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The roles of endomembrane trafficking in plant abiotic stress responses[FA]

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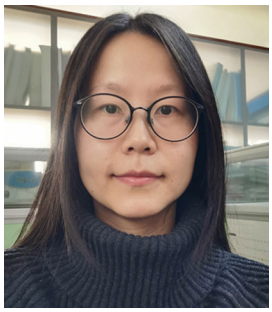
Invited Expert Review



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Abstract Endomembrane trafficking is a fundamental cellular process in all eukaryotic cells and its regulatory mechanisms have been extensively studied. In plants, the endomembrane trafficking system needs to be constantly adjusted to adapt to the ever-changing environment. Evidence has accumulated supporting the idea that endomembrane trafficking is tightly linked to stress signaling pathways to meet the demands of rapid changes in cellular processes and to ensure the correct delivery of stress-related cargo molecules. However, the underlying mechanisms remain unknown. In this review, we summarize the recent findings on the functional roles of both secretory trafficking and endocytic trafficking in different types of abiotic stresses. We also highlight and discuss the unique properties of specific regulatory molecules beyond their conventional functions in endosomal trafficking during plant growth under stress conditions.

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INTRODUCTION

Endomembrane trafficking is a fundamental cellular process conserved in eukaryotes to deliver materials between distinctive membrane-bound organelles, and performs the housekeeping functions to maintain essential cellular and developmental processes (Surpin and Raikhel 2004). The major endomembrane trafficking routes in plant cells include the secretory and endocytic pathways (Figure 1). In the early secretory pathway of eukaryotes, newly synthesized proteins with an N-terminal signal peptide or transmembrane domains enter the conventional protein secretory (CPS) pathway starting at the endoplasmic reticulum (ER), which is also an important site for lipid synthesis, before being transported to the Golgi apparatus (Nebenfuhr and Staehelin 2001; Brandizzi and Barlowe 2013; Oikawa et al. 2013; Stefano et al. 2014). After passing through the stacks of Golgi cisternae from

