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ARTICLE

Characterization and abiotic stress-responsive expression analysis of *SGT1* genes in *Brassica oleracea*

Ashokraj Shanmugam, Senthil Kumar Thamilarasan, Jong-In Park, Mi Young Jung, and Ill-Sup Nou

Abstract: *SGT1* genes are involved in enhancing plant responses to various biotic and abiotic stresses. *Brassica oleracea* is known to contain two types of *SGT1* genes, namely *suppressor of G2 allele of SKP1* and *suppressor of GCR2*. In this study, through systematic analysis, four putative *SGT1* genes were identified and characterized in *B. oleracea*. In phylogenetic analysis, the genes clearly formed separate groups, namely *BolSGT1a*, *BolSGT1b* (both *suppressor of G2 allele of SKP1* types), and *BolSGT1* (*suppressor of GCR2*). Functional domain analysis and organ-specific expression patterns suggested possible roles for *BolSGT1* genes during stress conditions. *BolSGT1* genes showed significant changes in expression in response to heat, cold, drought, salt, or ABA treatment. Interaction network analysis supported the expression analysis, and showed that the *BolSGT1a* and *BolSGT1b* genes are strongly associated with co-regulators during stress conditions. However, the *BolSGT1* gene did not show any strong association. Hence, *BolSGT1* might be a stress resistance-related gene that functions without a co-regulator. Our results show that *BolSGT1* genes are potential target genes to improve *B. oleracea* resistance to abiotic stresses such as heat, cold, and salt.

Key words: abiotic stress resistance, *BolSGT1*, *Brassica oleracea* var. *capitata*, gene expression.

Résumé : Chez les plantes, les gènes *SGT1* augmentent la réponse à divers stress biotiques et abiotiques. Le *Brassica oleracea* contient deux types de gènes *SGT1*, soit le *Suppressor of G2 allele of SKP1* et le *Suppressor of GCR2*. Dans ce travail, une analyse systémique a été employée pour identifier et caractériser quatre gènes *SGT1* putatifs chez le *B. oleracea*. Une analyse phylogénétique révèle l'existence de différents groups dont *BolSGT1a*, *BolSGT1b* (tous deux de type *suppressor of G2 allele of SKP1*) et *BolSGT1* (*suppressor of GCR2*). L'analyse des domaines fonctionnels et de l'expression dans les organes a suggéré de possibles rôles pour les gènes *BolSGT1* en conditions de stress. Les gènes *BolSGT1* présentent un changement significatif de leur expression en réponse aux stress de chaleur, de froid, de sécheresse, de salinité ou de traitement à l'ABA. Une analyse des réseaux d'interaction supporte les résultats de l'analyse d'expression et a montré que les gènes *BolSGT1a* et *BolSGT1b* sont fortement associés à des co-régulateurs en conditions de stress. Contrairement, le gène *BolSGT1* n'a montré aucune association forte. Ainsi, *BolSGT1* pourrait constituer un gène associé à la résistance au stress qui opère sans un co-régulateur. Ces résultats montrent que les gènes *BolSGT1* représentent des cibles potentielles en vue de l'accroissement de la résistance aux stress abiotiques tels que la chaleur, le froid et la salinité chez le *B. oleracea*. [Traduit par la Rédaction]

Mots-clés : résistance aux stress, *BolSGT1*, *Brassica oleracea* var. *capitata*, expression génique.

Introduction

Brassica oleracea is a major vegetable crop produced and consumed around the world, but its establishment, growth, and yield are highly affected by biotic and abiotic stresses such as bacteria, viruses, and fungi, and drought, cold, and salt (Ahmed et al. 2012; Thamilarasan et al. 2014). These stresses increase the level of reactive oxygen species (ROS), which causes injuries to the plants through oxidative damage at the cellular level. Plants have developed mechanisms for tolerance against biotic and abiotic stresses involving cellular, physiological, and developmental changes through expression of resistance-related genes that can be activated within hours or days (Yabuta et al. 2009). Interestingly, biotic resistance-related genes such as *thaumatin-like* genes in wheat; *DREB*, *AtRALFL8*, *AtMGL*, and some *cytochrome P450*

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genes in *Arabidopsis* exhibit crosstalk with abiotic stress responses and can be expressed during both forms of stresses (Agarwal et al. 2006; Atkinson et al. 2013; Deihimi et al. 2013; Fujita et al. 2006; Narusaka et al. 2004).

