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Research Article
SWEET Gene Family in Sugar Beet (*Beta vulgaris*): Genome-Wide Survey, Phylogeny and Expression Analysis

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Abstract

Background and Objective: The SWEET (Sugars Will Eventually be Exported Transporter) proteins play important roles in modulating the growth and development processes in plants. However, little information is available on the SWEET family in sugar beet (*Beta vulgaris*). The objectives of this present study were to genome-wide identify and characterize the BvSWEET family in sugar beet. **Materials and Methods:** Based on the available genome, proteome and transcriptome databases of sugar beet, various computational tools have been used to analyze the nucleotide and full-length protein sequences of members of the BvSWEET family. **Results:** A total of 16 members of the BvSWEET family has been identified in sugar beet at the genome-wide scale. Structural analysis indicated that the BvSWEET family exhibited variable characteristics. Furthermore, the BvSWEET family in sugar beet could be categorized into four distinct groups like in other plant species. Of our interest, we found that some *BvSWEET* genes exhibited strongly preferential expression in major organs/tissues under adverse environmental stimuli. **Conclusion:** The results provided a comprehensive foundation for further functional characterization of the *BvSWEET* gene family.

Key words: Identification, characterization, expression patterns, sugar beet, SWEET

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Competing Interest: The authors have declared that no competing interest exists.

Data Availability: All relevant data are within the paper and its supporting information files.

INTRODUCTION

Sugar beet or red beetroot (*Beta vulgaris*) has been known as one of the most essential dicotyledonous plants, which is widely grown in the world. Supplying approximately 30% of the global sucrose, sugar beet was recognized as the second-largest source of refined table sugar[1]. This economically important edible beet is also daily used as a source of a variety of natural pigments, like bioactive molecules (such as betalains, pectic-oligosaccharides and phenolics) and phytochemicals (such as flavonoid, carotenoid and vitamin)[2], which was reportedly related to numerous health benefits[3]. Thus, the efficiency of cultivation of this sugar-yielding crop has been comprehensively investigated.

To investigate and evaluate the molecular changes in sugar beets under adverse environmental conditions, many studies have been reported the roles of transporter protein families in the facilitation of sucrose accumulation[4]. Among them, one key sucrose transporter family has been known as 'SWEET-s' (Sugars Will Eventually be Exported Transporters). Participating in sucrose translocation and storage[5], the SWEET family has been reportedly modulated many biological processes during the growth and development of plants[6]. Recently, the SWEET families have been comprehensively identified and characterized in various crop species, like rice[7], tomato[8], soybean[9], oilseed rape[10], cucumber[11], banana[12], Chinese white pear[13], cotton[14], tea plant[15], apple[16], litchi[17], wheat[18], *Medicago truncatula*[19] and walnut[20]. Unfortunately, no report has been made to a genome-wide survey of this critical gene family in sugar beet.

Thus, the purpose of this research was to comprehensively identify and characterize the SWEET family in sugar beet. Particularly, a genome-wide survey has been performed to seek all putative members of the SWEET family. We also analyzed their general characteristics, like physic-chemical properties, subcellular localization, gene structure, phylogenetic tree and transmembrane helices. Furthermore, the expression patterns of the *SWEET* gene in major tissues/organs of sugar beet were determined by re-analyzing the previous transcriptome atlas.

MATERIALS AND METHODS

Study area: This study was carried out from March, 2021 to January, 2022. All analyses were conducted at Hanoi City and Vinh Phuc and Phu Tho provinces, Vietnam.

Genome-wide survey of the SWEET family in sugar beet: To comprehensively seek SWEET-s in sugar beet, the well-characterized domain of plant's SWEET[5] obtained from the Pfam tool[21] was applied to search against the latest assembly of sugar beet (Accession number: GCF_000511025.2)[22] in the NCBI (National Center for Biotechnology Information) and Phytozome 12.0[23] portals. The major annotated features of the identified SWEET-s, including peptide sequence, coding DNA sequence (CDS), genomic DNA sequence (gDNA), identifier code and chromosomal distribution were consequently obtained for further analyses.

