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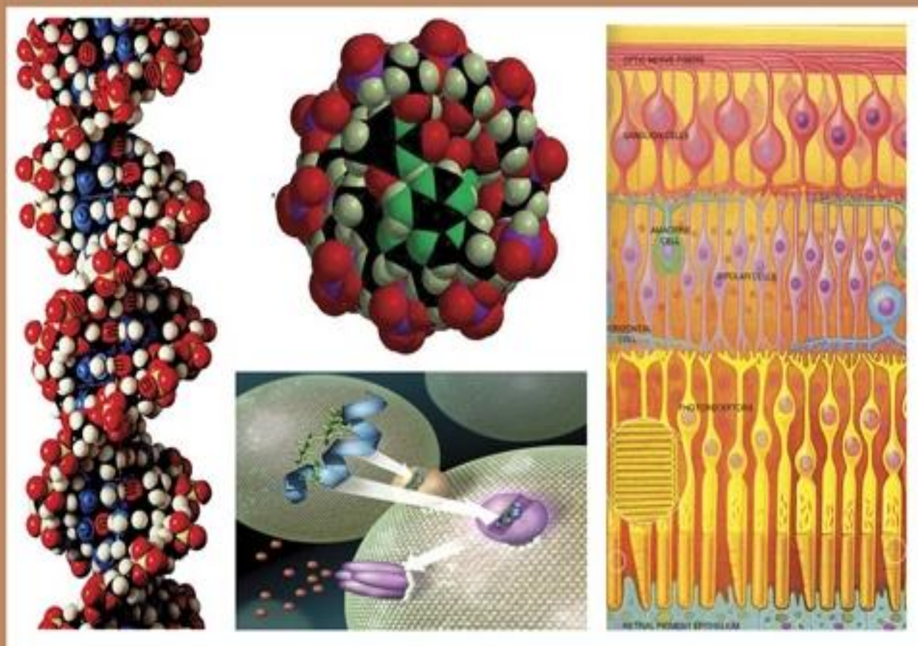

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Recent Advances in Synergy Among *SNARE* Proteins and Multi-Subunit Tethering Complexes (MTCs) in Vesicle Trafficking and Plant Development

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ABSTRACT

Plants comprise an expanded endomembrane system, and transport within the network requires well-organized and accurate vesicle transport. Tethering complexes facilitate the early, exact contact among donor and acceptor membranes, operate to bring vesicles into a closer proximity for trans-SNARE complex assembly docking; these are classified as either long coiled-coil proteins or multi-subunit tethering complexes (MTCs). Numerous MTCs that function at different membrane trafficking steps have been recognized, where they function as significant interfaces between SNARE proteins, Rabs, and phosphoinositides. SNARE proteins assemble into complexes that catalyze the fusion between a donor and a target membrane. Studies of the diverse SNARE proteins provided further valuable information about vacuole biogenesis and vacuolar trafficking pathways related to cell-type specificity, plant development, growth, and the plant developed a specific traffic route to overcome environmental stress. In conclusion, tethers' selective recruitment during membrane fusion is controlled via diverse small GTPases, such as those in the RAB family. The MTCs promote SNARE complex assembly by direct interactions of MTC subunits with Q-SNAREs. A subset of MTC subunits exploits structurally similar CATCHR domains to mediate inter-subunit interactions as well as SNARE protein interactions. MTCs are subdivided into CATCHR (complexes associated with tethering containing helical rods: Dsl1, COG, GARP, EARP, and exocyst) and non-CATCHR (TRAPP I, II and III, HOPS and CORVET) complexes based on the structure of their subunits. This review summarized new information about SNARE proteins and tethering complexes, highlight new insights about their function, and discuss current debates and future perspectives.

INTRODUCTION

1-All about SNAREs:

SNARE (soluble N-ethylmaleimide-sensitive fusion protein attachment receptors) small molecule protein composed of 100-300 amino acids.

Its structure is quite simple but plays a vital part in the transport of vesicles, confirms the transport of vesicles, and target membrane-specific recognition (Söllner *et al.,* 1993). SNARE proteins can be divided into two categories depending on the positioning: V-SNARE positioned on the transport vesicles and t-SNARE positioned on the target membrane. When the transport vesicles move along the cytoskeleton close to the target membrane, v-SNARE on the transport vesicles and t-SNARE on the target membrane interact, forming a multi-subunit SNARE complex to promote the membrane fusion process (McNew *et al.,* 2000). SNARE proteins can also be divided into four types depending on the core amino acids (glutamic acid and arginine) of the hydrophobic heptapeptide sequence of SNARE motif: 1 R-SNARE and 3 Q-SNARE. In mammals, a typical SNARE complex consists of Qa-(syntaxin1 positioned on the target membrane-like), Qb-(N-terminal half of SNAP25 like), Qc-(C-terminal half of SNAP25 like) SNARE, and R-SNARE (VAMP/synaptobrevin) on the donor membrane composition (Hong & Lev, 2014). Most R-SNARE is equivalent to v-SNARE; most Q-SNARE is equivalent to t-SNARE. However, there are exceptions, mammals R-SNARE Ykt6 and Sec22B as t-SNARE, while GS15, Bet1, and Slt1 as v-SNARE function SNARE motif interactions of each subunit form a four-Helix complex (Bock, Matern, Peden, & Scheller, 2001; Hong & Lev, 2014; Martens & McMahon, 2008). This form of complex composition has a certain conservatism in yeast, mammals, and plants (Sutter, Campanoni, Blatt, & Paneque, 2006). Syntaxin 1 in mammals was originally identified as Qa-SNARE, so Qa-SNARE is often referred to as syntaxins (Carr & Rizo, 2010). Qa-SNARE has a unique structure: three alpha-helices at the N-end, connected to SNARE motifs through a flexible sequence, and the C-end is a hydrophobic structure that can be anchored to the membrane (Carr & Rizo, 2010; Denic, 2012). The α-Helix can be folded back into SNARE motifs to form a“closed” conformation without fusion capability or separated from SNARE motifs to form an “open” conformation with fusion capability (Südhof & Rothman, 2009). Both Qb-SNARE and Qc-SNARE have a unique N-terminal helical structure connecting the unique SNARE motifs; C-terminal is also a hydrophobic structure. R-SNARE can be divided into two types depending on the N-terminal extension, the VAMP family, and the“longin” subfamily. The VAMP family contains VAMP1, VAMP4, VAMP5, and the “brevin” subfamily VAMP2 (synaptobrevin), VAMP3 (cellubrevin), and VAMP8 (endobrevin). R-SNARE belongs to the“longin” subfamily, such as VAMP7/TI-VAMP, SEC22, YKT6, and yeast protein Nyv1 belonging to this category. The N-terminal of these R-SNARE contains "longin domain" (Rossi *et al.,* 2004; Wen *et al.,* 2006). A functional SNARE complex is usually composed of specific 3 Q-SNARE and 1 R-SNARE by SNARE motif combined. When the transport vesicles are tied to the target membrane, the transport vesicles and the SNARE on the target membrane recognize each other to form the SNARE complex. SNARE complex has three binding forms: the first is positioned on the target membrane Qa - SNARE, Qb - SNARE, Qc-SNARE first combined to form a complex and then R-SNARE vesicles on the binding; the second is R-SNAREs and Qa-SNARE first interaction, conformational changes, exposing Qb - SNARE, Qc-SNARE affinity binding sites, and then Qb - SNARE, Qc-SNARE affinity binding sites. The SNARE forms a complex; the last is relatively simple if four SNARE proteins' simultaneous presence forms a complex (Jahn & Scheller, 2006). SNARE has certain conservatism in yeast, mammals, and