SGT1 (*suppressor of the G2 allele of skp1*) was first identified in yeast as a suppressor of *skp1-4*, a temperature-sensitive mutation of *SKP1* that arrests cell division in G2/M phase (Kitagawa et al. 1999). *SGT1* is expressed in association with several resistance-related genes like *HSP-90*, *Prf*, *RAR1*, and *Nod1*, and forms protein complexes that function in various biological processes in plants (Azevedo et al. 2002; Catlett and Kaplan 2006; Kud et al. 2013). *Brassica oleracea* contains *suppressor of the G2 allele of skp1*, as well as another related gene, *suppressor of GCR2*.

SGT1 proteins contain three functional domains, including tetratricopeptide repeats (TPRs), CHORD SGT1 (CS), and SGT1-specific sequence (SGS) (Kumar & Kirti 2015). TPR domains are generally involved in interprotein associations, whereas CS and SGS domains are responsible for stress resistance (Botër et al. 2007; Nyarko et al. 2007). *Arabidopsis* contains two SGT1 proteins, AtSGT1a and AtSGT1b, which bind to RAR1, a component required for the resistance through R proteins (Azevedo et al. 2006). Another type of SGT1 protein is characterized by the so-called SGT1 domain, similar to that found in human suppressor SGT1 protein (Sato et al. 1999).

These earlier reports revealed that *SGT1* plays an important role as a resistance-related gene and is expressed during various stress conditions in plants. Currently, no detailed studies report the expression of *SGT1* genes in abiotic stress responses in *B. oleracea*. In this study, *SGT1* genes are identified in the *B. oleracea* genome and characterized by in silico analysis. Also examined is their expression in response to abiotic stresses, finding evidence suggesting that these resistance genes respond during all stresses.

Materials and methods

Sequence analysis

Coding DNA and protein sequences for SGT1 of *B. oleracea* and *B. rapa* were retrieved from the *Brassica* database (http://www.brassicadb.org/brad/) using key word searches. Genomic structures of *BolSGT1* genes were determined by the Gene structure display server (http://gsds.cbi.pku.edu.cn/). Pairwise and multiple alignments were used for analyses of similarity and homology. Functional domains were analyzed with SMART (http://smart.embl-heidelberg.de/smart/set_mode.cgi?NORMAL=1). Predictions of pI, N-Glyc position, and molecular mass were made using the entire ORF and the pI/Mw tool at Expasy (http://web.expasy.org/protparam/). The subcellular localizations of *BolSGT1* genes were predicted using the PSORT software programs (Nakai and Horton 1999). Predicted protein interactions were identified using STRING software (Search Tool for the Retrieval of Interacting Genes/Proteins, http://string-db.org/) (Szklarczyk et al. 2011).

Phylogenetic tree

Phylogenetic analysis was conducted using MEGA6.06. Predicted protein sequences of *BolSGT1* and pathogenesis-related protein (thaumatin-like protein) genes were used for phylogenetic tree construction using the neighbor-joining method with the complete deletion option. Tree reliability was assessed using 1000 bootstrap replicates, and the numbers indicated for each clade represent bootstrap support values given as percentages (Thamilarasan et al. 2014).

Plant materials and abiotic stress conditions

Cabbage line 106 (*B. oleracea* var. *capitata*) plants were grown at the Department of Horticulture, Sunchon National University, South Korea. Fresh roots, stems, leaves, and flower buds of *B. oleracea* were harvested, frozen immediately in liquid nitrogen, and stored at −80 °C for RNA isolation followed by organ-specific expression. Plant treatments (cold, drought, heat, salt, and ABA) were started in the morning (08:00), and samples were collected at appropriate time courses and frozen immediately in liquid nitrogen. For the stress-responsive expression analysis, seeds of cabbage line 106 were sown and grown aseptically on half-strength MS agar medium in a culture room under a 16-h light photoperiod at 25 °C. After three weeks of growth, the seedlings were treated at 42 °C for 0, 0.5, 1, and 3 h time courses for heat stress. For salt and ABA treatments, the seedlings were transferred to fresh liquid MSH (half-strength MS medium without sucrose) medium containing 250 mmol/L NaCl or 100 mmol/L abscisic acid (ABA). To induce cold stress, the seedlings were maintained at 4 °C. Drought treatment was applied by keeping the seedlings on filter paper at 28 °C. The samples were subjected to stresses for 0 (control), 1, 3, 6, 12, and 24 h. Afterward, the second and third leaves were collected and frozen immediately in liquid nitrogen and stored at −80 °C until RNA isolation. The total RNA was extracted from the 100 mg of frozen samples of the roots, stems, leaves, and flower buds of healthy plants and leaves of plants treated with abiotic stress using an RNeasy mini kit (Qiagen, USA), after which RNA was treated with RNase-free DNase (Promega, USA) to remove genomic DNA contamination. The purity of isolated RNA was quantified and checked by ND-1000 Spectrophotometer and NanoDrop v3.7 software (NanoDrop Technologies, USA). Synthesis of cDNA from RNA extracts was performed with Superscript III® First-strand Synthesis Supermix kit (Invitrogen, USA) following the manufacturer's instructions.