Analysis of protein properties of the SWEET family in sugar beet: The physic-chemical characteristics of the SWEET proteins, like length, molecular weight, iso-electric point, aliphatic index, hydropathicity, were theoretically calculated by the ExPASY Protparam tool[24] as previously guided[25,26].

Prediction of the subcellular localization of the BvSWEET-s: The subcellular localization of the SWEET proteins were predicted by using the web-based YLOC tool[27]. The full-length protein sequence of each member of the SWEET family in sugar beet was used as a query for a search in the YLOC system[27]. Particularly, a total of 10 locations, including the nucleus, cytoplasm, mitochondrion, plasma membrane, extracellular space, endoplasmic reticulum, peroxisome, Golgi apparatus, vacuole and chloroplast were predicted for the plant model[27].

Analysis of the membrane-bound SWEET proteins in sugar beet: To predict the transmembrane helices in SWEET proteins in sugar beet, the TMHMM 2.0 tool[28] was used. The full-length protein sequences of the SWEET family in sugar beet were used as seed sequences for seeking the transmembrane helices[28].

Construction of phylogenetic tree of the SWEET family in sugar beet: To construct the phylogenetic tree of the SWEET family, the full-length protein sequences of all members of the SWEET family in sugar beet were collected as raw material for the MEGA (Molecular Evolutionary Genetics Analysis) 7.0 software[29]. The Maximum Likelihood estimation with 1,000 bootstrapped replications was used as the statistical model for generating the phylogenetic tree. Additionally, also collected the full-length protein sequences of the SWEET families from *Arabidopsis thaliana*[30], rice[7] and cassava in the Phytozome[23] to analyze the categorization of the SWEET families.

Analysis of gene structures of the *SWEET* family in sugar beet: The number of exons and introns of genes encoding the SWEET family in sugar beet was analyzed by using the GSDS (Gene Structure Display Server) 2.0 website[31]. The order of members of the *SWEET* gene family was arranged based on the Maximum-Likelihood-based phylogenetic tree[29]. The result was then illustrated by using Adobe Illustrator[25,26].

Analysis of the expression patterns of the *SWEET* family in sugar beet: To investigate the expression patterns of the *SWEET* gene family in sugar beet, we re-analyzed the previous transcriptome databases by searching against the NCBI GEO (NCBI Gene expression omnibus)[32], like GSE135555[33], GSE138039[34], GSE107627[35] and GSE114968[36]. Particularly, the first microarray database (GSE135555) provided expression data of fifteen-day-old roots of the sugar beet plants treated with a beet cyst nematode, namely *Heterodera schachtii*[33], while the second dataset (GSE138039) contained expression data of leaves on five-week-old sugar beet plants inoculated with a fungal pathogen, namely *Sclerotinia sclerotiorum* [34]. Additionally, we also downloaded two datasets, GSE107627[35] and GSE114968[36], which provided two expression data of leaf tissues from alkaline-treated seedlings and root tissues from salinity-treated seedlings, respectively. Differentially expressed gene was assigned by a fold-change cut-off (|fold-change|>2.0). The cluster heatmap of the *SWEET* genes in sugar beet was then visualized in R software with the g plots[37].

RESULTS AND DISCUSSION

Identification, annotation and chromosome localization of the SWEET family in sugar beet: First of all, we seek the SWEET family in sugar beet by Blast-ing a conserved domain of SWEET molecules, namely 'PF03083'[5] against the available sugar beet's assembly[22] from Phytozome[23] and NCBI databases. As a result, a total of 16 putative members of the SWEET family has been found and validated in sugar beet in Table 1.

