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Research Article

SWEET transporter gene expression in barley during drought stress at the grain filling stage

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ABSTRACT- *SWEET* (Sugars Will Eventually be Exported Transporters) genes facilitate the mobilization of photosynthetic products from source leaves to sinks. They contribute to sucrose translocation and respond to abiotic stresses. This research examined the *HvSWEET* genes within the barley genome, focusing on their phylogenetic relationships, structural characteristics, chromosomal positions, and gene expression profiles in response to drought stress at 21 and 28 days post-anthesis (two important time points in seed filling). In silico analysis revealed 23 *SWEET* genes in barley, including information on chromosomal location, phylogenetic relationships, gene structures, conserved motifs, and *cis*-elements in promoter regions. Phylogenetic analysis grouped barley and maize *SWEET* sequences into five clusters. *HvSWEET12/13c/14* genes contain multiple binding sites in their promoter regions, indicating involvement in multiple abiotic/biotic stress responses. Gene expression analysis showed up-regulation of *HvSWEET7/12/13c/14* at 21 and 28 days after anthesis under drought conditions. The role of sucrose transport in grain filling at 21 and 28 days after anthesis in barley was highlighted. *SWEET* transporters influence source/sink relationships, presenting opportunities for genetic modification to enhance stress tolerance. These results offer valuable insights into the various functions of *HvSWEET* genes and highlight their potential application in enhancing barley resilience against stress.

INTRODUCTION

Sugar transporters are evolutionarily conserved genes found in several species of bacteria, fungi, and plants. They aid in the transmembrane transport of sugars (Lemoine et al., 2013). Plants utilize carbon for synthesizing metabolites essential for their survival and development. Carbohydrate transport involves the uptake and distribution of sugars from source leaves to sink tissues, such as flowers and roots, thereby playing a crucial role in plant growth (Saidi and Hajibarat, 2020a). Developmental stages influence plant tolerance to abiotic and biotic stresses (Chen et al., 2010). Conventional breeding has made significant advancements in altering carbohydrate transport in crops like maize, barley, and potato, but the underlying genes and regulatory mechanisms still need further exploration. The *SWEET* (Sugars Will Eventually be Exported Transporters) family represents a novel class of sugar transporters. These transporters function as bidirectional uniporters/facilitators, enabling the diffusion of sugars across cell membranes down a concentration gradient (Chen et al., 2010). Ongoing research has shed light on the comprehensive dynamics of sugar biosynthesis and transport within the photosynthetic organs of plants. SWEETs, a family of sugar transporters typically possessing seven transmembrane domains (TM) and two MtN3 motifs, play a role in loading sucrose into the phloem and sink tissues (Hajibarat and Saidi, 2023). In *Arabidopsis thaliana*, *SWEET* genes have been categorized into four phylogenetic clusters: cluster I (*SWEET1-SWEET3*), cluster II (SWEET4-SWEET8), cluster III (*SWEET9-SWEET15*), and cluster IV (SWEET16-SWEET17) (Eom et al., 2015). Under abiotic stress, sugar synthesis is enhanced, and the types of accumulated sugars can vary depending on the plant species (Chen et al., 2012). Most sugar transporters are essential for grain filling. Research on *SWEET* genes has been predominantly conducted in model plants, focusing on glucose and sucrose transport functions (Chen et al., 2012). Certain SWEETs, such as *AtSWEET16* and *AtSWEET17*, play multifaceted

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roles in monosaccharide and polysaccharide transport and are highly expressed in roots (Guo et al., 2014). Some *SWEETs* have been linked to plant reproductive stages (Sun et al., 2013). *AtSWEET5* gene expression is up-regulated in the female gametophyte (Yuan et al., 2010; Klemens et al., 2013). Up-regulation of *AtSWEET16* improves *A. thaliana* tolerance to cold and drought stress (Yuan and Wang, 2013). SWEETs from other plant species (barley and tomato) also contribute to abiotic stress and senescence regulation (Yuan and Wang, 2013). This study investigated *HvSWEET* genes in the barley genome, analyzing their phylogenetic relationships, gene structures, chromosome locations, and gene profiles under drought stress at two time points.

