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News and views into the SNARE complexity in *Arabidopsis*

Sang-Jin Kim*[1,2] *and Federica Brandizzi*[1,2,3]

[1] *Great Lakes Bioenergy Research Center, Michigan State University, East Lansing, MI, USA*
[2] *Plant Research Laboratory, Department of Energy, Michigan State University, East Lansing, MI, USA*
[3] *Department of Plant Biology, Michigan State University, East Lansing, MI, USA*

Edited by:
Robert Mullen, University of Guelph, Canada

Reviewed by:
Jurgen Denecke, University of Leeds, UK
Mary Lai Preuss, Webster University, USA

****Correspondence:***
Federica Brandizzi, Plant Research Laboratory, Department of Energy, Michigan State University, East Lansing, MI 48824, USA.
e-mail: fb@msu.edu

Secretory organelles are engaged in a continuous flux of membranes, which is believed to occur mostly via transport vesicles. Being critical in maintaining several cellular functions, transport vesicles are membrane-enclosed sacs that temporarily store and then deliver membrane lipids, protein, and polysaccharides. SNAREs have a crucial role in vesicle traffic by driving membrane fusion and conferring fidelity through the formation of specific SNARE complexes. Additionally, specific roles of SNAREs in growth and development implicate that they are versatile components for the life of a plant. Here, we summarize the recent progress on the understanding of the role of SNAREs and highlight some of the questions that are still unsolved.

Keywords: *Arabidopsis*, SNARE, vesicle trafficking, membrane fusion

INTRODUCTION

Generally, vesicle trafficking occurs via three important steps: vesicle budding from the donor organelle, movement towards a target organelle, and fusion. Several proteins are involved in docking and fusion of vesicles for target recognition and driving membrane fusion (Malsam et al., 2008). Among the proteins for vesicle trafficking, SNAREs (soluble *N*-ethylmaleimide-sensitive fusion protein attachment protein receptors) were described a critical role in membrane fusion (Sollner et al., 1993). SNAREs can be categorized into two types: v-SNAREs, as SNAREs on the vesicle, and t-SNAREs, as SNAREs on the target membrane. When a vesicle moves close to its target, a v-SNARE on the vesicle interacts with three t-SNAREs on the target membrane, forming a hetero-tetrameric *trans*-SNARE complex that drives membrane fusion (McNew et al., 2000). According to the core amino acid in the hydrophobic heptad repeats in the SNARE motif, SNAREs can be divided into four groups: Qa-, Qb-, Qc-, and R-SNAREs (Fasshauer et al., 1998). In mammals, a typical SNARE complex consists of Qa- (syntaxin 1 like), Qb- (N-terminal half of SNAP25 like), and Qc- (C-terminal half of SNAP25 like) SNAREs on the target membrane, and R-SNAREs on the vesicle (Bock et al., 2001). The same combination seems to be conserved also in plants (Sutter et al., 2006a). It has been reported that there may be as many as 65 SNAREs in *Arabidopsis* (**Table 1**; Sanderfoot, 2007; Saito and Ueda, 2009). A large number of SNAREs in *Arabidopsis* may help facilitate trafficking in a complex endomembrane system that include distinct secretory and vacuolar trafficking steps mediated by two times more SNAREs than unicellular or mammalian systems (Sanderfoot, 2007). Studies to date on the same family of plant SNAREs have often revealed redundancy but also functional specificity. Here, we summarize the roles of SNAREs in *Arabidopsis* and present additional thoughts for future SNARE studies.