As compared with the SWEET families in other plant species, we found that the amount of members from this important family is critically variable[38]. For example, 21 putative members have been identified and characterized in rice[7]. In the cucumber and tea plant, 17 and 13 members of the SWEET family have been reported recently, respectively[11,15], while 25 SWEET-s were found in Medicago's assembly[19]. In four cotton species, 22, 31, 55 and 60 members of the SWEET family have been listed in *Gossypium arboreum*, *G. raimondii*, *G. hirsutum* and *G. barbadense*, respectively[14]. The number of members of the SWEET family could also reach 52 and 108 in soybean and wheat, respectively[9,18]. Quite recently, a total of 25 members of the SWEET family has been studied in walnut[20]. Here, our genome-wide survey indicated that the number of SWEET family in sugar beet (16) is more than in tea plant (13)[15] but less than many plant species, like cucumber (17)[11], rice (21)[7], *G. arboreum* (22)[14], Medicago (25)[19], walnut (25)[20], *G. raimondii* (31)[14], soybean (52)[9], two other cotton species (55 and 60 in *G. hirsutum* and *G. barbadense*, respectively)[14] and wheat (108)[18].

Next, the chromosomal locations of all 16 members of the SWEET gene family were manually retrieved from the NCBI database. According to the chromosomal localization of SWEET genes in Fig. 1, we named 16 annotated genes, from *BvSWEET01* to *16* by their order of occurrence on the chromosomes. It was noted that 16 *BvSWEET* genes were located on the sugar beet genome with an even ratio. Particularly, the chromosomes 2, 6 and 7 harboured only one *BvSWEET* gene each, while two chromosomes, like 3 and 5

Table 1: BvSWEET family in sugar beet

Gene name	Locus name	Length	Mass	pI	AI	GRAVY	SL	TMH
BvSWEET01	EL10Ac1g00932	234	26.39	9.27	115.30	0.70	PM	7
BvSWEET02	EL10Ac1g01460	255	27.95	9.50	116.59	0.59	PM	7
BvSWEET03	EL10Ac2g02891	162	18.71	8.71	121.42	0.81	PM	4
BvSWEET04	EL10Ac3g05343	251	27.86	8.89	113.03	0.49	PM	7
BvSWEET05	EL10Ac3g06628	246	27.22	8.35	121.99	0.68	PM	6
BvSWEET06	EL10Ac3g06631	241	26.47	7.70	109.13	0.53	PM	7
BvSWEET07	-	162	18.61	8.47	122.04	0.79	PM	5
BvSWEET08	EL10Ac4g08428	234	26.03	6.25	112.48	0.81	PM	7
BvSWEET09	EL10Ac4g09802	262	29.42	8.93	117.14	0.59	PM	7
BvSWEET10	EL10Ac4g09898	223	24.49	8.93	130.67	0.89	PM	7
BvSWEET11	EL10Ac5g10774	234	26.74	9.22	122.35	0.72	PM	6
BvSWEET12	EL10Ac5g11351	324	36.27	6.52	105.49	0.34	PM	7
BvSWEET13	EL10Ac5g12959	257	28.22	9.59	123.62	0.77	PM	7
BvSWEET14	EL10Ac5g12960	273	30.36	8.99	114.62	0.58	PM	7
BvSWEET15	EL10Ac6g13562	258	28.86	9.25	123.49	0.65	PM	7
BvSWEET16	EL10Ac7g17402	335	37.62	8.19	108.81	0.30	PM	7

pI: Iso-electric point, AI: Aliphatic index, GRAVY: Grand average of hydropathicity, SL: Sub-cellular localization, TMH: Transmembrane helices and PM: Plasma membrane

