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Genome-wide identification and expression profiling of MST, SUT and SWEET
transporters in *Dendrobium catenatum*

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Abstract:

Background

Sugar transporters (STs) play a critical part in the transporting of sugar, be involved in plant growth and development, stress/defense and signal transduction. *Dendrobium catenatum* (also name as *Dendrobium officinale*, here after *D. catenatum*) is an important traditional Chinese medicinal herb with remarkable medicinal functions and high economic value. Polysaccharides are the primary active components exerting various pharmacological activities in *D. catenatum*. Sugar transporters function as material supplier and may play the essential roles in the polysaccharide biosynthesis, as well as the key player in the abiotic stress signaling and responses in *Dendrobium* plants. However, there is still a lack of comprehensive analysis of sugar transporters in *D. catenatum*, and limits the understanding of sugar partitioning in *D. catenatum*.

Results

In this work, we identified the members of MST, SUT, and SWEET gene families in four *Dendrobium* plants. Phylogenetic analysis, structural arrangement, regulatory networks, expression profiles, and potential functions of sugar transporters were systematic study in *D. catenatum*. Seven DcSTs involved in polysaccharide

biosynthesis was identified using WGCNA. Red-blue light is an effective way to improve the accumulation of polysaccharides, and influences the expression of polysaccharide biosynthesis related genes.

Conclusions

This study provide insight into the evolution and functional annotation of sugar transporters in *Dendrobium*, and lays a foundation for future functional research of sugar transporters involved in polysaccharide biosynthesis and stress response.

Keywords: MST; SUT; SWEET; *Dendrobium catenatum*; polysaccharide biosynthesis

Introduction

Carbohydrates (sugars) serve as one of the most important carbon and energy resource in higher plants, also function as signal and functional molecules in many biological processes [1]. Plants synthesize sugars in the chloroplast of phototrophic cells during the daytime, and transport sugars throughout the plant to support the demand of consumption and storage. Sucrose represents the predominant transport sugar for long-distance transport via the phloem in many species, it is mainly imported the sieve elements–companion cell complex (SE-CC) via symplasmic or apoplasmic pathways [2, 3]. After phloem unloading, sucrose is either directly transported into sink cells, or is hydrolyzed to monosaccharides (glucose and fructose) for sugar uptake of sink cells [4, 5]. In addition, hexoses and sucrose are distributed to different subcellular compartments to sustain the carbon and energy supplies. The intercellular and intracellular transport of sugars requires several essential transport steps across membranes, in which sugar transporters play the pivotal role [6]. Plants have three major types sugar transporters to coordinate the transport of monosaccharide and disaccharide: monosaccharide transporter (MST), sucrose transporter (SUT, also called SUC for sucrose carrier), and SWEET (Sugars Will Eventually be Exported Transporter) [7].

MST belongs to the major facilitator superfamily (MFS) class of transporters, is the largest family of plant STs. There are 53 AtMSTs and 65 OsMSTs in *Arabidopsis thaliana* and *Oryza sativa*, respectively [8, 9]. MST family includes seven subfamilies

which have one common origin [10]. Sugar transport proteins (STPs) are plasma membrane hexose/H⁺ symporters, and responsible for the uptake of hexoses of sink cells [5, 11]. Vacuolar glucose transporters (VGTs) are tonoplast or chloroplast localized glucose/H⁺ antiporter [5, 12]. Polyol/monosaccharide transporters (PLTs) localize in the plasma membrane, and act as broad-spectrum H⁺-symporter for linear polyols and sugars, including sorbitol, mannitol, xylitol, ribose, myo-inositol, pentoses and hexoses [5, 13]. Inositol transporters (INTs) localize to plasma membrane or tonoplast, and are responsible for the transport of myo-inositol which involved in the synthesis of raffinose [14, 15]. Tonoplast monosaccharide transporters (TMTs) are tonoplast-localized sucrose/H⁺ antiporters, and responsible for the influx of sugars into the vacuole [16]. Plastidic glucose translocators (pGLTs) localize to chloroplast inner envelope membrane or Golgi stacks, act as hexose transporter [17, 18]. Early Response to Dehydration 6-like (ERD6-like or ESL) is the largest subfamily of MST family in *Arabidopsis*, some ERD6 proteins have been characterized as tonoplastic glucose exporters in *Arabidopsis* [19].

SUT so far is found exclusively in plants, functions as sucrose–H⁺ symporter and plays a pivotal role in the long-distance transport of sucrose from source to sink [20]. Most SUT proteins transport sucrose and maltose, while some members transport esculin and biotin as their substrates [21, 22]. SUT proteins belong to the of MFS superfamily, have 12 transmembrane domains and always localize to plasma membrane, whereas some members localize to tonoplast and responsible for the efflux of sucrose from vacuole to cytosol [23]. There are nine *AtSUCs* and five *OsSUTs* in the genome of *Arabidopsis* and rice [11, 24]. In higher plants, SUT proteins could divide into three clades (Type I, II and III) which originated from two ancient groups (AG1 and AG2) in the ancestral bryophyte [25]. Type I SUTs are origin from AG1 and lost in the monocot lineages, Type IIB are origin of Type II in monocot species [25]. Type I and Type IIB members localize to plasma membrane and involved in apoplastic phloem loading [26, 27]. Type II members are plasma membrane- or cytoplasmic-localized, but their function is still unclear [24, 25]. Type III members localize to and responsible for sucrose efflux from vacuole [2].

SWEET is the recently identified sugar transport family, which mediate the translocation of sugars across cell membranes, especially the efflux of cell-to-cell transport and the secretion of sugars [28, 29]. In plants, SWEET is a class of low-affinity sugar transporter, and may function as uniporters involved in the transport of neutral sugars such as glucose, fructose, and sucrose [29]. SWEET proteins always have seven transmembrane helices (TMs) that harbor two MtN3/saliva (PF03083) domains [28, 30], and localize to different cellular compartments, such as plasma membrane, tonoplast, and Golgi [31]. There are 17 SWEETs in Arabidopsis, and 21 SWEET members have been identified in the rice genome [30]. The evolutionary analysis showed that four major clades were perceived in plant SWEET proteins, from clade I to clade IV [32]. In Arabidopsis, SWEET members of clades I, II, and IV transport predominantly hexose, clade III SWEETs mainly transport sucrose [31]. Besides sugar loading and unloading, SWEETs also be involved in the plant development, resistance to environmental stresses, hormone regulation, plant-pathogen and symbiotic interactions [33].

Dendrobium is one of the largest genera in Orchidaceae, and naturally grows on the severe environment as tree trunks and cliffs. *Dendrobium* plants have enormous ornamental and medicinal values for their spectacular flowers and various types of secondary metabolites [34]. A typical characteristic of *Dendrobium* is that with the fleshy stems/leaves be rich of polysaccharide, which is a class of active macromolecules display antioxidant, anticancer, and immunomodulatory [34]. The transport of photosynthetic carbohydrate products from leaf to stem is critical to the biosynthesis and accumulation of polysaccharide in *Dendrobium*. Sugar transporters function as material supplier and may play the essential roles in the polysaccharide biosynthesis, as well as the key player in the abiotic stress signaling and responses in *Dendrobium* plants. Up to now, several genomes of *Dendrobium* medicinal herb have been finished, including *D. catenatum* (also name as *D. officinale*, here after *D. catenatum*) [35-37], *D. huoshanense* [38], *D. nobile* [39], and *D. chrysotoxum* [40]. Although some SWEET and SUT genes have been identified in some *Dendrobium* plants [41-43]. However, there is still a lack of comprehensive analysis of sugar

transporters in *Dendrobium*, and limits the understanding of sugar partitioning in *Dendrobium*.

In this study, the sugar transporters were identified in the genome of four *Dendrobium* plants and one Orchid plant *Apostasia shenzhenica* [44]. Then, the evolution history of sugar transporters was analyzed in *Dendrobium* plants. Furthermore, *D. catenatum*, the well-known and widely cultivated *Dendrobium* plant, was used for the comprehensive study of sugar transporters, including the structural arrangement, *cis*-element analysis, regulatory networks, and expression profiles. Finally, the polysaccharides content and gene expression in different organs of *D. catenatum* under various light conditions were analyzed. The results laid the foundation of functional studies of the sugar transporters to understand the process of polysaccharide biosynthesis in *Dendrobium*, and allow their efficient use in the germplasm improvement in *Dendrobium* plants.

Results

Genome-wide identification and phylogenetic analysis of *sugar transporter* genes in *Dendrobium* plants

The members of the MST, SUT and SWEET sugar transporter gene families in have been identified using combined BLAST and HMM methods in the genome of *A. shenzhenica* and four *Dendrobium* plants (*D. catenatum*, *D. chrysotoxum*, *D. huoshanense*, and *D. nobile*). As shown in Table 1 and Table S1, a total of 341 sugar transporters were identified in these five Orchid plants, including 61 members in *A. shenzhenica*, 73 members in *D. catenatum*, 66 members in *D. chrysotoxum*, 60 members in *D. huoshanense*, and 81 members in *D. nobile*.

MST is the largest sugar transporter family in *A. shenzhenica* (39 members), *D. catenatum* (34 members), and *D. huoshanense* (28 members). The members of MST could be classified into seven subfamilies based their evolutionary relationship in most *Dendrobium* plants (Table 1 and Fig. 1), as well as that of Arabidopsis and rice.

STP and ERD-6 like always be the largest subfamilies of MST gene family in plants [19, 45]. However, we found that STP is the largest subfamily in *Dendrobium* plants, ERD-6 like subfamily undergo contraction and loss events in *Dendrobium* plants and *A. shenzhenica*, especially in *D. chrysotoxum* and *D. huoshanense*. There are similar number of members in the subfamilies of PLT, VGT, TMT, INT, and pGlcT.