ROLE OF ER AND GOLGI SNAREs

In the endoplasmic reticulum (ER) and Golgi apparatus, 21 SNAREs (three Qa-SNAREs: AtSYP81 and two AtSYP3; seven Qb-SNAREs: AtSEC20, two AtMEMB1, two AtGOS1, and two AtUSE1; seven Qc-SNAREs: three AtSYP7, two AtBS14, and two AtSFT1; four R-SNAREs: two AtSEC22, AtVAMP714, and AtVAMP723) have been localized at a subcellular level by microscopy with fluorescent protein fusions along with *in silico* analyses (Uemura et al., 2004; Chatre et al., 2005; Sanderfoot, 2007; Bubeck et al., 2008). In general, a Qa-SNARE is the core SNARE that regulates a SNARE complex formation at the target membrane. Interestingly, several Qa-SNARE null mutants have been reported to be lethal, supporting that Qa-SNAREs are essential (Sanderfoot et al., 2001b). Two Qa-SNAREs (AtSYP81 and AtSYP31) have been shown to be involved in ER–Golgi traffic (Bubeck et al., 2008). When secretory and ER retention markers were used to investigate alteration of ER–Golgi traffic, it was found that AtSYP81 overexpression inhibited both anterograde and retrograde membrane traffic, while AtSYP31 overexpression only inhibited anterograde traffic (Bubeck et al., 2008). In yeast, the ortholog of AtSYP31 has been reported to interact with the yeast counterparts of AtSEC22 and AtMEMB11 (Tsui et al., 2001). Interestingly, in tobacco leaf epidermis a strong redistribution of Golgi proteins into the ER was also observed in conditions of overexpression of AtSEC22 or AtMEMB11 (Chatre et al., 2005), implicating also these proteins in traffic at the ER/Golgi interface. At least for AtSEC22, this may be a conserved function. For example, yeast Sec22p was found to have a role in both anterograde and retrograde traffic between ER and Golgi (Spang and Schekman, 1998). Furthermore, components of the COPII machinery in mammalian cells, Sec24a and Sec24b, were found to interact directly with Sec22p (Mancias and Goldberg, 2008). In plants, we do not know whether AtSEC22 interacts with either COPI or

Table 1 | Localization of SNAREs.

	ER/Golgi	Dual localization	Reference
Qa	AtSYP81		
	AtSYP31		
	AtSYP32		
Qb	AtSEC20		
	AtMEMB11		
	AtMEMB12		
	AtGOS11		
	AtGOS12		
	AtUSE11		
	AtUSE12		
Qc	AtSYP71	PM/endosome	Suwastika et al. (2008)
	AtSYP72		
	AtSYP73		
	AtBS14a		
	AtBS14b		
	AtSFT11		
	AtSFT12		
R	AtSEC22		
	AtSEC22-like		
	AtVAMP714		
	AtVAMP723		
TGN/ENDOSOME/VACUOLE			
Qa	AtSYP41		
	AtSYP42		
	AtSYP43		
	AtSYP21	PVC/vacuole	Uemura et al. (2010)
	AtSYP22	PVC/vacuole	Uemura et al. (2010)
	AtSYP23	Cytosol/PVC/vacuole	Shirakawa et al. (2010)
Qb	AtVTI11	PVC/vacuole	Ebine et al. (2008)
	AtVTI12		
	AtVTI13		
	AtVTI14		
Qc	AtSYP61	TGN/endosome/PM	Drakakaki et al. (2011)
	AtSYP51	PVC/vacuole	Sanderfoot et al. (2001a), Ebine et al. (2008)
	AtSYP52	PVC/vacuole	Sanderfoot et al. (2001a)
	AtSYP5-like		
	AtSYP5-like		
R	AtYKT61		
	AtYKT62		
	AtVAMP711		
	AtVAMP712		
	AtVAMP713		
	AtVAMP727	Endosome/PM/vacuole	Ebine et al. (2011)
PLASMA MEMBRANE			
Qa	AtSYP111		
	AtSYP112		
	AtSYP121		
	AtSYP122		
	AtSYP123		
	AtSYP124		
	AtSYP125		
	AtSYP131		
	AtSYP132		
Qb	AtNPSN11		
	AtNPSN12		
	AtNPSN13		
Qb + Qc	AtSNAP29		
	AtSNAP30		
	AtSNAP33		
R	AtVAMP721		
	AtVAMP722		
	AtVAMP723		
	AtVAMP724		
	AtVAMP725		
	AtVAMP726		
	TOMOSYNa		
	TOMOSYNb		

Localization of SNAREs are either experimentally investigated or predicted (Uemura et al., 2004; Sanderfoot, 2007; Saito and Ueda, 2009). SNAREs with multiple localization are specified in the table with references.