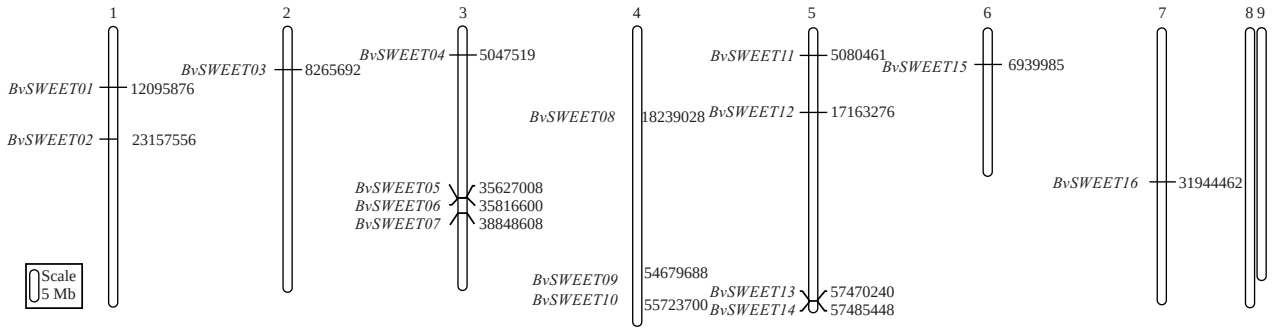

Fig. 1: Chromosomal distribution of the *SWEET* gene family in sugar beet genome

contained the highest number of *BvSWEET* genes (four each) (Fig. 1). We also found that two and three *BvSWEET* genes were mapped on chromosomes 1 and 4, respectively (Fig. 1). However, no *BvSWEET* gene was found on chromosomes 8 and 9.

Interestingly, two *BvSWEET* genes, like *BvSWEET13* and *14* were mapped on the sub-telomeric areas of chromosome 5. This trend was also reported in the *SWEET* gene families in other plant species, like rice[7], soybean[9], cucumber[11], tea plant[15], four cotton species[14], Medicago[19] and wheat[18]. We hypothesized that genes on the sub-telomeric region of the chromosome, like two *BvSWEET* genes in this study, may act in the chromosome pairing and recognition during the meiosis process in sugar beet, as previously reported in other plant species[39].

Investigation on the physic-chemical properties of the SWEET family in sugar beet: To get insight into the BvSWEET family in sugar beet, the physic-chemical characteristics of each BvSWEET's member were analyzed by the online ExPASy Protparam tool[24]. Particularly, five parameters, including protein length, mass, iso-electric point, aliphatic index and hydropathicity were explored by applying the full-length protein sequences to tool[24]. All features of the BvSWEET family were then provided in Table 1.

The results revealed that the lengths of gDNA *SWEET*-s varied from 489 (*BvSWEET03* and *07*) to 15046 bp (*BvSWEET15*), whereas, the protein lengths ranged from 162 (BvSWEET03 and 07) to 335 amino acid residues (BvSWEET16) (Table 1). Moreover, the molecular weights of the BvSWEET family were changed from 18.61 (BvSWEET07) to 37.62 kDa (BvSWEET16) (Table 1). A majority of the BvSWEET proteins (15 out of 16) had alkaline properties (the pI values were more than 7.0), whereas, only BvSWEET08 had acidic property (the pI value was less than 7.0) (Table 1). Interestingly, *in silico* analysis indicated that all members of the BvSWEET family are hydrophilic with positive GRAVY values (Table 1), while all these molecules contained a large amount of aliphatic amino acid residues, with the aliphatic index ranging from 105.49 (BvSWEET12) to 130.67 (BvSWEET10) (Table 1). Findings suggested that the variable features of the BvSWEET family may be related to their potential roles during the growth and development of sugar beet plants[12].

Previously, great efforts have been recorded to investigate the physic-chemical properties of the SWEET families in other plant species. For example, the SWEET family from tomato, oilseed rape, banana, apple and litchi were varied from 233-308, 56-303, 171-333 (with relative molecular weight between 19.1-37.4 kDa), 215-340 and 229-300 (with relative molecular weight between 25.6-33.6 kDa) amino acid residues, respectively[8,10,12,16,17]. Recently, the walnut SWEET proteins have been reported to vary from 154-301 amino acid residues in size, their molecular weights ranged from 16.63-33.24 kDa[20]. Moreover, a majority of the members (22 out of 25) of the SWEET family from banana had basic properties (iso-electric points ranging from 7.56-9.83)[12], while all 16 members of the SWEET family in litchi also exhibited alkaline properties[17]. The pI values of 21 (out of 25) members of the SWEET family in walnut had also basic properties[20].