MATERIALS AND METHODS

Characteristics of the HvSWEET gene family

Two methods were used to identify possible *HvSWEET* genes in barley: protein homology searching and retrieval using a Hidden Markov Model (HMM). The protein homology search utilized accessible SWEET protein sequences from *A. thaliana* and *Oryza sativa*. The HMM retrieval utilized the SWEET protein sequence number PF03083 from the Pfam HMM library to retrieve *SWEET* sugar transporter sequences. The *A. thaliana* protein sequences were acquired from the TAIR database, and the rice protein sequences were sourced from the RAP-DB database. Existing NCBI-sourced *A. thaliana* SWEET protein sequences served as query sequences for the tBLASTn program, enabling the identification of similar sequences in barley. To validate the putative sequences, the SMART database and InterProScan were used. Twenty-three non-redundant candidates were identified as HvSWEET proteins following analysis. Using the ExPASy server (http://web.expasy.org/computepi/), the theoretical isoelectric point (pI) and molecular weight (kDa) were estimated for each SWEET protein. The conserved SWEET domains of the SWEET proteins were aligned using ClustalW software with standard settings to perform a multiple sequence alignment analysis.

The Maximum Likelihood method utilized bootstrap tests with 1000 replications in the construction of the phylogenetic tree. Pairwise deletion of gaps and missing data was used in the construction of the phylogenetic tree. The genomic DNA and CDSs for each predicted *SWEET* gene were obtained from the NCBI database for gene structural analysis in barley. Gene structures were determined through the utilization of the GSDS program (http://gsds.cbi.pku.edu.cn). The MEME program was utilized to identify conserved motifs in the SWEET proteins. Default parameters were used, with the exception of setting the maximum number of motifs to 9. Exon-intron structures of *SWEET* genes were visualized with TBtools. Chromosomal distribution of *SWEET* genes was illustrated using the online tool (http://visualization.ritchielab.org/phenograms/plot). Genomic sequences of *SWEET* genes were acquired, encompassing 2000 base pairs (bp) upstream of the transcription start region, with the aid of TBtools.

Plant materials and growth conditions

The plant material was sourced officially from the Seed and Plant Improvement Institute (SPII), Ministry of Jihad-e-Agriculture, located in Karaj, Iran. The Jolgeh barley cultivar was evaluated in a field trial under both normal and water-deficit conditions during the 2022-2023 growing season at the Karaj Agricultural Research Station. Water-deficit stress poses a significant problem in these areas. This experiment was performed based on a randomized complete block design (RCBD) with three replications. Jolgeh barley genotype, a tolerant genotype to water stress, was planted on a two, 60 cm rows, each having three lines of plants with 20 cm distance. The experiment consisted of two treatments: a water-deficit treatment and a well-watered control treatment. Irrigation was applied once at planting in the autumn and three times in the spring, during the tillering, stemming, and flowering stages, while water deficit was imposed at 50% flowering. Sampling of penultimate stem (internode) was performed for the three replications at 21 and 28 days after anthesis. The first furrow irrigation applied in the spring contained about 1000 cubic meters of water per hectare and the following irrigations were relatively light and about 500 cubic meters of water per hectare. In normal years, four to five irrigations with a total volume of about 4000 cubic meters of irrigation water per hectare are applied to barley fields per season. After anthesis and the beginning of seed filling stages, each irrigation volume was reduced to 500 cubic meters per hectare.