COPII; however, an essential role in ER/Golgi membrane traffic has been further supported by analyses of loss-of-function mutants. Specifically, the *atsec22* mutation was reported to affect Golgi morphology and cause ER retention of a plasma membrane (PM) SNARE in pollen (El-Kasmi et al., 2011). Similarly to mammalian cells, AtSEC22 might interact with COPII coat components; however, in general, an interaction between coat proteins and SNAREs has not been reported in plants yet. The *Arabidopsis* genome encodes a large number of genes for coat proteins, often outnumbering other eukaryotes isoforms (Robinson et al., 2007). Possibly, specific SNARE–COPII protein interactions may at least partially explain the diversification of the ER and Golgi SNAREs and coat proteins in plants.

Evidence is emerging that some of the plant SNAREs may have dual localization. For example, AtSYP71 is distributed both at the ER and PM. Although in conditions of overexpression AtSYP71 was found in the ER, AtSYP71 expressed using its endogenous promoter was found to localize at PM in the *Arabidopsis* root as well as ER and PM localization in the dividing root cells (Suwastika et al., 2008). This suggests that SYP71 might form at least two different SNARE complexes on the ER and PM, or that AtSYP71 is a SNARE for the ER–PM traffic during cell division. No AtSYP71 homolog has been identified in mammals, suggesting that AtSYP71 may be involved in plant-specific membrane traffic events. Thus, identification of other SNAREs in the AtSYP71 SNARE complex may clarify the nature of the plant-specific role of AtSYP71, perhaps by providing important insights on understudied traffic route(s) that may occur between the ER and PM.

Two types of electron-dense vesicles originating from the ER have been suggested for the transport of storage proteins or proteases to storage or lytic vacuoles in pumpkin seeds and castor bean (Hara-Nishimura et al., 1998; Toyooka et al., 2000; Hayashi et al., 2001). However, trafficking components required for budding and cargo selection in such traffic routes have not been identified yet. Proteomics analyses of these dense vesicles may reveal important clues on the machinery and SNAREs that allows membrane transport to plant-specific organelles such as the protein storage vacuole.

ROLE OF TGN, ENDOSOMAL, AND VACUOLAR SNAREs

At the TGN, endosome, and vacuoles, 21 SNAREs (six Qa-SNAREs: three AtSYP4 and three AtSYP2; four Qb-SNAREs: AtVTI1; five Qc-SNAREs: AtSYP61, three AtSYP5, and two AtSYP5-like proteins; six R-SNAREs: two AtYKT6, three AtVAMP71, and AtVAMP727) have been identified (Uemura et al., 2004; Saito and Ueda, 2009; Shirakawa et al., 2010). The TGN is a tubular and vesicular organelle facing the *trans* side of the Golgi apparatus. Mounting evidence supports that the TGN represents a cross-road for post-Golgi protein traffic because it appears that vesicles containing vacuolar or secretory cargo can bud from the TGN, but also that endocytic markers such as the dye FM4-64 can be internalized to the TGN (Nakamura et al., 1993; Ahmed et al., 1997; Dettmer et al., 2006; Toyooka et al., 2007; Scheuring et al., 2011). Thus, complex vesicle budding and fusion events take place at the TGN, and it is likely that membrane transport is highly regulated at this organelle. In this view, specific SNAREs should facilitate anterograde or retrograde traffic between the TGN and endosomes, vacuoles, and PM. In particular, two Qa-SNAREs, AtSYP41 and AtSYP42 were found to form separate complexes in distinct TGN domains (Bassham et al., 2000). Furthermore, the corresponding knock-out mutants were found to be gametophytic lethal, suggesting that these SNAREs have specific and essential functions (Sanderfoot et al., 2001b). Recently, another SNARE, AtSYP61, has been implicated in traffic at the TGN. AtSYP61 is a component of the AtSYP4 SNARE family complexes and it is involved in salt and drought stress tolerance (Sanderfoot et al., 2001a; Zhu et al., 2002). Proteomic analysis of vesicles containing AtSYP61 has identified trafficking components at the TGN and PM along with enzyme cargos (Drakakaki et al., 2011). These results suggest that AtSYP61 has possibly a dual role as a t-SNARE at the TGN but also as a SNARE for TGN–PM traffic. Previously, AtSYP42 was co-immunoprecipitated with AtSYP61 (Sanderfoot et al., 2001a), but AtSYP42 was not found in the proteomic analysis in contrast to previous results. It would be interesting however to assay the proteome of the vesicles containing either AtSYP41 or AtSYP42 because we may learn about the function of AtSYP41 and AtSYP42, and, perhaps, determine whether the TGN exists as a uniform compartment or whether there may be TGNs with different composition due to specific functions or maturation stages.