Sub-cellular localization and membrane-bound analysis of the SWEET family in sugar beet: It is thought that the subcellular localization of proteins may be strongly related to their specific function[40]. Thus, the study carried out a prediction of the sub-cellular distribution of BvSWEET proteins in sugar beet by using the YLOC portal[27]. As expected, we found that all 16 BvSWEET proteins may be localized on the plasma membrane (Table 1). Findings were also confirmed in the SWEET proteins in other plant species, like tomato[8], walnut[20]. For example, five members of the SWEET family in tomato were predicted to distribute on the plasma membrane[8], while 22 (out of 25) SWEET proteins from walnut were also localized on the plasma membrane[20]. Moreover, the prediction of subcellular localization in a previous study showed that all 168 SWEET proteins from four cotton species were located in the plasma membrane[14].

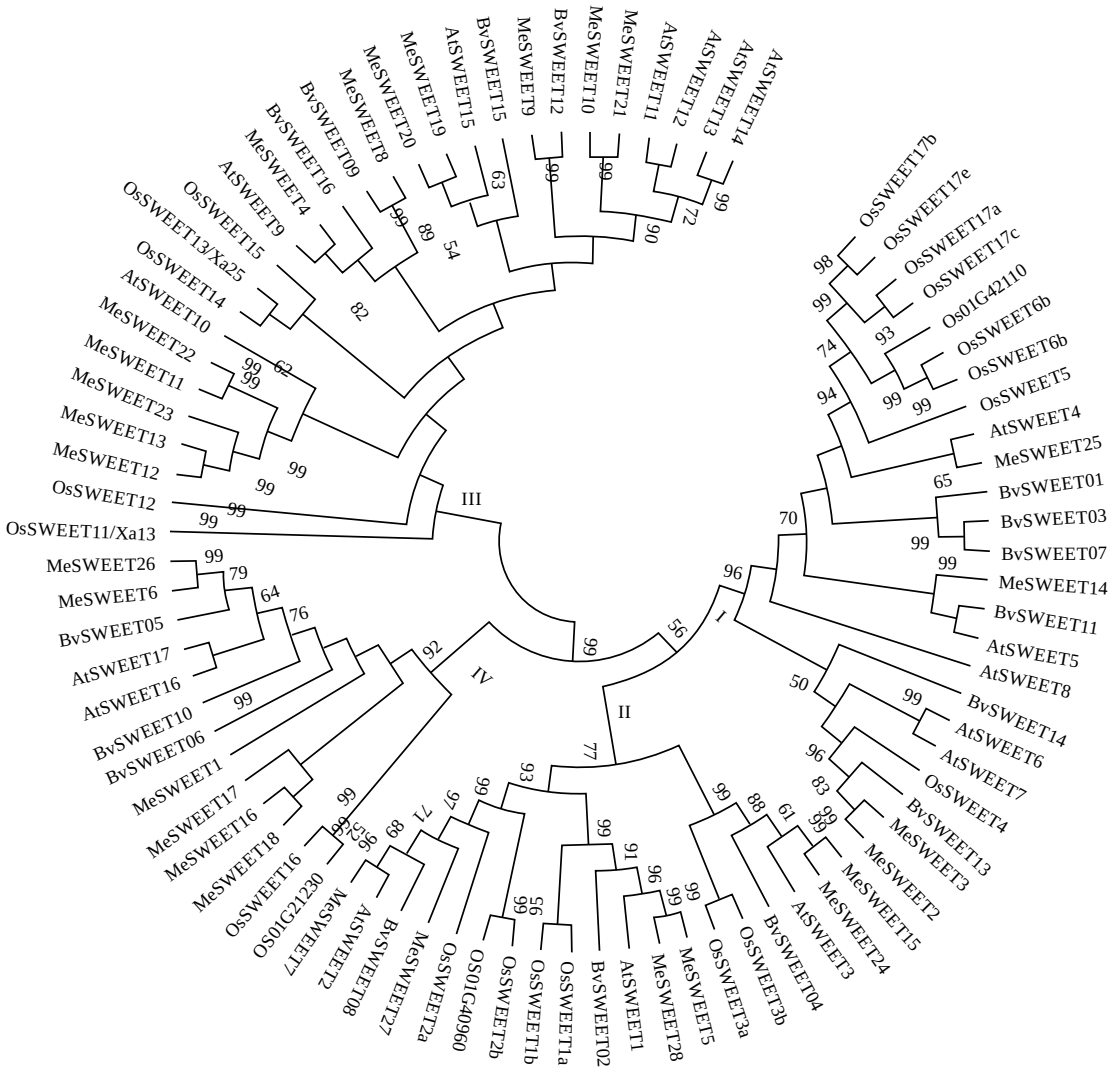

Fig. 2: Phylogenetic tree diagram of SWEET families from sugar beet, *Arabidopsis thaliana*, rice and cassava