Gene expression analysis of HvSWEET genes

RNA was extracted from the penultimate stem under both normal and drought conditions using RNX-Plus, following the manufacturer's instructions. Stem internode samples were collected 21 and 28 days post-anthesis for analysis of 10 *SWEET* genes. cDNA was synthesized following the prescribed protocol of the Easy cDNA Synthesis Kit. Gene expression analyses were conducted in triplicate, referencing the barley *Actin* gene as the internal control. SYBR Green Supermix was used for real-time qPCR according to the manufacturer's instructions. The $2^{-\Delta\Delta Ct}$ method was used to calculate relative gene expression. Tukey's comparisons test was used for statistical analysis of treatment means, with a significance threshold of *P-value* < 0.05. The primer sequences for RT-qPCR can be found in Table 1.

RESULTS AND DISCUSSION

In this investigation, we discovered 23 *SWEET* transporter genes in the barley genome (Table 2). Bioinformatics analyses, including phylogenetic tree construction, gene structure, protein motif identification, chromosomal localization, *cis*-element prediction, and gene expression analysis at 21 and 28 days after anthesis, were performed. The *HvSWEET* genes exhibited varying protein lengths, ranging from 82 to 333 amino acids. The predicted isoelectric points (pI) of the *HvSWEET* genes ranged from 4.94 to 9.83, while their estimated molecular weights (MW) varied from 9.08 to 35.47 kDa. Table 2 provides a comprehensive overview of all *HvSWEET* genes, including their gene names, gene details, amino acid lengths, and isoelectric points.

Table 1. Primers used for *HvSWEET* genes in this study

No.	Primer name	Sequence 5'→ 3'	Product of primer (bp)
1	*Hvsweet12 F*	GTCGTCGGCTGGATCTGCGTC	130
	Hvsweet12 R	GATGCCGAAGACGAAGCCCA	
2	*Hvsweet13c F*	CAAGTGATCAGGACCAAGAGCG	180
	Hvsweet13c R	ATCTTAGCTTAGCTCGCGTGCG	
3	*Hvsweet17 F*	TCTGGAGGATCGTGAGGAGCA	110
	Hvsweet17 R	CGTAGATGGTCTCCATGACGG	
4	*Hvsweet4F*	GAGAAACGAGAACTCCCTGCA	140
	Hvsweet4R	CTGTCAACGGTGTTCTTTGCG	
5	*Hvsweet5F*	CTTGTGCTACTACAACTCGACCC	120
	Hvsweet5R	CAGAGGACAATGGTTGGC	
6	*Hvsweet14F*	CAGCGTCATCGTAAGCAACTGAGC	110
	Hvsweet14R	GATGTTGTTCACGTACAGCGAC	
7	*Hvsweet7F*	GCTCATCCTCTGTCTGGTCCA	150
	Hvsweet7R	ATCGAGGTAGACAGGGGTATG	
8	*Hvsweet7aF*	CTGGGCCTGATGCAGCTCAT	130
	Hvsweet7aR	CTCATGCACACATCGCACGCTC	
9	*Hvsweet4aF*	TGTGACCCTCCACTCTTGCC	170
	Hvsweet4aR	GGCATGTACTCCACACTCTTGG	
10	*Hvsweet5aF*	TGTACTGCTTGCTTGCAGGGT	180
	Hvsweet5aR	CTGTTAGATCGATGCGGAG	
11	Actin F	GGTCCATCCTAGCCTCACTC	129
	Actin R	GATAACAGCAGTGGAGCGCT	

Table 2. Details of the identified *SWEET* genes in barley (*HvSWEET*) in this study