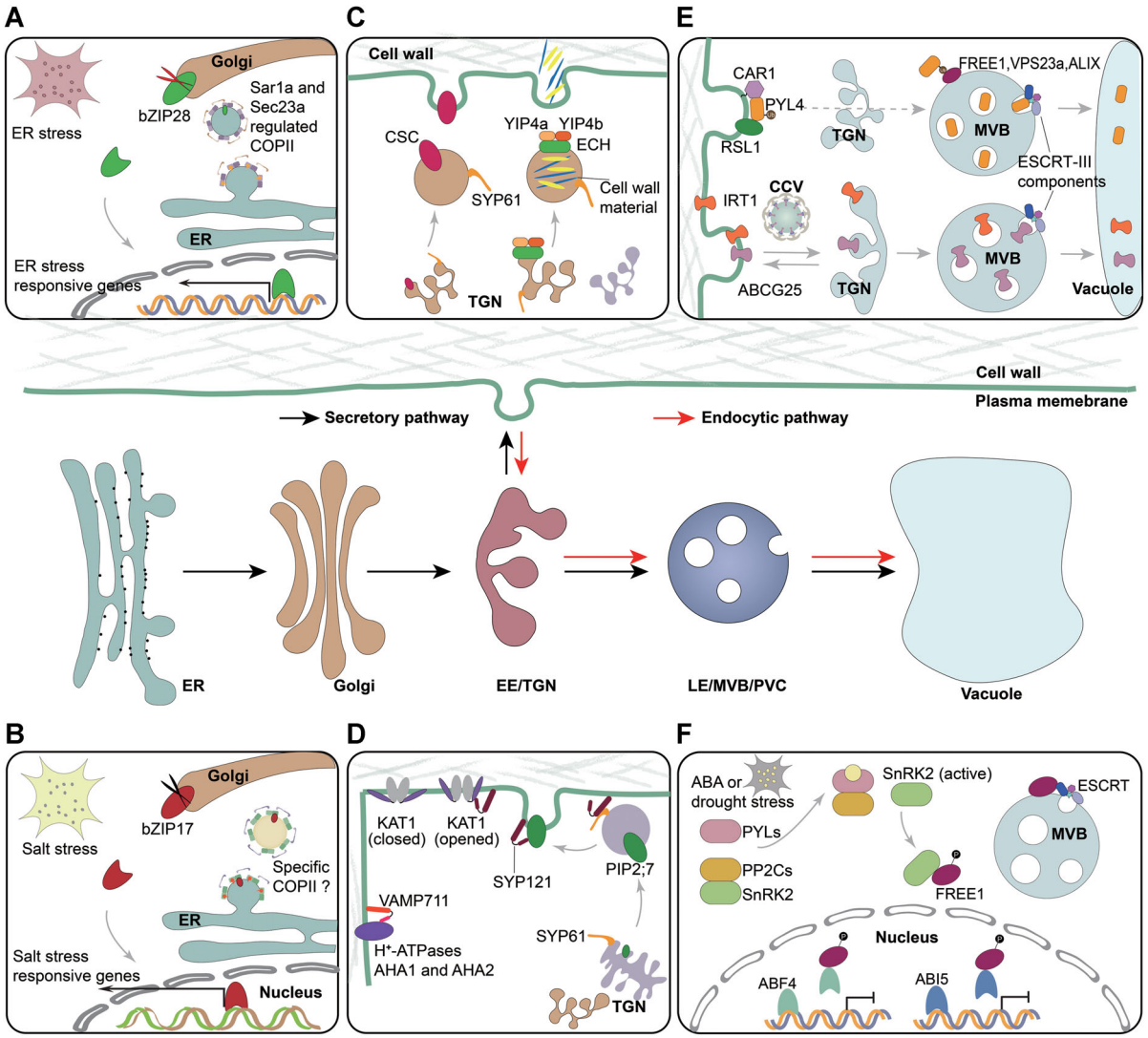

Figure 1. Endomembrane trafficking in the plant abiotic stress response

The major endomembrane trafficking routes in plant cells include the secretory and endocytic pathways, which are intensively involved in plant stress response to ensure the correct delivery of stress related cargoes. **(A)** Sar1a in *Arabidopsis* defines a specific population of COPII vesicles, which mediates the endoplasmic reticulum (ER) proteins export to the Golgi. Under ER stress, the COPII vesicles with Sar1a specifically mediate the ER export of transcription factor bZIP28, which could sense the ER stress and is cleaved at the Golgi. The cytosolic part of bZIP28 could be translocated into the nucleus to active the expression of downstream ER stress responsive genes. **(B)** Under salt stress, bZIP17 undergoes similar process with bZIP28. But whether it is mediated by a specific population of COPII vesicles is unknown. **(C)** SYP61 defined TGN compartments transport the cellulose synthesis complex (CSC) to the plasma membrane (PM) and deliver the cell wall materials to the apoplast with the help of ECH-YIP4a-YIP4b complex. **(D)** SYP61 could interact with SYP121 to facilitate the trafficking of PIP2;7 to the PM. Interestingly, SYP121 could perform its noncanonical function by interacting with the K^+ channel KAT1 and directly regulating its activity. Likewise, VAMP711 could interact with the PM localized H^+-ATPase AHA1 and AHA2 to inhibit their activities, regulating stomatal movement and plant sensitivity to drought stress. **(E)** PM localized abscisic acid (ABA) exporter ABCG25 and iron transporter IRT1 undergoes the clathrin mediated endocytosis (CME) for vacuolar degradation and recycling back to the PM. Similarly, ABA receptor PYL4, which associate with the membranes via the interaction with CAR1 protein, could be ubiquitinated by the E3 ligase RSL1 localized on the PM, and recognized by the ESCRT components FREE1, VPS23a and ALIX for vacuolar sorting and degradation. **(F)** Under ABA treatment or drought stress, FREE1 could be phosphorylated by SnRK2 protein kinase, and translocated into the nucleus to perform its unique function. Phosphorylated FREE1 could interact with transcription factors ABF4 and ABI5 and repress their transcriptional activities, thus attenuating the ABA response and contributing to the fine balance of plant survival and growth under stress conditions.

the *cis* side to the *trans* side, the secreted cargo molecules reach the *trans*-Golgi network (TGN) for further sorting to the plasma membrane (PM) and apoplast, or to the endosomes and vacuoles (Hwang and Robinson 2009; Robinson and Pimpl 2014). Proteins without signal peptides can also gain access to the cell exterior through unconventional protein secretion (UPS) pathways in plants either via non-vesicular secretion bypassing the Golgi or through some specific vesicles and organelles (Ding et al. 2014; Robinson et al. 2016). During the endocytic pathway, proteins are first internalized at the PM and transported to the TGN, the plant equivalent of the early endosome (EE) (Lam et al. 2007; Viotti et al. 2010). After reaching the TGN, endocytic cargos can be either recycled back to the PM, or be further transported to the vacuoles via the multivesiclular body (MVB)/prevacuolar compartment (PVC), which is equivalent to the late endosome in plant cells and is formed by maturation from specific subdomains of TGN (Viotti et al. 2010; Cui et al. 2014).

