Gene 642 (2018) 284–292

Contents lists available at ScienceDirect

Gene

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

Research paper

# Genome-wide identification of the SWEET gene family in wheat

Yue Gao[a,1], Zi Yuan Wang[a,1], Vikranth Kumar[b,1], Xiao Feng Xu[a], De Peng Yuan[a], Xiao Feng Zhu[a], Tian Ya Li[a], Baolei Jia[c,*], Yuan Hu Xuan[a,*]

[a] College of Plant Protection, Shenyang Agricultural University, Dongling Road 120, Shenyang 110866, China
[b] Division of Applied Life Science (BK21 Plus Program), Plant Molecular Biology & Biotechnology Research Center (PMBBRC), Gyeongsang National University, Jinju 52828, Republic of Korea
[c] School of Bioengineering, Qilu University of Technology, Jinan 250353, China

ARTICLE INFO

*Keywords:*
Sweet
Sugar transporter
Stem rust
Interaction
Wheat

ABSTRACT

The SWEET (sugars will eventually be exported transporter) family is a newly characterized group of sugar transporters. In plants, the key roles of SWEETs in phloem transport, nectar secretion, pollen nutrition, stress tolerance, and plant–pathogen interactions have been identified. SWEET family genes have been characterized in many plant species, but a comprehensive analysis of SWEET members has not yet been performed in wheat. Here, 59 wheat SWEETs (hereafter TaSWEETs) were identified through homology searches. Analyses of phylogenetic relationships, numbers of transmembrane helices (TMHs), gene structures, and motifs showed that TaSWEETs carrying 3–7 TMHs could be classified into four clades with 10 different types of motifs. Examination of the expression patterns of 18 SWEET genes revealed that a few are tissue-specific while most are ubiquitously expressed. In addition, the stem rust-mediated expression patterns of SWEET genes were monitored using a stem rust-susceptible cultivar, 'Little Club' (LC). The resulting data showed that the expression of five out of the 18 SWEETs tested was induced following inoculation. In conclusion, we provide the first comprehensive analysis of the wheat SWEET gene family. Information regarding the phylogenetic relationships, gene structures, and expression profiles of SWEET genes in different tissues and following stem rust disease inoculation will be useful in identifying the potential roles of SWEETs in specific developmental and pathogenic processes.

## 1. Introduction

Sugars are the predominant carbon and energy sources for living organisms (Walmsley et al., 1998), and cellular sugar uptake and export across the plasma membrane are critical for growth and development (Chen et al., 2012; Walmsley et al., 1998). The SWEET (sugars will eventually be exported transporter) family is a newly characterized group of sugar transporters in plants and mammals (Chen et al., 2010). SWEET members have been identified in many plant species, including *Arabidopsis*, rice, maize, soybean, citrus, cassava, grapevine, tomato, sorghum, *Brassica*, potato, *Medicago*, pear, and cotton (Chen et al., 2010; Chong et al., 2014; Cohn et al., 2014; Cox et al., 2017; Feng et al., 2015; Hu et al., 2014; Jian et al., 2016; Kryvoruchko et al., 2016; Li et al., 2017; Manck-Gotzenberger and Requena, 2016; Mizuno et al., 2016; Patil et al., 2015; Sosso et al., 2015). In plants, an average of 20 SWEET paralogs have been identified in most genomes (Feng and Frommer, 2015). Phylogenetic analysis of plant SWEETs has revealed that SWEET members can be classified into four clades (Chandran, 2015). Clade I and II members prefer hexose, and clade III members are efficient sucrose transporters. Clade IV SWEETs are located on the tonoplast membrane and likely transport fructose in *Arabidopsis* (Chen et al., 2012; Klemens et al., 2013). Typical eukaryotic SWEET proteins consist of seven transmembrane helices (TMHs) (Feng and Frommer, 2015). However, an ExtraSWEET protein from *Vitis vinifera* carrying 14 TMHs has recently been reported (Patil et al., 2015), suggesting a diversity of TMH structures in SWEET proteins.