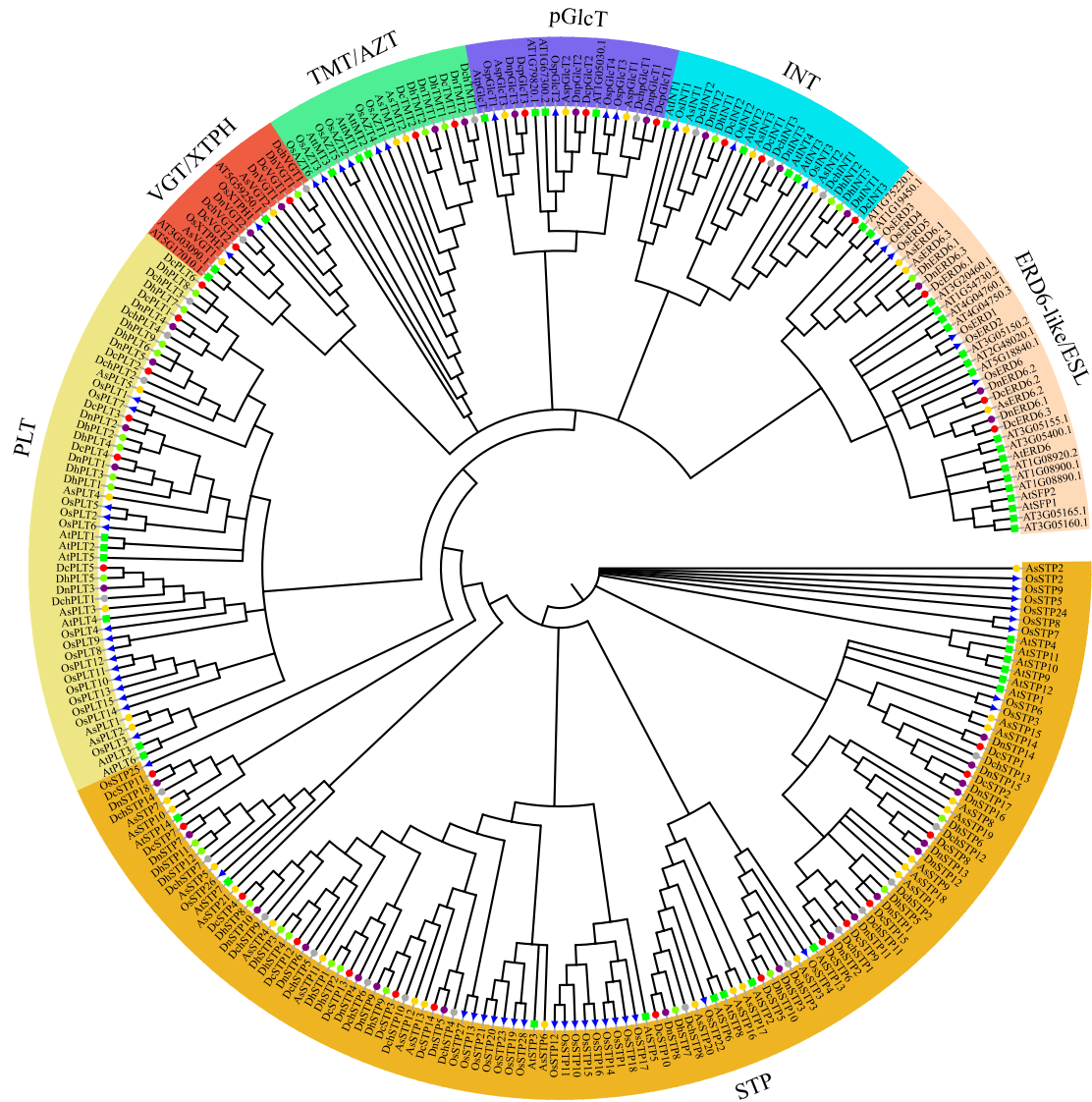


Fig. 1. Phylogenetic tree and subgroup classification of MST proteins in *A. thaliana*, *O. sativa*, *A. shenzhenica*, *D. catenatum*, *D. chrysotoxum*, *D. huoshanense*, and *D. nobile*. The phylogenetic tree was constructed by the neighbor-joining (NJ) method with 1000 bootstrap replicates. The green rectangle, blue triangles, yellow cycle, red cycle, grey cycle, yellowgreen cycle, purple cycle represent proteins from *A. thaliana*, *O. sativa*, *A. shenzhenica*, *D. catenatum*, *D. chrysotoxum*, *D. huoshanense*, and *D. nobile*.

SUT contains 5 to 9 members in *Dendrobium* plants and *A. shenzhenica*, and could be classified into four clades (Table 1 and Fig. 2), including clade I, clade IIa, clade IIIa/b. There is one member in both clade I and clade IIa in most *Dendrobium* plants. Clade IIb is a dicotyledon-specific clade of SUT gene family, and there is no clade IIb members in rice, *A. shenzhenica*, and four *Dendrobium* plants. Clade III is a monocotyledon-specific clade of SUT gene family, we found that it could be further divided into two subclade, and clade IIIb is the Orchid-specific clade of SUT gene family. There are two members in *A. shenzhenica* (AsSUT3/4), three members in *D. catenatum* (DcSUT1/2/5) and *D. chrysotoxum* (DchSUT4/5/7), four members in *D. nobile* (DnSUT4/5/6/7), and five members in *D. huoshanense* (DhSUT3/5/6/7/8).

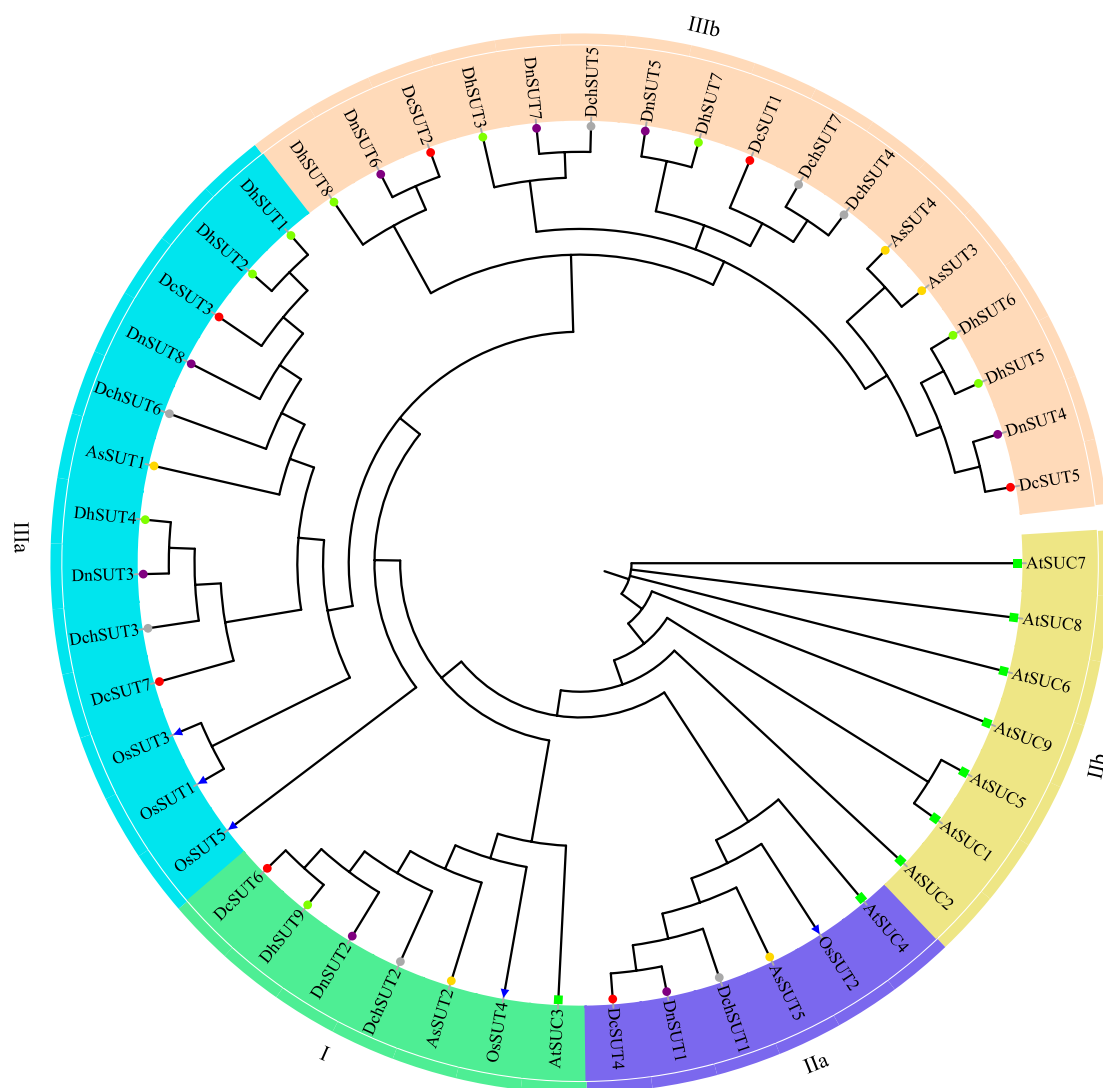


Fig. 2. Phylogenetic trees and subgroup classification of SUT proteins in *A. thaliana*, *O. sativa*, *A. shenzhenica*, *D. catenatum*, *D. chrysotoxum*, *D. huoshanense*, and *D. nobile*. The

phylogenetic tree was constructed by the neighbor-joining (NJ) method with 1000 bootstrap replicates. The green rectangle, blue triangles, yellow cycle, red cycle, grey cycle, yellowgreen cycle, purple cycle represent proteins from *A. thaliana*, *O. sativa*, *A. shenzhenica*, *D. catenatum*, *D. chrysotoxum*, *D. huoshanense*, and *D. nobile*.

Compared to MST, SWEET is the largest sugar transporter family in *D. chrysotoxum* (34 members) and *D. nobile* (37 members). As shown in Fig. 3, SWEET proteins could be classified into five clades, including clade I, clade IIa, clade IIb, clade III, and clade IV in five plants. There are 3 to 5 members of clade I in *A. shenzhenica* and *Dendrobium* plants. In the clade IIa, the members of Arabidopsis and rice cluster into the single clades, and AsSWEET6 cluster with the members of Arabidopsis. Clade IIb is a monocotyledon-specific clade of SWEET gene family, there are one member in rice (OsSWEET4), three members in *A. shenzhenica* (AsSWEET15/16/17), and expanded dramatically in *Dendrobium* plants. In clade III and IV, the members from different plants always mixed with each other.