In both the secretory and endocytic pathways, the movement of cargo from organelle to organelle is facilitated by vesicles, the formation of which ensures the enclosure of selective cargos and shares conserved sequential processes as well as the major molecular machineries (Valencia et al. 2016). Protein cargos are first recruited into the vesicles formed at the donor membrane via coat and adaptor proteins. These vesicles are further transported and targeted to the destination. Tethering factors help to bring the donor vesicle membrane close to the target membrane, facilitating the subsequent efficient fusion mediated by SNARE complexes. Importantly, small GTPases, for example, ARF and Sar1 GTPases, are the core governors in multiple steps in vesicle formation by recruiting coat proteins (clathrin, COPI, and COPII coatomers), and Rab GTPases in vesicle transport, vesicle tethering and endosomal maturation by selectively recruiting tethering or other specific effector proteins. The activities of small GTPases are regulated by guanine nucleotide exchange factors (GEFs) and GTPase-activating proteins (GAPs), which cycle between GTP-bound active and GDP-bound inactive forms. The retromer complex mediates the recycling of specific membrane cargos from endosomes back to the TGN/Golgi apparatus or to the PM (Robinson et al. 2012; Heucken and Ivanov 2018). Membrane cargo proteins may also be ubiquitinated and sorted into intraluminal vesicles (ILVs) inside MVBs, and are finally released into the vacuole lumen for degradation upon the fusion between MVB and vacuole (Cui et al. 2016). Consistent with the unique morphology of ILV-containing MVBs, the biogenesis and protein sorting at the MVB are specifically regulated by an "endosomal sorting complex required for transport" (ESCRT) machinery, which consists of ESCRT-0, -I, -II, -III, and VPS4 complexes (Cai et al. 2014; Gao et al. 2017). The characterization and functions of these molecular players in plants have been extensively studied and well summarized in several recent reviews (Fan et al. 2015; Valencia et al. 2016; Gao et al. 2017).

In plants, endomembrane trafficking is indispensable for the response and adaptation to environmental stresses (Yu and Xie 2017; Rosquete and Drakakaki 2018). As sessile organisms, plants need to constantly monitor environmental changes and rapidly reprogramme their metabolism and gene-expression profiles to adapt to unfavorable conditions, such as soil salinity, drought, extreme temperatures, nutrient imbalance, and toxic metals (Zhu 2016; Yang and Guo 2018; Ding et al. 2019). In the past decades, much evidence points to plants having evolved effective and complicated response systems to cope with stress conditions, including the primary and secondary stress perception, and signaling transduction in the cells (Zhu 2016). For example, under salt stress, both the composition of the cell wall changes and PM-localized leucine-rich repeat receptor kinases (LRR-RKs) proteins sense the cell wall integrity (CWI) thereby contributing to the perception of salt signaling (Yang and Guo 2018). Moreover, it has been recently found that a PM lipid glycosyl inositol phosphorylceramide (GIPC) binds Na^+ and controls Ca^{2+} influx channels (Jiang et al. 2019). Salt stress perceived by multiple pathways further activates the salt overly sensitive (SOS) pathway including SOS2 kinase and PM-localized SOS1 Na^+ antiporter to export excessive Na^+ out of the cell, facilitating plant survival, and growth (Yang and Guo 2018). The detailed mechanisms of plant responses to salt stress and other stresses have been well summarized in excellent reviews (Zhu 2016; Yu and Xie 2017; Shi et al. 2018; Yang and Guo 2018; Ding et al. 2019; Wang and Mao 2019). It is intriguing that the compartmentalization and abundance of various macromolecules, including expressed proteins, lipids, and polysaccharides, are essential and constantly regulated in plant stress responses. Since most macromolecules are produced far away from their sites of function, it is not surprising that plant stress responses frequently and

largely rely on the endomembrane trafficking to ensure the correct delivery of stress-related cargos, which are in turn dynamically regulated by the stress signals to meet the specific demands caused by adapting to the constantly changing environment. Here, we will review the recent advances and discuss the involvement of endomembrane trafficking in plant abiotic stress responses.

