

SNARE Genes in Brassica napus

Subjects: [Biochemistry & Molecular Biology](#)

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SNAREs (soluble N-ethylmaleimide-sensitive factor attachment protein receptors) are central components that drive membrane fusion events during exocytosis and endocytosis and play important roles in the different biological processes of plants.

Brassica napus

SNARE

gene family

Sclerotinia sclerotiorum

expression profile

hormone stimuli

1. Introduction

Vesicle trafficking is essential for diverse biological processes including cell polarity, growth, development, and adaptation [1,2,3,4,5]. The cargo exchange of trafficking vesicles promotes the vesicle-mediated communication among eukaryotic cells through the exocytic and endocytic pathways. These exocytic and endocytic processes are dependent on the targeted membrane fusion of vesicles that delivers membranes, proteins, and soluble cargos between subcellular membranous compartments and the plasma membrane [6]. This membrane fusion mechanism is highly conserved in all eukaryotes [7] and the central components driving the actual membrane fusion events are a set of proteins dubbed as SNAREs (soluble *N*-ethylmaleimide-sensitive factor attachment protein receptors) [8].

SNAREs can be classified into v-SNAREs (associated with transport vesicles) and t-SNAREs (associated with the target compartments) [9]. Considering that some SNARE proteins may have multiple functions, another classification method is generally accepted: Qa-, Qb-, Qc-, Qbc-, and R-SNAREs according to the central amino acid present in the hydrophobic heptad repeats of the proteins [10]. The fusion of vesicles with their target membrane is driven by a cluster of four coiled-coil helices, termed Qa, Qb, Qc, and R, each of which is contributed by three or four individual SNARE proteins (a single Qbc-SNARE protein carries two SNARE helices: Qb and Qc) [11]. The specific interaction between v-(R)SNARE and a cognate set of t-(Q)SNAREs is an important part of the mechanisms that partly influence the accuracy of the transport. SNARE proteins form a superfamily of diverse proteins with at least 64 members in *Arabidopsis thaliana* [11], 60 members in rice [11], 63 members in tomato [12], 69 members in *Populus trichocarpa* [13], and 173 members in wheat [14]. Compared to other eukaryotes, plants so far have the highest number of identified SNAREs; *Homo sapiens* has 38 SNAREs [15], *Drosophila melanogaster* has 26 [16], and there are between 21 and 25 of them in *Saccharomyces cerevisiae* [17,18]. Sansebastiano and Piro were of the opinion that this increase in the number of SNAREs in plants was a result of gene expansion of partially redundant genes in conserved subfamilies and not the evolution of new isoforms [13].

The expansion of SNARE encoding genes in plants implies the importance of this superfamily during the growth and development of the plants, as well as for biotic and abiotic stress responses [19].

During the last 20 years, evidence for the diverse functions of SNAREs at multiple stages of plant development rapidly accumulated. At the cellular level, SNARE proteins express in diverse organelles such as the plasma membrane, ER, transport vesicles, Golgi apparatus, and trans-Golgi network (TGN). The proteins are previously reported to mediate the processes of vacuole biogenesis, vacuolar transport, vesicle fusion, secretion, cell growth, and ion homeostasis. AtVAMP721 interacts with the potassium channels AtKAT1 and AtKC1 to maintain the currency of the K⁺ channels in *A. thaliana* [20]. Members of AtSYP4 (AtSYP41, AtSYP42, AtSYP43) localize on the same TGN compartment and maintain the morphology of both the Golgi apparatus and TGN [21]. The homodimer form of the ER-localized R-SNARE protein AtSEC22 plays a major role during anterograde and retrograde transports by promoting efficient membrane fusion and assisting in the assembly of higher-order complexes. Furthermore, the Qc-SNARE AtBET12 together with the Qb-SNARE AtMEMB12 negatively regulates the secretion of pathogenesis-related protein 1(PR1) in *A. thaliana* [22].

At the tissue level, several types of SNAREs were reported to play vital roles in root growth, pollen tube growth, and seed maturation. For example, the membrane-localized Qa-SNARE AtKNOLLE (AtSYP111) is highly expressed in organs containing dividing cells and is specifically involved in cytokinetic vesicle fusion [23]. AtSYP123 is expressed and accumulated in the cells present at the tip region of root hairs during root development, while AtSYP124, AtSYP125, and AtSYP131 only express in pollen and are involved in pollen tube growth [24].