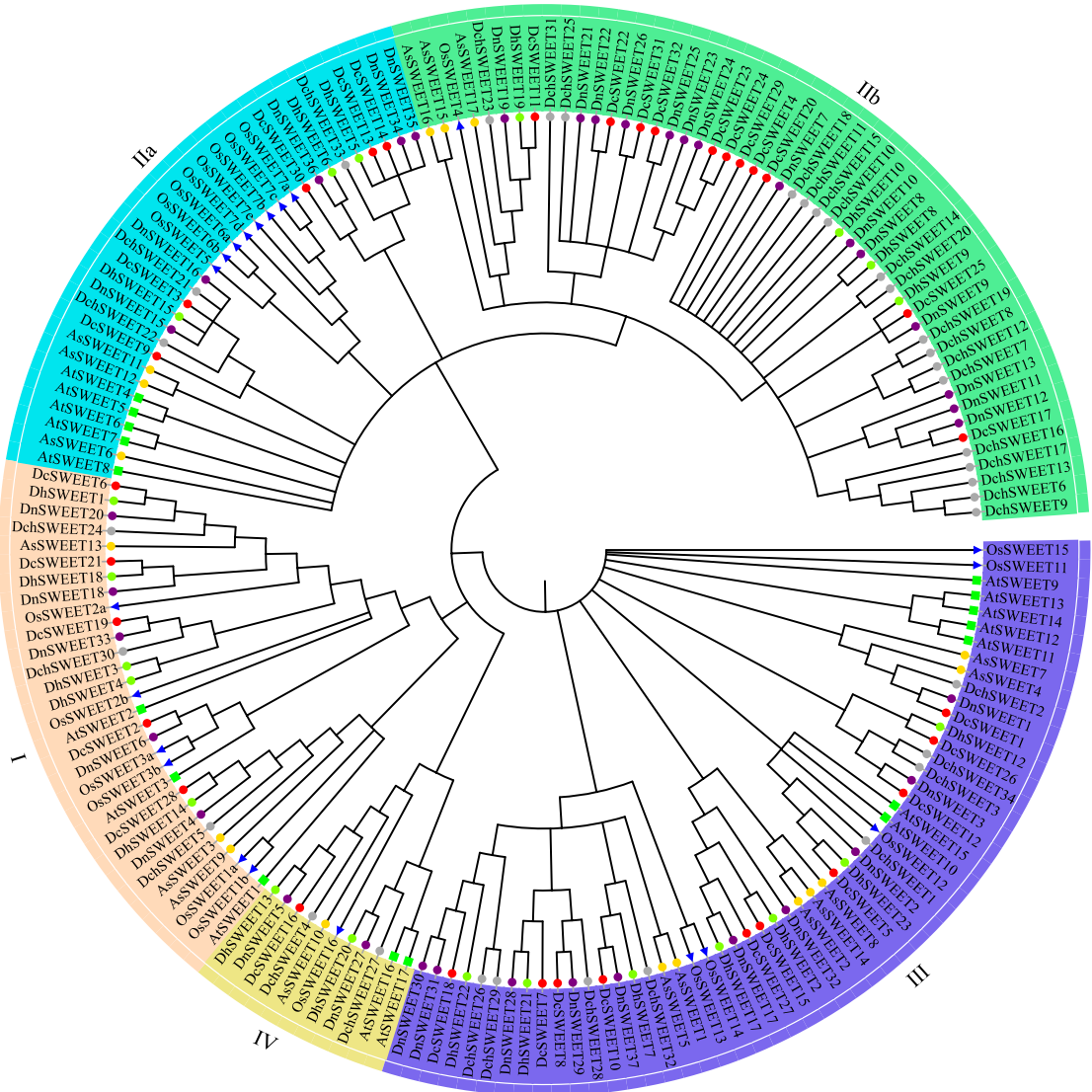


Fig. 3. Phylogenetic trees and subgroup classification of SWEET proteins in *A. thaliana*, *O. sativa*, *A. shenzhenica*, *D. catenatum*, *D. chrysotoxum*, *D. huoshanense*, and *D. nobile*. The phylogenetic tree was constructed by the neighbor-joining (NJ) method with 1000 bootstrap replicates. The green rectangle, blue triangles, yellow circle, red circle, grey circle, yellowgreen circle, purple circle represent proteins from *A. thaliana*, *O. sativa*, *A. shenzhenica*, *D. catenatum*, *D. chrysotoxum*, *D. huoshanense*, and *D. nobile*.

To investigate the evolution history of *sugar transporter* genes, we identified and calculated the K_a/K_s ratio of the homologous gene pairs of *DcSTs*. As shown in Table S2, there are 66 *DcST* paralogous gene pairs (including 31 *DcMST* gene pairs, 5 *DcSUT* gene pairs, and 30 *DcSWEET* gene pairs) were identified, 41 orthologous gene pairs (25 *MST* gene pairs, 3 *SUT* gene pairs, and 14 *SWEET* gene pairs) that between *D. catenatum* and *O. sativa*, 74 orthologous gene pairs (38 *MST* gene pairs, 10 *SUT*

gene pairs, and 26 *SWEET* gene pairs) that between *D. catenatum* and *A. shenzhenica*, 77 orthologous gene pairs (23 *MST* gene pairs, 4 *SUT* gene pairs, and 50 *SWEET* gene pairs) that between *D. catenatum* and *D. chrysotoxum*, 58 orthologous gene pairs (29 *MST* gene pairs, 7 *SUT* gene pairs, and 22 *SWEET* gene pairs) that between *D. catenatum* and *D. huoshanense*, 74 orthologous gene pairs (35 *MST* gene pairs, 7 *SUT* gene pairs, and 32 *SWEET* gene pairs) that between *D. catenatum* and *D. nobile*. The *Ka/Ks* ratio ranged from 0.05 to 0.40 (median 0.19) among the *DcMST* paralogs, 0.11 to 0.23 (median 0.15) among the *DcSUT* paralogs, 0.08 to 0.53 (median 0.21) among the *DcSWEET* paralogs (Table S2). As shown in Fig. 4A, the *Ka/Ks* ratio among the *DcMST* orthologs is similar to that of. However, the *Ka/Ks* ratio of *DcSUT/DcSWEET* orthologous gene pairs between *Dendrobium* plants is significantly higher than that of rice and *A. shenzhenica*. The results suggests that sugar transporter homologous genes are under the purifying selection pressure in *D. catenatum*, *SUT* and *SWEET* genes under the relative positive selection among *Dendrobium* plants.

The duplication events of *DcST* genes were analyzed using DupGen_finder [46]. As shown in Fig. 4D, a total of 66 duplicated gene pairs were identified among 61 *DcST* genes. Dispersed duplication (42 duplicated gene pairs) and tandem duplication (13 duplicated gene pairs) were the main duplicated types of sugar transporter genes in *D. catenatum*. There are seven tandem duplication-derived clade II type *DcSWEETs*, including a gene cluster that consisted of five *DcSWEET* genes (*DcSWEET22/23/24/31/32*) were identified in the clade II type *DcSWEETs*, and a duplicated gene pair of *DcSWEET4* and *DcSWEET29*. It indicated that tandem duplication events are responsible for the expansion of clade II type *DcSWEETs*.

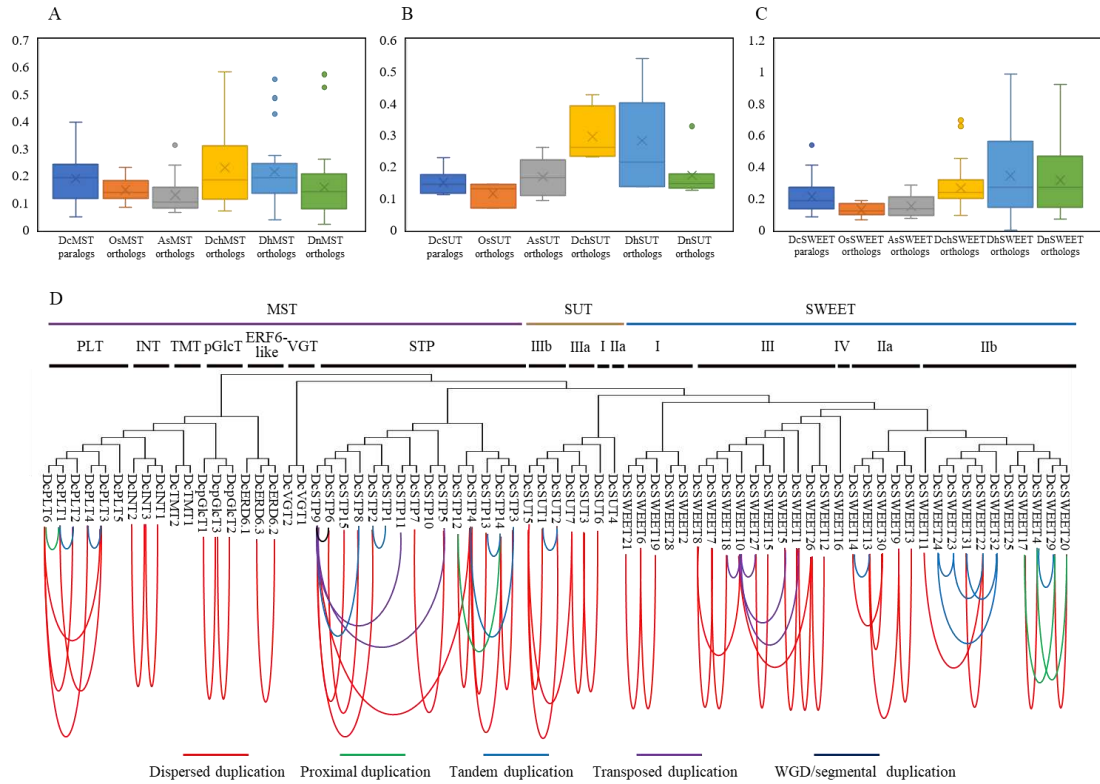


Fig. 4. Inference of *DcST* gene duplications. A) Box and whisker plots representing the distribution of K_a/K_s ratio in *MST* Orthologues; B) *SUT* Orthologues; C) *SWEET* Orthologues; D) Phylogenetic relationship and gene duplications pairs among *DcSTs*.