THE SECRETORY PATHWAY IN PLANT ABIOTIC STRESS RESPONSE

Participation of the early secretory pathway in plant environmental adaptation

The first stage of the secretory pathway is mediated by the coat protein complex II with the ensuing COPII vesicles serving as the anterograde vectors for cargo transport from the ER to the Golgi (Chung et al. 2016). The COPII machinery was first identified in yeast and is conserved in both mammals and plants. It comprises the small GTPase Sar1, the inner coat complex (Sec23-Sec24) and the outer coat complex (Sec13-Sec31) (Novick et al. 1980; Zanetti et al. 2013). One unique feature of the plant COPII machinery is the presence of multiple COPII paralogs due to gene duplication, with five *Sar1*, two *Sec13*, two *Sec31*, seven *Sec23*, and three *Sec24* in *Arabidopsis*. A recent study by Zeng et al. (2015) has identified a specific pair of Sar1a and Sec23a in *Arabidopsis* with specialized functions in the ER export of specific cargos, compared to Sar1c which has a more general function in ER export (Zeng et al. 2015). Strikingly, one unique cargo of the Sar1a-regulated COPII is bZIP28, which is an ER resident protein sensing ER stress and is exported from ER to Golgi followed by cleavage and translocation of the cytosolic tail into nucleus thus functioning as a transcription factor (Figure 1A). Moreover, microarray analyses have shown that the expression of *Sar1a and Sec31a* is significantly upregulated under ER stress and such an increase is significantly impaired in a *bzip28bzip60* double mutant (Song et al. 2015; Chung et al. 2016). These results have demonstrated the unique role of Sar1a in ER stress and ER homeostasis in *Arabidopsis*. ER stress involves the accumulation of unfolded or misfolded proteins, which can be induced by multiple abiotic stresses (Zhu 2016). A previous study also reported a similar signaling cascade in the salt stress response that has shown that the ER localized transcription factor bZIP17 is transported to the Golgi under salt stress, whereby the cytosolic domain of bZIP17 is cleaved followed by its translocation into the nucleus to activate the expression of downstream salt stress responsive genes (Figure 1B) (Liu et al. 2007). However, the detailed mechanism of how bZIP17 senses salt and whether bZIP17 is transported by a specific COPII machinery need to be determined. It will be interesting to get more information on the functions of specific COPII proteins in other plant stress responses. Most recently, both Hu et al. (2019) and Mitterreiter et al. (2019) reported that the component of the translocon complex Sec62 in *Arabidopsis* is involved in plant stress response in addition to its function in plant growth (Hu et al. 2019; Mitterreiter et al. 2019). *sec62* mutants show higher sensitivity to ER stress induced by dithiothreitol (DTT) or tunicamycin (TM). Moreover, the survival rate of mutant plants under high temperature stress is obviously lower than that of wild-type plants. Together with the interesting observation that Sec62 colocalizes with the autophagosome marker Atg8 upon TM treatment, it is likely that *Arabidopsis* Sec62 is involved in the autophagy-dependent clearance of excess ER proteins under stress conditions (Hu et al. 2019). Indeed, Sec62 in mammalian cells has been proved to be an autophagy receptor, though the direct evidence for this in plants is still lacking (Fumagalli et al. 2016).

Roles of TGN to PM trafficking in plant abiotic stress responses

The plant TGN is a versatile organelle with a tubular-vesicular structure and has different sub-populations including Golgi-associated TGN and free TGN (Dettmer et al. 2006; Lam et al. 2007; Kang and Staehelin 2008; Toyooka et al. 2009; Kang 2011; Gendre et al. 2015). The SNARE protein Syntaxin of Plants 61 (SYP61) defines a sub-population of TGN compartments. Zhu et al. (2002) first identified the *osm1* (for osmotic stress-sensitive mutant)/*syp61* exhibiting hypersensitivity to both salt and osmotic stresses in a large scale screening of *Arabidopsis* mutants (Zhu et al. 2002). In addition, the water loss of detached shoot from *osm1* mutant was significantly higher than in wild type plants, and abscisic acid (ABA) induced stomatal closure was impaired in the mutant. These observations point to the involvement of SYP61 in the plant response to abiotic stresses, including salt stress, osmotic stress, and drought. A subsequent proteomic study of purified SYP61 compartments provided some clues as to the specific cargos of SYP61-labeled TGN and their presumable functions in plant