At the whole-plant level, SNAREs are mainly activated in response to stresses such as drought/osmotic stress, high salinity, abscisic acid (ABA)-induced stress, and pathogen stimuli. For example, AtSYP121 is involved in ABA-dependent drought stress in tobacco and non-host resistance against powdery mildew as well as oomycete attack in *A. thaliana* [2,23,25]. As a paralog of AtSYP121, AtSYP122 is phosphorylated in response to the elicitor flagellin [26] and has redundant functions with AtSYP121 in plant immunity and general secretion events [27,28]. Another Qa-SNARE, SYP132 also plays roles in bacterial defense and symbiosome definition in *Nicotiana benthamiana* and *Medicago truncatula*, respectively [29,30]. AtSYP61 plays an important role in osmotic stress tolerance and the ABA-dependent regulation of stomatal responses [31]. ShNPSN11 plays a positive role in defense activation and host resistance to *Oidium neolycopersici* in tomato [25].

Brassica napus is a major oil crop in temperate regions of the world. It belongs to the family *Brassicaceae*. The amphidiploid *B. napus* (2n = 38, AACCC) was formed as a hybrid between progenitors of *B. rapa* (2n = 20, AA) and *B. oleracea* (2n = 18, CC) ~7500 years ago [32], both of which underwent whole-genome triplication [33,34]. More ancient polyploidization events [35,36] along with the recent hybridization and subsequent gene loss shaped the *B. napus* genome and determined the size of the entire gene complement ~100,000 genes as well as the individual gene families [37]. This evolutionary process and the close relationship of *B. napus* with *A. thaliana* make *B. napus* an ideal material for gene family evolutionary research. However, the number, nature, general relationships, and functions of the various SNARE proteins present in *B. napus* remain in the dark.

Therefore, in this study, we first used an *in silico* approach to carry out global identification of the members of the SNARE family in *B. napus* and then systematically analyze their structural similarities, evolutionary relationships, and transcriptional profiles under the influences of the necrotrophic fungus *Sclerotinia sclerotiorum*, oxalic acid (OA), methyl jasmonate (MeJA), salicylic acid (SA), and abscisic acid (ABA).

2 Identification of SNARE Genes in *B. napus*

To identify all members of the SNARE family in *B. napus*, three methods including Pfam analysis, conserved domains search, and orthologous sequence BLAST were used. A total of 237 *BnaSNAREs* were identified. Of these genes, six (6) couples sharing 100% identity on the amino acid level but different nucleotide sequences were considered to be different *BnaSNAREs*. All candidate *BnaSNAREs* were named according to their best hit in *Arabidopsis*. Each gene name starts with an abbreviation for the species name *B. napus* (*Bna*), followed by the name of the most prominent *Arabidopsis* gene from this subclade (e.g., “*BnaSYP122*” for *AtSYP122*-like genes, “*BnaSEC20*” for *AtSEC20*-like genes, “*BnaYKT61*” for *AtYKT61*-like genes). Exceptions are *BnaSNAP33s*, *BnaSNAP30s*, and *BnaSNAP29s* which are named according to their protein molecular weight (e.g., “*BnaSNAP31*” represents the protein molecular weight is approximate 31 kDa). Genes on different chromosomes belonging to the same subclade were consecutively numbered according to their chromosome number from low-to-high values (e.g., four *KNOLLE*-like genes *BnaC05g06210D*, *BnaA06g04950D*, and *BnaA08g26870D*, *BnaC08g13620D* were named separately as “*BnaKNOLLEa*”, “*BnaKNOLLEb*”, “*BnaKNOLLEc*”, and “*BnaKNOLLEd*”). In the case of *SYP4s*, our phylogenies did not provide clear orthologous relationships among *SYP41s*, *SYP42s*, and *SYP43s* genes from *B. napus* and *Arabidopsis*. We therefore named the *SYP4* subclade genes of *B. napus* as *BnaSYP44*, *BnaSYP45*, and *BnaSYP46*, taking up the current code of *Arabidopsis*. A similar strategy was adopted to name *USE1*, *SFT1*, *MEMB1*, and *YKT62*-like genes. *VAMP724*, *VAMP726*, and *VAMP728* genes were similar to the case of *BnaSYP4s*, but the strategy did not fit this case because the codes in *Arabidopsis* are up to eight (*VAMP728*). “Slash” was rather used in naming these genes (e.g., “*BnaVAMP724/6/8a*”, “*BnaVAMP724/6/8b*”).