Gene name	Accession number	Chromosomal location	Protein length	MW (kDa)	pI
HvSWEET4	HORVU1Hr1G079940.6	chr1H: 524164619 - 524166937	82	9.08	8.98
HvSWEET5	HORVU2Hr1G006520.2	chr2H: 13644166 - 13646353	87	9.57	4.94
HvSWEET5a	HORVU2Hr1G006510.1	chr2H: 13613171 - 13614579	246	27.02	9.32
HvSWEET7	HORVU3Hr1G084860.2	chr3H: 609690156 - 609693280	264	28.89	6.89
HvSWEET7a	HORVU3Hr1G091230.9	chr3H: 634920942 - 634924075	144	15.88	9.73
HvSWEET5b	HORVU3Hr1G107780.1	chr3H: 673285306 - 673291122	273	29.93	6.70
HvSWEET12b	HORVU5Hr1G076770.1	chr7H: 551930918 - 551932663	321	35.30	9.07
HvSWEET13	HORVU6Hr1G029520.8	chr6H:120201027-120203926	253	28.52	9.83
HvSWEET12	HORVU7Hr1G030160.8	chr5H: 58906370 - 58909157	292	31.68	6.90
HvSWEET12a	HORVU7Hr1G054710.2	chr7H: 221745072 - 221747441	303	32.49	8.11
HvSWEET12d	HORVU6Hr1G089600.4	chr6H: 570135624 - 570137778	282	30.70	8.98
HvSWEET4c	HORVU7Hr1G067000.1	chr7H: 346595507 - 346597601	90	10.19	9.13
HvSWEET4a	HORVU7Hr1G117490.1	chr7H: 645251293 - 645253295	260	25.03	7.9
HvSWEET13a	HORVU6Hr1G089540.6	chr6H: 570019107 - 570021234	216	23.92	9.24
HvSWEET12c	HORVU1Hr1G010210.7	chr1H: 23166693 - 23169065	290	31.82	8.63
HvSWEET13c	HORVU3Hr1G013170.3	chr3H: 28461697 - 28464387	249	27.50	9.30
HvSWEET14	HORVU6Hr1G000440.5	chr6H: 1053657 - 1056009	293	32.15	9.13
HvSWEET7c	HORVU6Hr1G055960.7	chr6H: 356677679 - 356682060	129	14.59	7.77
HvSWEET17	HORVU0Hr1G010080.9	chr4: 57404637 - 57427236	256	27.72	6.71
HvSWEET17a	HORVU1Hr1G029920.6	chr1H: 167986996 - 167989745	240	26.89	9.01
HvSWEET13b	HORVU4Hr1G053450.3	chr4H: 445034384 - 445035969	130	14.30	9.41
HvSWEET4b	HORVU4Hr1G070740.1	chr4H: 577425380 - 577427479	90	10.18	9.13
HvSWEET7b	HORVU6Hr1G086010.1	chr7H:515717214-515906633	333	35.47	9.61

Phylogenetic tree, gene structures of the SWEET transporter genes in barley, and chromosomal location

Phylogenetic analysis revealed five clusters of *SWEET* genes encoding sugar transporter proteins in diverse species like barley and maize (Fig. 1). In barley, the *HvSWEET* genes exhibited exon numbers ranging from one to six, with four genes containing a single exon, suggesting conserved domains. Gene structure analysis (Fig. 2a) showed that most genes, including *HvSWEET5a/12/13/14/17* contained multiple introns and exons. The gene structure of *HvSWEET* genes within the same subfamily aligned with the phylogenetic tree (Fig. 2b), with most genes classified in the same subfamily. The *HvSWEET* genes were distributed across all barley chromosomes (Fig. 3), with chromosomes 3, 6, and 7 carrying the highest number of genes (three genes). Chromosome 5 harbored a single gene, *HvSWEET12*, while chromosome 2 contained two genes. *SWEET* transporters are crucial for energy metabolism, osmotic regulation, and signaling molecules influencing plant growth and development. Phylogenetic analysis classified *HvSWEET* genes into five clusters. *SWEET* genes in *A. thaliana* exhibit diverse exon counts ranging from 1 to 13. Protein structure analysis is vital for comprehending the functional mode of SWEET transporters. Gene structure analysis aligns with phylogenetic findings. Our results parallel those of Chen et al. (2010), suggesting five clusters within the *SWEET* gene family in *A. thaliana*.