abiotic stress responses (Drakakaki et al. 2012). One cargo is the cellulose synthase complex (CSC), the motile transmembrane protein complex responsible for the synthesis of cellulose microfibrils (Figure 1C). CSC has also been proved to function in salt stress, since cellulose deficient mutants show hypersensitivity to salt stress (Zhang et al. 2016). Another cargo ECHIDNA (ECH) has later been identified to form a complex with RAB GTPase interacting proteins YIP4A and YIP4B (Figure 1C) (Gendre et al. 2011, 2013). Both the *ech* mutant and *yip4ayip4b* double mutant showed significant defects in cell elongation and pectin mucilage secretion in the seed coat, indicating their functions in secretory trafficking of cell wall polysaccharides. Previous studies in wheat and soybean have demonstrated that there is higher level of pectin in the drought tolerant wheat cultivar and salt tolerant soybean cultivar (Konno et al. 2008; Leucci et al. 2008; Tenhaken 2014). However, direct evidence showing the function of ECH-YIP4A-YIP4B complex in plant abiotic stress responses is still lacking. Last but not least, the TGN-localized syntaxins SYP42 and SYP43 have also been identified in the proteome of the SYP61 compartment and the *syp42 syp43* double mutants were hypersensitive to salt and osmotic stress (Uemura et al. 2012), albeit the underlying molecular mechanisms are totally unknown. In summary, whether the TGN-localized syntaxins functions in stress responses through secretory trafficking of cell wall materials and whether different TGN populations performs distinctive roles in plant stress responses still need further investigation.

SYP121 is a PM-localized SNARE protein, and assembles together with other SNAREs, including TGN-localized VAM721/722 and SNAP33, to form the SNARE complex, driving the vesicle fusion at the PM and likely delivering stress-related cargos to the PM. It has been two decades since the first identification of SYP121 function in response to drought and ABA in tobacco (Leyman et al. 1999). However, Hachez et al. (2014) have recently shown that SYP121 is required for the proper trafficking of the aquaporin PIP2;7 to the PM in *Arabidopsis* (Figure 1D) (Hachez et al. 2014). Intriguingly, SYP61 was shown to interact with SYP121 to form a SNARE complex mediating the trafficking of PIP2;7 to the PM. Disruption of either SYP61 or SYP121 leads to a decrease in plant cell membrane water permeability, which is likely due to a defect in the trafficking of aquaporins to the PM (Besserer et al. 2012). However, the evidence is still lacking to show whether the physical interaction between PIP2;7 and SNAREs can directly regulate the activity of PIP2;7. Taken together, these studies indicate that the TGN and PM localized SNAREs can directly interact with the transmembrane cargo molecules like aquaporins to mediate their secretory trafficking or recycling between the PM and TGN, thereby modulating plant adaptation to drought stress. Besides SNAREs, it has been shown that the TGN-localized RabA1 GTPase is also involved in plant salinity stress tolerance, though the underlying mechanisms remain unclear (Asaoka et al. 2013).

Unconventional functions of VSRs in plant abiotic stress response

Soluble cargo proteins like aleurain that are synthesized in the ER and transported to the vacuoles are recognized and sorted by vacuolar sorting receptors (VSRs) (Cui et al. 2016). Recently, the novel function of one *Arabidopsis* VSR homolog VSR1 in osmotic stress tolerance has been identified (Wang et al. 2015b). The mutant *vsr1/ced2* was first identified as a new regulator of ABA synthesis, which is one of the most important phytohormones involved in abiotic stress responses and many other physiological processes. Osmotic stress triggers ABA accumulation to balance growth and stress response. However, the expression of the ABA synthesis gene *NCED3* and ABA levels were both reduced in the *ced2* mutant, which exhibited enhanced sensitivity to osmotic stress. Moreover, similar phenotypes were observed in plants with overexpression of dominant-negative form of VSR1 that interferes with its vacuolar sorting functions, indicating that VSR1-mediated vacuolar protein trafficking is required for stress-induced ABA synthesis and osmotic stress response.