Characteristic features and structural arrangement of *DcSTs* in *D. catenatum*

A total of 73 *DcST* genes were identified in *D. catenatum* genome, including 34 *DcMST*, 7 *DcSUT* and 32 *DcSWEET* genes (Fig. 4D). The detailed information of these 73 ST genes were listed in Table 2, including the gene ID, genomic location, protein length, exon number, molecular weight (MW), and subcellular localization.

The protein length of *DcMSTs* ranges from 461 (*DcPLT6*) to 754 (*DcTMT2*) amino acids (aa). *DcMST* proteins always have 10-12 TMHs (transmembrane helix) except *DcSTP3* (8 exons) and *DcPLT6* (9 TMHs) (Fig. 5A and Table 2). There are 7 subfamilies in the *MST* gene family in *D. catenatum*, as well as that of Arabidopsis and rice. The length of *DcSUT* proteins ranges from 491 (*DcSUT7*) to 638 aa (*DcSUT6*). As well as *DcMSTs*, *DcSUT* proteins always have 10-12 TMHs. Compared to *MST* and *SUT* proteins, *DcSWEETs* have the size (196 (*DcSWEET17*) to 296 aa (*DcSWEET6/16*)), the less TMHs (5-7). Most sugar transporter proteins are

located in the plasma membrane, vacuole, and chloroplast.

As shown in Fig. 5B, most of the DcMST proteins have one complete Sugar_tr (Sugar (and other) transporter, PF00083) domain except five DsMSTs (DcVGT2, DcTMT1/2, and DcINT1/3). The Sugar_tr domain consist of eight core conserved motifs (motif 3/4/5/6/11/12/14/15) in DcMSTs. Most DcSTPs have two additional motifs (motif 9 and 10) in the N-terminal of their Sugar_tr domain. MFS_SLC45_SUC (Solute carrier family 45 and similar sugar transporters of the Major Facilitator Superfamily (MFS) of transporters, cd17313) domain is a conserved domain in plant sucrose transporters. Each of the seven DcSUTs have one complete MFS_SLC45_SUC domain and two conserved motifs (motif 14 and 15) in the N-terminal. All the DcSWEET proteins harbor two MtN3_slv (Sugar efflux transporter for intercellular exchange, PF03083) domains, and each of MtN3_slv harbored two conserved motifs (motif 2 and 7 in N'-MtN3_slv, motif 1 and 8 in C'-MtN3_slv). Compared to other subfamilies of DcSWEET, the members of clade II have an additional conserved motif (motif 13) among two MtN3_slv domains. There are some incomplete MtN3_slv domains in DcSWEETs, including N-terminal MtN3_slv of DcSWEET2/12/28 and the C-terminal MtN3_slv of DcSWEET15/17/30.

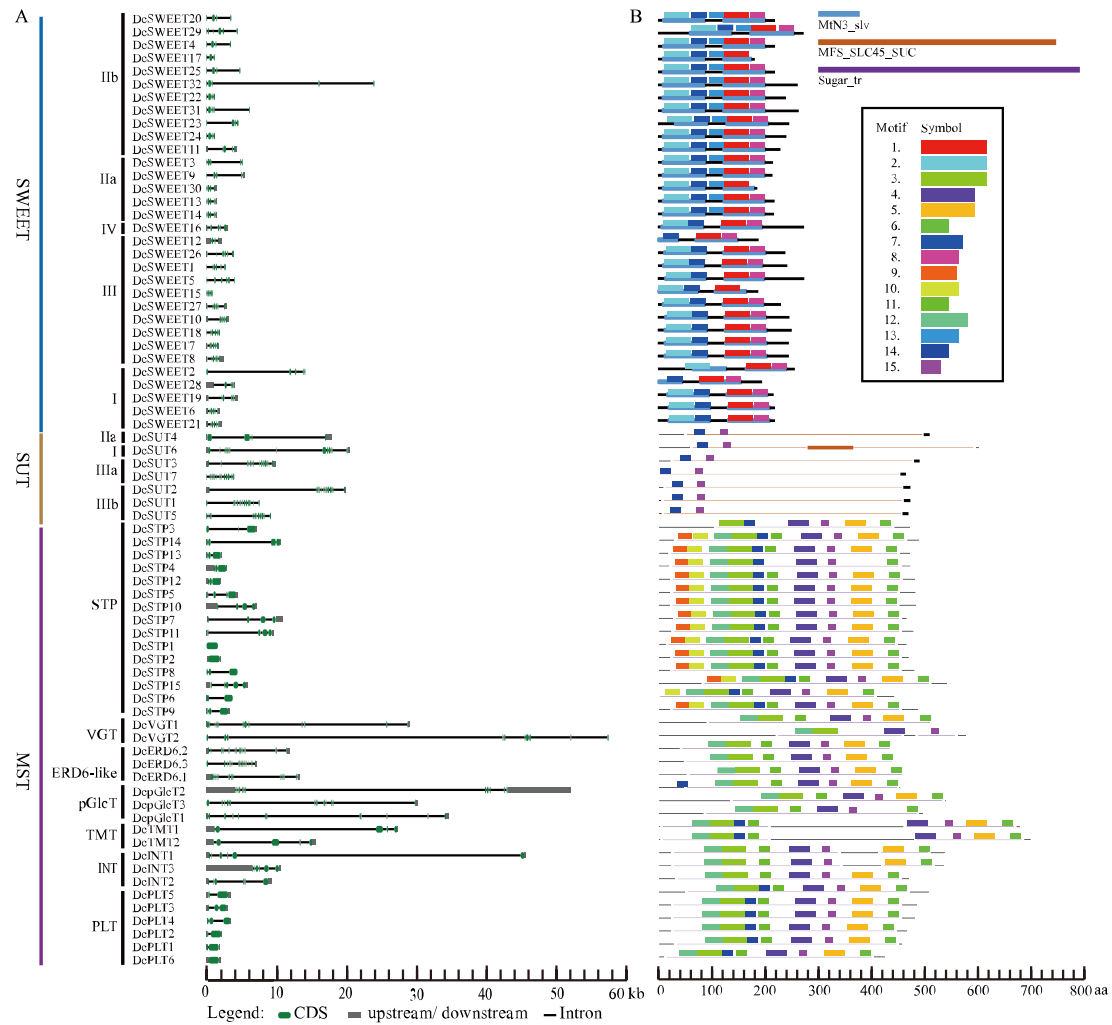


Fig. 5. Gene and protein structure of sugar transporters in *D. catenatum*. A) The intron–exon structures of *DcST* genes; B) Conserved domains and motifs (1–15) distribution of sugar transporter proteins in *D. catenatum*. Heterochromatic boxes represent different domains and motifs, indicated in the middle.

Cis-regulatory element analysis of the sugar transporter genes

The upstream 2000 bp promoter regions of 73 *DcSTs* were retrieved to analyze their *cis*-acting elements. As shown in Fig. 6A, the top 20 abundant *cis*-element involved in transcription factor (TF) recognition and binding (MYB, W box, MYB-like sequence, Myb-binding site), light responsiveness (Box 4, G-box, TCT-motif, GT1-motif, GATA-motif), stress responsiveness (STRE, ARE, WRE3, WUN-motif, MBS, TC-rich repeats), and hormones responsiveness (CGTCA-motif, TGACG-motif, ABRE,

ERE). MYB (core *cis*-element for MYB TFs recognition and binding), Box 4 (conserved DNA module involved in light responsiveness), CGTCA-motif (*cis*-acting regulatory elements involved in the methyl jasmonate (MeJA) responsiveness) were the most abundant elements in *DcSTs*. Most *DcSTs* are abundant in light responsiveness and hormone responsiveness *cis*-elements (Fig. 6B), suggesting them may be involved in the growth and development of *D. catenatum*. *DcSTP1/3*, *DcERD6.3* and *DcSWEET27* contain amounts of stress responsiveness *cis*-elements, implying their involvement in the response to environmental stresses. Furthermore, we analyzed the transcriptional regulatory network of sugar transporter genes and transcription factors in *D. catenatum*. A total of 40 TF families are involved in the transcriptional regulatory of *DcSTs*, and most of the *DcST* genes are regulated by multiple TFs (Fig. 6C). In accordance with the results of *cis*-regulatory element analysis (Fig. 6A), most *DcST* genes are targeted by MYB TFs. In addition, B3, C2H2, Dof, ERF, HD-ZIP, MIKC_MADS TFs also participate in the regulation of *DcSTs* expression extensively.