plants; there are 65 kinds of SNARE proteins in the model plant Arabidopsis, distributed in various transport routes (Jahn & Scheller, 2006; A. Sanderfoot, 2007). These SNAREs play an important role in the transport of vesicles in complex intimal systems (Jahn & Scheller, 2006). The plant SNARE family's current study found that it often appears functional redundancy, but there is a certain specificity. SNARE is involved in various biological processes, including growth, metabolism, stress, and immunity (N. C. Collins *et al.,* 2003; El Kasmi *et al.,* 2013). Fluorescence subcellular localization and proteomics analysis showed that on the endoplasmic reticulum and Golgi, there are 21 SNARE protein: 3 QA-SNARE, AtUfe1 and 2 AtSYP3; 5 Qb-SNARE, AtSEC20, 2 AtMEMB1, 2 AtGOS1; 9 Qc-SNARE, 2 AtGOS1; 9 Qc-SNARE, 2 AtGOS1; 9 Qc-SNARE, 2 AtGOS1; 9 Qc-SNARE, 2 Atgos1; 9 Qc-SNARE AtSYP7,2 atuse1, 2 AtBS14 and 2 AtSFT1; 4 R-SNARE, 2 ATSEC22, AtVAMP714 and AtVAMP723 (Bubeck *et al.,* 2008; Chatre, Brandizzi, Hocquellet, Hawes, & Moreau, 2005; El Kasmi *et al.,* 2013; Uemura *et al.,* 2004). In general, Qa-SNARE is the core of the SNARE complex; some Qa-SNARE deletion mutations lead to plant death, indicating that this Qa-SNARE is essential for plant survival (A. A. Sanderfoot, Pilgrim, Adam, & Raikhel, 2001).

2-The Expression of SNARE Protein-Encoding Genes in Arabidopsis Developmental Stages:

In Arabidopsis, there are 64 SNARE protein-coding genes expressed in 79 orangs during Arabidopsis' developmental stages; these SNARE-coding genes during the Arabidopsis development stage show a wide variety of expression levels and different regulations. In Arabidopsis, the SNARE encoding genes are grouped and based on their expression in various organs. In leaf as well as in internode, there are five SNARE protein-coding transcripts expressed (SNAP33, SYP121, SYP22, VAMP723 and VAMP722). There are two SNARE-encoding genes (VTI13 and SYP112) that are richly expressed in flowers. In another, almost twenty SNARE genes are significantly expressed (USE12, SYP72, SYP123, SYP124, SYP131, SYP31, SYP43, SYP81, SYP61, SYP125, VAMP725, VAMP711, VAMP725, NPSN13, NPSN11, COS11, YKT62, SEC20, SEC22, and SNAP30*)*. Four Arabidopsis genes (SYP124, SYP131, SYP123 and SYP125) are essential for the pollen tube growth during exocytosis (Ichikawa *et al.,* 2014; Kato, He, & Steger, 2010; Silva, Ul-Rehman, Rato, Di Sansebastiano, & Malhó, 2010; Slane, Reichardt, El Kasmi, Bayer, & Jürgens, 2017; Ul-Rehman, Silva, & Malhó, 2011). The one SNARE gene (SEC20) is necessary for the gametophyte development as well as maintenance of Golgi-stack integrity in Arabidopsis (El-Kasmi *et al.,* 2011). There are about nine SNARE protein-coding genes abundantly expressed in the silique and seeds. Five SNARE protein-coding genes are abundant in the meristem and flower (SYP132, SYP32, SYP71, GOS12, and BS14b). The four SNARE protein-coding genes are strongly expressed in anther, silique, and seeds (SYP22, MEMB12, SFT12, and SYP42), and seven genes are highly expressed in meristems (VTI12, NPSN12, VAMP713, VAMP721, VAMP728, SYP111, and SYP24) (Gu, Brennan, Wei, Guo, & Lindsey, 2020; Klepikova, Kasianov, Gerasimov, Logacheva, & Penin, 2016).

3-Importance of SNARE Interaction With Tethered Complexes During Vesicle Transport:

The connection of cells, and compartments, relies upon membrane structure and function, which is vital for growth, progression, and responses toward environmental stress for the plant and animal. The controlled dynamics of membranes, and the related proteins, are facilitated via the membrane trafficking