Almost all of the identified SNAREs in *B. napus* showed the same conserved domain with their respective orthologs in *Arabidopsis* according to NCBI batch CD search, except for the 11 *SYP6*-like proteins, which just contain 1 N-terminal syntaxin-6 (PF09177) domain but lost a C-terminal SNARE domain. Furthermore, of these 11 *SYP6*-like proteins from *B. napus*, 3 orthologs from *Arabidopsis* were not previously identified. Considering the fact that the conserved N-terminal syntaxin-6 domain is unique to the SNARE family, we believe that the 11 genes belong to the SNARE family and we classified them as SYN-sub-family.

The *BnaSNARE* proteins have varying physicochemical characteristics. Isoelectric points (pIs) of the proteins are between 4.44 and 11.84, and their molecular weights (MWs) range from 9.02 to 120.51 kDa. Exceptions are *BnaSYP31d* with 7.15 kDa, and both *BnaSYP112e* and *BnaSYP112f* have MW of 8.05 kDa, which fall below the range; *BnaVTI11e*, however, has an MW of 184.07 kDa which falls above the stated range. Subcellular localization prediction for the *BnaSNARE* proteins indicated that they are localized at the plasma membrane, ER, Golgi, vacuole, and a small group were located in the cytoplasm, mitochondrion, and nucleus.

3 *Bna*SNAREs Belong to Well-Defined Subfamilies That Were Correlated to Their Gene Structures and Conserved Motifs

A maximum-likelihood phylogenetic tree of all the *SNARE* genes from *A. thaliana* and *B. napus* shows that the *B. napus* genome retains all the orthologs of *A. thaliana* *SNARE*s and the gene phylogeny roughly followed species phylogeny. In several subclades, one *SNARE* in *A. thaliana* is closely related to a double of two *B. napus* homologs (e.g., *SFT1*, *USE1* **Figure 1** and **Table S4**) which is consistent with the chromosome multiples of *B. napus* and *A. thaliana* as *B. napus* is heterotetraploid while *A. thaliana* is diploid. In many subclades, *SNARE* homologs in *B. napus* are significantly expanded compared to those in *A. thaliana*. Measured from the total point of view, the number of *SNARE*s in *B. napus* is much more than double of those in *A. thaliana*, in fact, nearly four times (e.g., *TYN1*, *SEC20*, *SYP5* subclades **Figure 1** and **Table S1**). The topology in *BnaSYP12*, *BnaYKT6*, *BnaSYP6*, and *BnaVAMP72* subclades (**Figure 1** and **Table S1**) is more complex, suggesting multiple duplication events, before and/or after polyploidization of *B. napus*. The *Bna*SNARE proteins displayed the same five groups described previously (Q (a-, b-, c-, bc-) and R) in *A. thaliana* and presented a similar proportion of members compared to *A. thaliana* (**Table S5**). Therefore, Qa-, Qb-, and Qc-*Bna*SNAREs are composed of 69, 44, and 37 (+11) genes, respectively. Qbc-*Bna*SNAREs have 10 members and R-*Bna*SNAREs have 65 members.