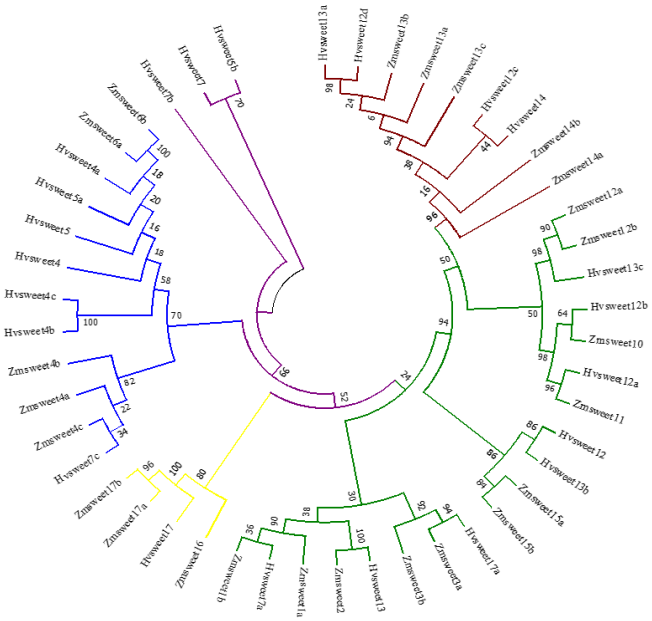

Fig. 1. Phylogenetic tree of the *SWEET* genes created by the neighbor-joining (NJ) method. SWEET genes were grouped into five clusters. Orthologous genes were in the same cluster.

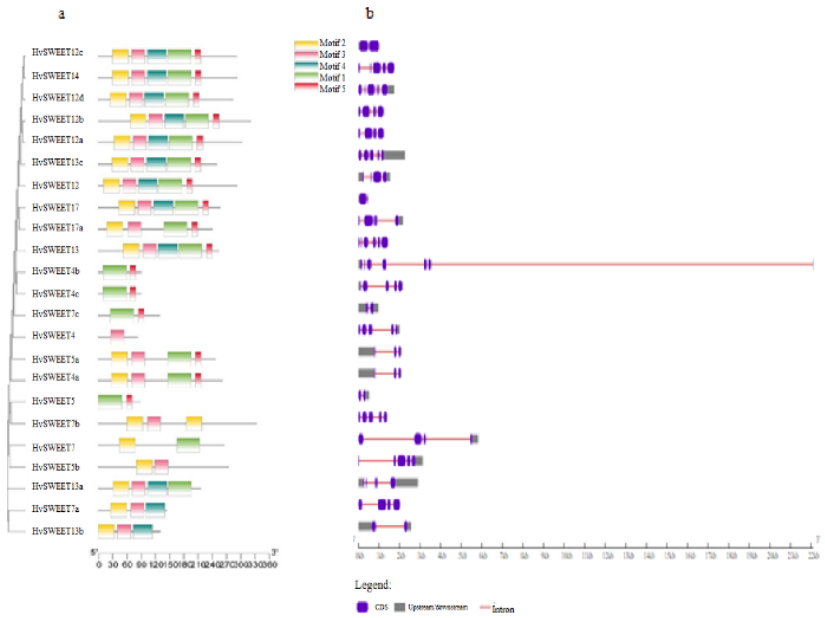

Fig. 2. (a) Distribution of conserved motifs within SWEET transporter proteins. (b) Exon-intron structure of barley genes, organized according to their phylogenetic relationships. Blue and gray regions, generated using the GSDS database, indicate gene exons and introns, respectively.