THE ENDOCYTIC PATHWAY IN PLANT ABIOTIC STRESS RESPONSE

The crucial functions of CME and recycling in plant adaption to abiotic stresses

Proteins at the PM are constantly damaged when exposed to outside environmental stresses. To ensure the normal activities of the PM in plants, it is necessary to remove damaged proteins and maintain the proper abundance and quality of functional proteins through the endocytic pathway, mainly by clathrin mediated endocytosis (CME) (Fan et al. 2015). The coat protein clathrin is

first recruited to the PM to form clathrin coated pits (CCPs), and cargo proteins are further selected into this region via an interaction with the adaptor protein 2 (AP2) complex. After the recruitment of accessory proteins and coat assembly, matured clathrin coated vesicles (CCVs) eventually detach from the PM and are transported to the EE/TGN, where the endocytosed cargo proteins are either recycled or further sorted for vacuolar degradation. Many important PM-localized proteins, such as the auxin transporters PINs, the BR receptor BRI1, and the pattern recognition receptor FLS2, are subject to the CME for protein turnover (Fan et al. 2015; Dubeaux and Vert 2017; Liu et al. 2018). Recently, the ABA exporter ABCG25 has also been reported to undergo the CME for vacuolar degradation and its spatial regulation is important for ABA homeostasis under stress conditions (Figure 1E) (Kuromori et al. 2010; Park et al. 2016; Nguyen et al. 2018). More endosomal localizations of ABCG25 were observed when treated with NaCl, indicating that salt stress enhances the endocytosis of ABCG25 to reduce the efflux of ABA and increase the ABA content inside the cells. Similar observations in mutants with defective ABA synthesis and signaling demonstrate that salt stress induced endocytosis of ABCG25 does not rely on the concentration or the signaling of ABA. Thus, the exact mechanism through which the endocytosis of ABCG25 is activated is still unclear. Interestingly, treatment with exogenous ABA increased the recycling of ABCG25 back to the PM, maintaining a high level of ABA efflux. These observations indicate that the spatial regulation of ABA transporters by CME and recycling is an effective mechanism to fine-tune the ABA level according to the environmental change. One matter we need to mention is that CME-regulated plant stress responses are definitely not specific to ABCG25, as it also functions in the internalization of other PM-localized stress regulators like receptor like kinase ACR4, the aquaporin PIP2;1, the boric transporter BOR1, and the iron transporter IRT1 (Takano et al. 2005; Barberon et al. 2011; Ueda et al. 2016; Qin et al. 2019).

In particular, the research on trafficking of IRT1 in the past decade have demonstrated the critical roles of CME and recycling in plant nutrient homeostasis under complicated environmental conditions (Figure 1E) (Barberon et al. 2011, 2014; Shin et al. 2013; Ivanov et al. 2014; Zelazny and Vert 2015; Dubeaux et al. 2018). IRT1 is the primary determinant of iron absorption in plants, and also mediates the transport of other non-iron metals such as manganese, zinc, cobalt, and cadmium. Although most endogenous IRT1 localized to the TGN/EE in the steady state, specific localization of IRT1 was observed at the PM upon pharmacological treatment with the CME inhibitor Tyrphostin A23 (TyrA23) or in the plants expressing the dominant-negative clathrin HUB to disrupt CME (Barberon et al. 2011, 2014). Later, another study showed that IRT1 could partially colocalize with retromer complex component SNX1 and the loss-of-function mutant of *SNX1* exhibited enhanced IRT1 degradation (Ivanov et al. 2014). These results together indicate that IRT1 dynamically cycles between PM and TGN/EE through the CME-dependent internalization and the SNX1-mediated recycling. Surprisingly, the localization and dynamic of IRT1 are not regulated by iron availability, but rather by the secondary substrates like zinc and manganese (Barberon et al. 2011, 2014; Dubeaux et al. 2018). The depletion of these metals resulted in the enrichment of IRT1 at the PM, while the addition of excess metals triggered the endocytosis of IRT1 from PM to endosomes and eventually to vacuole for degradation. Interestingly, the post-translational modifications of IRT1 are critical for its dynamic and are also regulated by the availability of non-iron metals. Multi-monoubiquitination by the E3 ligase IDF1 is essential for the internalization of IRT1 from PM to TGN/EE (Barberon et al. 2011). However, when IRT1 senses the high influx of non-iron metals through direct metal binding to its histidine residues, CIPK23 kinase is recruited to phosphorylate IRT1 and enhances the interaction between IDF1 and IRT1, which in turn extends the multi-monoUb into K63-linked polyUb chains and facilitates IRT1 turnover (Dubeaux et al. 2018). Altogether, these results unraveled the elaborate regulatory mechanisms of IRT1 partition through the endomembrane system, which allows the plants to optimize the iron absorption and prevent the harmful accumulation of other metals.