In *Arabidopsis*, SWEET11 and 12 export sucrose from parenchymal cells for import into sieve element/companion cells by SUC2 (Chen et al., 2012), and SWEET9 is necessary for nectar secretion (Lin et al., 2014). In addition, mutations in *AtSWEET11*, *12*, and *15* severely delay embryonic development (Chen et al., 2015). ZmSWEET4 and OsSWEET4/11 have been reported to play important roles in grain filling in maize and rice, respectively (Ma et al., 2017, Sosso et al., 2015). MtSWEET11 transports sucrose and is specifically expressed in nodules

*Abbreviations:* SWEET, sugars will eventually be exported transporter; TMHs, transmembrane helices; LC, Little Club; Ta, *Triticum aestivum*; MSAs, multiple sequence alignments; NJ, Neighbor-joining; SEM, scanning Electron Microscope

* Corresponding authors.
*E-mail addresses:* baoleijia@cau.ac.kr (B. Jia), xuanyuanhu115@syau.edu.cn (Y.H. Xuan).
[1] These authors contributed equally to this work.

https://doi.org/10.1016/j.gene.2017.11.044
Received 8 September 2017; Received in revised form 2 November 2017; Accepted 15 November 2017
Available online 16 November 2017
0378-1119/ 

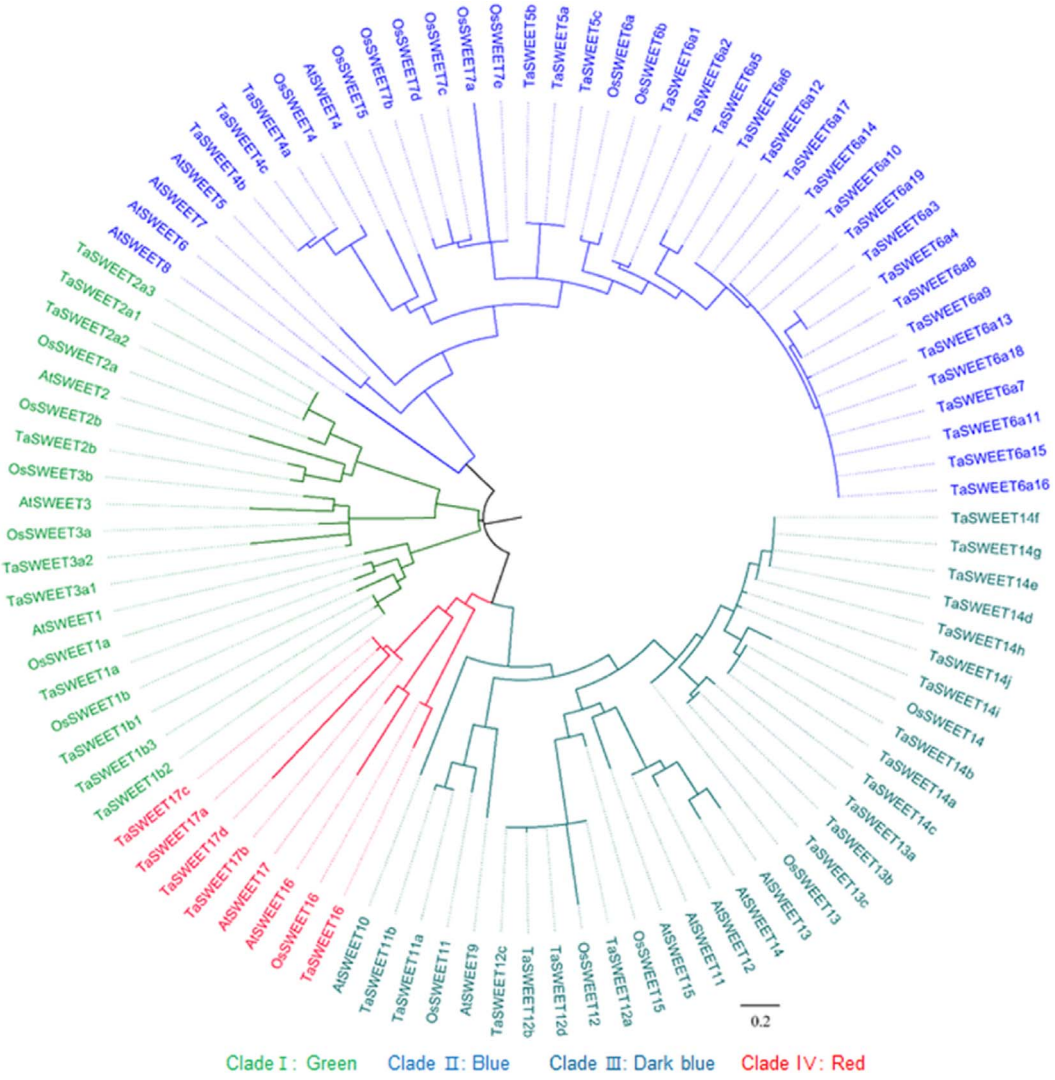


**Fig. 1.** Phylogenetic tree of SWEETs from *Oryza sativa*, *Arabidopsis thaliana*, and *Triticum aestivum*. The phylogenetic tree was constructed using the maximum likelihood method. The tree was generated using ClustalW in MEGA 7.0 using SWEET amino acid sequences from *Oryza sativa* (OsSWEETs), *Arabidopsis thaliana* (AtSWEETs), and *T. aestivum* (TaSWEETs). The four clades are indicated in green (Clade I), blue (Clade II), dark blue (Clade III), and red (Clade IV). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

in *Medicago truncatula* (Kryvoruchko et al., 2016). Furthermore, SWEET genes are known as susceptibility (S) genes, acting as targets of effector proteins during host–microbe interactions in many plant species. For example, *Xa13/OsSWEET11*, *Xa25/OsSWEET13*, and *OsSWEET14* were identified as targets of *Xanthomonas oryzae* pv. *oryzae* effectors in rice (Antony et al., 2010; Hutin et al., 2015; Zhou et al., 2015). In cotton, expression of the sucrose transporter *GhSWEET10* is activated by Avrb6, a TAL