system. The membrane trafficking system in plants includes three essential pathways: (i) biosynthetic secretory pathway, (ii) endocytic pathway, and (iii) the vesicle transport pathway. The organelles involved in all methods use small membrane-enclosed transport vesicles to exchange molecular information. There are four vital steps in the vesicle trafficking system, budding, vesicle movement, tethering, and fusion (Fig. 1) (Gu, Brennan, *et al.,* 2020; Uemura & Ueda, 2014). Through the budding process, coat proteins and GTPases form vesicles in the donor compartment and distort the native membrane till the vesicle is released through scission. The cargo and v-SNAREs are assimilated in budding vesicles via binding on coat subunits; the released vesicle during the movement phase travels to the acceptor compartment via the combining of cytoskeletal motors, namely kinesin and myosin (Matanis *et al.,* 2002; Shorter, Beard, Seemann, Dirac-Svejstrup, & Warren, 2002). After that, the tethering and docking factors function in combination with Rab GTPases, and the SNAREs tether at the acceptor membrane to the vesicle (Cai, Reinisch, & Ferro-Novick, 2007). At the last step, the t-SNARE complex is designed by the single v-SNARE molecule; after that, the t-SNARE complex lets the vesicle recognize the objective compartment and finalize membrane fusion as well as delivery of cargo (Bassham, Brandizzi, Otegui, & Sanderfoot, 2008; Cai *et al.,* 2007). Tethered to stay factor-mediated transport vesicles in initial contact with the target membrane, the transport vesicles tethered to remain on the target membrane, to identify whether the vesicles can be fused with the target membrane. Tethering factors interact with the corresponding transport vesicles to regulate membrane fusion processes. Tethered element has certain conservatism in plants, animals, and fungi, more thorough research in yeast and mammals, Arabidopsis tethered factor research is still in its infancy. Tethering factors can be divided into long spiral protein molecules and multi-subunit tethering complexes (MTCs) (Cai *et al.,* 2007). Currently, identified long curled tethering factors include positioning in the Golgi body and endosome. Placed on the Golgi Golgins protein family (probably having 20 members) mainly includes GM130, Golgin-45, Golgin-97, Golgin-245, and p115, etc. (Barr & Short, 2003), regulated by the Rab and Arl family GTPases, between the membrane on the Golgi, the role of tethered between the membrane and the cytoskeleton. Positioning on the inner body is mainly EEA1, Rabaptin-5, Rabenosyn-5, and Rabip4 (Aoki et al., 2009; Gillingham & Munro, 2003).

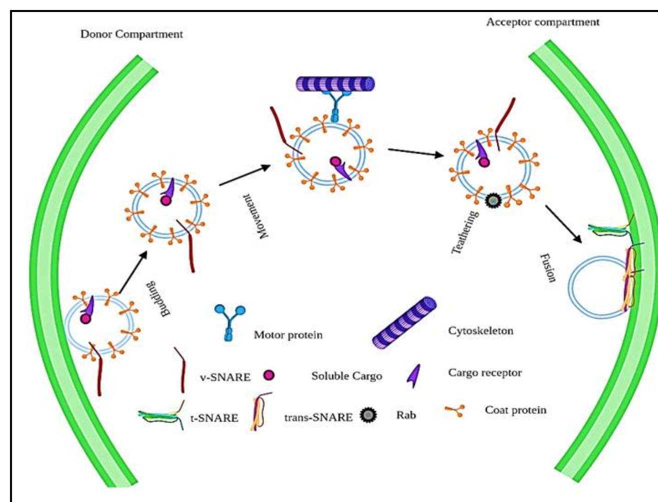

Fig. 1: (Cai et al., 2007; Uemura & Ueda, 2014): Tethering and SNARE through vesicle trafficking.

The nine kinds of multi-subunit complexes, namely CORVET (class C core vacuum/endosome tethering), HOPS (homotypic fusion and protein sorting)and GARP (Golgi-associated retrograde protein)/VFT (Vps fifty-three, Vps-vacuum protein sorting), TAPPI (transport protein particle), Dsl1 (depends on SLY1-20), TRAPPll, TRAPPlll, COG (preserved oligomeric Golgi) and exocyst, which function in different parts (Fig. 2) (Çivril *et al.,* 2010; Yu & Hughson, 2010).Multi-subunit complex (MTCs) is divided into two main categories, including helical complex (CATCHR) and Class C vacuole protein sorting receptor (Vps) complex. The Dsl1, COG, GARP belong to the CATCHR family; although the sequence homology is low, they all contain a conservative helical beam structure (Peterson & Emr, 2001). The HOPS and CORVET belong to Class C vacuole protein sorting receptors, regulating trans-Golgi to the endosome/lysosome tethering process (Vukašinović & Žárský, 2016). The TRAPP complex I/II/III is also considered a tethered factor, but TRAPP complex I/II/III has a small GTPase factor function compared with another tethered factor. Since then, studies have found that most of the tethering factors are Rab or Ar1 effector factors, in GTP-bound directly interact with GTPases (Asensio *et al.,* 2011; Sohda *et al.,* 2007), such as CORVET, HOPS, COG, exocyst (Leshem et al., 2006; Sohda *et al.,* 2010).Tethered retention factor through different mechanisms associated with different endometriosis, such as through specific domains (such as some Golgin family GRIP domain), by binding to phospholipids interaction with some small GTPases, etc. (Barr & Short, 2003; Gillingham & Munro, 2003). Although MTCs and long spiral protein molecules are involved in the vesicle transport tethered stay process, it is speculated that long spiral protein molecules may be involved in tethered stay initial dynamic stage because it can form a low affinity instantaneous reversible interaction (Asensio *et al.,* 2011). The MTCs may be involved in the regulation of late SNARE assembly, MTCs on the target membrane. Data show that Tip20p plays a role in identifying capsid proteins or the formation of SNARE complexes, or in both (Spang, 2012).Recent results also suggest that the process of decontamination of COPII vesicles in the endoplasmic reticulum to the Golgi pathway may occur only in or after the tethering process with the Golgi body (Lord *et al.,* 2011). The excess COPII coat component Sec23p does not affect COPII vesicles' formation in the endoplasmic network and COPII vesicles and Golgi membrane tethering activity, but in the late membrane fusion process with Golgi is suppressed (Barlowe, 1997).Therefore, the coating composition may play the identification role by tethering to leave the complex to complete the initial identification and the vesicle closer to the target membrane. Tip20p and Sec39p on tethered complex and endoplasmic reticulum from the connecting role and Dsl1p is a bridge connecting Tip20p and Sec39p and is responsible for identifying the coat complex subunits in particular α and δ-COP (Andag & Schmitt, 2003; Diefenbacher, Thorsteinsdottir, & Spang, 2011; Kraynack *et al.,* 2005; Meiringer *et al.,* 2011; Ren *et al.,* 2009; Tripathi, Ren, Jeffrey, & Hughson, 2009).Therefore, Dsl1p is most likely to endoplasmic network COPI vesicles closer and make it with the subunit's t-SNARE phase action. This tethering process is not only essential for the fusion process of vesicles and endoplasmic reticulum, but it may also be a key step to promote or even lead to COPI vesicles to clothing quilt. Schmitt's laboratory plotted Dsl1p on the site of interaction with the coat quilt protein and found that these sites and the coat quilt complex necessary to stabilize the site overlap (Zink, Wenzel, Wurm, & Schmitt,