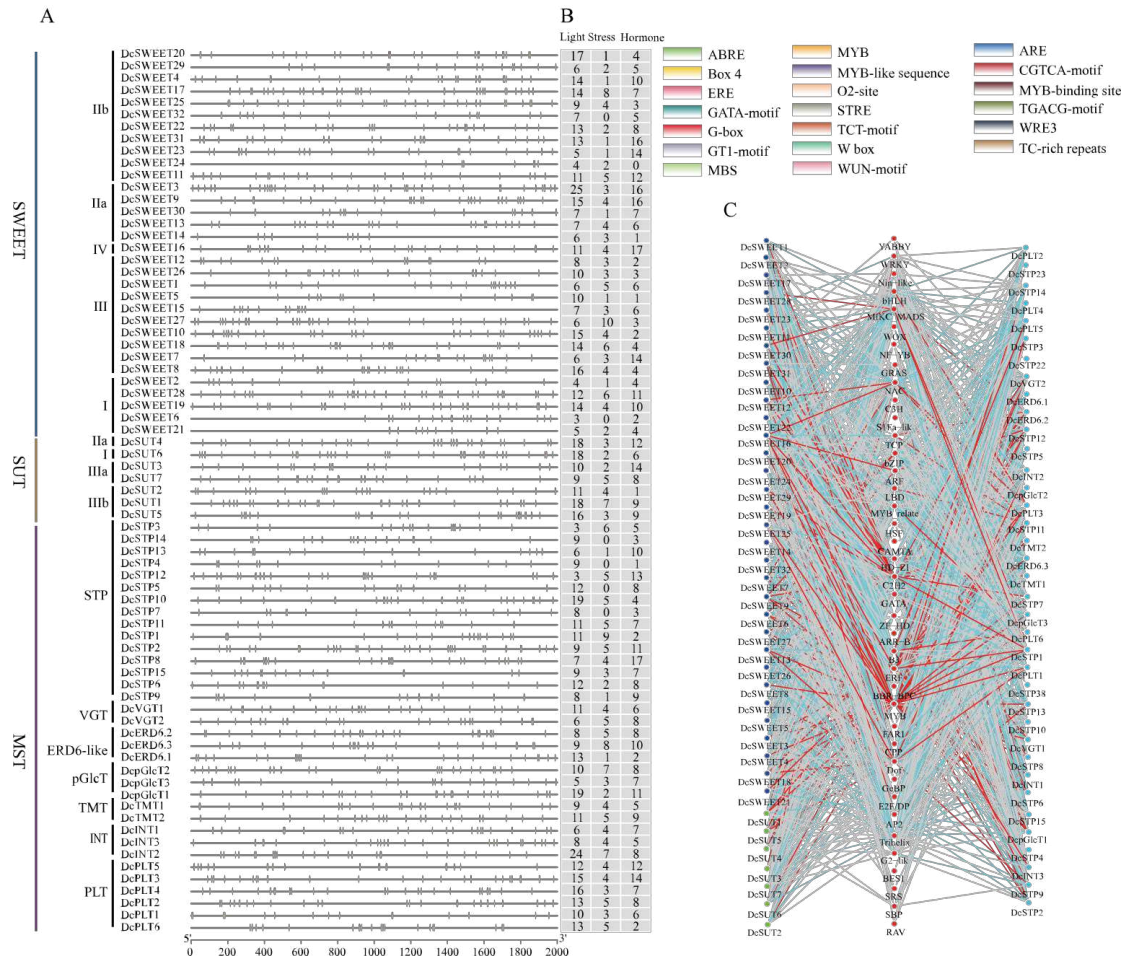


Fig. 6. Cis-regulatory element analysis of sugar transporter proteins in *D. catenatum*. A) The distribution of 20 cis-acting elements in the 2000 bp upstream promoter; B) the frequency of the cis-element response to light, environmental stresses, and plant hormones; C) Regulation networks between DcSTs and potential transcription factors. The color of line represents the number of TF binding sites in the promoter region of DcST genes, grey 1-3, blue 4-9, red ≥ 10 .

Post-transcription regulation of DcST genes

MicroRNAs (miRNAs) play the critical roles in the post-transcriptional regulatory networks. As shown in Fig. 7D, 27 out of 73 sugar transporters are regulated by 64 miRNAs of 23 miRNA families. Most of these conserved miRNAs are function in the development of plant and the responses to biotic and abiotic stresses, such as miR156, miR172, miR397, miR399, miR529, and miR535. Five *DcSTs* (*DcINT3*, *DcSTP15*, *DcSUT5*, and *DcSWEET21/25*) are regulated by miR397 members, which mainly target the laccase (*LAC*) genes that be involved in lignin synthesis [47]. MiR156, miR529 and miR535 share the similarity sequence, both target SQUAMOSA promoter binding protein-like (*SPL*) genes to negatively regulate the immunity in

plants. *DcSWEET16* is mainly targeted by miR156 members while *DcpGlcT2* is both targeted by miR156 and miR172 that be involved in reproductive growth and flower development. *DcpGlcT3*, *DcINT1* are mainly regulated by miR535, *DcSWEET8/15* are targeted by miR529. *DcSWEET7/18* are targeted by miR399, which is the critical regulator of phosphate homeostasis in plants.

Fig. 7. Interaction of miRNAs and sugar transporter genes.

The RNA-seq data of *D. catenatum* was analyzed to explore the expression patterns of *sugar transporter* and *CSLA* genes (Fig. 8A). Compared to vegetative tissues (leaf, stem, and root), most ST genes are relatively high expressed in flowers. Furthermore, some ST genes are flower-specific expressing, including the members of clade II SWEET family (*DcSWEET4/14/17/20/25/29/30*), *DcSUT5/7* from clade III *SUT* family, and *DcSTP1/8* from *STP* subfamily of *MST* (Fig. 8B). The result indicated that these sugar transporters may be involved in the development of flower, such as the production of nectar and sugar rich secretion. *DcSWEET11* is the only constitutive expression member of clade II SWEET family in whole plants, as well as *DcSWEET16* from clade IV, *DcSWEET8/10* from clade III, and *DcSWEET28* from clade I. *DcSUT3/4/6* show constitutive expression pattern in *D. catenatum*, and *DcSUT3/4* are relatively high-expressed in stem. Compared to *SWEET* and *SUT* family, most of *MST* genes are constitutive expressing. Photosynthetic sugars are

transported from photosynthetic tissue to non-photosynthetic tissue to allocate the resource of carbon and energy in the whole plants. *DcSWEET28* and *DcSTP9* are relatively high-expressed in the daytime and downregulated during the night (Fig. 8C). Some ST genes are down-regulated in the daytime, including *DcSWEET8*, *DcSTP11*, *PLT2/3/4*. *DcSWEET16/19*, *DcSUT3*, *DcSTP5/9*, *DcPLT1/2/3/4* are different expressed between the drought and rewatered treatments. in comparison, more ST genes are involved in the in the response to cold stress, including *DcSWEET6/10/11/12/16/18/19/21*, *DcSTP4/5/9/12/13/14*, *DcVGT1/2*, *DcERD6.1*, *DcINT1/2*, *DcPLT1/2/3/4/5*. *DcSWEET8/19* are downregulated under exogenous hormone treatment, including NAA, 6-BA, combined NAA and 6-BA treatment. In contrast, *DcSWEET28* is upregulated under exogenous hormone treatment.

Fig. 8. Expression profiles of *DcST* genes. The expression data were obtained from RNA-seq data and shown as log2 values based on TPM values (Transcripts Per Kilobase of exon

model per Million mapped reads). A) Heatmap of the expression pattern of *DcST* genes; B) *DcSTs* with high expression level in different tissues of *D. catenatum*; C) *DcSTs* involved in circadian, and the response to environmental stress and exogenous hormones.

The co-expression network of *sugar transporter* genes in *D. catenatum*

To identify the potential cooperative genes of *sugar transporters* in *D. catenatum*. WGCNA was performed using 26 RNA-seq data of *D. catenatum* under different treatments. As shown in Fig. 9A, we found that the genes were clustered into 28 modules, 16 *DcST* genes were assigned to 5 modules. As shown in Fig. 6A, *DcINT1* and *DcSUT3* assigned to MEblack module, 8 *MST* genes (*DcpGlcT3*, *DcSTP3/5/12*, *DcPLT1/5*, *DcERD6.3*, *DcVGT2*) and 2 *SWEET* genes (*DcSWEET8* and *DcSWEET16*) assigned to MEturquoise module, *DcERD6.2* assigned to MEyellow module, *DcSTP11* and *DcSUT4* assigned to MEblue module, *DcPLT4* assigned to MEgreen module. Then, the GO (Gene Ontology) enrichment analysis was performed in the genes sets of those five modules. Two enriched GO terms that related to polysaccharide biosynthesis were found in the MEturquoise module, including carbohydrate derivative binding (GO:0097367) and carbohydrate derivative metabolic process (GO:1901135) (Fig. 9B). GO:0097367 also enriched in black module while none of the polysaccharide biosynthesis-related GO terms were in other three modules. The central genes which involved in polysaccharide biosynthesis were identified in turquoise module (Fig. 9C), including seven *sugar transporter* genes (*DcSWWT8/16*, *DcSTP3/12*, *DcVGT2*, *DcpGlcT4*, and *DcPLT5*), two *CSLA* genes (CELLULOSE SYNTHASE-LIKE A genes, *LOC110107854_DcCSLA4* and *LOC110108926_DcCSLA8*), and *GUX1* (UDP-glucuronate:xylan alpha-glucuronosyltransferase 1, *LOC110102381*).