Roles of MVB-mediated protein sorting and degradation in plant stress adaptation

The ubiquitinated membrane proteins for degradation are sorted into intraluminal vesicles (ILVs) inside LE/MVB governed by a multi-subunit membrane remodeling complex termed as ESCRT (Gao et al. 2017). Interestingly, recent work has highlighted a surprising role of ESCRT in cytosolic cargo proteins and in plant abiotic stress responses through engagement in plant ABA signaling (Belda-Palazon et al. 2016). The perception of ABA is

mediated by the soluble receptor pyrabactin resistrance1 (PYR1)/pyr1-like (PYL)-regulatory components of aba receptors (RCAR) (Miyakawa et al. 2013). In the presence of ABA, PYR/PYLs interact with clade A protein phosphatase type 2Cs (PP2Cs), reducing the phosphatase activities of PP2Cs and releasing the ABA-activated sucrose non-fermenting 1-related protein kinase (SnRK2s). SnRK2s phosphorylate downstream ABA-responsive transcription factors and other proteins regulating cellular activities (Umezawa et al. 2013; Wang et al. 2013). Although PYR/PYL receptors are soluble proteins without a transmembrane domain, they can partially associate with the PM via an interaction with CAR1 protein containing a lipid binding C2 domain (Rodriguez et al. 2014). The receptors are further ubiquitinated by the PM-localized E3 ligase RSL1, allowing the membrane associated PYL receptors to be recognized by the ESCRT components and to be sorted into an endosomal compartment (Figure 1E). FYVE DOMAIN PROTEIN REQUIRED FOR ENDOSOMAL SORTING 1 (FREE1) is a plant specific ESCRT component which binds to ubiquitin and phosphatidylinositol 3-phosphate (PI3P), and interacts with multiple ESCRT proteins including VPS23 in ESCRT-I, SNF7 in ESCRT-III and AtBRO1/ALIX in accessory protein complex (Gao et al. 2014; Gao et al. 2015; Belda-Palazon et al. 2016). It was recently reported that the N terminus of FREE1 directly interacts with the ABA receptor PYL4 and mediates the vacuolar degradation of ubiquitinated PYL4 (Belda-Palazon et al. 2016). A *free1/fyve1* heterozygous mutant with reduced expression of *FREE1* displayed enhanced sensitivity to ABA treatment, because of the accumulation of functional PYL4 in the mutant. In addition, other plant ESCRT components including VPS23 and ALIX have also been shown to use a similar mechanism to recognize a subfraction of ubiquitinated ABA receptors and to regulate their vacuolar sorting and degradation, thereby negatively modulating plant ABA signaling and drought stress response (Yu et al. 2016; Garcia-Leon et al. 2019).

In another study, however, the ESCRT accessory protein LIP5 was demonstrated to play a positive role in ABA signaling as the *lip5* mutant was insensitive to ABA treatment and more sensitive to drought stress, although the underlying mechanism is unknown (Xia et al. 2016). Besides the drought stress response, LIP5 was also shown to play a critical role in plant responses to salt and heat stresses presumably by regulating the vacuolar degradation of ubiquitinated aggregated proteins under stress conditions (Wang et al. 2015a). Consistent with the critical role of ESCRT in plant stress adaption, the expression levels of several ESCRT-related genes, such as *LIP5* and *SKD1*, were upregulated upon salt stress; as a consequence plants with reduced expression of *SKD1* displayed an imbalanced Na^+/K^+ homeostasis and a reduced salinity tolerance (Ho et al. 2010). Another ESCRT accessory protein ALIX was also proved to regulate the vacuolar degradation of high-affinity phosphate transporters PHT1 and maintain the phosphate homeostasis in *Arabidopsis* (Cardona-Lopez et al. 2015). Besides the ESCRT complex, MVB and vacuole localized Rab small GTPases are also involved in plant abiotic stress responses. For example, overexpression of the tonoplast-localized RabG3e gene in *Arabidopsis* leads to an increase in tolerance to salt and osmotic stresses and reduced accumulation of reactive oxygen species (Mazel et al. 2004), while overexpression of a constitutively active mutant of the plant unique Rab5 protein ARA6(Q93L) enhanced tolerance to salt stress (Ebine et al. 2011). Future work will be to characterize the stress-induced cargos that are sorted by MVB-mediated transport using a combination of omics approaches and to figure out the link between stress signaling and vacuolar sorting pathway.

