by log2 is visualized in the heatmap. The intensity of red color indicates the levels of transcriptional expression, while the white color indicates no expression was detected.

Fig. 6. Distribution of some stress- and/or hormone-related *cis*-acting elements in promoter regions of sugar transporter genes. The 2.0 kb promoter regions upstream transcription start sites were acquired for the analysis.

segmental duplications occur frequently (Cannon et al., 2004). Here, 49 (40.2%) sugar transporter genes were found to undergo tandem duplication (Supplementary Fig. S7), suggesting that tandem duplication plays an important role in the expansion of sugar transporter genes in soybean. Similarly, around 30% of sugar transporter genes were found to be tandem duplicated in *Arabidopsis* and rice (Buettner, 2007; Deng et al., 2019), while the ratio is about 60% in sugarcane (Zhang et al., 2020). Among these sugar transporter genes, 71 pairs of genes were possibly duplicated through WGD or segmental duplication (Fig. 4; Supplementary Table S5). The time frame of WGD/segmental duplication of these gene pairs was estimated to be between 5.29 and 265.0 MYA (Supplementary Table S5). Thus, the WGD/segmental duplication could play a major role in the expansion of sugar transporter genes in soybean. Consistently, other gene families like calcium transporters and SWEET transporters in soybean were expanded mainly by