Expression analysis

Gene-specific primers were designed from coding DNA sequences of *SGT1* genes by using Primer3 software for

Table 1. Primers for expression analysis.

Gene	Forward	Reverse	Product length (bp)
Primers for RT-PCR			
BoActin	GCTATGTATGTCGCTATTC	TTGGAAGTCTCCATCTC	329
BolSGT1a	GCCGGTAAAAGTTGATCAGAC	TCAATCTTGTCCCAGTCCTTC	420
BolSGT1b_1	CCACTCCACCACTAGCAAC	AAACCGCTGATGCGACATTGG	372
BolSGT1b_2	AAGATGGATGGCGAAGGAAC	AACAGGAGCAGCATCAGC	454
BolSGT1	CACCTCCAAATCATCGACTTC	TCTAACCCTAACGCGATGC	519
Primers for RT-qPCR			
BoActin	TTCTCTCTTCCACACGCCAT	CTTGTCCTGCGGGTAATTCG	265
BolSGT1a	AAGTTGATCAGACCCCTGTG	TTGGAGATGATACGCTTCCTC	194
BolSGT1b_1	CCACTCCACCACTAGCAAC	ATAAGCTTCCTCTCCAGCAAC	200
BolSGT1b_2	AAGATGGATGGCGAAGGAAC	ACTCGATGGCTTTGTTGGC	200
BolSGT1	CACCTCCAAATCATCGACTTC	ATGCGGAAGAGGAGGAAGAC	200

RT-PCR and Real-time PCR (qPCR). Primers were designed with 18–21 bp length, 45%–55% of GC content, and 58–60 °C annealing temperature as default parameters. Actin, a commonly used housekeeping gene for expression study, was used as a reference gene (Table 1) in RT-PCR and qRT-PCR experiments (Dekkers et al. 2012; Hee-Jeong et al. 2014). RT-PCR was performed for organ-specific expression using 50 ng cDNA (1 μL), 20 pmol primer pairs (2 μL), Emerald master mix (8 μL), and sterile H_2O to a total volume of 20 μL. Condition was set at 30 cycles of 60 °C for 30 s and 72 °C for 45 s, followed by a final extension at 72 °C for 5 min. The PCR products were resolved on a 2% agarose gel. For qRT-PCR, 1 μL cDNA with 10 μL iTaq SYBR Green Super-mix with ROX (California, USA) was used with three step amplification (annealing temperature 60 °C) and melting peak with two technical replicates. Amplification, detection, and data analysis were carried out using a Light Cycler® 96 Instrument (Roche Diagnostics, United States). Efficiency was determined based on different cDNA concentration and primer specificity using melting peak (supplementary data, Fig. S1[1]).

Results and discussion

Identification and characterization of *SGT1 genes*

Extensive searches were conducted in the *Brassica* database to identify *SGT1* genes, and retrieved sequences based on annotation. Among the 17 *B. oleracea* genes, eight were annotated as *SGT1a*, seven as *SGT1b*, and two as *SGT1* based on *Arabidopsis* nomenclature in the *Brassica* database. Coding sequences of eight *SGT1a* genes range from 159 to 1032 bp, and the seven *SGT1b* genes range from 168 to 963 bp. The two *SGT1* genes are 1947 and 342 bp. Sequence similarities were identified between *SGT1a* genes, which also showed the highest similarity between the genes, and between *SGT1b* genes. Likewise, the two *SGT1* genes showed high levels of similarity to each other. Even though the remaining genes are complete sequences, they lack functional domains and are short in length. Despite the presence of a promoter region in these genes, they showed no expression during organ-specific analysis. Hence, we omitted these genes from further analysis. In pairwise alignments, short sequences with high similarity between the sequences were found, suggesting that *SGT1* genes may have been duplicated in the *B. oleracea* genome (Table S1[1]). These duplicated genes in *B. oleracea* evolved during evolutionary events, and 4365 duplicated genes are identified in 1825 gene clusters. Duplication and triplication of the genes are a result of evolutionary events in *Brassicaceae* lineage, and during this event, genes possibly mutated into pseudogenes or non-functional genes (Liu et al. 2014; Lynch et al. 2001; Town 2006; Yao et al. 2015). In *Arabidopsis*, Noël et al. (2007) reported that *SGT1* encodes three functional domains (TPR, CS, and SGS) that are essential for activation of suppressor of G2 allele of SKP1 protein. Domain analysis revealed that among eight annotated *SGT1a* genes, only one (Gene id: Bol006218) encoded all three functional domains, and that gene was named *BolSGT1a*. Similarly, among the seven genes annotated as *SGT1b*, only two (Gene ids: Bol006784 and Bol025710) encoded proteins containing all three functional domains, and those genes were named *BolSGT1b_1* and *BolSGT1b_2*. The remaining genes encoded only one domain (TPR/SGS) or no domains. Only one of the two annotated *SGT1* genes encoded the SGT1 functional domain, and that gene was named *BolSGT1*. Additionally, RT-PCR was performed for genes that did not encode functional domains and expression was not observed (data not shown). This domain and expression analysis suggested that the functional domains are essential for expression of *BolSGT1* genes. The domain-containing sequences were used for further studies, and they are described in Table 3.