Other SNAREs have been localized in post-Golgi routes. For example, three AtSYP2 family members, AtSYP21, AtSYP22, and AtSYP23, have been shown to localize on the prevacuolar compartment (PVC), vacuole, and cytoplasm, respectively. Individual single mutants are viable, with only a gravitropic defect reported for the *atsyp22* mutant (Yano et al., 2003). However, the *atsyp21*/*atsyp22* double mutant is known to be lethal (Shirakawa et al., 2010). A complete complementation of *atsyp22* with *AtSYP21* under *AtSYP22* promoter suggests that AtSYP21 and AtSYP22 may have redundant functions (Uemura et al., 2010). Overexpression of SYP21 resulted in homotypic fusion of PVC as well as the accumulation of vacuolar cargo in the PVC and partial secretion of vacuolar proteins (Foresti et al., 2006), suggesting that overexpression of SYP21 inhibits anterograde trafficking in the PVC–vacuole route. These observations open the question on the molecular basis for the role of AtSYP21 in two different biological events. In other words, it would be interesting to test whether vacuolar trafficking defects and homotypic fusion of PVC observed in conditions of AtSYP21 overexpression are due to the collapse of one or multiple fusogenic machineries. AtSYP23 has a similar protein sequence with AtSYP21, but it does not have transmembrane domain. AtSYP23 can make a SNARE complex with AtVTI11 and AtSYP5, and high expression of AtSYP23 can complement an *atsyp22* mutant (Shirakawa et al., 2010). Thus, AtSYP23 may function in vacuolar trafficking like AtSYP21 and AtSYP22. Considering the lack of transmembrane domain in AtSYP23, AtSYP23 may function by specific manner differently from other Qa-SNAREs. Therefore, either other regulatory proteins may recruit AtSYP23 at the active site for the SNARE complex formation or that AtSYP23 may interact with a preformed SNARE complex. *In vitro* liposome fusion assays may allow distinguishing the two models.

Similar to AtSYP61, members of the AtVAMP71 family (AtVAMP711, AtVAMP712, AtVAMP713, and AtVAMP714) have been found to be involved in drought stress response by regulating stoma closure (Leshem et al., 2010). Stoma aperture is directly regulated by the volume of the vacuole (Blatt, 2000; Sirichandra et al., 2009). Therefore, the AtVAMP71 family may be involved in membrane fusion to tonoplast or vesicle budding from vacuole so as to control the size of vacuole through modulating the tonoplast size. So far, the composition of the AtVAMP71 family complexes has not been determined, but the presence of three AtVAMP71 SNAREs (AtVAMP711, AtVAMP712, AtVAMP713) on the tonoplast suggests that these SNAREs could have either overlapping functions or that they may form distinct SNARE complexes on the tonoplast for tissue- and developmental-specific roles. Another R-SNARE, AtVAMP727 is localized on the endosome/PVC and PM (Uemura et al., 2004; Ebine et al., 2008, 2011). It forms a complex with AtSYP22, AtVTI11, and AtSYP51 on the PVC/vacuole and forms a complex with AtSYP121 at the PM (Ebine et al., 2008, 2011). Roles in vacuolar trafficking was shown that in the *atsyp22/atvamp727* double mutant, storage vacuolar cargo such as 2 s albumin was secreted (Ebine et al., 2008). The double mutant contained multiple small vacuoles instead of large vacuoles found in wild-type and in *atvamp727* and *atsyp22* single mutants (Ebine et al., 2008), supporting that AtSYP22 and AtVAMP727 may form a SNARE complex for membrane fusion between PVC and vacuole. In addition, Rab-GTPase, Ara6 has been identified to regulate the formation of AtVamp727 SNARE complex with AtSYP121 at PM under salt stress (Ebine et al., 2011), suggesting AtVAMP727 has another role in PM, presumably triggered by salt stress. These