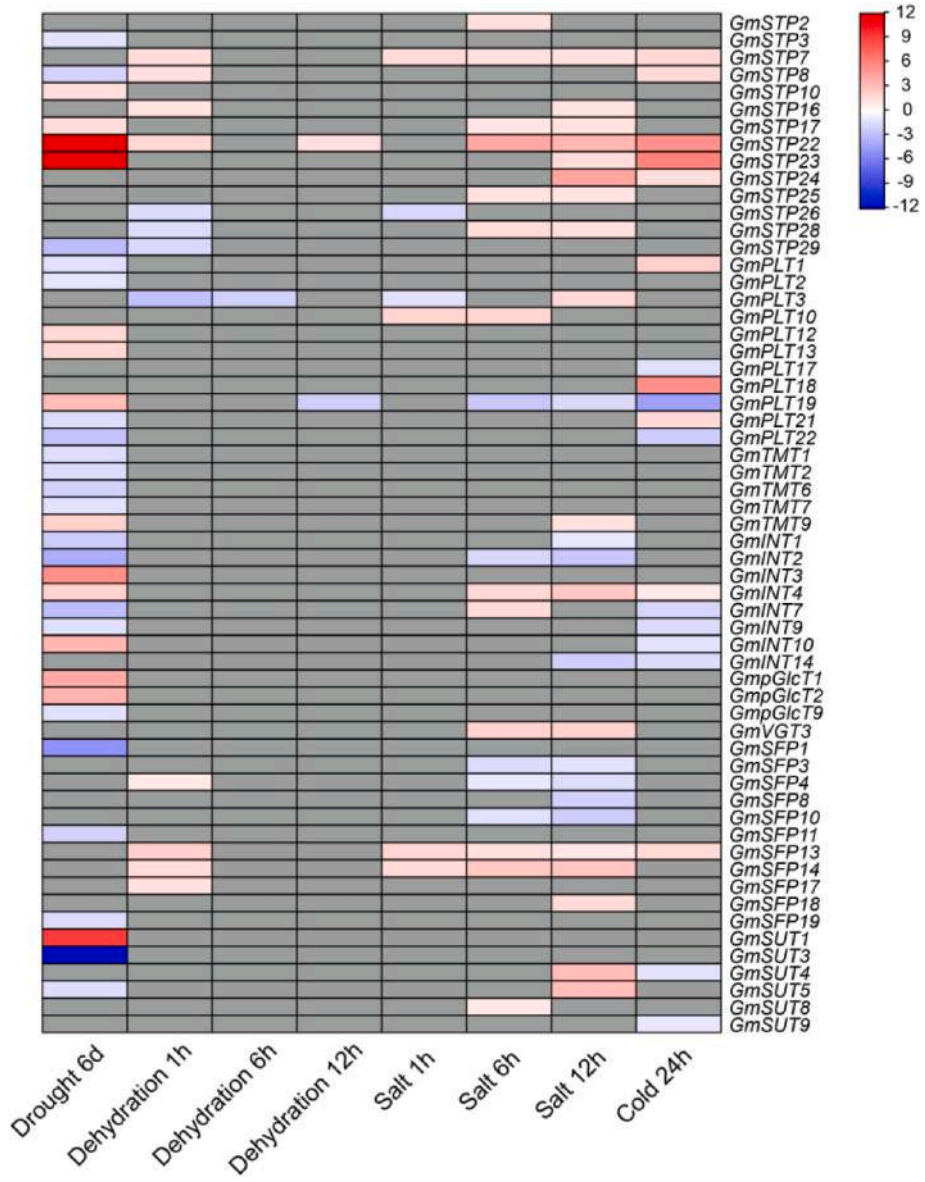

Fig. 7. Heatmap representation for expression profiles of sugar transporter genes in response to drought, dehydration, salt and cold. The intensities of the color represent the relative magnitude of fold changes in log2 values according to microarray or RNA sequencing data. Only the genes significantly differentially expressed (fold change >2, and p-value <0.05) were shown. Red color indicates induction, blue color indicates repression, and gray color means no significant change.

WGD/segmental duplication (Zeng et al., 2020; Patil et al., 2015). Duplicated genes could increase the adaptation of soybean to ever-changing surrounding environments during the evolution.

In this study, most of the sugar transporter genes (87%) were detected in at least one of the tissues, and the majority of them were expressed in multiple tissues (Fig. 5; Supplementary Table S6), suggesting that these sugar transporter genes identified here are authentic. The expression of some genes, such as *GmSTP4/5/9*, *GmSFP6/15/16*, *GmPLT20*, *GmTMT7*, and *GmINT8/13/15*, which could not be detected in tissues of soybean, may be expressed in tissues under specific conditions. Interestingly, many duplicated gene pairs, such as *GmSTP1/GmSTP2*, *GmSTP22/GmSTP23*, *GmSUT1/GmSUT2*, and *GmSUT4/GmSUT5*, have similar tissue expression patterns, suggesting that they may exert redundant functions. These duplicated genes may also play distinct roles under specific environmental conditions. But lots of genes belonging to the same subfamily exhibited distinct tissue expression patterns, suggesting that they may have different physiological functions. Notably, many genes were constitutively expressed in diverse tissues, such as *GmSTP6/8*, *GmINT9/10*, *GmpGlcT1/2/7*, *GmTMT3/4/6*, *GmPLT12/13/17*, *GmSUT8/10/11*, *GmSFP13/19/20*, and *GmVGT1*, suggesting that they may function in regulating the growth and development of soybean. In addition, some genes exhibited tissue-specific expression patterns. For instance, *GmSUT6/7* and *GmSTP3/19/*31 that were predominantly expressed in flowers. It has been reported that some sugar transporter genes play critical roles in plant growth and development. For example, *Arabidopsis SWEET10* and *SUC9* regulate flowering, because overexpression of *SWEET10* and silencing of *SUC9* increase the sugar content in the phloem near the shoot apex, and thereby stimulate inflorescence formation (Andrés et al., 2020; Sivitz et al., 2007). It has also been found that some sugar transporter genes, such as TST subfamily genes, are correlated with sugar contents in fruit crops like watermelon and apple (Ren et al., 2018; Zhu et al., 2021). But whether the tissue-specifically expressed genes play roles in tissue development by regulating sugar transport and allocation in soybean deserves further studies.

As a legume, soybean is able to establish both symbioses with nitrogen-fixing bacteria and with mycorrhizal fungi. Through these mutually advantageous associations, soybean is able to obtain essential