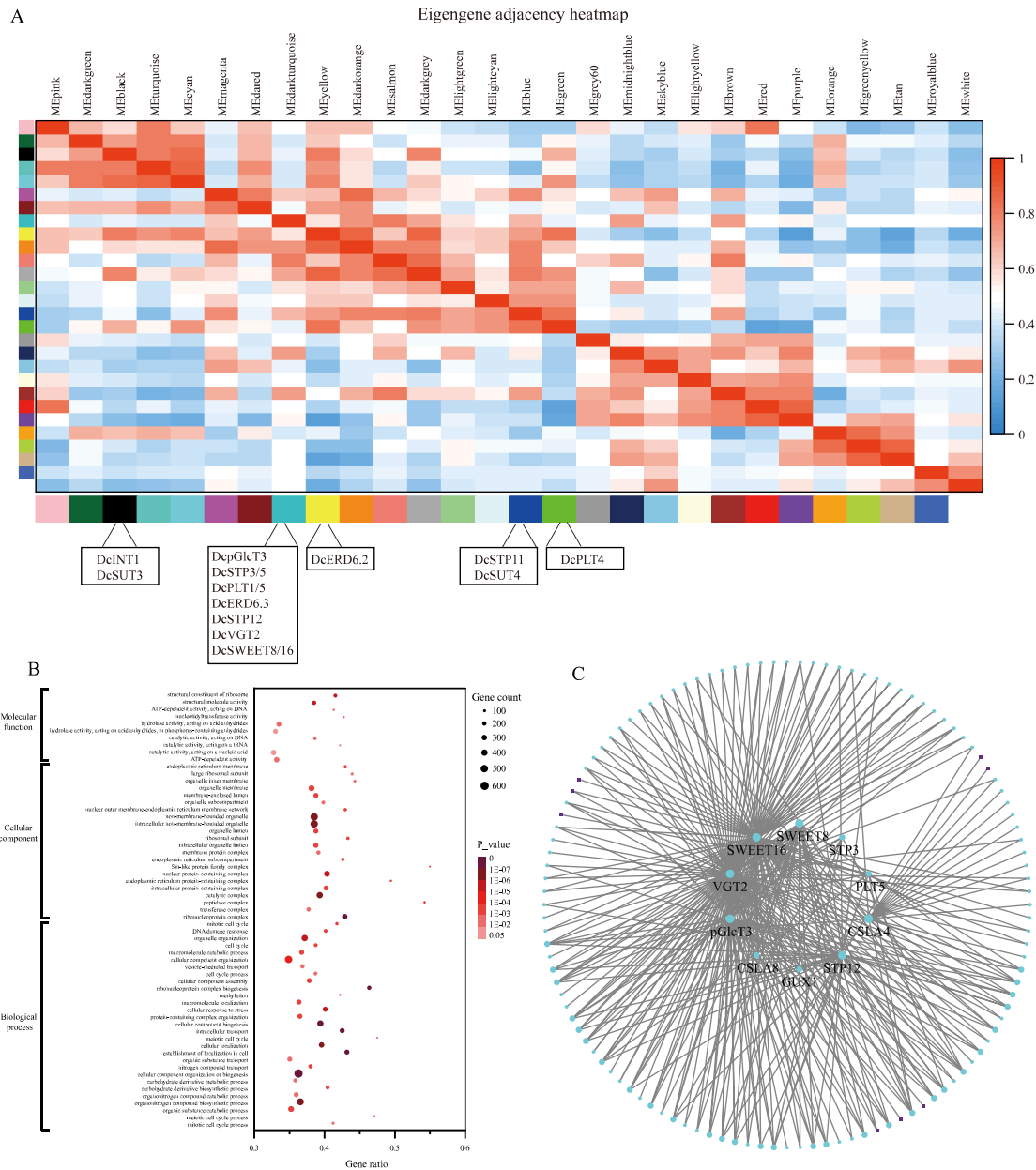


Fig. 9. The key sugar transporter genes involved in polysaccharide biosynthesis. A) Module eigengene (ME) adjacency heatmap of 28 co-expression modules; B) GO enrichment analysis of the gene sets of MEturquoise module; C) Co-expression network of DcST and polysaccharide biosynthesis related genes in the turquoise module, blue circle represents protein-coding genes, purple square represents noncoding genes.

Polysaccharides content and expression profiles of central genes under different light conditions

To further clarify the potential function of *sugar transporter* genes in the process of polysaccharide biosynthesis under different light conditions. *D. catenatum* were cultivated under white light (W, control, CK), white-red-blue-UV light (WRBU), and

white-red-blue light (WRB) for seven days. Then, the polysaccharides content and expression profiles of central genes in leaf and stem were analyzed.

As shown in Fig 10A, there were no significant morphological difference among three treatment groups, besides the weakly anthocyanin accumulation in the leaf of WRBU group, which may be induced by UV radiation. Compared CK group ($23.79 \pm 1.52\%$), the content of polysaccharides in the leaf was up-regulated slightly in the WRB group ($29.57 \pm 1.23\%$), while down-regulated weakly in the WRBU group ($19.50 \pm 3.74\%$), both without significant difference (Fig. 10B). In the stem, polysaccharides contents both were upregulated under WRBU and WRB treatment (CK $20.13 \pm 4.34\%$, WRBU $23.05 \pm 2.73\%$, WRB $25.41 \pm 1.54\%$). It suggesting that Red + Blue light could enhance the biosynthesis and accumulation of polysaccharides in both leaf and stem, but UV radiation will diminish this positive effect.

the expression profiles of seven *sugar transporter* genes (*DcSWEET8/16*, *DcSTP3/12*, *DcVGT2*, *DcPLT5*, *DcpGlcT3*) and three polysaccharide biosynthesis related genes (*DcCSLA4*, *DcCSLA8*, *DcGUX1*) were verified using qRT-PCR. As shown in Fig. 10C, *DcSWEET8/16* were down-regulated in the leaf under WRBU and WRB treatment, while up-regulated in the stem under WRB treatment. *DcSTP3* was up-regulated in the stem under WRB treatment. *DsSTP12* was up-regulated in Leaf-WRB group, although it did not be detected in the Stem-W group, the expression was increasing dramatically when suffer Red + Blue light treatment. *DcPLT5* and *DcpGlcT3* both were down-regulated in Leaf-WRBU and Leaf-WRB groups, while up-regulated in Stem-WRBU and Stem-WRB groups. Three polysaccharide biosynthesis related genes both have the higher relative expression level in the stem than leaf. *DcCSLA4* was down-regulated in Leaf-WRBU and Leaf-WRB groups, and up-regulated in Stem-WRB group. *DcCSLA8* was up-regulated in Leaf-WRB group, and up-regulated in Stem-WRBU and Stem-WRB groups. *DcGUX1* was down-regulated in Leaf-WRB group and up-regulated in Stem-WRB group.

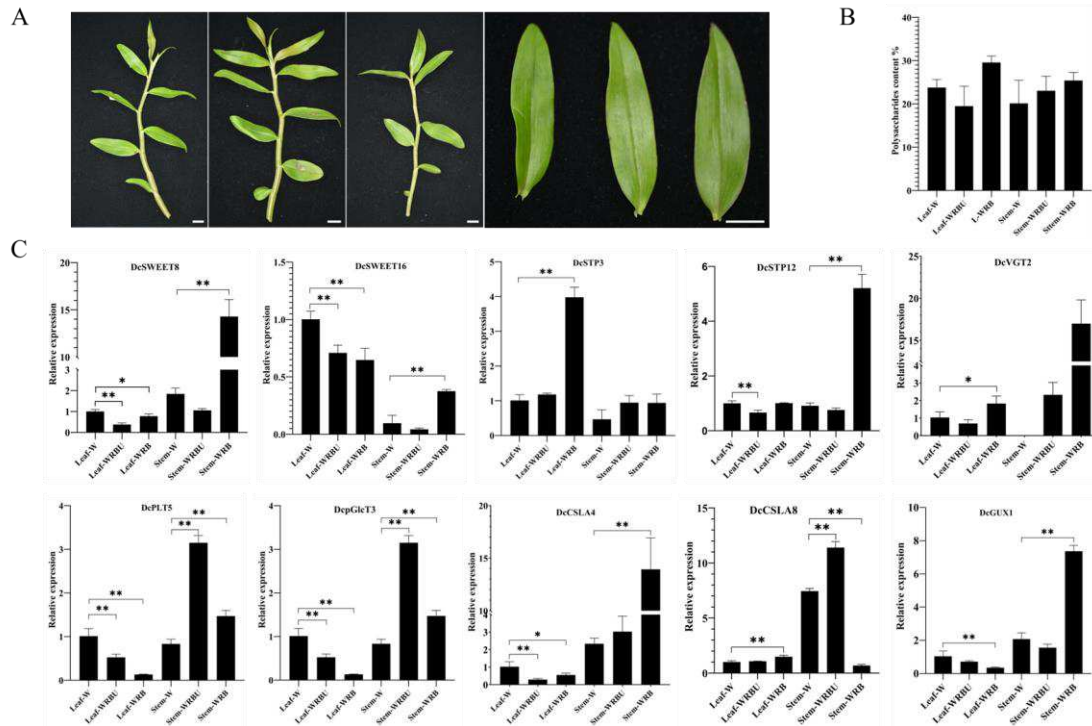


Fig. 10. Morphological, polysaccharides content, and expression profiles of polysaccharide biosynthesis related central genes in *D. catenatum* under different light conditions. A) Morphological of *D. catenatum* under different light conditions, from left to right: Stem-W, Stem-WRB, Stem-WRBU, Leaf-W, Leaf-WRBU, and Leaf-WRB; B) the content of polysaccharides in leaf and stem; C) the expression of ten central genes in leaf and stem. Each data point represents mean value $\pm$ standard deviation (SD) ($n = 3$). Error bars indicate standard deviation. Asterisks indicate the significant degree of expression level compared to the value of the control (* < 0.05 , ** < 0.01).

Discussion

Translocation of sugar plays an indispensable role in plant growth, development, stress/defense and signal transduction [29]. Sugar transports are mainly responsible for sugars translocation, and classified into MST, SUT, and SWEET gene families [29, 48]. The evolutionary and functional research of sugar transporter have been well studied in some plants, such as Arabidopsis [9, 49, 50], rice [9, 51], sorghum [52], pineapple [53], and Lilies [54]. However, there is still a lack of the thorough comprehension of sugar transporters in *Dendrobium* plants.

In present study, we identified the members belong to MST, SUT, and SWEET

gene families in four *Dendrobium* plants, including *D. catenatum*, *D. chrysotoxum*, *D. huoshanense*, and *D. nobile*. The members of sugar transporter gene families also be identified in *A. shenzhenica* to study the evolution history of sugar transporters. MST and SWEET contains the largest number of gene family members and SUT contains fewest members in *Dendrobium* plants, as well as Arabidopsis and other reported plants [9]. The phylogenetic analysis showed that ERD6-like subfamily has experienced dramatically contraction and loss in *Dendrobium* plants, even *A. shenzhenica*. ERD6-like is the largest subfamily of MST gene family in Arabidopsis due to the segmental and tandem duplications events in their evolutionary histories [9, 55]. Previous report showed that ERD6-like genes mainly participate in the transport of different hexoses, and the biological functions of most ERD6-like genes remain largely unknown [55]. We also found that clade IIIb of SUT gene family and clade IIb of SWEET gene family have experienced expansion in *Dendrobium* plants. Clade IIIb is the Orchid-specific clade of SUT gene family, which may be originated from the dispersed duplication event during the speciation of ancestor of Orchid and undergo expansion in *Dendrobium* plants (Fig. 2, Fig. 3, and Fig. 4D). Zhang et al. reported the expansion of SWEET gene family expansion in *D. chrysotoxum*, and deduced that the expansion events are related to the abundant medicinal compounds and fleshy stems of *Dendrobium* [40].

D. catenatum is an important traditional Chinese medicinal herb with remarkable medicinal functions and high economic value. Polysaccharides are the primary active components exerting various pharmacological activities in *D. catenatum* [56]. Sugar transporters are responsible for intra- or inter-cellular transport processes of sugar [29], and highly involved in the perception and response of biotic and abiotic stresses via regulate sugar partitioning in plants [48]. They could provide monosaccharide substrate for polysaccharide biosynthesis, and participate in the adaptation to harsh environments. Thus, we preformed the comprehensive analysis of DcDTs in present work.