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/gen-2015-0128.

Table 2. Sequence characteristics of *BolSGT1* genes used in this study.

Name	Accession No.	Nucleotide length (bp)	ORF (bp)	Chromosome No.	Exon position
BolSGT1a	Bol042107	1879	1032	C06	1–160 516–585 683–807 888–969 1056–1152 1227–1292 1369–1507 1587–1879
BolSGT1b_1	Bol006784	2022	963	C09	1–160 406–475 553–677 776–893 990–1086 1177–1242 1326–1464 1566–1645 1915–2022
BolSGT1b_2	Bol025710	2189	687	C03	1–108 968–1064 1148–1274 1388–1512 1697–1766 2030–2189
BolSGT1	Bol009238	2178	1947	C03	1–186 264–543 628–966 1037–2178

Note: ORF, Open reading frame; bp, base pair.

Table 3. Sequence characteristics of BolSGT1 proteins used in this study.

Name	Accession No.	Length (aa)	Domain				N-Glyc (Asn) position	Mol. wt. (kDa)	pI	Instability index
			TPR	CS	SGS	SGT1				
BolSGT1a	Bol042107	343	2–103	145–221	260–341	—	51, 312	38.535	5.49	42.39
BolSGT1b_1	Bol006784	320	2–103	157–233	273–318	—	51, 289	35.302	5.23	41.94
BolSGT1b_2	Bol025710	228	2–103	160–207	192–226	—	51, 102, 197	24.859	4.71	45.16
BolSGT1	Bol009238	648	—	—	—	22–609	—	73.167	4.69	54.64

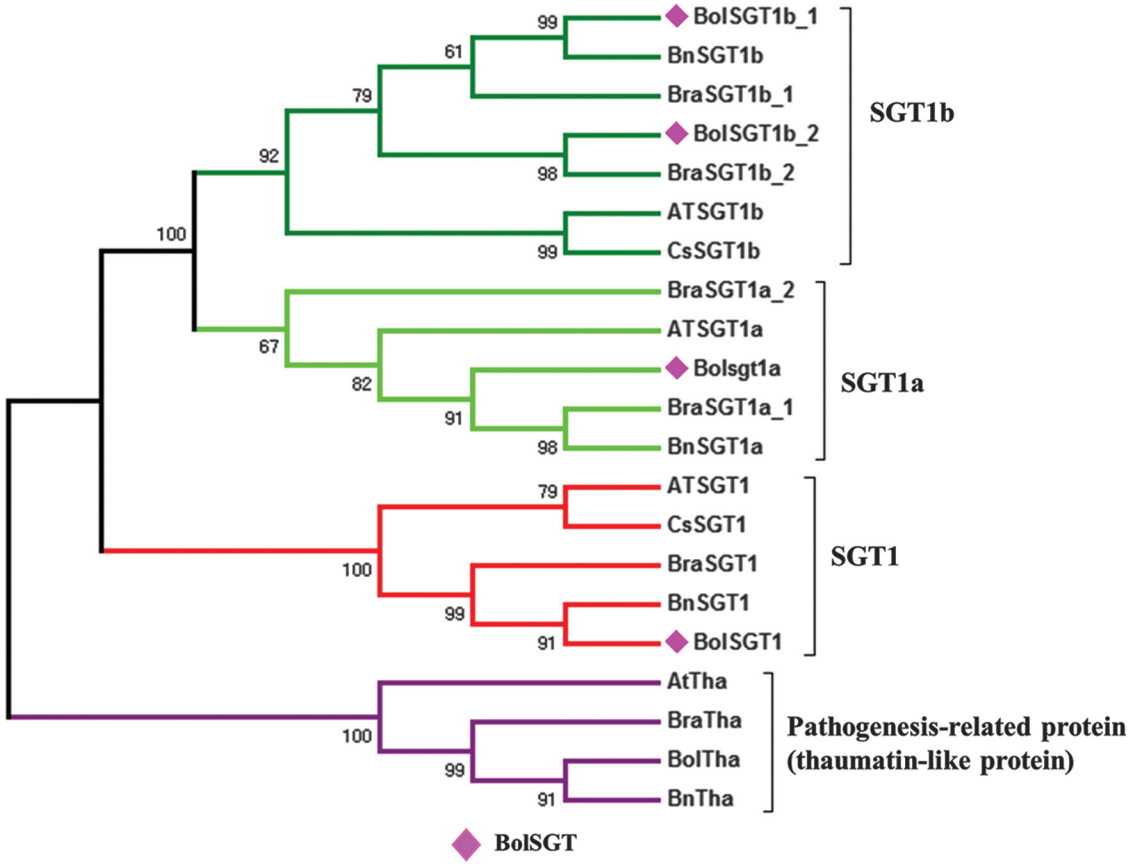
Note: aa, amino acid; pI, isoelectric point; kDa, kilodalton.