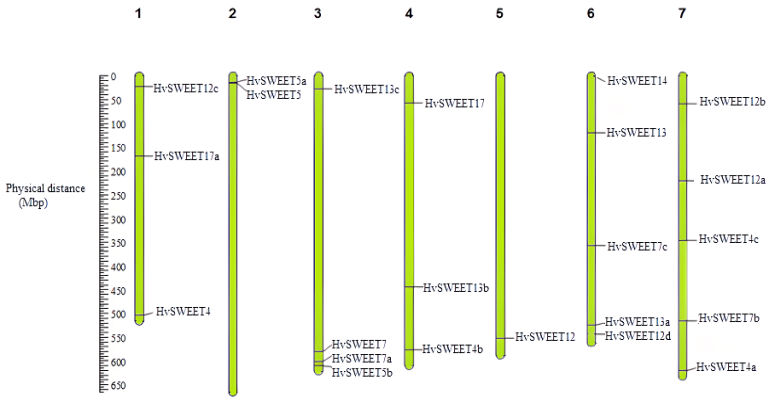

Fig. 3. The physical map of the identified *HvSWEET* genes in barley using MapChart software.

Quantitative RT-PCR analysis of SWEET genes expression under drought conditions

qRT-PCR validation confirmed the expression patterns of *SWEET* genes under drought stress. In Jolgeh, 10 *HvSWEET* genes exhibited expression in the penultimate stem internode at 21 and 28 days after flowering (Fig. 4), suggesting their involvement in seed development. Notably, *HvSWEET5/12/13c/7/14/17* were expressed at 21 days after anthesis as compared to other *SWEET* genes (Fig. 4). *HvSWEET*17 gene showed a significant decrease in expression as compared to normal. *HvSWEET5/7/12/13c/14* genes showed a significant increase in expression as compared to normal (Fig. 4a). At 28 days after anthesis, *HvSWEET4a/5/5a/7/7a/13/14* genes showed a significant difference in expression as compared to normal. All genes showed a decrease in expression as compared to normal at 28 days after anthesis (Fig. 4b). In Jolgeh genotype, *HvSWEET13* displayed a significant expression for both treatments (Fig. 4a and Fig. 4b). Drought stress altered sugar levels in the leaves and roots of three rice genotypes (IR 64, Nagina 22, and Pokkali). Under drought stress, the expression of the *OsSWEET13* sucrose transporter is upregulated, indicating its role in sucrose transport. The *OsSWEET13* gene is expressed in phloem juice, facilitating efficient sucrose distribution under drought stress (Mathan et al., 2021). Research indicates a strong link between abscisic acid (ABA) signaling and drought stress response, as evidenced by the high expression of ABA-induced genes under drought conditions (Nakashima et al., 2013). Mathan et al. (2021) identified *OsSWEET13* and *OsSWEET15* as key *SWEET* transporters influenced by drought. Their findings suggest that the elevated ABA levels during drought stress promote the induction of *OsSWEET13* and *OsSWEET15* via ABA-responsive transcription factors, demonstrating the binding of OsbZIP72 to the promoters of these *SWEET* transporters. This confirms the potential of the OsbZIP72-*OsSWEET* module as a target for regulating sucrose dynamics in rice under drought stress (Mathan et al., 2021). This mechanism may offer a target for maintaining stable sugar levels in rice plants experiencing drought. The *OsSWEET11*, *OsSWEET12*, and *OsSWEET14* genes are primarily involved in sucrose transport (Eom et al., 2015). Our findings demonstrated the role of *SWEET* transporters in grain development and seed maturation, corroborating previous research (Asseng and Van Herwaarden, 2003). Sugar accumulation is a response to drought stress and triggers the expression of *SWEET* genes, enhancing abiotic stress tolerance (Ferrandino and Lovisolo, 2014). This study highlights the crucial role of *SWEET* transporters in sucrose metabolism under both normal and drought conditions. Regulating sucrose transporters in crops like barley is critical for improving grain yield. Similarly, a separate study revealed that rice employs both apoplasmic and symplasmic pathways to export sucrose from mature leaves to seeds. *OsSWEET5*, a gene in rice encoding a sugar transporter protein, plays a role in galactose transport. Plants overexpressing *OsSWEET5* exhibited auxin signaling inhibition and translocation, altered sugar metabolism and transport, and ultimately, and retarded growth in the early seedling stage (Mathan et al., 2021). Abiotic stress triggers adjustments in sucrose allocation between source and sink tissues, a process mediated by plant sucrose transporters (Durand et al., 2016; Hajibarat et al., 2018). For instance, the expression of sucrose transporter genes like *AtSWEET11*, *AtSWEET12*, and *AtSUC2* increases in *A.thaliana* leaves under stress, resulting in enhanced sucrose transport (Durand et al., 2016). Together, these findings indicate that sucrose distribution and transport play a vital role in plant survival when facing stressful environmental conditions.