The promoter region of *DcSTs* contained many *cis*-element involved in light/stress/hormones responsiveness and TF binding. The result suggesting most

DsSTs may be influenced by light condition and involved in photosynthate partitioning of *D. catenatum*. Transcriptional regulatory network showed that most sugar transporter genes are targeted by MYB TFs (Fig. 6C). MYB is one of the largest TF families in the plants, play important roles in plant growth and development, and responses to environmental stimulus [57]. Previous study showed that MYB TFs are involved in the synthesis of multiple secondary metabolites, such as flavonoids, phenolic acids, terpenoids, alkaloids, and polysaccharides [58]. Some MYB TFs are essential for the polysaccharides biosynthesis, such as AtMYB5/46 targeted to AtCSLA9 in Arabidopsis [59, 60], and DoMYB75 in *D. catenatum* [61]. Considering that sugar transporters are highly involved in polysaccharides biosynthesis, the DcMYBs which are targeting DcSTs maybe the important regulators of polysaccharides biosynthesis in *D. catenatum*. Meanwhile, some conserved miRNAs were found regulate the expression of DcSUTs, it suggesting that these miRNAs also play important roles in the process of sugar partitioning.

Dendrobium plants are rich of polysaccharide in the stem and leaf, we found some *DcST* genes are highly expressed in stem and leaf, especially *DcSUT3/4* and *DcSWEET8/10/11/28*. Most sugar transporter are relatively high expressed in flowers, while some members are flower-specific expression. In accordance with previous reports in *Petunia axillaris* [62] and some Orchid plants [42, 43]. *DcSWEET28* and *DcSTP9* are upregulated in the daytime, while some sugar transporters genes are upregulated during night. The results suggesting that sugar transporters are responsible for the sugar translocation to different sink organs and involved in various physiological process, such as photosynthesis, flowering, and polysaccharides biosynthesis. Environmental stresses may trigger the accumulation of soluble sugars and polyols in plants, sugar transporters modulate sugar partitioning to counterbalance the negative impacts of biotic stresses [48]. We identified some *DcST* genes responded to the environment stimuli, especially SWEET members. Mannan polysaccharides are promising bioactive polysaccharides and key ingredient in *D. catenatum* [34]. *CSLA* genes encode mannan synthases which responsible for glucomannan biosynthesis [63, 64]. A total of 13 DcCSLAs were identified, and play

an important role in the biosynthesis of mannan polysaccharides in *D. catenatum* [63, 65, 66]. We found that *DcSWWT8/16*, *DcSTP3/12*, *DcVGT2*, *DcpGlcT4*, and *DcPLT5* are central genes in polysaccharide biosynthesis, as well as *DcCSLA4/8* and *DcGUX1*.

Most *DcST* genes contains abundant light responsiveness *cis*-elements in their promoter region (Fig. 6B), while 7 *DcSTs* were identified as central genes in the polysaccharide biosynthesis process (Fig. 9C). The results indicated that light condition is an important influencing factor of polysaccharide biosynthesis in *D. catenatum*. Previous studies showed that light condition, especially light quality, is a key factor for controlling the growth and polysaccharide production in alga and plants [67-69]. Red-blue light was beneficial for the accumulation of dry matter and polysaccharides in *Dendrobium* plants [70, 71]. We further investigated the content of polysaccharides and the expression of relevant genes in *D. catenatum* under different light quality. And found that red-blue light could promote the accumulation of polysaccharides in both leaf and stem, conversely, UV light suppress polysaccharide accumulation in leaf. The expression of ten central genes were influenced significantly under different light conditions, indicated they might be closely related to the response to light condition and polysaccharide biosynthesis. The further work is the functional determination of these sugar transporters and uncover their roles in the polysaccharide biosynthesis of *D. catenatum*.

Materials and methods

4.1. Identification of MST, SUT and SWEET proteins in *D. catenatum*

All the MST, SUT, and SWEET family members of *A. thaliana* and *O. sativa* were downloaded from The Arabidopsis Information Resource (<http://www.arabidopsis.org/>) and the Rice Genome Annotation Project (<http://rice.plantbiology.msu.edu/>). The Hidden Markov Model HMM profiles of Sugar_tr (PF00083), MtN3/saliva (PF03083), and MFS_SLC45_SUC (cd17313) domain were downloaded from the Pfam database (<http://pfam.xfam.org/>) and Conserved Domain Database (<https://www.ncbi.nlm.nih.gov/Structure/cdd>). The genome of *D. catenatum* (GCF_001605985.2), *D. nobile* (GCA_022539455.1), *D. chrysotoxum* (GCA_019925795.1), *A. shenzhenica* (GCA_002786265.1), and *D.*

huoshanense (CNP0000830) were downloaded from NCBI (<https://www.ncbi.nlm.nih.gov>) and CNGbDb (<https://db.cngb.org/>).

The protein sequences of MST, SUT and SWEET in Arabidopsis and rice were used for seed to find the candidate proteins in three *Dendrobium* genome using BLASTP program with an E-value cutoff set as $1e^{-10}$. Then, HMMER program (<http://hmmer.org/>) was used to identify the candidate MST proteins harboring Sugar_tr domain, SUT proteins harboring MFS_SLC45_SUC domain, and SWEET proteins harboring MtN3/saliva domain with the E-value of $1e^{-5}$ [72].

4.2. Basic physicochemical properties and phylogenetic analysis of sugar transporters in *D. catenatum*

The molecular weight (MW), isoelectric point (pI) and grand average of hydropathicity (GRAVY) of sugar transporter proteins were calculated using ProtParam (<https://web.expasy.org/protparam/>) [73]. The subcellular localization information were predicted using WoLF PSORT (<https://wolfsort.hgc.jp/>) [74], Cell-Ploc (<http://www.csbio.sjtu.edu.cn/bioinf/Cell-PLoc-2/>) [75] and Bologna Unified Subcellular Component Annotator (BUSCA, <http://busca.biocomp.unibo.it>) [76], and final decided based on consensus localization for two or more algorithms.

The information of transmembrane domain (TM) and conserved domain was obtained using InterPro (<https://www.ebi.ac.uk/interpro/search/sequence/>). The conserved motifs of MST, SUT, and SWEET proteins were analyzed by MEME (<http://meme-suite.org>) with the following parameters: maximum number of motifs, 15; motif length, 6 to 50 [77]. The structure of *sugar transporter* genes was visualized using the online tools Gene Structure Display Server 2.0 (GSDS 2.0, <http://gsds.gao-lab.org/index.php>) [78].

MST, SUT, and SWEET proteins were aligned respectively using MAFFT online service (<https://mafft.cbrc.jp/alignment/server/>) [79]. A neighbor-joining (NJ) phylogenetic tree was constructed in MEGAX (<http://www.megasoftware.net/>) based the multiple sequence alignment with 1000 bootstrap replicates, and displayed using Interactive Tree of Life (<https://itol.embl.de/>).

4.3. Gene duplication and *Ka/Ks* analysis

The duplication events of *DcSTs* were defined based on the collinearity analysis of candidate gene pairs using DupGen_finder [46]. The orthologous gene pairs were

identified using OrthoFinder [80]. The non-synonymous substitution rate (K_a) and synonymous substitution rate (K_s) of the duplication and orthologous gene pairs were calculated using PAMLX [81].

4.4 Promoter analysis of *DcST* genes

Cis-acting elements in the promoter region of *DcST* genes were predicted and analyzed using PLANTCARE (<http://bioinformatics.psb.ugent.be/webtools/plantcare/html/>) [82]. The potential binding sites of TFs in the promoter region of *DcST* genes were predicted using PlantRegMAP (http://plantregmap.gao-lab.org/binding_site_prediction.php) and visualized using Cytoscape 3.7.0 [83, 84].

4.5. Interaction analysis of *sugar transporter* genes and miRNAs in *D. catenatum*

The miRNA data of *D. catenatum* were downloaded from the previous study [85]. The *sugar transporter* mRNAs targeted by Dca-miRNA were predicted using psRNATarget (<http://plantgrn.noble.org/psRNATarget/>) [86]. The mRNA-miRNA interaction network was visualized using Cytoscape 3.7.0 [84].

4.6. Transcript abundance analysis of *sugar transporter* genes in *D. catenatum*

To explore the expression patterns of *DcST* genes, a total of 46 RNA-seq of *D. catenatum* was downloaded from NCBI. All the Sequence Read Archive accession numbers were displayed in Table S3. The gene expression levels were calculated and normalized to the TPM (Transcripts Per Kilobase of exon model per Million mapped reads). The expression profile of *DcST* genes were extracted and visualized using RStudio.

4.7. WGCNA analysis

Weighted correlation network analysis (WGCNA) was performed using WGCNA package 1.63 in R. The co-expression network modules were identified and the gene sets were extracted for GO enrichment analysis. The signed weighted correlation network was visualized using Cytoscape 3.7.0.

4.8. Plant materials and treatment

Two years old *D. catenatum* plants were grown in the greenhouse under the condition of 12/12 h photoperiod (white light, $180 \mu\text{mol m}^{-2} \text{s}^{-1}$) and temperature of 25 °C. *D. catenatum* were treated with three light conditions, including white light (control, CK),

white-red-blue-UV light (60 white LED + 18 red LED (660 nm) + 16 blue LED (440 nm) +2 UV LED (395 nm), WRBU), white-red-blue light (60 white LED + 18 red LED + 16 blue LED, WRB), The second to fifth adult leaves and stem nodes were sampled at 7th day after treatment, immediately frozen in liquid nitrogen and then then stored at -80°C.

4.9. Measurement of polysaccharide content

The content of total polysaccharide in leaf and stem were measured using the phenol–sulfuric acid method following the protocol provided in the Pharmacopeia of the People's Republic of China (2020). The absorbance at 488 nm was determined using Microplate Reader (FlexStation 3, Molecular Devices, USA). Three replicates were obtained for each treatment.