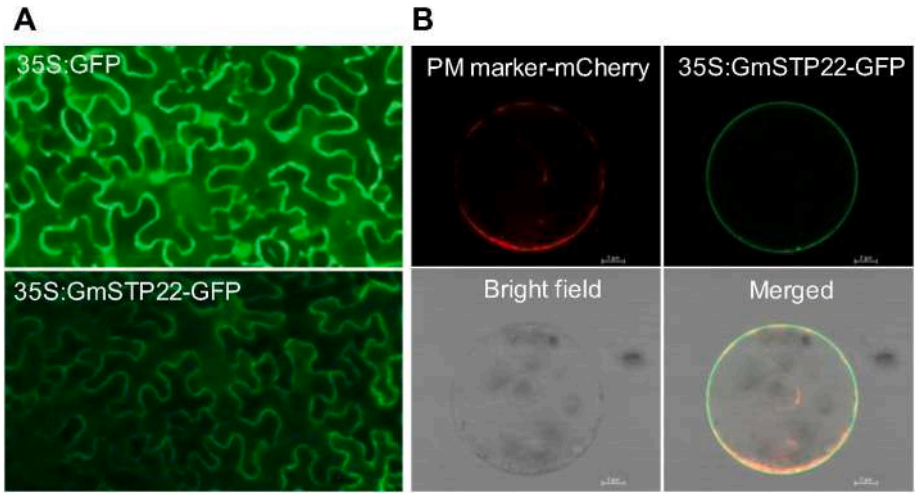

Fig. 8. Subcellular localization of GmSTP22. (A) The subcellular localization of GmSTP22 was analyzed by transiently expressing the GmSTP22-GFP fusion protein in tobacco leaves. 35S:GFP was used as the positive control. (B) 35S:GmSTP22-GFP fusion constructs was introduced into rice protoplast cells along with the plasma membrane (PM) marker mCherry fusion construct (35S:AtCBL1-mCherry). Fluorescence signals from GFP, mCherry, and the merged and bright-field images are shown. Scale bars = 5 μm.

nutrients, such as nitrogen and phosphate, that are crucial for its growth and development. Sugar transporters function during the symbioses with mycorrhizal fungi and rhizobia (Doidy et al., 2012). Recently, it has been found that GmSUT1/SUC1 plays a role in promoting soybean nodulation by mediating sucrose transport to nodules (Deng et al., 2022). GmSWEET6, which is induced by arbuscular mycorrhizal fungi, was found to be essential for arbuscular mycorrhizal symbiosis by mediating sucrose efflux across periarbuscular membrane to fungi (Zheng et al., 2023). Here, it is interesting that most (78%) of the sugar transporter genes identified here were expressed in root hairs with or without rhizobia inoculation (Supplementary Fig. S8). Some sugar transporter genes, such as *GmSTP21*, *GmSFP8*, and *GmPLT5/6/7/8/9* were predominantly expressed in nodules (Fig. 5), suggesting that they may play roles in nodule development. Notably, *GmPLT8* was significantly induced by the inoculation of rhizobia in a short-term (Supplementary Fig. S8), suggesting its potential role in the establishment of symbiosis with rhizobia. Previously, *LjPLT3*, *LjPLT4*, and *LjPLT14* from *Lotus japonicus* were found to be significantly induced in roots by the inoculation with rhizobia (*Mesorhizobium loti*)(Tian et al., 2017). Plant polyols can function as sugars for carbohydrate translocation and energy transfer between sources and sinks, and also as osmoprotective solutes and antioxidants (Saddhe et al., 2021). *Arabidopsis* PLT5 has been characterized as a low specificity H^+-symporter that mediates the energy-dependent uptake of inositol, linear polyols, hexoses, and pentoses across the PM (Klepek et al., 2005; Reinders et al., 2005). Further studies are required to investigate the potential function of PLTs as well as other kinds of sugar transporters in the nodulation and symbiosis in legumes.

Alteration of sugar transport and allocation mediated by various sugar transporters has been known to be an adaptation strategy under biotic and abiotic stresses (Yamada and Osakabe, 2018). For example, *Arabidopsis* ESL1 has been suggested to be involved in exporting sugar out of the tonoplast under drought and salinity stresses (Yamada et al., 2010). *Arabidopsis* ERDL6 was reported to putatively mediate glucose efflux from the vacuole by acting as a glucose/H^+ symporter, and overexpression of the closest sugar beet homolog to AtERDL6 reduces freezing tolerance in *Arabidopsis* (Klemens et al., 2014; Poschet et al., 2011). The abundance of glucose and fructose in the vacuole was found to be increased under cold stress (Schulze et al., 2012). Tonoplast-localized sugar transporters, TSTs (previously named TMTs), can transport both glucose and sucrose (Wormit et al., 2006; Schulz et al., 2011). The concentrations of glucose, fructose and sucrose were found to be decreased under cold stress in leaves of knockout mutants of all three TSTs in *Arabidopsis*, suggesting that the vacuole functions as a reservoir of sugars (Wormit et al., 2006). *Arabidopsis* TST1 and TST2 have been reported to participate in freezing tolerance (Klemens et al., 2014). Tomato TST2 was found to be critical for soluble sugar accumulation in response to drought stress (Zhu et al., 2024). By obtaining previous microarray and RNA-seq transcriptome data, the expression of 59 sugar transporter genes (48.4%) was found to be significantly influenced by stresses like salt, drought, and cold (Fig. 7). Their responses to stresses can be verified by qRT-PCR analysis (Fig. 9A). Interestingly, all these genes contain at least two type of stress/hormone-related cis-elements in promoters (Fig. 6). The stress-responsive expression of these sugar transporter genes suggest their potential involvement in stress responses. Further researches through the combination of physiological, biochemical, molecular, and genetic approaches are required to dissect the potential roles of these sugar transporters in stress response and tolerance.