2009). The Deletion of Dsl1p causes COPI vesicles to cluster and remain in the cytoplasm, unable to fuse with the target membrane. More interestingly, α-and δ-COP binding sites on Dsl1p are very close, indicating that at a particular time, only one subunit can be combined with Dsl1p.Therefore, there may be a transfer mechanism: Dsl1p first contact with the outer layer of the coat is Composite α-COP occurs, and then, Dsl1p and responsible for cargo identification and binding of the coat is composite inner layer δ-COP binding (Cosson, Demolliere, Hennecke, Duden, & Letourneur, 1996).In other words, Dsl1p contact with α-COP is to identify each other; the next binding with δ-COP can weaken the interaction of cargo protein and caprolactone protein, help caprolactone complex from the vesicle. Through these processes, the v-SNARE protein in the transport vesicles buried under the coat is exposed and then interacts with the t-SNARE on the endoplasmic reticulum to form a complex, promoting vesicle anchoring and membrane fusion (Uemura & Ueda, 2014). About Sec39p in the tethering to stay in the specific function is not very clear; due to the instability of Sec39p, its function is difficult to study in vitro (Tsui, Tai, & Banfield, 2001). In vivo study data support sec39p tethering function, when COPI vesicles close to the target membrane, Sec39p, and Use1p interaction promote SNARE complex (Kraynack *et al.,* 2005). MTCs on different organelles, SNARE interact with, GARP, DSL1, and COG complex subunits, on the endoplasmic reticulum or Golgi can simultaneously interact t-SNARE and enhance the stability of t-SNARE sub-complex assembly (Laufman, Hong, & Lev, 2013; Pérez-Victoria & Bonifacino, 2009; Pérez-Victoria *et al.,* 2010; Ren *et al.,* 2009). The MTC plays a vital role in recruiting SNARE subunits; the t-SNARE sub-complex formation is an intermediate step in forming the t-SNARE complex (Malsam, Kreye, & Söllner, 2008); MTC in the recruitment of SNARE subunit is conducive to the late assembly of SNARE driven membrane fusion process. Still, this process also avoids the uncorrelated SNARE in the wrong assembly of cells. Recent studies have shown that the COG4 subunit is actively involved in the assembly of paired SNARE complexes on the Golgi body, preventing improper assembly (Peng & Gallwitz, 2002). The exocyst subunits Sec6 and Sec9 interact to prevent the formation of Sec9-Sso1 t-SNARE complexes before the exocyst is raised to Sec1. The MTCs can also inhibit the assembly of non-fused SNARE on biofilm or premature assembly of fused SNARE. In vitro studies have shown that SM protein can prevent the assembly of non-fused SNAREs, such as SM protein Sly1p, by interaction with Sed5p (Stx5 in mammals) to prevent its assembly with non-fused SNARE (Peng & Gallwitz, 2002). In addition to the SNARE recruitment function, the tethered retention factor can also enhance SNARE protein's stability or SNARE complex, thus affecting the SNARE pin's assembly. The COG6 can interact directly with Stx6 and stabilize Stx6. The deletion of the COG6 subunit leads to abnormal degradation of Stx6 by the proteasome. Affecting the assembly of the Stx6-Stx16-Vti1a-VAMP4 SNARE complex hinders the reverse transport of lysosomes to the Golgi body (Laufman, Hong, & Lev, 2011). Golgi SNARE GS28 and GS15 abnormal degradation by proteasome also appear in other cog subunits mutant cells (Oka, Ungar, Hughson, & Krieger, 2004). The latest study found that GS28 and COG4 interaction (Laufman *et al.,* 2013).MTCs and SNARE these interactions enable SNARE conformational changes to protect it from degradation, as previously proposed SM protein Sly1 can interact with the endoplasmic reticulum t-SNARE Ufe1p, Ufe1p can be protected from ERAD degradation (Braun & Jentsch, 2007), Vps45p and yeast Stx16 homologous protein Tlg2p interaction to

protect it from proteasome degradation (Bryant & James, 2001). The HOPS complex has different mechanisms to stabilize the trans-SNARE complex, inhibit Sec17p/Sec18p (SNAP/NSF) dismantling (Xu, Jun, Thompson, Yates, & Wickner, 2010). The HOPS interacts with various vacuole SNARE to promote SNARE complexes' formation, HOPS Capable of interacting with t-and v-SNARE inhibit Sec17p and Sec18p and another SNARE disassembly (K. M. Collins, Thorngren, Fratti, & Wickner, 2005). As described above, the tethering factor can induce SNARE recruitment by multiple interactions, stabilize the SNARE complex, or activate the SNARE complex assembly by interacting with the SM protein (Rizo & Südhof, 2012; Shen, Tareste, Paumet, Rothman, & Melia, 2007). However, the tethered factor and SNARE impact is mutual; in some cases, SNARE affects the tethered factor's positioning. SNARE can enhance HOPS and liposomes' link and stabilize the interaction between HOPS and vacuoles (Stroupe, Hickey, Mima, Burfeind, & Wickner, 2009). Similarly, the interaction of DSL1 with the endoplasmic reticulum SNARE may also be necessary for DSL1 to be associated with the membrane because DSL1 does not interact with the Rab small GTPase mediated vesicle recruitment (Diefenbacher *et al.,* 2011; Ren *et al.,* 2009). DSL1 interacts with the COPI subunit (Andag, Neumann, & Schmitt, 2001), and HOPS interacts with the APL5 subunit of the AP-3 coat (Heider & Munson, 2012). The interaction of these capsid proteins with SNARE may be necessary to coupling tethered factors into the membrane fusion process. In yeast, t-SNARE positioned on the endoplasmic reticulum is Ufe1p, Use1p, and Sec20p, V-SNARE Sec22p positioned on the target membrane participate in retrograde transport from the Golgi to the endoplasmic reticulum, DSL1 complex by Tip20p and Sec39p and Sec20p and Use1p binding (Sacher, Kim, Lavie, Oh, & Segev, 2008). Mammalian homologous proteins of Tip20p and Sec39p are RINT1 and NAG, binding to SNARE p31 and BNIP1, respectively, to regulate retrograde transport of the Golgi to the endoplasmic reticulum (L. Li *et al.,* 2006). Multi-subunit tethering complexes (MTCs) plays important role in plant immunity (Table 1).