4.10. Quantitative real-time PCR

Total RNA was extracted using Fruit-mate™ for RNA Purification (TaKaRa, Dalian, China) and Ominiplant RNA Kit (CoWin Biosciences, Beijing, China). The cDNA was synthesized using the PrimeScript™ RT reagent Kit with gDNA Eraser (TaKaRa, Dalian, China). qRT-PCR was conducted on Bio-Rad CFX96 touch Real Time PCR System (Bio-Rad, Hercules, CA, USA) using the TB Green® Premix Ex Taq™ (TaKaRa, Dalian, China). The oligonucleotide primers were designed using primer-premier 6 (Table S4), *actin* (ACT) gene was used as an internal control. Each reaction was analyzed in triplicate and the $2^{-\Delta\Delta CT}$ method was used to analyze the data [87].

5. Conclusion

In this study, we identified 341 sugar transporters in *A. shenzhenica*, *D. catenatum*, *D. chrysotoxum*, *D. huoshanense*, and *D. nobile*. Then, the evolution history, expansion and contraction of *sugar transporter* gene families was analyzed in *Dendrobium* plants. The phylogenetic analysis, structural arrangement, regulatory networks, expression profiles, and potential functions of 73 sugar transporters in *D. catenatum* were analyzed. Seven DcSTs were found that be involved in polysaccharides biosynthesis process. Red-blue light is an effective way to improve the accumulation of polysaccharides. This study provides insight into the evolution and functional

annotation of MST, SUT, and SWEET gene families in *D. catenatum*, and provide valuable information for the functional study of sugar transporter genes involved in stress response and polysaccharides biosynthesis in *Dendrobium* plants.

Author Contributions

Conceptualization, X.-Y.Z. and H.-W.H.; writing—original draft preparation, W.-W.F.; formal analysis, H.-S. G., L.Z and D.-D.M.; methodology, Y.-Y.L., L.-F.Z. and J.-T.L.; writing—review and editing, X.-Y.Z. and H.-W.H.; All authors have read and agreed to the published version of the manuscript.

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Declarations

Ethics approval and consent to participate

Not applicable.

Competing Interest

The authors report no declarations of interest.

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Table 1

The number of different type sugar transporters in 7 plants.

Speices	MST								SUT						SWEET						Total
	STP	PLT	VGT	TMT	pGlcT	INT	ERD6-like	Total	I	IIa	IIb	IIIa	IIIb	Total	I	IIa	IIb	III	IV	Total	
<i>A. thaliana</i>	14	6	3	3	4	4	19	53	1	1	7	0	0	9	3	5	0	7	2	17	79
<i>O. sativa</i>	29	15	2	6	4	3	6	65	1	1	0	3	0	5	6	8	1	5	1	21	91
<i>A. shenzhenica</i>	21	5	2	2	3	3	3	39	1	1	0	1	2	5	3	3	3	7	1	17	61
<i>D. catenatum</i>	15	6	2	2	3	3	3	34	1	1	0	2	3	7	5	5	11	10	1	32	73
<i>D. chrysotoxum</i>	14	4	2	1	1	3	0	25	1	1	0	2	3	7	3	3	18	8	2	34	66
<i>D. huoshanense</i>	12	9	1	2	0	3	1	28	1	0	0	3	5	9	5	4	5	7	2	23	60
<i>D. nobile</i>	18	5	2	2	3	3	3	36	1	1	0	2	4	8	5	6	14	10	2	37	81

Table 2

Characteristic features of sugar transporters in *D. catenatum*.

S. No	Protein ID	Protein length (aa)	Molecular weight	Exons	THMs	Subcellular location
DcERD6.1	XP_020690096.1	497	53619	17	12	plasma membrane and vacuole
DcERD6.2	XP_020701355.1	474	51494.47	18	12	plasma membrane and vacuole
DcERD6.3	XP_020702150.1	481	51494.84	17	12	plasma membrane
DcINT1	XP_020675104.1	581	63279.1	6	12	plasma membrane and vacuole
DcINT2	XP_020676904.1	509	54680.9	6	12	plasma membrane
DcINT3	XP_020696092.1	579	63420.1	6	12	plasma membrane and vacuole
DcpGlcT1	XP_020699357.2	537	58411.23	12	11	plasma membrane and chloroplast
DcpGlcT2	XP_020671882.1	491	52786.05	13	10	plasma membrane

DcpGlcT3	XP_020672325.2	583	61401.43	13	11	plasma membrane and chloroplast
DcPLT1	XP_020689528.1	496	53417.9	2	10	plasma membrane and vacuole
DcPLT2	XP_020689572.2	505	54039.13	2	10	plasma membrane and vacuole
DcPLT3	XP_020693533.2	525	56358.75	3	12	plasma membrane and vacuole
DcPLT4	XP_020693540.1	522	55692.14	3	12	plasma membrane and vacuole
DcPLT5	XP_020696863.1	549	58933.98	2	11	plasma membrane and vacuole
DcPLT6	XP_028551540.1	461	49985.54	1	9	plasma membrane and vacuole
DcSTP1	XP_020673769.1	504	55621.81	1	11	plasma membrane and vacuole
DcSTP2	XP_020673820.1	508	55929.32	1	12	plasma membrane and vacuole
DcSTP3	XP_020676035.2	511	57155.97	3	8	plasma membrane and vacuole
DcSTP4	XP_020676038.1	512	56568.53	3	11	plasma membrane and vacuole
DcSTP5	XP_020678679.1	522	57723.61	4	12	plasma membrane and vacuole
DcSTP6	XP_020682728.1	479	52510.74	2	10	plasma membrane
DcSTP7	XP_020690754.1	504	54603.33	4	11	plasma membrane and vacuole
DcSTP8	XP_020692064.1	520	56587.14	3	12	plasma membrane and vacuole
DcSTP9	XP_020692077.1	527	57029.1	3	11	plasma membrane and vacuole
DcSTP10	XP_020695794.1	523	57967.25	4	12	plasma membrane and vacuole
DcSTP11	XP_020700131.1	518	56636.82	4	10	plasma membrane and vacuole
DcSTP12	XP_020704792.1	521	57001.69	3	11	plasma membrane and vacuole
DcSTP13	XP_020704799.1	511	56210.29	3	11	plasma membrane and vacuole
DcSTP14	XP_020704818.1	529	57159.1	4	12	plasma membrane and vacuole
DcSTP15	XP_028548876.1	585	64189.57	6	12	plasma membrane
DcTMT1	XP_020676096.1	733	79105.15	5	10	plasma membrane and vacuole
DcTMT2	XP_020702404.1	754	81183.79	5	10	plasma membrane and vacuole
DcVGT1	XP_020690641.1	555	59351.64	13	12	plasma membrane and chloroplast
DcVGT2	XP_028551786.1	624	69089.88	12	11	plasma membrane and vacuole
DcSUT1	XP_020695242.1	500	53276.48	14	11	plasma membrane and vacuole

DcSUT2	XP_020695324.1	500	53406.88	14	12	plasma membrane
DcSUT3	XP_020698795.1	518	55639.42	14	10	plasma membrane and vacuole
DcSUT4	XP_020700410.1	538	57434.5	5	12	plasma membrane
DcSUT5	XP_020702803.1	496	52805.96	14	10	plasma membrane and vacuole
DcSUT6	XP_020703969.1	638	68894.38	14	11	plasma membrane
DcSUT7	XP_028557242.1	491	53217.55	14	9	plasma membrane and vacuole
DcSWEET1	XP_020671992.2	262	29221.23	6	7	plasma membrane and vacuole
DcSWEET2	XP_020672052.1	277	30999.59	5	6	plasma membrane and vacuole
DcSWEET3	XP_020674019.1	233	26201.75	5	7	plasma membrane
DcSWEET4	XP_020674476.2	237	26775.07	4	7	plasma membrane and vacuole
DcSWEET5	XP_020675146.2	296	33103.11	7	7	plasma membrane and vacuole
DcSWEET6	XP_020675601.1	237	26619.75	6	7	plasma membrane, chloroplast, chloroplast
DcSWEET7	XP_020681423.1	265	29628.48	6	7	plasma membrane and vacuole
DcSWEET8	XP_020681431.1	265	29548.47	6	7	plasma membrane and vacuole
DcSWEET9	XP_020682347.1	232	25952.07	5	7	plasma membrane
DcSWEET10	XP_020686358.1	266	29937.55	6	7	plasma membrane and vacuole
DcSWEET11	XP_020687552.1	248	27452.87	5	7	plasma membrane, chloroplast, chloroplast
DcSWEET12	XP_020694055.1	204	23383.16	4	5	plasma membrane and vacuole
DcSWEET13	XP_020694837.1	236	26368.85	5	7	plasma membrane and vacuole
DcSWEET14	XP_020694842.2	235	26270.7	5	7	plasma membrane and vacuole
DcSWEET15	XP_020695376.1	203	23090.31	4	7	plasma membrane and vacuole
DcSWEET16	XP_020695524.1	296	33105.05	6	6	plasma membrane and vacuole
DcSWEET17	XP_020698470.1	196	22184.7	3	6	plasma membrane and vacuole
DcSWEET18	XP_020699529.1	271	30501.38	6	7	plasma membrane and vacuole
DcSWEET19	XP_020700202.1	234	26016.98	6	7	plasma membrane and vacuole
DcSWEET20	XP_020700756.1	237	26594.95	4	7	plasma membrane and vacuole
DcSWEET21	XP_020701878.1	237	26577.42	6	7	plasma membrane, chloroplast, chloroplast

DcSWEET22	XP_020706020.1	259	28917.85	4	7	plasma membrane and vacuole
DcSWEET23	XP_020706032.1	266	30208.04	4	6	plasma membrane and vacuole
DcSWEET24	XP_020706043.1	260	28848.86	4	7	plasma membrane
DcSWEET25	XP_028548619.1	237	26514.24	4	7	plasma membrane and vacuole
DcSWEET26	XP_028549267.1	258	29397.21	6	7	plasma membrane and vacuole
DcSWEET27	XP_028551223.1	249	27592.3	6	7	plasma membrane and vacuole
DcSWEET28	XP_028554265.1	211	23202.44	4	5	plasma membrane and vacuole
DcSWEET29	XP_028556203.1	295	33080.46	6	6	plasma membrane and vacuole
DcSWEET30	XP_028556661.1	201	22443.16	4	6	plasma membrane and vacuole
DcSWEET31	XP_028557180.1	285	31999.37	5	7	plasma membrane
DcSWEET32	XP_028557181.1	283	31646.02	5	7	plasma membrane

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