STPs have been regarded as an H^+/sugar symporter for a broad range of substrates, such as fructose, glucose, galactose, and mannose (Buttner, 2010). Here, we showed that *GmSTP22* was induced by short-term salt and dehydration stresses (Fig. 9). Under high salt conditions, root epidermal and cortex cell layers are severely damaged, and plants attempt to minimize carbon leakage from damaged tissues by retrieving sugars under salt stress (Yamada and Osakabe, 2018). Studies have revealed a major role of STPs in monosaccharide uptake into roots under salt stress (Yamada et al., 2011; Wang et al., 2020). *AtSTP13*, the closest homology of *GmSTP22* in *Arabidopsis*, has also been reported to be induced by drought and salt stress, and *Arabidopsis atstp13* mutant plants showed carbon loss to liquid media under salt stress (Yamada et al., 2011). *Arabidopsis* STP13 was found to be localized in the PM, and overexpression of *STP13* could promote glucose uptake and increase growth under low nitrogen conditions (Schofield et al., 2009). In this study, GmSTP22 was also found to be localized in the PM, and it could positively regulate salt stress tolerance potentially by facilitating glucose transport (Figs. 9–10). Therefore, the role of STP transporter in salt stress tolerance could be conserved in higher plants. STP proteins are also involved in plant responses to other environmental stresses. For example, rice STP6 positively regulates plant resistance to cold stress (Luo et al., 2024); *Arabidopsis* STP1 and STP13 are involve in plant defense against pathogenic bacteria (Yamada et al., 2016). Based on the responsiveness of several *STP* genes to various stresses in soybean (Fig. 7), it is possibly that these genes could play a role in plant stress