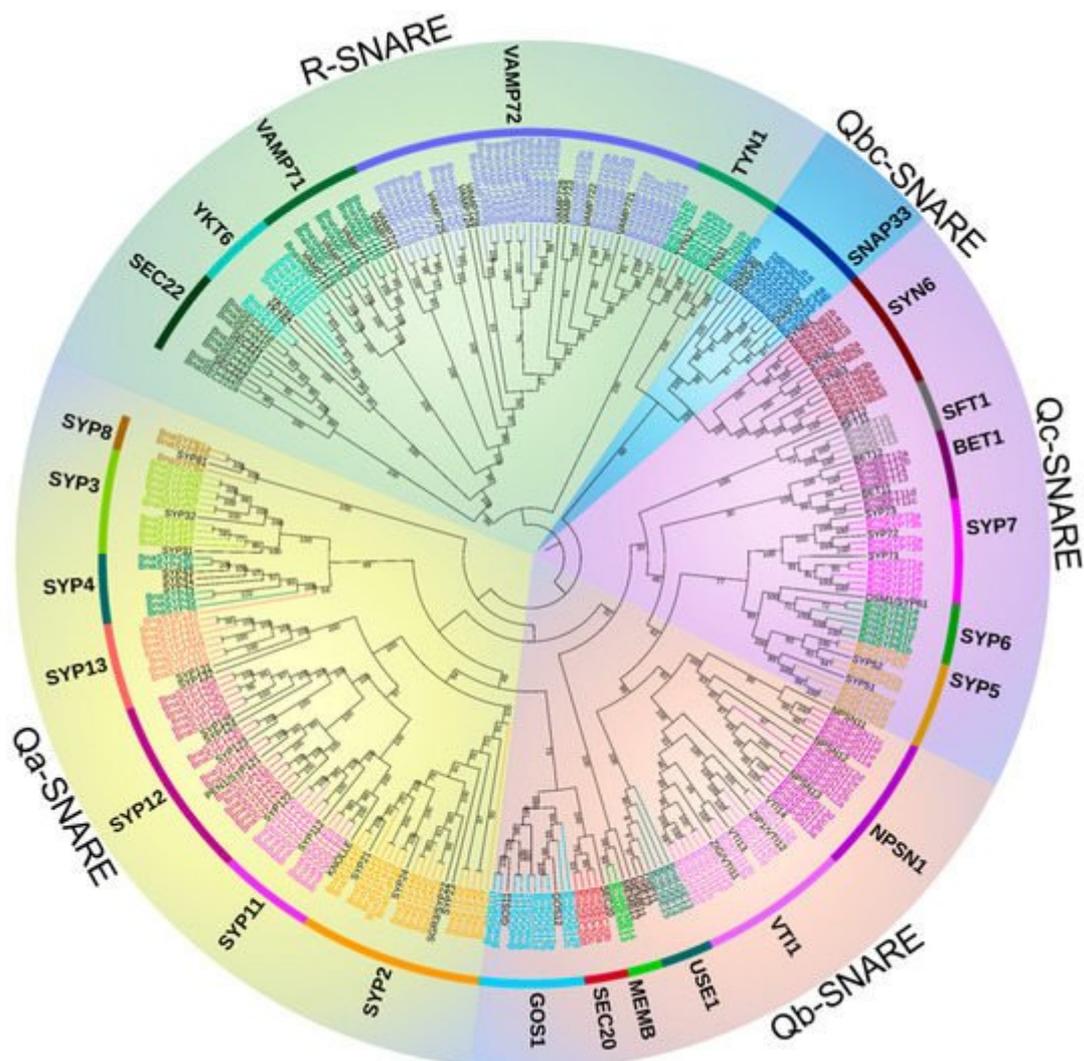
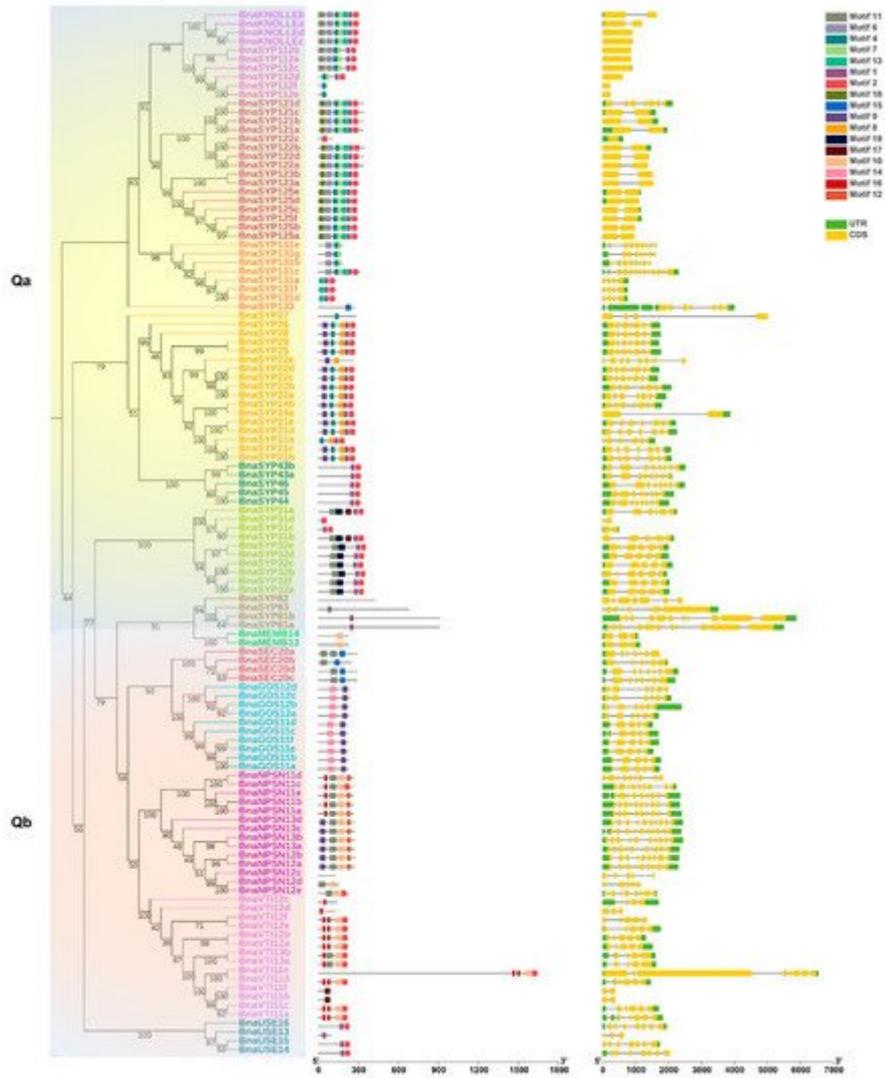