Genomic DNA sequences for all four genes were obtained from the *B. oleracea* genome sequence. Exon positions were determined for the *BolSGT1* genes (Table 2). Amino acid sequence characteristics, molecular weight, and pI for the four predicted BolSGT1 proteins are presented in Table 3. Both the BolSGT1a and BolSGT1b proteins were predicted to be located in cytoplasm, mitochondrial matrix space, and the endoplasmic reticulum, whereas BolSGT1 was predicted to be in the chloroplast and cytoplasm. Previously, subcellular localization in *Arabidopsis* was studied by Noël et al. (2007), who found that SGT1 and HSC70 proteins co-localize in the cytosol and in the nucleus to regulate biotic and abiotic stress responses. The predicted characteristics of the BolSGT1 proteins are consistent with similar functions in stress responses in *B. oleracea*. Based on these results, further analysis of these *BolSGT1* genes was carried out.

Phylogenetic analysis

Fu et al. (2009) reported that *Glycine max SGT1* is 60%–65% identical to *A. thaliana SGT1*, and greater than 70% identical to tobacco *NbSGT* and barley *HvSGT*. Chung et al. (2006) generated a phylogenetic tree of *SGT1* genes from different plant species, which showed that *AtSGT1* and *BolSGT1* are closely related. However, no studies have reported the phylogenetic relationships of *BolSGT1a*, *BolSGT1b*, and *BolSGT1* among different plant species. Accordingly, we constructed a phylogenetic tree using 17 SGT1 protein sequences from five species, including *A. thaliana*, *B. oleracea*, *B. rapa*, *B. napus*, and *Camelina sativa*, of the family *Brassicaceae* (Fig. 1). Additionally,

Fig. 1. Phylogenetic tree of SGT1 proteins of the Brassicaceae constructed by the neighbor-joining method. The tree was grouped into SGT1a, SGT1b, and SGT1 clades. Abbreviations: At, *Arabidopsis thaliana*; Bol, *Brassica oleracea*; Bra, *Brassica rapa*; Bn, *Brassica napus*; Cs, *Camelina sativa.* Accession numbers are listed in the supplementary data, Table S2[1] .



pathogenesis-related protein (thaumatin-like protein) is used as an outgroup gene in the phylogenetic tree (Fig. 1), which is also expressed during abiotic stress (Deihimi et al. 2013). In the phylogenetic tree, the proteins clearly formed separate SGT1a, SGT1b, and SGT1 groups, indicating that all three proteins arose before the divergence of these species. The tree shows that *SGT1* is diverged from *SGT1a* and *SGT1b*, whereas *SGT1a* and *SGT1b* are more closely related. Consistent with the close relationship of the two species, *BolSGT1a* is most closely related to *BrSGT1a*, and *BolSGT1b* is clustered with *BrSGT1b*. Likewise, *BolSGT1* is grouped with *SGT1* of *B. rapa.*