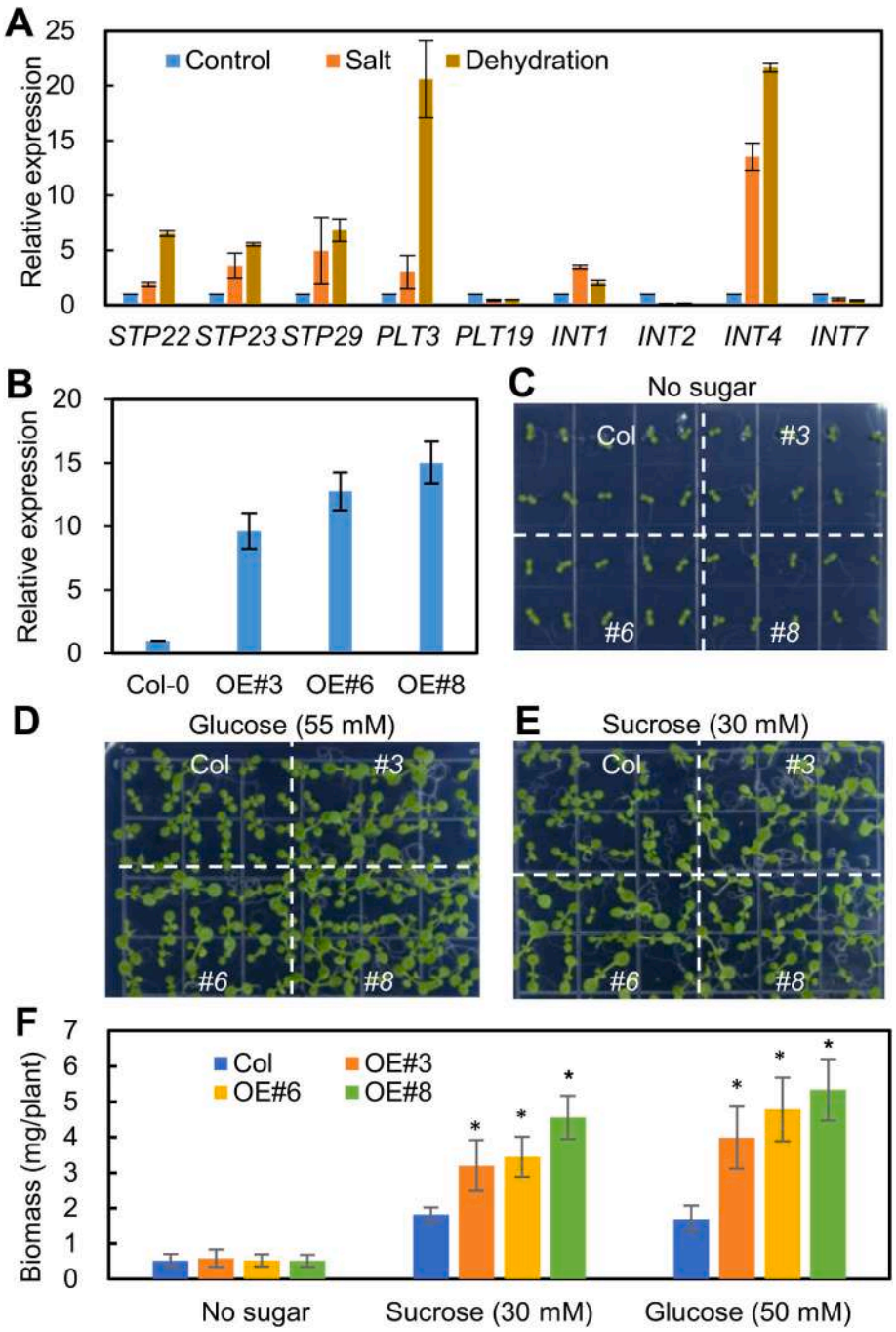

Fig. 9. Expression analysis of sugar transporter genes in response to short-term salt and dehydration stress by qRT-PCR and the growth of transgenic plants with *GmSTP22*-overexpression. (A) Nine sugar transporter genes were selected to analyze their relative expression levels under short-term (6 h) salt and dehydration stresses by qRT-PCR. The relative expression levels under control treatment were normalized to 1. Error bars represent ± SD from three biological replicates. (B) Relative abundance of *GmSTP22* transcript in three independent *GmSTP22*-overexpression lines (OE#3, OE#6, OE#8) measured by qRT-PCR. Seedling growth phenotypes of GmSTP22-overexpression lines grown under half-strength MS media without sugar (C), with 55 mM glucose (D), and with 30 mM sucrose (E). (F) Fresh weight of plants grown in the half MS media supplemented without sugar, or with 55 mM glucose or 30 mM sucrose. Data are the means ± SD (from four biological replicates, each replicate contains 10 seedlings). Asterisks indicate significant difference between wild-type plants and transgenic plants ($P < 0.05$, student's t-test).

tolerance. Further researches are needed to reveal their exact roles and the underlying mechanism in stress responses in order for their exploitation in crop improvement.

5. Conclusion

A total of 122 sugar transporter genes have been identified in soybean genome. According to their phylogenetic relationships and their conserved protein domains and motifs, these transporters can be classified into 8 subfamilies, including 32 STP/HTs, 22 PLT/PMTs, 9 TMT/TSTs, 15 INTs, 9 pGlcTs, 4 VGTs, 20 SFPs, and 11 SUTs. These sugar transporter genes can be mapped to all the 20 chromosomes, and tandem duplication, and WGD/segmental duplication contribute to their expansion. Expression analyses reveal their tissue and stress-responsive expression patterns. Functional analyses by ectopic expression suggest that GmSTP22 could facilitate plant growth and salt stress tolerance possibly by mediating sugar transport. This study provides basic information and lays the foundation for further functional analyses