Next, the presence of transmembrane helices was then investigated on the full-length protein sequences of the BvSWEET family in sugar beet. The predicted result was provided in Table 1. We found that a majority of members (12 out of 16) of the BvSWEET family contained seven transmembrane helices (Table 1). Two members, including BvSWEET05 and 11, were noted to contain six transmembrane helices, while BvSWEET07 and 03 harboured five and four transmembrane helices, respectively (Table 1). Previously, SWEET families in litchi[17] and some other plant species[9] were recognized to contain seven transmembrane helices[5]. Taken together, suggested that BvSWEET proteins, with the presence of these transmembrane helices, may function as membrane receptors[41].

Phylogenetic analysis of the SWEET family in sugar beet: To categorize the BvSWEET family in sugar beet, a maximum-likelihood-based phylogenetic tree of full-length SWEET proteins from sugar beet, *A. thaliana*[30], rice[7] and cassava has been successfully constructed in Fig. 2. As provided in Fig. 2, all members of the BvSWEET family from sugar beet could be classified into four distinct groups. Six members, including BvSWEET01, 03, 07, 11, 13 and 14 have been fall into group I, while three (BvSWEET02, 04 and 08) and three (BvSWEET05, 06 and 10) members were categorized into group II and III, respectively (Fig. 2). Finally, group IV contained four remaining members, like BvSWEET09, 12, 15, 16 (Fig. 2). Here, we realized that proteins in the same branch shared similar characteristics (Fig. 2, Table 1). For example,

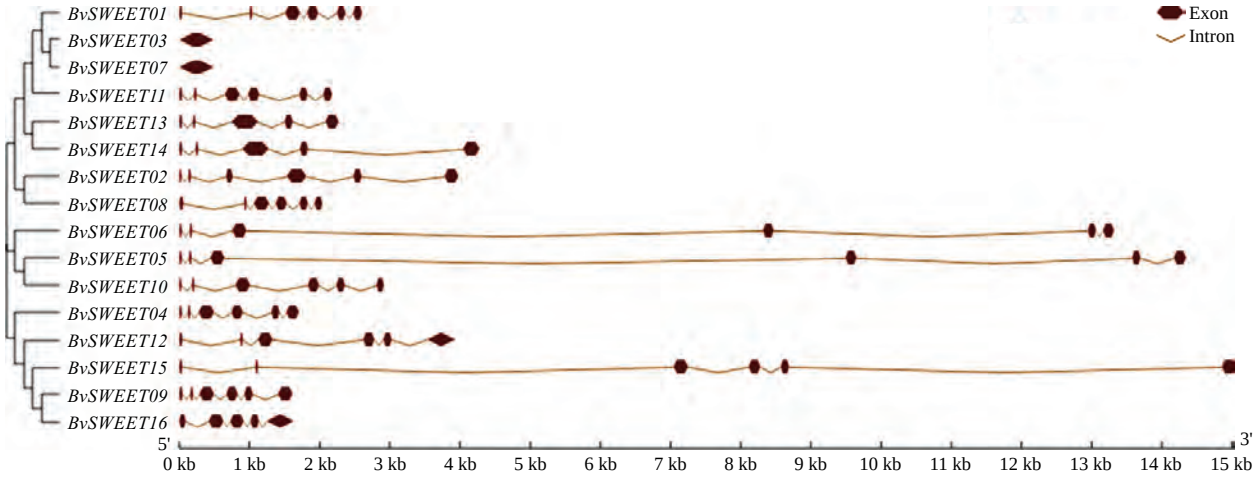

Fig. 3: Gene organizations of the *BvSWEET* gene family in sugar beet

BvSWEET03 and 07 were localized in the same clade of group I (Fig. 2), they shared similar protein sizes, molecular weights, iso-electric points, aliphatic index and average grand of hydropathy). Thus, we suggested that these same-clade-SWEET proteins may share similar functions.