effector of *Xanthomonas citri* subsp. *malvacearum* (*Xcm*), during *Xcm* invasion (Cox et al., 2017). The TAL effectors are delivered into the plant cytoplasm through the type III secretion system and enter the nucleus to induce the expression of specific SWEET genes, ensuring sucrose delivery into the apoplasts of colonized cells (Manck-Gotzenberger and Requena, 2016).

Wheat (*Triticum aestivum*) is a major crop, exhibiting the largest cultivation area worldwide; therefore, technologies to increase the allocation of sugar into grain and protect wheat plants from pathogens have become ever more sophisticated. Stem rust (caused by *Puccinia graminis* f. sp. *tritici*; *Pgt*) is often regarded as potentially the most destructive rust disease of wheat worldwide (Pardey et al., 2013). Recently, its impact has become severe in wheat production areas owing to the generation of TTTTF that has threatened thousands of hectares of durum wheat in Sicily (Bhattacharya, 2017). However, information on SWEET family genes and their impact on the interactions between pathogens and wheat is lacking. In this study, we identified and characterized SWEET genes in wheat plants (TaSWEETs). The 59 identified TaSWEET genes were compared with those from other species using phylogenetic and multi-alignment analyses. The TMH and domain architectures of TaSWEET proteins were analyzed, and their tissue-specific or *Pgt* infection-mediated expression patterns were determined. This is the first report to identify SWEET gene family members and their influence on interactions with stem rust disease in wheat.

## 2. Materials and methods

### 2.1. Molecular phylogenetic analysis using maximum likelihood

To identify SWEETs in wheat, rice SWEET and Arabidopsis AtSWEET sequences were used as queries to search the UniProt database (http://www.uniprot.org/) using BLAST with e-value cutoff of e-10. Even wheat genome sequence are available (IWGSC, 2014), but it is chromosome-based draft sequence and the limited information for transcripts and annotations are provided. The Uniprot database covers the information presented wheat genome database, and the TaSWEETs identified in the Uniprot database were also searched in the wheat