Figure 1. Maximum-likelihood phylogeny of SNARE proteins from *B. napus* and *A. thaliana*. A phylogenetic tree of SNARE proteins from *B. napus* and *A. thaliana* was constructed using IQ-TREE. The colored *B. napus* genes are subclade-specific, whereas *A. thaliana* genes were in black. Subfamilies were indicated using *A. thaliana* gene names, and sub-family names according to priority rule [11] were shown in brackets if different from the *A. thaliana* gene names. Despite the absence in other research, the *A. thaliana* genes SYN61, SYN62, and SYN63 and their orthologous in *B. napus* were included in the phylogeny. A version of the tree with untransformed branches and including the accession numbers can be found in [Figure S2](#).

The conserved motifs of each BnaSNARE protein sequence were identified by MEME and analyzed with the InterProScan tool (**Figure 2b** and [Table S6](#)). In brief, proteins in the same subclade seemed to share a similar motif composition, corresponding to the phylogenetic classification of BnaSNARE proteins. Motifs one and two correspond to the SNARE domains found in both Q- and R- SNARE proteins. Motifs six, seven, and eight, were found to be related to the syntaxin domains present in Q-SNAREs of *B. napus*, while motifs three, four, five, sixteen, and eighteen were found to be related to the Synaptobrevin and Longin domains present in R-SNAREs. In addition, motif fifteen is specific to Qbc SNARE, while motif nineteen is just present in *BnaSYP3s*. Along with the conserved motifs, the distribution of introns and exons in the 237 *BnaSNAREs* was analyzed with GSDS 2.0 (**Figure 2c**). We found a conserved number of introns within the subclades which is consistent with the phylogenetic classification. In detail, *Qa-SNAREs* contain various introns between 0 and 11. Among them, *BnaSYP11s* and *BnaSYP12s* contain the minimal introns 0 or 1. *BnaSYP13s* contain the most variable number of introns which are from 3 to 11. Almost all of the *BnaSYP2s* had six introns with two exceptions: *BnaSYP22e* and *BnaSYP27* having eight and three introns, respectively. A similar situation also occurred in other types of *BnaSNAREs* (**Figure 2c**). *Qb-SNAREs* contain various introns between 1 and 9; *Qc-SNAREs* contain 3 to 11 introns; *Qbc-SNAREs* contain 3, 4, or 6 introns while *R-SNAREs* contain 1 to 23 introns. More so, *R-SNAREs*, *BnaTYN11a*, *BnaTYN11b*, *BnaTYN11c*, and *BnaTYN11d* harbor 23 introns each, which is the largest number detected in all the *SNAREs* in *B. napus*.