Organ-specific expression

Organ-specific expression analysis was conducted using mRNA isolated from roots, stems, and leaves (second and third leaf) of 3-week-old non-treated seedlings, and flower buds were collected from 14-week-old seedlings of *B. oleracea* by RT-PCR at different experimental profiles. Expression is observed in all four *BolSGT1* genes in all tested organs. *BolSGT1a* was highly expressed in root, stem, and leaves but showed lower expression in flower bud. *BolSGT1b_1* was highly expressed in stem and moderately expressed in leaves and flower bud, whereas it had lower expression in root. *BolSGT1b_2* showed high expression in flower bud, moderate expression in stem and leaves, and lower expression in root. *BolSGT1* was strongly expressed in stem, moderately expressed in leaves and flower bud, but expressed in root only to very low levels (Fig. 2). Organ-specific expression analysis showed that the *BolSGT1* genes are differentially expressed in all organs at various experimental conditions (data not shown). This proposes that *BoSGT1* genes are

Fig. 2. Organ-specific expression of *BolSGT1* genes. Abbreviations: R, root; S, stem; L, leaf; Fb, flower bud; Bol, *Brassica oleracea.*

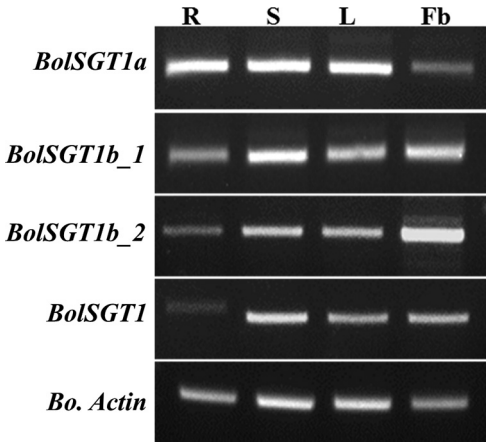
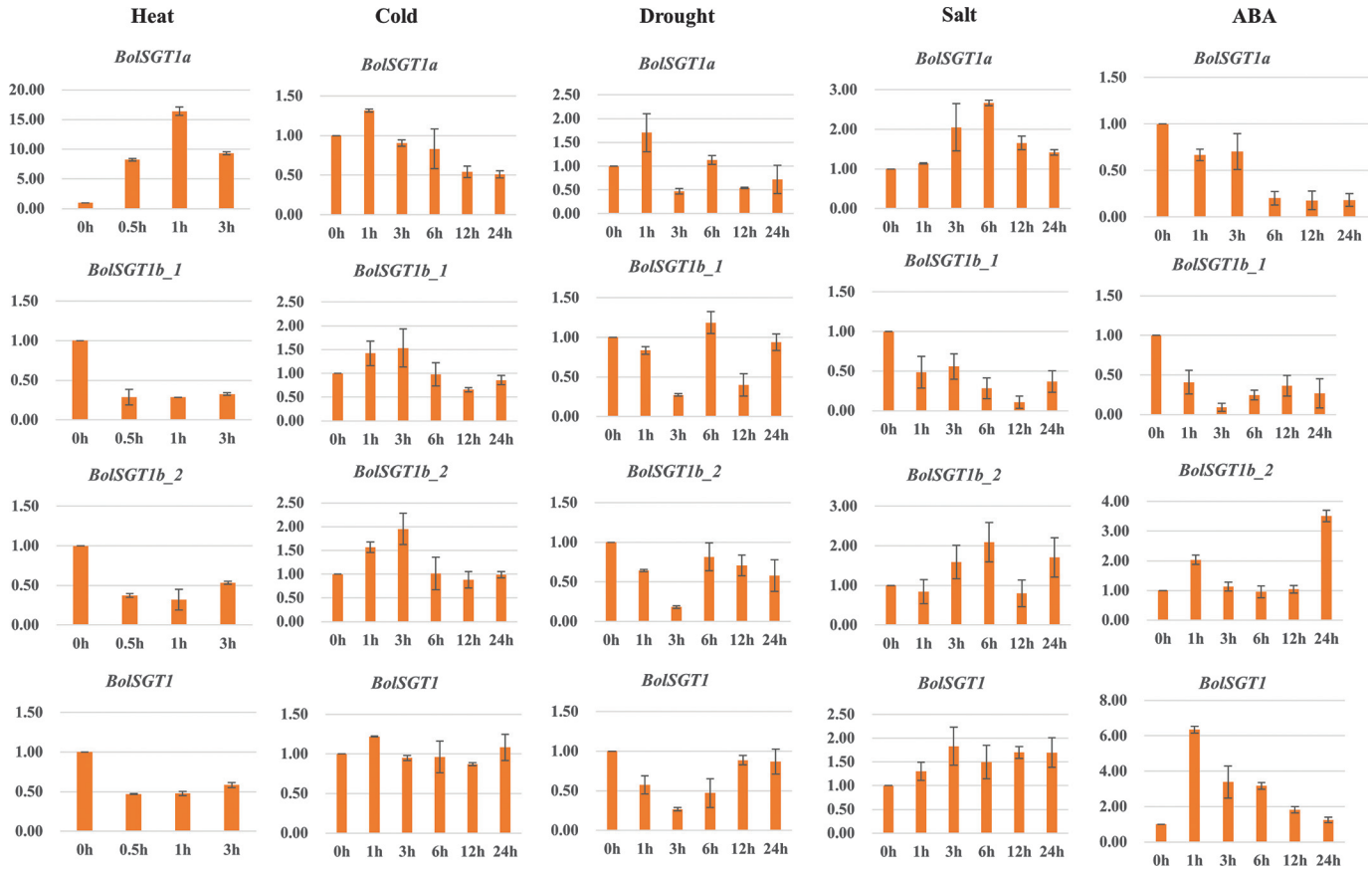