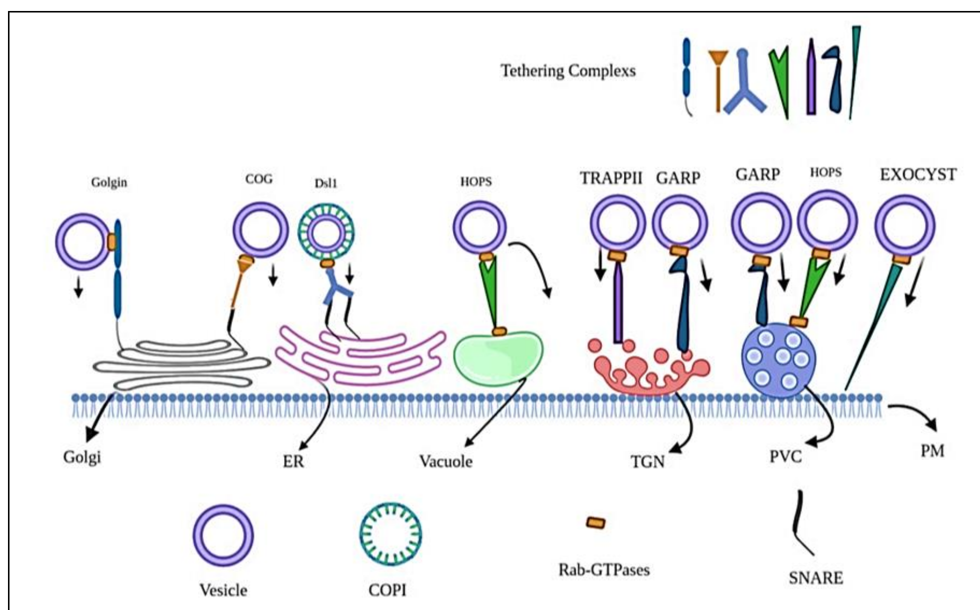

Fig. 2: (Ravikumar, Steiner, & Assaad, 2017): Distribution of tethering complexes in cellular compartments according to their location

Table 1: Distribution localization and functions of multi-subunit tethering complexes (MTCs) in plants

S.NO	MTCs	Functions	Localization	Trafficking	References
1	COG	Pollen tube growth, Embryo development and meristem organization	Golgi	Intra Golgi	(Ishikawa et al., 2008; Ostertag, Stammler, Douchkov, Eichmann, & Hückelhoven, 2013; Tan et al., 2016)
2	TRAPPII	Cytokinesis, Leaf venation patterns and Root hair tip growth	TGN	Post-Golgi membrane trafficking	(Jaber et al., 2010; Naramoto et al., 2014; Qi, Kaneda, Chen, Geitmann, & Zheng, 2011; Thellmann, Rybak, Thiele, Wanner, & Assaad, 2010)
3	DSL1	Storage protein transport, Enhanced sensitivity to salt stress, osmotic stress, heat stress and ER stress response	ER	Golgi to ER	(L. Li et al., 2013; L. Li et al., 2006; Zhao et al., 2013)
4	GARP	Pollen tube germination and growth; embryo development, heat and osmotic stress	TGN and PVC	PVC/Golgi	(Guermonprez et al., 2008; C.-F. Lee et al., 2006; Pahari et al., 2014; L.-C. Wang et al., 2011; Wu, Locy, Shaw, Cherry, & Singh, 2000)
5	HOPS	Vacuole biogenesis, Pollen tube penetration	Vacuole and PVC	PVC to vacuole	(Hao, Liu, Zhong, Gu, & Qu, 2016; Rojo, Gillmor, Kovaleva, Somerville, & Raikhel, 2001; Rojo, Zouhar, Kovaleva, Hong, & Raikhel, 2003)
6	EXOCYST	Pollen tube germination, growth, Cytokinesis, Vascular development, Trichome development, Response to pathogens and Penetration resistance	Plasma membrane	Secretion	(Fendrych et al., 2013; Fendrych et al., 2010; Kulich et al., 2015; S. Li et al., 2010; Y. Li et al., 2017; Tan et al., 2016; Vukašinović et al., 2017; Vukašinović & Žárský, 2016)

4-Role of SNAREs Abiotic and Biotic Stress Responses in Plants:

Inside the plants, cells compromise the physiological and molecular activities due to high salinity, ionic, and osmotic imbalance, which leads to a loss of the plant's competency (Macková *et al.,* 2013). This affects the plant activates and leads to a chain of mechanisms that decrease the loss of water in the cell, bring detoxification of ROS, and regulate the absorption of ions (Baral, Shruthi, & Mathew, 2015). That needs a fast mobilization of proteins towards the tonoplast and plasma membrane; subsequently, the ions gathered inside the vacuole or transferred to the extracellular medium via ion transporters and proton pumps include V-ATPase/ H+-ATPase (Pizarro & Norambuena, 2014). The transportation of proteins, lipids among various cellular compartments will primarily be carried out via membranous vesicles. Soluble N-ethylmaleimide-sensitive factor attachment protein receptor (SNARE) plays a vital function in membrane fusion, targeting and delivering proteins, soluble cargo, and proteins among the membranous compartments (Uemura, Ueda, & Nakano, 2012).

4.1. Importance of SNAREs in Abiotic Stress:

Plants' life cycles are affected by many abiotic stresses include high salinity cold, freezing, drought, heat, UV-B, and osmotic stresses. The presence of numerous SNARE genes in plants suggests that, at minimum, fraction of SNAREs infection involved in abiotic stress responses (A. Sanderfoot, 2007). Plants have developed ordered trafficking mechanisms through several SNAREs to uphold cellular homeostasis against environmental stresses, plant vacuoles, and trans-Golgi network function in plant responses to stressful environments. Several endosomal definite SNARE proteins, namely SYP51 VTI11 and SYP22, interact through various members in the VAMP71 family, which are involved in guiding the vesicle transport to the vacuole and plasma membrane (Ebine *et al.,* 2008; A. Sanderfoot, 2007). The SNARE proteins, namely Qa SNAREs and