Prediction of Cis-elements in the SWEET genes

Promoter regions of the 23 *HvSWEET* genes contain various known stress-related *cis*-elements. *SWEET* promoters comprise diverse *cis*- elements associated with drought and hormonal signaling (Fig. 5). Stress-responsive *cis*-elements identified in this study encompass MYB, MYC, G-box, ABRE, SA, and JA responsive elements. Promoters of *HvSWEET14*, *HvSWEET7/7a/13/13c/14/17* genes exhibit the highest number of *cis-elements*. Among the investigated *SWEET* genes, *HvSWEET7/7a/13* displayed the most *cis-elements* in their promoter regions whereas, *HvSWEET5* possessed the fewest *cis-elements* within its promoter region. Previous research has demonstrated the responsiveness of *SWEET* genes to various stresses and stimuli in plants such as *A. thaliana*, tomato, and soybean (Saidi and Hajibarat, 2020b). *HvSWEET12/12c/12d/13a/17a* genes exhibited the highest number of light-responsive *cis*-elements. Understanding the interplay between *cis*-elements and their corresponding transcription factors could enhance the transcriptional regulation of genes under drought stress. Most of *cis*-elements are involved in drought stress such as drought stress and light responsive elements. Also, hormonal stress such as methyl jasmonate responsive elements and ABA responsive elements (Fig. 5).

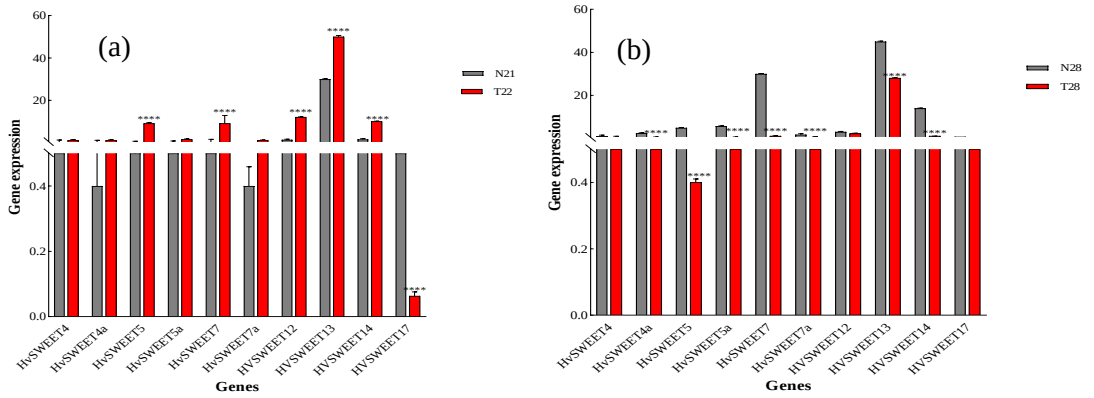

Fig. 4. The qRTPCR expression of 10 Jolgeh barley genes in stem penultimate internode samples at (a) 21 days and (b) 28 days after anthesis under drought stress, N21; normal treatment at 21 days after anthesis, T21; drought treatment at 21 days after anthesis, N28; normal treatment at 28 days after anthesis, and T28; drought treatment at 28 days after anthesis. **** denotes a significant difference ($P < 0.0001$).