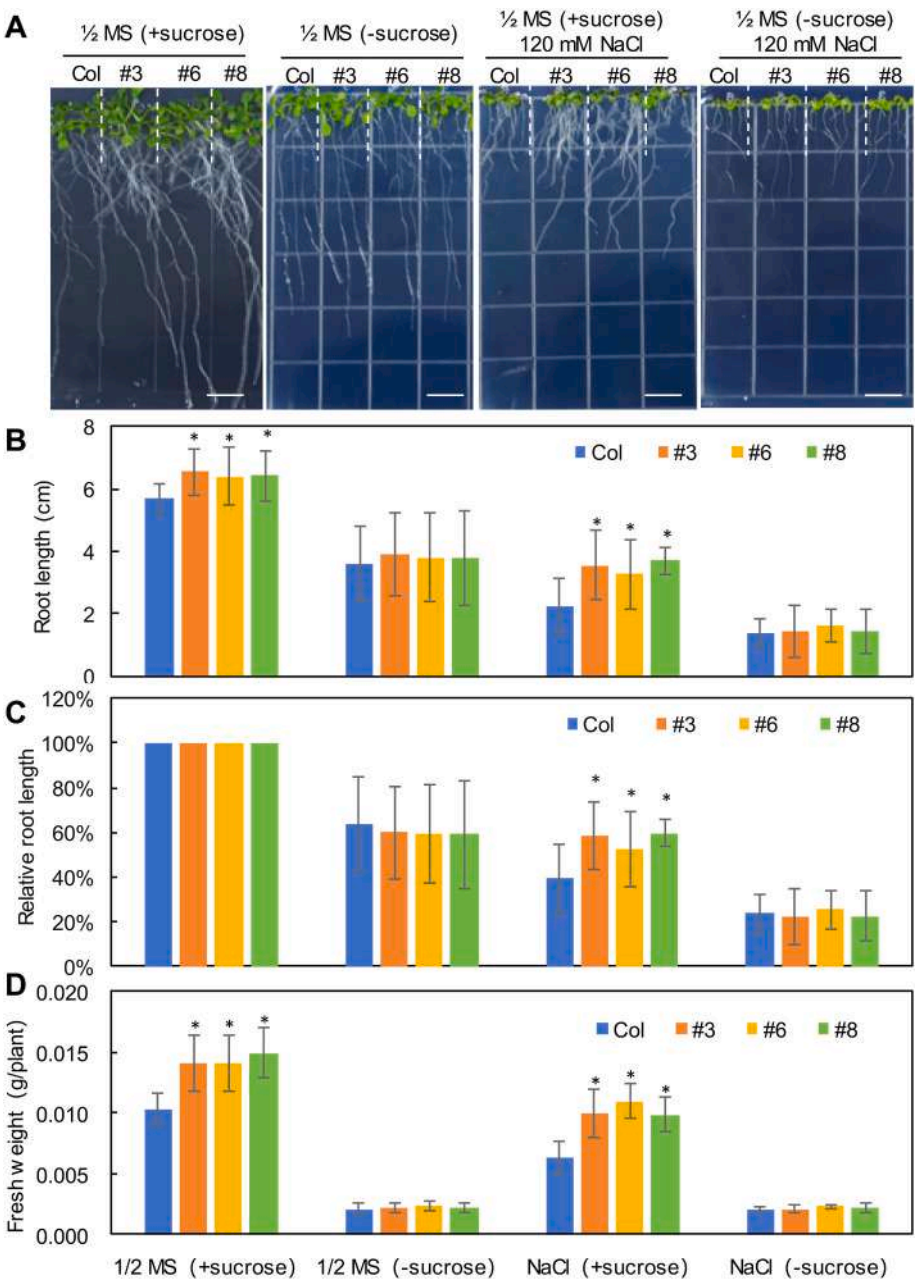

Fig. 10. Ectopic expression of *GmSTP22* increases root growth under salt stress in the presence of sucrose. (A) Growth of wild-type and *GmSTP22*-overexpressing *Arabidopsis* plants under salt stress in the presence or absence of sucrose. Four-day-old seedlings grown in the half MS media containing 1% sucrose were transferred to the half MS media containing 120 mM NaCl with or without sucrose. Photos were taken after treatment for 8 days. The scale bar represents 1 cm. (B) Average root length of *Arabidopsis* after treatment of salt stress for 8 days. (C) Relative root length of Arabidopsis seedlings after treatment of salt stress for 8 days. (D) Fresh weight of *Arabidopsis* seedlings after treatment of salt stress for 8 days. Data are the means ± SD (n = 12). Asterisks indicate that significant difference between wild-type plants and *GmSTP22*-overexpression lines ($P < 0.05$, student's t-test).

and potential genetic manipulation of sugar transporters aiming to the improvement of plant growth, seed yield, and stress resistance in soybean.

Funding

This work was supported by grants from the National Natural Science Foundation of China (32372802), the Scientific Research Fund of Zhejiang Provincial Education Department (Y202351654), Zhejiang Provincial College Students' Science and Technology Innovation Project (the Xinmiao Talent Program of Zhejiang Province).

Author contributions

Houqing Zeng conceived the study. Hang Guo, Zhengxing Guan, Yuanyuan Liu, Kexin Chao, Qiuqing Zhu, Yi Zhou, and Haicheng Wu performed the bioinformatic analyses and the experiments. Hang Guo, Erxu Pi, Huatao Chen and Houqing Zeng analyzed the data. Houqing Zeng and Hang Guo wrote the manuscript. All the authors have approved the contents of the manuscript.

Declaration of competing interest

The authors declare the following financial interests/personal

relationships which may be considered as potential competing interests:

Houqing Zeng reports financial support was provided by Hangzhou Normal University. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.plaphy.2024.109095.

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