R SNAREs, are involved mainly in endosomal trafficking via carrying cargos containing storage proteins and ROS to respond to abiotic stresses (Leshem, Golani, Kaye, & Levine, 2010). In Arabidopsis, the suppression of AtVAMP71 enhanced water loss and changed the control of stomatal opening as well as closing through unsuitable reactive oxygen species localization under drought stress (Leshem et al., 2010; Salinas-Cornejo, Madrid-Espinoza, & Ruiz-Lara, 2019). Arabidopsis plants heterologously overexpressing GhSNAP33 or GsSNAP33 showed increased drought tolerance (Nisa *et al.,* 2017; P. Wang *et al.,* 2018). Furthermore, SNARE proteins interacting with SNAP25 homologs in plants such as AtVAMP721/722 and NtSYP121 are regulated by abscisic acid for abiotic stress responses (Yi, Park, Yun, & Kwon, 2013). The AtVAMP7C genes' suppression includes AtVAMP711, AtVAMP712, AtVAMP713, and AtVAMP714 enhanced tolerance to salt stress (Gu, Fonseka, *et al.,* 2020; Leshem *et al.,* 2006). A study on the extreme halophyte Salicornia brachiate a novel salt-inducible gene SbSLSP S. brachiata SNARE-like superfamily protein (SbSLSP), confers salt, and drought tolerance (B. Singh, Khurana, Khurana, & Singh, 2018). In tobacco lines overexpressing of the SbSLSP gene shows higher tolerance to salt and drought stresses via modifying membrane stability, K^+/Na^+ ratio, and reactive oxygen species levels (D. Singh, Yadav, Tiwari, Agarwal, & Jha, 2016). The GsCBRLK interacting protein, GsVAMP72, is recognized as a vesicle-associated membrane protein in Glycine soja. The GsVAMP72 protein contains longin domain to its N-terminus end and belongs to the R-SNARE family. GsVAMP72 is extensively regulating plant responses to salt as well as ABA stresses. Overexpression of GsVAMP72 in Arabidopsis significantly reduced salt tolerance by altering the ionic content and down-regulating expression of stress-responsive genes, including RD29A and COR47, KIN1, COR15A, and RAB18. Furthermore, GsVAMP72 overexpression enhanced plant abscisic acid (ABA) sensitivity and rehabilitated ABA-responsive genes' expression levels (Nisa *et al.,* 2017; Sun *et al.,* 2013). The plants Qa-SNARE as well as the group of SYP4, these are localized on the trans-Golgi network (TGN), to regulate two pathways, the secretory and vacuolar pathways. With regards to the secretory role, the SYP4 proteins are essential for extracellular resistance to fungal pathogens. The phenotypes a *syp4*-mutant concerned with salinity and osmotic response play the physiological functions of the SYP4 group in the abiotic stress response (Rosquete & Drakakaki, 2018; Uemura, Ueda, *et al.,* 2012; Xiangfeng Wang *et al.,* 2020). The overexpression of the SFT12 gene of Arabidopsis thaliana, codes for a Qc-SNARE protein located in the Golgi complex, confers tolerance to salt stress in Arabidopsis thaliana plants via accumulating excess sodium in the vacuole (Tarte *et al.,* 2015). It has been observed that the role of vesicle transport in salt secretion, the virus-induced gene silencing (VIGS) used to downregulate the gene encoding a SNARE protein LbSYP61, has the capability of recretohalophyte Limonium bicolor to secrete salt through salt glands (Lu *et al.,* 2020).

4.2. Importance of SNAREs in Biotic Stress:

Plants exclusively rely on cell-autonomous innate immunity because of the lack of circulatory systems and mobile immune cells. By an exterior receptor termed as pattern recognition receptor (PRR), plants detect a pathogen by identifying a pathogen-associated molecular pattern (PAMP) (Dodds & Rathjen, 2010; Jones & Dangl, 2006; Nishad, Ahmed, Rahman, & Kareem, 2020), and eject extracellular pathogens, secrete immune molecules to protect pathogen-attempting sites (Yun & Kwon, 2017). There are two different pathways

recognized up to date, the transporter-mediated secretion; this contains mitochondrial, peroxisome localized AtPEN2 (penetration 2) myrosinase, plasma residing AtPEN3 (penetration 3) ABC transporter the second is SNARE-assisted exocytosis (Fuchs *et al.,* 2016; C. Kwon, Bednarek, & Schulze-Lefert, 2008; Lipka *et al.,* 2005; Stein *et al.,* 2006; Yun & Kwon, 2017). The Qa-SNARE AtSYP121 (Arabidopsis PM-residing), also known as AtPEN1, is the first recognized SNARE essential for plant immunity. AtSYP121 barley ortholog is known as HvROR2, necessary for *mlo*-specified disease resistance 2) (N. C. Collins et al., 2003; Ma, Li, Li, Li, & Zhang, 2020). SYP121 is vital for resistance to fungal and oomycete and pathogens SYP132 is engaged in immune responses to bacterial pathogens, and this interacts in plant cells with AtVAMP721 or AtVAMP722. The important SNAP25-like gene AtSNAP33 is expressed in the leaf tissue, possibly SYP132-SNAP33-VAMP721 or VAMP722; this complex in plants derives the immune exocytosis to bacterial pathogens (C. Kwon, Neu, *et al.,* 2008; Martinière & Moreau, 2020). The lastest proteomic approaches or apoplastic leaf segments identified that Arabidopsis seedling-grown liquid media containing plant secreted proteins discovered that AtVAMP721 or AtVAMP722 AtSYP121 essential for the secretion of several cell wall-related proteins (Uemura et al., 2019; P. Wang et al., 2018).The caffeoyl-CoA O-methyltransferase1 (CCOAOMT1) (lignin biosynthetic enzyme), transported out of plant cell via AtVAMP721/ AtVAMP722 vesicles, and it has founded that AtVAMP722 travel to the fungal entry directionally locations where AtSYP121 gathered at PM (H. Kwon, Lee, Nam, Kwon, & Yun, 2020). At the fungal places in plant cells, AtSYP121 as well as AtVAMP721/ AtVAMP722 essential for the development of secondary cell walls known as papillae on time; this proposes AtVAMP721/ AtVAMP722 transport cell wall-modifying proteins at the pathogen attempting areas (Kim *et al.,* 2014; C. Kwon, Neu, et al., 2008). Soluble N-ethylmaleimide sensitive factor attachment protein receptors (SNAREs) are important regulators that control the trafficking of cargo proteins to their final destinations and play a vital role in plant development; though, their roles in plant defense remain mostly unidentified. Furthermore, defect in the secretory and folding machinery in the ER reduces pathogenesis-related (PR) proteins' secretion, letting extra bacterial growth in plants (D. Wang, Weaver, Kesarwani, & Dong, 2005). Appropriately folded proteins then exit the ER and transportable to the PM along with the Golgi and trans-Golgi network (TGN) by vesicles. This might clarify why nearly all the plant compartments, including the nucleus, ER and Golgi, are focally repositioned to the pathogen attacking sites, likely to shorten the time between synthesis and secretion of immune molecules (Qin *et al.,* 2020; D. Takemoto, Jones, & Hardham, 2003; D. Wang et al., 2005). Indeed, some successful pathogens, including even an aphid, have invented effectors to inhibit this immune secretory route for virulence in host plants (Bozkurt *et al.,* 2011; Kalde, Nühse, Findlay, & Peck, 2007; Nomura *et al.,* 2006; Nomura et al., 2011; Rodriguez, Escudero-Martinez, & Bos, 2017). In this sense, it is not surprising to find that most SNAREs identified so far for their immune functions are localized to the ER, Golgi, TGN, or PM; the best candidates are PR proteins (Table 2). Indeed, PR1 is less noticed in extracellular space in plants missing the Golgi-localized MEMB12 Qb-SNARE or the PM-residing SYP132 Qa-SNARE, leading to impaired immunity (Kalde *et al.,* 2007; X. Zhang *et al.,* 2011). Reduced PR1 secretion in plants mutated in Sec61, DAD1 or BiP2 gene whose product is involved in translocation, folding, and maturation of nascent proteins in the ER (Sun *et al.,* 2013) suggests that PR proteins flow from the ER via