In the previous study, a phylogenetic analysis of the SWEET families in tomato and two other plant species, like rice and *A. thaliana* has been performed[8]. As expected, the SWEET family in three targeted plant species could be categorized into four classes[8]. Furthermore, a comprehensive phylogenetic tree of 173 SWEET proteins from 13 plant species, including four dicots, two monocots, two bryophytes and five algae has been well-described[9]. As expected again, four distinct clades were perceived[9]. Taken together, findings revealed that the SWEET family in sugar beet, perhaps in plant species, could be categorized into four major groups.

Gene structure of the *SWEET* family in sugar beet: To investigate the structure of the gene encoding BvSWEET proteins, we analyzed the exon/intron organization of each member of the *BvSWEET* gene family by using the GSDS tool[31]. The gene organizations of all *BvSWEET* genes were then generated and provided in Fig. 3. We found that most members (14 out of 16) of the *BvSWEET* gene family contained introns in their genomic sequences, whereas, two genes, including *BvSWEET03* and *07* were noted to be intronless. Next, three genes, like *BvSWEET13*, *14* and *16* contained five exons, while the remaining *BvSWEET* gene family members (11 out of 16) harboured six exons (Fig. 3).

Significantly, such a similar phenomenon of six exons in the *BvSWEET* gene family was also confirmed in the *SWEET* families from many crop species. In tomatoes, some *SWEET* genes (23 out of 29) contained six exons and five introns[8]. Also, 51 (out of 68), 12 (out of 17), 12 (out of 18) members of the *SWEET* families from oilseed rape, cucumber, Chinese white pear, respectively[10,11,13] contained six exons. Recently, many members of the *SWEET* gene families in the tea (11 out of 13) and litchi (14 out of 16) have been reported to harbour six exons[15,17]. Taken together, our comparisons strongly indicated that the majority of the *SWEET* gene families in plant species might have the conserved motif of six exons and five introns.

Expression patterns of the *SWEET* family during the growth and development of sugar beet: As the main part of this study, the expression patterns of the *BvSWEET* gene family members were explored by re-analyzing four available RNA-Seq datasets[33-36] in the NCBI GEO[32]. A heatmap was then generated and provided in Fig. 4. Noted that two genes, including *BvSWEET03* and *07* not expressed in all datasets. The expression of all remaining members of the *BvSWEET* gene family displayed spatial variation in major organs/tissues of sugar beet plants.

Under the alkaline stress[35], only three genes, like *BvSWEET04*, *10* and *11* exhibited a significantly different expression in root tissues (Fig. 4). Among them, *BvSWEET10* and *11* were noted to strongly induce and reduce in alkaline-treated roots, respectively (Fig. 4). Under the salt stress[36], eight genes, like *BvSWEET01*, *02*, *06*, *09*, *12*, *14*, *15* and *16* were differentially expressed in leaves from alkaline-treated seedlings. Interestingly, one (*BvSWEET12*) and two (*BvSWEET14* and *15*) genes were highly up-regulated and down-regulated in leaf tissues under the alkaline treatment, respectively. Next, under the infection of a fungal pathogen[34], six (*BvSWEET04*, *05*, *06*, *09*, *12* and *14*) and one (*BvSWEET10*) genes were highly reduced and induced in leaf tissues, respectively (Fig. 4). Finally, under the inoculation of *H. schachtii*[33], only two genes, *BvSWEET10* and *14* were