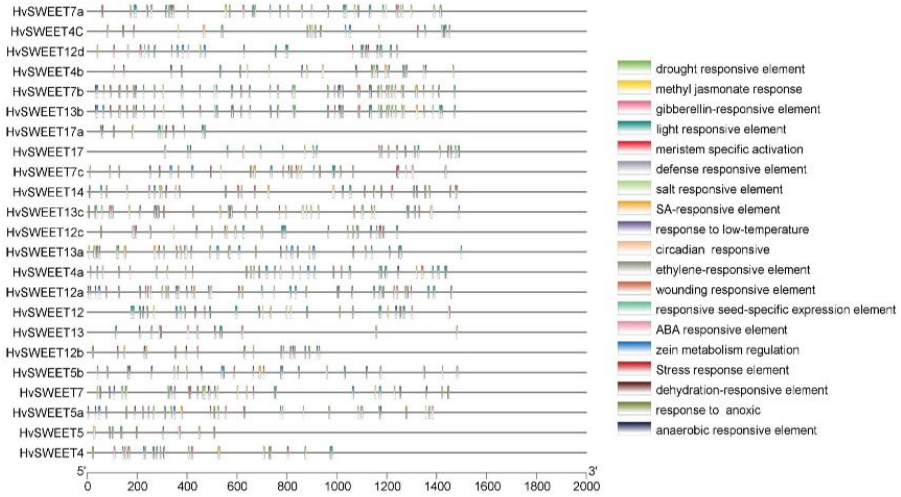

Fig. 5. *Cis*-elements detected in the upstream of promoter regions and their frequencies in each gene. Light responsive element (G-box and Sp1), methyl jasmonate response (CGTCA-motif and TGACG-motif), drought responsive element (MYC and MYB), and ABA responsive element (ABRE).

CONCLUSION

In this study, 23 *SWEET* transporter genes were identified in barley. Analysis of gene structure, biochemical characteristics, and phylogenetic tree indicates high conservation of the *SWEET* gene family throughout plant evolution. Gene expression analysis of 10 *HvSWEET* genes are expressed in penultimate stem at 21 and 28 days after anthesis, suggesting diverse functional roles of *SWEET* gene members under drought stress. The identified *cis*-elements (MYB, MYC, G-box, ABRE, and JA responsive elements) in the *SWEET* gene promoters are crucial for drought stress response. Among the investigated *SWEET* genes, *HvSWEET12/13c/14* genes possess multiple *cis*-element binding sites in their promoters, enabling them to play a pivotal role in mitigating various environmental stresses. This research provides a basis for subsequent investigations into the function of *HvSWEET* genes in barley growth, development, and drought stress responses. These results not only enhance our comprehensive understanding of the *HvSWEET* family in barley, but also identify a promising candidate gene for application in future barley breeding programs.

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CRediT AUTHORSHIP CONTRIBUTION STATEMENT

Conceptualization: Zohreh Hajibarat and Abbas Saidi; Methodology: Abbas Saidi; Software, Mohammad Reza Ghaffari; Validation: Ahmad Mosuapour Gorji and Abbas Saidi; Formal analysis: Mehrshad Zienalabedini; Investigation: Zohreh Hajibarat; Resources: Habibollah Ghazvini; Data curation: Zohreh Hajibarat; Writing—original draft preparation: Abbas Saidi; Writing—review and editing: Habibollah Ghazvini; Visualization: Abbas Saidi; Supervision: Zohreh Hajibarat; Project administration: Abbas Saidi.

DECLARATION OF COMPETING INTEREST

The authors declare no conflicts of interest.

ETHICAL STATEMENT

Not applicable

DATA AVAILABILITY

The data presented in this study are uploaded during submission as a supplementary file and are openly available for readers upon request.

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