Fig. 3. Real-time PCR expression analysis of *BolSGT1* genes after stress treatment in *Brassica oleracea*. The error bars represent the standard error of the means of two technical replicates.



functional during essential plant development stages. Together, our results indicate that *BolSGT1* genes are expressed to different degrees in different organs. *SGT1* genes are expressed in different organs of *Capsicum annuum* and *Haynaldia villosa*, which are involved in different development stages and are substantially expressed during different stresses (Chung et al. 2006; Xing et al. 2013). This similarity suggests that the *BolSGT1* genes may also play roles during abiotic stress conditions. Hence, the *BolSGT1* genes were studied using quantitative PCR in the abiotic-treated *B. oleracea*.

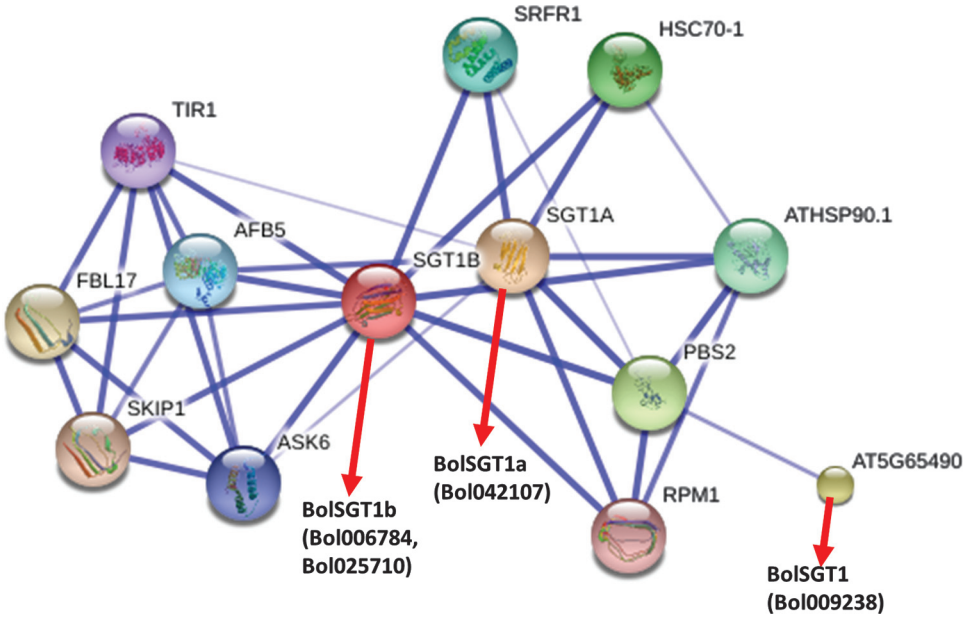
Analysis of *BolSGT1* gene expression during abiotic stresses

To analyze the expression pattern of *BolSGT1* genes, RT-qPCR was carried out on samples from plants treated with abiotic stresses such as heat, cold, drought, salt, and ABA. Our results revealed that *BolSGT1a* expression was highly upregulated by heat stress until 1 h, and then subsequently decreased. During salt and cold stress, *BolSGT1a* expression increased until 6 and 1 h, respectively, and then decreased. Drought and ABA treatments did not induce notable expression during the time courses. During ABA stress, *BolSGT1a* decreased and showed similar expression after treatment at 1 and 3 h, followed by a decrease and similar expression at 6, 12, and 24 h.