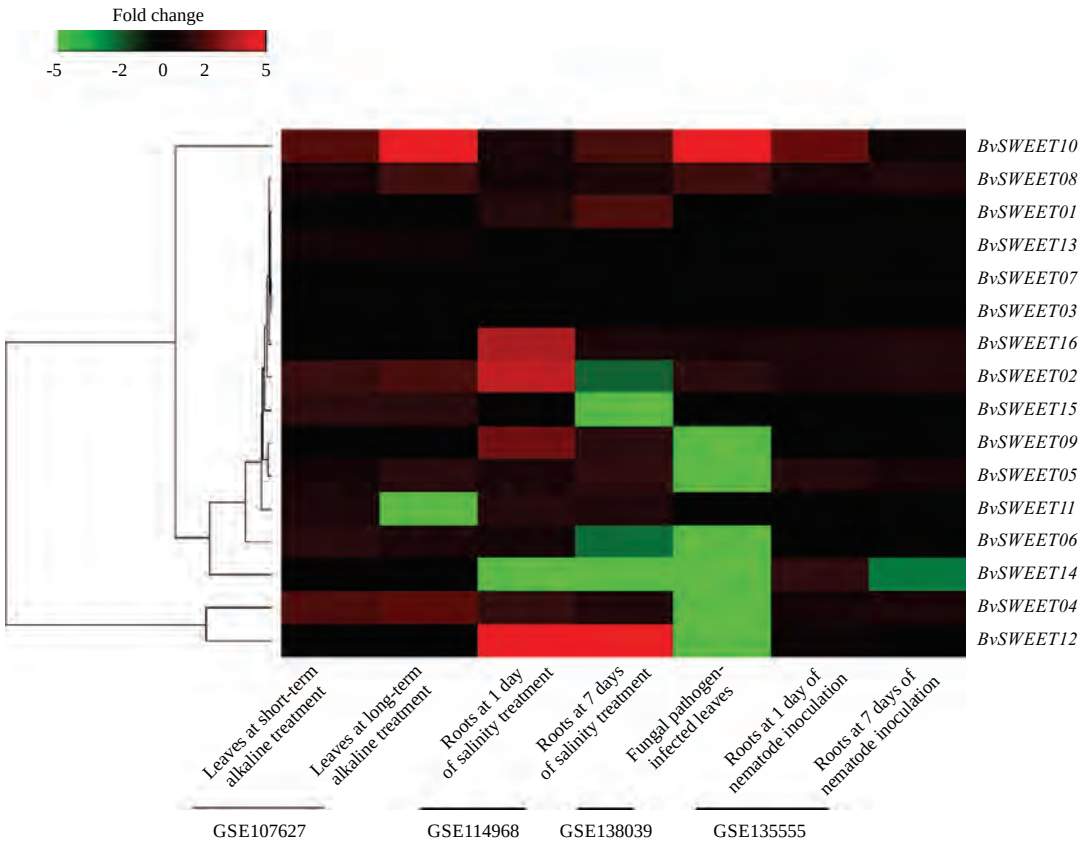

Fig. 4: Expression patterns of the *BvSWEET* gene family during the growth and development of sugar beet plants

noted to be up-regulated and down-regulated in root tissues (Fig. 4). Previously, various efforts have been recorded to investigate the role of *SWEET* genes in response to abiotic stress(es) in higher plants, such as banana[12], cotton[14], *P. equestris* and *D. officinale*[42] and *M. truncatula*[19]. Taken together, our re-analysis suggested that the *BvSWEET* gene family is differentially expressed in various organs/tissues under numerous abiotic/biotic stress conditions, which may suggest their potential functions during growth and development processes and perhaps in responses to adverse environmental conditions.

CONCLUSION

In this present study, a comprehensive analysis of 16 members of the BvSWEET family has been investigated in sugar beet. Various information of the BvSWEET family, like chromosomal locations, physic-chemical properties, subcellular localizations, exon/intron organizations, phylogenetic trees, gene structures has been analyzed by using computational tools. We re-analyzed four transcriptome datasets to explore the expression profiles of the *BvSWEET* gene family in major organs/tissues during the growth and development processes. To sum up, the data provide valuable information for further functional characterization of sugar beet *BvSWEET* genes.

SIGNIFICANCE STATEMENT

The features and expression analyses of sugar beet *SWEET* genes were originally presented in this paper. The findings laid the groundwork for future functional studies, especially those involving the *BvSWEET* gene in these important crops.

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Dr. La Viet Hong,

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Regards

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