Golgi/TGN finally into the apoplast, specific interaction of VAMP721/722 with SYP121/132 in plant cells (C. Kwon, Neu, et al., 2008; Yun et al., 2013). This suggests that VAMP721/722 vesicles might transport PR proteins to SYP121/132 PM sites to release them, though the exact nature of cargo delivered by VAMP721/722 vesicles has not been identified yet. Late callose deposition in response to the fungal attack in Pen1, VAMP721/722 silenced plants (Assaad *et al.,* 2004; Ellinger *et al.,* 2013), and accumulation of vesicle-like structures containing the callose generating PMR4 enzyme (Z. Zhang *et al.,* 2007). This suggests that secondary cell wall components and enzymes might also be transported within VAMP721/722 vesicles. The specific immune activity of SYP121 and SYP132 to fungal and bacterial pathogens, correspondingly, furthermore suggests that VAMP721/722 vesicles may transport different cargo to the SYP121 and SYP132 PM sites. Partial co-localization between VAMP722 and the TGN-localized SYP43 Qa-SNARE suggests that the cargo-loaded VAMP721/722 vesicles bud from the TGN (Uemura, Kim, *et al.,* 2012). Bacterial HopE1 and HopZ1a effectors were found to disrupt plant microtubule function, resulting in the reduced apoplastic discharge of a secretory marker protein, PR1, and callose accompanied by high bacterial growth (Guo, Kim, Li, Elowsky, & Alfano, 2016; A. H.-Y. Lee *et al.,* 2012). Therefore, it is likely that VAMP721/722 vesicles loaded with PR proteins and cell wall materials transfer from the TGN to the target PM sites along microtubules (Yun & Kwon, 2017). R-SNARE VAMP727 and Qa-SNARE SYP22 were previously reported to associate with vacuolar protein deposition and brassinosteroids (BRs) receptor BRI1 plasma membrane targeting. It has been identified that VAMP727 and SYP22 are induced by infection of root-knot nematode (RKN), a plant pathogen, which causes severe growth defect and yield loss. This suggests that VAMP727-SYP22 SNARE complexes regulate plant defense via the control of abundances of BRI1 on the plasma membrane (Zhu *et al.,* 2019). Arabidopsis plants overexpressing GhSNAP33 showed significant resistance to *V. dahliae*, with reduced disease index and fungal biomass and elevated expression of PR1 and PR5. GhSNAP33 positively mediates plant defense against stress conditions and *V. dahliae* infection, rendering it a candidate for the generation of stress-resistant engineered cotton (P. Wang *et al.,* 2018). The role of FvSyn1 in hyphal growth, localization, cell wall stress response and virulence in *F. verticillioides***.** FvSyn1 belongs to a family of SNARE proteins that play critical roles in various developmental processes (H. Zhang, Yan, & Shim, 2019). The positive role of SNARE genes (*SNARE3, SNARE5*, and *SNARE6*) transcripts have in resistant and susceptible wheat plants during incompatible and compatible interaction, respectively, in response to *puccinia triticina* induced leaf-rust infection. The studies suggested a role for SNARE genes in vesicle-mediated resistance to leaf-rust in wheat (Chandra, Halder, Kumar, & Mukhopadhyay, 2017).

Table 2. The SNAREs play a vital role in immunity

S. No	SNAREs	Plant name	Position	Protection against	Reference
1	SYP121	Arabidopsis Barley	PM	Blumeria & Erysiphe fungi	(N. C. Collins et al., 2003)
2	SYP132	Tobacco	PM	Pseudomonas bacterium	(Kalde et al., 2007)
3	SYP31	Soybean	Golgi	Heterodera nematode	(Pant et al., 2014)
4	SYP42/43	Arabidopsis	TGN	Erysiphe fungus	(Uemura, Kim, et al., 2012)
5	MEMB12	Arabidopsis	Golgi	Pseudomonas bacterium	(X. Zhang et al., 2011)
6	NPSN11	Wheat	Vesicle	Puccinia fungus	(Xiaodong Wang et al., 2014)
7	SYP71	Rice Arabidopsis, tobacco Wheat	ER ER/Chloroplast PM	Magnoporthe fungus TuM virus Puccinia fungus	(Bao et al., 2012) (Wei, Zhang, Hou, Sanfaçon, & Wang, 2013)(Liu et al., 2016)
8	VAMP714	Rice	Chloroplast/Vacuole	Magnaporthe fungus	(Sugano et al., 2016)
9	VAMP721/722	Arabidopsis	Vesicle	Blumeria, Erysiphe & Golovinomyces fungi Hyaloperonospora oomycete	(C. Kwon, Neu, et al., 2008)
10	VAMP727-SYP22	Arabidopsis	PM	Root-knot nematode	(P. Wang et al., 2018)
11	GhSNAP33	Cotton ,Arabidopsis	PM, vesicle	Verticillium dahlia	(H. Zhang et al., 2019)
12	SNARE3, SNARE5& SNARE6	Wheat	Vesicle	Puccinia triticina	(Chandra et al., 2017)

5-Tethering and SNARE Complexes Facilitated Membrane Fusion at The Vacuole in Plants:

In plant cells, vacuoles are vital organelles that sustain cellular homeostasis, serving as reservoirs for numerous molecules and function as lytic organelles to break down and recycle cellular components. Thus, vacuoles are dynamic for several methods, like cell elongation, programmed cell death, and toxic compound sequestration. Vacuoles are important organelles in plants, playing vital parts, such as cellular material degradation, ion and metabolite storage, and turgor maintenance. Vacuoles obtain material by the endocytic, secretory, and autophagic pathways. Membrane fusion is the final step throughout which prevacuolar compartments (PVCs) and autophagosomes fuse with the vacuole membrane (tonoplast) to transport cargoes. Protein components of the canonical intracellular fusion machinery conserved across organisms, including *Arabidopsis thaliana,* with complexes, such as SNAREs, catalyze membrane fusion and homotypic fusion. Vacuole protein sorting (HOPS) helps as adaptors that tether cargo vesicles to target membranes for fusion under RAB-GTPases regulation (Rodriguez-Furlan *et al.,* 2019). Tethering proteins play a vital mechanical part in the terminal stage of membrane fusion that is likely to be conserved at multiple vesicular traffic steps. So, SNAREs and tethering proteins are known a single, non-dissociable device that drives fusion (Cui et al., 2019). Studies in vacuolar protein sorting in yeast identified a tethering complex, the HOPS complex, that plays a vital role in vacuole biogenesis. HOPS complex contains four core subunits (Vps11, Vps16, Vps18 and Vps33) and two specific subunits (Vps41 and Vps39). Arabidopsis comprises homologs for all HOPS subunits, each of which is encoded via a single gene. Functions of numerous subunits in the HOPS complex had been discovered, such as atvps16 (vcl1) mutant is congested in vacuole formation in the embryo, shows altered development, and accumulates small vesicles and autophagosomes, the defects led to embryo lethality at the torpedo stage. AtVps16, AtVps33 and AtVps11 formed a complex in vivo and localized on PVC and

tonoplast. An additional examined HOPS subunit is Vps41; it plays a vital role in controlling pollen tube stigma communication in Arabidopsis. AtVps41 mutations disrupted pollen tubes' diffusion into the transmitting tissue, leading to failed male transmission; multiple small vacuoles were detected in the AtVps pollen tubes. This phenotype is more severe than that in the vcl1 pollen tube, suggesting that the AtVps41 subunit might play some functions independent of the HOPS-core subunits (Tan, Wei, Li, Wang, & Bao, 2017). In plants, homologs for all subunits of the HOPS and CORVET complexes are conserved, some of which play essential roles in embryogenesis and gametophyte functions. The Arabidopsis vacuoless1 (vcl1) mutant, which harbors a mutation in the VPS16 gene, shows severe vacuole biogenesis defects. Recently, VPS11 and VPS41 were also essential for vacuole biogenesis during embryogenesis and pollen tube growth (Hao *et al.,* 2016; Tan *et al.,* 2017; Vukašinović & Žárský, 2016). The reported interaction among the HOPS and CORVET core complex with SYP22 in Arabidopsis, HOPS and CORVET's different functions may result from different interactions with two SYP22 covering vacuolar SNARE complexes using diverse R-SNAREs: one containing VAMP713 and the other VAMP727 (Fujiwara *et al.,* 2014; Rojo *et al.,* 2003). Another pathway is accountable for SYP22 transport, which resembles the CORVET-dependent transport pathway, identified as SYP22, also requires CORVET function for vacuolar localization. The plant detailed the R-SNARE VAMP727 pathway, which was suggested by strong colocalization and coimmunoprecipitation of CORVET and VAMP727, which contains RAB5, CORVET, and the VAMP727 containing SNARE complex (Fig. 3). It is accountable for the fusion among multivesicular endosomes and the vacuolar membrane, based on the observation that VAMP727 mediates the fusion between these membranes (Ebine et al., 2008; K. Takemoto *et al.,* 2018). The other unit covers RAB7, HOPS, and the VAMP71 containing the SNARE complex. This unit facilitates homotypic fusion among vacuoles, considering the colocalization of HOPS components and VAMP71 at the interaction sites among vacuoles and the fragmented vacuole phenotype brought via depletion of VAMP71 or HOPS components. This transport pathway resembles the RAB5 and RAB7 dependent pathway (Ebine *et al.,* 2014; Leshem *et al.,* 2010).

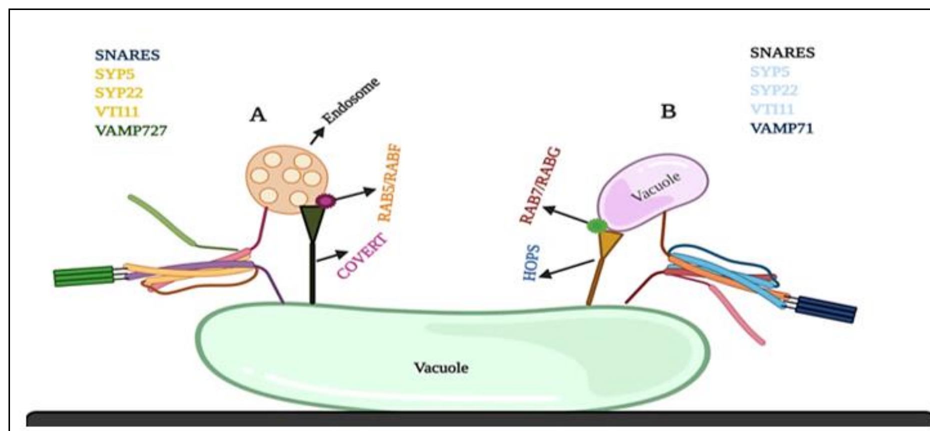

Fig. 3: HOPS and CORVET mediate specific membrane fusion events at the vacuole in Arabidopsis: (**A**) CORVET facilitates membrane fusion among multivesicular endosomes as well as the vacuole, in coordination with RAB5 and the VAMP727 having SNARE complex. HOPS acts with the VAMP713 holding SNARE complex and RAB7 to facilitate membrane fusion among vacuoles (**B**) HOPS acts with the VAMP713 holding SNARE complex and RAB7 to facilitate membrane fusion among

vacuoles (K. Takemoto et al., 2018).

6-Conclusion

This review discussed that SNARE proteins play very important roles in plant development; SNAREs have a central role in vesicle traffic via driving membrane fusion and conferring fidelity via forming specific SNARE complexes. Many SNAREs in Arabidopsis implicate SNARE complexes' diversified roles in membrane traffic events during growth and development and responses to biotic and abiotic stresses. It is also important to consider that MTCs contribute to the function of SNAREs, thus increasing the level of complexity and fidelity and regulation of the biological processes mediated by SNAREs.

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