BolSGT1b_1 and *BolSGT1b_2* showed similar expression patterns in response to heat, cold, and drought stresses. During heat and drought stress, no significant differential expression pattern was observed. During cold stress, expression gradually increased until 3 h, followed by a decrease. In salt stress, *BolSGT1b_2* was upregulated until 6 h, and then suddenly decreased at 12 h. ABA treatment led to decreased *BolSGT1b_1* expression. However, *BolSGT1b_2* responded positively at 1 h, and then decreased until 12 h. *BolSGT1* expression in response to salt stress and ABA treatment was upregulated and downregulated, respectively. During salt stress, *BolSGT1* expression gradually increased until 3 h, slightly decreased at 6 h, and then increased. During ABA treatment, *BolSGT1* expression suddenly increased at 1 h, followed by a gradual decrease (Fig. 3).

These observations support the idea that *BolSGT1* genes could play roles during stress conditions. In *Arabidopsis*, *SGT1a* is more highly upregulated in heat stress than other *SGT1* genes (Noël et al. 2007). Although *BolSGT1a* and *BolSGT1b* genes share similar domain structures, they display contrasting expression patterns during heat stress (Fig. 3), which is similar to the situation in *Arabidopsis* (Yabuta et al. 2009). In cold stress, *BolSGT1a* and *BolSGT1b* genes were downregulated, unlike *BolSGT1*. Along with previous reports, our results suggest that the

Fig. 4. Interaction network (confidence view) of *BolSGT1* genes identified in *Brassica oleracea* and related genes in *Arabidopsis*. Stronger associations are represented by thicker lines.



HSP90/SGT1 complex might be co-regulated during cold stress condition, which is expressed as downregulation, and it may be slightly induced by heat stress (Fu et al. 2009). In *Arabidopsis*, *HSC70-1*, encoding an interactor of SGT1, shows significant responses during salt stress (Cazalé et al. 2009). Our results also revealed that *BolSGT1a*, *BolSGT1b_2*, and *BolSGT1* have a differential expression pattern during salt stress conditions, which might be co-regulated by *HSC70-1* (Cazalé et al. 2009). In *Arachis diogoi*, *SGT1* was upregulated during ABA treatment (Kumar and Kirti 2015), consistent with the report of Cazale et al. (2009) that *HSC70/SGT1* act directly or indirectly during stress conditions. Our results revealed that the *BolSGT1* gene is repressed and that all other *BolSGT1* genes have no differential expression pattern during ABA treatment, responses to which may, therefore, not be co-regulated by *HSC70/SGT1*. Previous results revealed that *BolSGT1* genes may be co-regulated and induced by all stresses excluding drought; in drought stress, *BolSGT1* genes were not expressed well, suggesting that they may not function in drought stress responses (Fu et al. 2009).

To further explore the possible functions of these genes, we generated an interaction network by in silico methods, which revealed many genes as co-regulated with *BolSGT1* genes. Interestingly, many proteins that may act as co-regulators (HSC70-1, ATHSP90.1, SRFR1, PBS2, RPM1, and AFB5) of BolSGT1s (BolSGT1a and BolSGT1b) showed strong interaction with all proteins except BolSGT1 (Fig. 4). In SGT1, the CS domain is involved in interaction with Hsp90 and RAR1 (Takahashi et al. 2003; Wang et al. 2015). However, BolSGT1 has not shown any interaction with RAR1, though previously reported in other plants. Our results suggest that BolSGT1 does not strongly interact with other proteins during stress conditions, but it might be expressed individually. Notably, although *AtSGT1* is functionally annotated as an unknown gene, based on our results, we can suggest that *BolSGT1* is a stress-related gene involved in drought, salt, and ABA responses in *B. oleracea*.

Conclusion

In summary, four *SGT1* genes were identified in *B. oleracea* and their expression patterns were characterized in response to different abiotic stresses. This is the first systematic investigation of *B. oleracea SGT1* genes. Quantative PCR analysis of the *BolSGT1* genes found that they have potential for use as target genes to improve plant resistance to abiotic stresses such as heat, cold, and salt in *B. oleracea*. Interaction network analysis supported the expression analysis, and showed that these genes are associated with co-regulators during stress conditions, with the exception of *BolSGT1*. *BolSGT1* was functionally annotated as an unknown gene; our results show that it can be considered a stress-related gene that is expressed individually in response to drought, salt, and ABA.

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