results are important milestones in our understanding of vacuole biogenesis and stress response. Analyses of the diverse SNARE complexes at the tonoplast will provide further valuable information about vacuole biogenesis and vacuolar trafficking pathways possibly in relation to cell type specificity, along with plant development and growth, and plant may have developed specific traffic route to overcome environmental stress.

ROLE OF PLASMA MEMBRANE SNAREs

A total of 23 SNAREs (nine Qa-SNAREs: two AtSYP11, five AtSYP12, and two AtSYP13; three Qb-SNAREs: AtNPSN1; three Qb + Qc-SNAREs: AtSNAP29, AtSNAP30, and AtSNAP33; eight R-SNARE: six AtVAMP72 and two Tomosyn) have been localized at the PM (Uemura et al., 2004; Sanderfoot, 2007). A large number of Qa-SNAREs at the PM may allow the delivery of different types of vesicles to the PM in response to specific development and biotic/abiotic cues. For example, it has been shown that AtSYP121 is involved in the regulation of K^+ channels and resistance against barley powdery mildew (Collins et al., 2003; Sutter et al., 2006b; Honsbein et al., 2009). However, an *atsyp122* mutant did not show any defects on non-host resistance, contrary to the *atsyp121* mutant, although both AtSYP121 and AtSYP122 are involved in the regulation of salicylic acid and jasmonic acid (Assaad et al., 2004; Zhang et al., 2007). Growth defects were only seen in the *atsyp121/atsyp122* double mutant (Assaad et al., 2004). Therefore, AtSYP121 and AtSYP122 might have overlapping functions in plant growth and development, but distinct roles in disease resistance, presumably by mediating fusion of different types of vesicles containing cargo to resist pathogens.

Two AtSYP121 SNARE complexes have been identified with AtSNAP33 and AtVAMP721 or AtVAMP722 as components in the complexes (Kwon et al., 2008). AtSNAP33 also forms a SNARE complex with AtSYP111 and individual mutants showed incomplete cytokinesis, a process that requires massive vesicle traffic at the cell plate (Lukowitz et al., 1996; Lauber et al., 1997; Heese et al., 2001). The existence of multiple AtSNAP33 complexes suggests that this protein may have multiple roles in plant development, and transport machinery of AtSNAP33 to either cell plate during cell division or PM may rely on specific traffic machinery. For example, investigation on the trafficking of AtSYP111 during cytokinesis has established that AtSYP111 is delivered to the cell plate by secretory pathways. In mitotic cells, AtSYP111 was found to localize at the TGN and cell plate, and inhibition of ER–Golgi trafficking accumulated AtSYP111 in the ER (Reichardt et al., 2007; Chow et al., 2008). These results suggest that AtSYP111 traffics through the secretory pathway, and that distribution of AtSYP111 at the cell plate depends on a clathrin and dynamin-related protein A dependent endocytosis (Boutte et al., 2010). However, there is no evidence that AtSYP111 is directly delivered from TGN to cell plate. Considering endocytosis dependent polar distribution of auxin transporter (PIN1; Dhonukshe et al., 2008), AtSYP111 may be secreted to PM first by the default pathway and then relocalized to the cell plate by endocytosis.