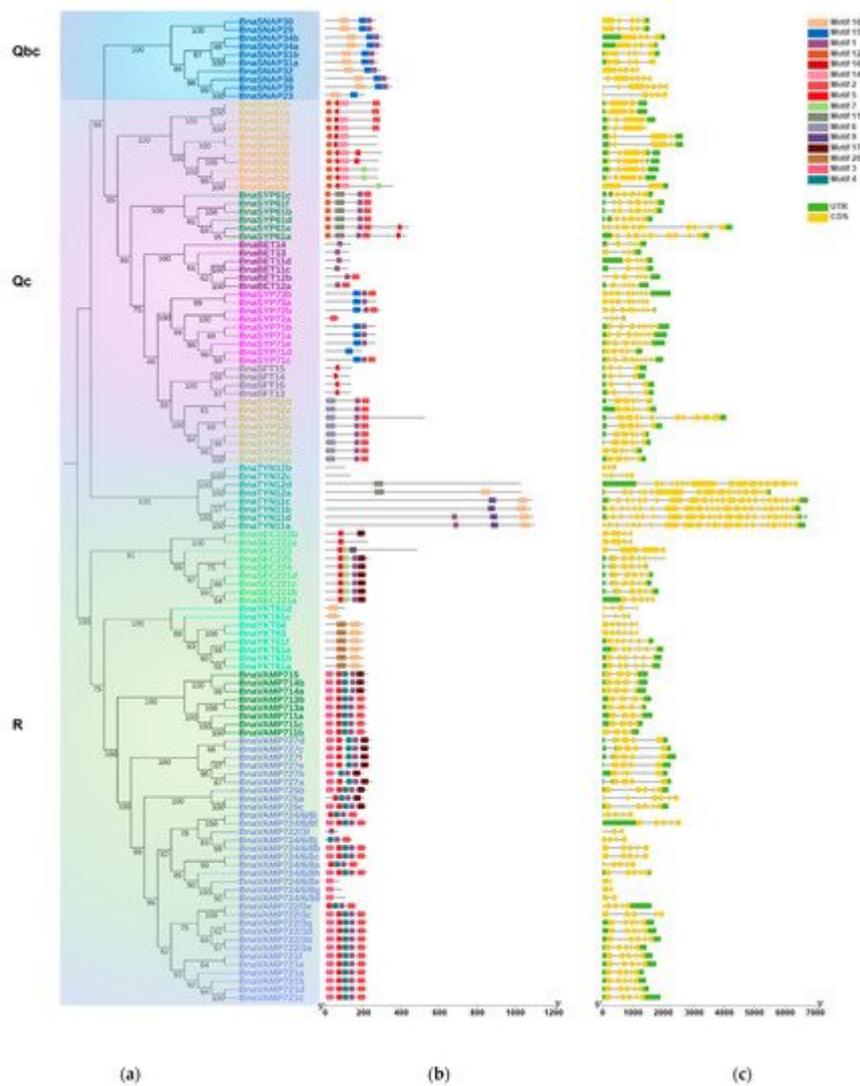


Figure 2. Gene intron/exon structures and protein conserved motifs of BnaSNAREs. (a) Phylogenetic tree of BnaSNARE proteins. (b) Conserved motif arrangements of BnaSNAREs. Twenty conserved motifs labeled with different colors were found in the BnaSNAREs sequences using the MEME program. Sequences of the conserved motif are presented in [Table S5](#). (c) Exon-intron organizations of *BnaSNAREs*. The green boxes represent 5' or 3' untranslated regions, yellow boxes represent exons, and black lines represent the introns. The lengths of the exons and introns can be determined by the scale at the bottom.

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