Recent discovery for a role of Qa-SNAREs (AtSYP11, AtSYP12, and AtSYP13 families) at the PM supports a diversified but redundant function of Qa-SNAREs at this compartment. It was found that *AtSYP132* could complement an *atsyp111* mutant (Reichardt et al., 2011). Also, replacement of the SNARE domain of AtSYP111 with that of AtSYP132 rescued the *atsyp111* mutant. However, neither AtSYP121 nor the AtSYP111 chimera containing the SNARE domain of AtSYP121 was able to complement the *atsyp111* mutant (Reichardt et al., 2011). These results support that while AtSYP132 may have an overlapping function with other SNAREs at the PM, AtSYP111, and AtSYP121 may have distinct roles, perhaps by forming highly specialized complexes. For example, although AtSYP111 and AtSYP121 interact with SNAP33 (Heese et al., 2001; Kwon et al., 2008), AtSYP111 may form a SNARE complex with different R-SNAREs. Identification of the R-SNAREs in the AtSYP111 and AtSYP121 complexes along with structural analyses of the SNARE complexes by X-ray crystallography may provide fundamental information on the difference between AtSYP111 and AtSYP121 SNARE complexes.

CONCLUSION

The large number of SNAREs in *Arabidopsis* implicates diversified roles of SNARE complexes in membrane traffic events during growth and development as well as responses to biotic and abiotic stresses. It is also important to consider that other proteins may contribute to the function of SNAREs, thus increasing the level of complexity as well as fidelity and regulation of the biological processes mediated by SNAREs. For example, the Sec1/Munc18 (SM) protein family was reported to regulate a SNARE complex formation by controlling a Qa-SNARE in mammalian and yeast cells (Malsam et al., 2008). Similarly in plants, AtSYP41 and AtSYP42 form distinct SNARE complexes at different subdomains of TGN with AtSYP61, AtVTI12, and a SM protein, AtVPS45 (Bassham et al., 2000; Sanderfoot et al., 2001a). *AtVPS45* RNAi plants showed decreased amount of AtSYP41 compared to wild-type, suggesting that AtVPS45 may be important for the stability of AtSYP41 (Zouhar et al., 2009). These findings support that SM proteins regulate SNARE-mediated membrane fusion, as well as stability or turnover of SNAREs. In *Arabidopsis*, six putative Sec1-like proteins in the SM protein family have been predicted to exist (Schwacke et al., 2003). Thus, investigation of the uncharacterized SM proteins will be necessary to define one of the possible regulatory mechanisms of SNARE complexes. Related to this, tethering factors and GTPases can play important roles in membrane fusion (Malsam et al., 2008). In yeast, tethering factors are involved in the SNARE complex assembly and docking for membrane fusion by interacting with GTPases (Price et al., 2000; Seals et al., 2000; Shorter et al., 2002), supporting that SNARE complex assembly is a multifaceted process based on the interplay of multiple components. Therefore, a study focused on SNARE specificity in vesicle trafficking should take into account an analysis of several components for membrane fusion to better define an overall picture of the function of the SNAREs.

So far, valuable approaches to characterize the role of SNAREs have been developed and have provided important data in plants. However, there are still several unsolved questions on the function of SNAREs and the nature of the complexes that they can form *in vivo* in plant cells. *Arabidopsis* has a large number of SNAREs and several SNARE complexes that partially share the same components. We need to understand the physiological relevance of the number of SNARE and of the SNARE complexes.

With no doubt, we are living in an exciting moment for research in plants thanks to a wealth of genetics, genomics, and molecular resources. *In vitro* fusion assays using SNAREs and other regulatory proteins may help specify the roles of SNARE complexes with similar but not identical components. The combination of *in vitro* and *in vivo* studies on cargo trafficking and membrane fusion will also provide important insights into the mechanisms and regulatory pathways of vesicle transport along with a better understanding of their role in plant growth, development, and response to stress.

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