THE ROLES OF UNIQUE SNARE AND ESCRT: BEYOND TRAFFICKING IN PLANT ABIOTIC STRESS RESPONSES

Non-endosomal function of SNAREs in plant stress responses

SYP121 and SYP122 shares 76% amino acid similarity, similar expression patterns with no tissue specificity and have a similar ability to form SNARE complexes at the PM. What is more, growth is greatly repressed in only *syp121syp122* double mutants but not single mutants, indicating their redundancy in plant growth (Assaad et al. 2004). However, it is intriguing to note that stomatal reopening was only delayed in the *syp121* mutant but not in the *syp122* mutant, showing the unique function of SYP121 in stomatal movement and abiotic response (Eisenach et al. 2012). More strikingly, Honsbein et al. (2009) showed that SYP121, but not SYP122, directly interacts with the regulatory K^+ channel KC1 on the PM to form a tripartite complex with KC1 and the K^+ channel AKT1, thus regulating

channel activity to promote K^+ uptake. The mutant *syp121*, but not *syp122*, showed a similar phenotype with *kc1* and *akt1* mutants in the low K^+ condition with the presence of $NH4^+$. Subsequent studies have demonstrated a direct interaction between SYP121 and another K^+ channel KAT1, and have shown that the addition of SYP121 could enhance the whole cell current when coexpressed with KAT1 in *Xenopus oocytes*. Studies with temporal kinetics of the channel gating showed that expression of *SYP121* significantly alters the lifetime of KAT1 in both open and close states (Figure 1D) (Lefoulon et al. 2018). These findings confirmed the unique function of SYP121 in the direct regulation of K^+ channel activities. Likewise, in a more recent study, the R-SNARE protein VAMP711 was shown to directly interact with the *Arabidopsis* PM H^+-ATPases AHA1 and AHA2 to inhibit their activities (Figure 1D). Deletion of VAMP711 in *Arabidopsis* results in a higher PM H^+-ATPase activity and slower stomatal closure in response to ABA, thereby making the mutant plants more sensitive to drought treatments (Xue et al. 2018). Together, these studies demonstrate the unique roles of SNAREs in directly modulating the activity of their transmembrane cargos, which function as transporters or channels, besides their conserved function as vesicle fusion modulators in mediating the endosomal trafficking and targeting of cargo proteins.

Non-endosomal function of plant unique ESCRT component FREE1 in plant environmental adaptation

Besides the canonical function of ESCRT in endosomal trafficking of stress-response cargo molecules as discussed above, a more recent study has also demonstrated a non-endosomal function of ESCRT subunit FREE1 as a transcriptional regulator in plant responses to ABA signaling (Figure 1F). FREE1 was previously shown to interact with both ESCRT components and autophagy regulators like SH3P2 and the PI3K complex (Gao et al. 2015). Consistent with these diverse interaction partners, FREE1 performs dual functions in both endosomal trafficking and autophagic pathways. Loss of function mutant *free1* is seedling lethal, showing abnormal MVBs, defective vacuolar transport and accumulation of autophagosomes (Gao et al. 2014, 2015). Interestingly, the newly generated *free1* weak allele using CRISPR-Cas9 makes it possible to uncover the novel function of FREE1 (Li et al. 2019). The mutant named as *free1-ctmut is* hypersensitive to ABA treatment without obvious defects in MVB biogenesis and vacuolar degradation. Moreover, both the full length FREE1 and FREE1(FYVE) with deletion of the PI3P-binding FYVE domain complemented the ABA hypersensitive phenotype, while the FREE1-CTmut could not, indicating the importance of the C terminal coiled-coil domain in the involvement of FREE1 in ABA signaling independent of its conventional functions in endosomal trafficking. Further detailed analysis revealed that exogenous ABA treatment significantly increased nucleus localized FREE1, relying on the phosphorylating residues residing in the C-terminal coiled-coil region of FREE1 by SnRK2 protein kinase. And in turn, FREE1 in the nucleus could interact with transcriptional factor ABF4 and ABI5 to repress their DNA binding ability and transcriptional activities, thus attenuating the ABA response and releasing the inhibitory effect on plant growth. This study, together with the previously mentioned ESCRT mediated ABA receptor turnover, providing an interesting demonstration of the elegant coordination of endosomal trafficking and unique protein function in the balance of plant survival and growth under stress conditions.

CONCLUDING REMARKS

In this review, we have discussed recent studies supporting the involvement of endomembrane trafficking in plant abiotic stresses and revealing their potential underlying mechanisms (Figure 1; Table 1). However, we are still far away from the finalized picture as to how the plant integrates numerous environmental signals and flexibly adjusts its endomembrane trafficking and growth. In addition to stress-related protein cargos, other macromolecules are also delivered through the endomembrane system and play essential roles in plant stress responses, including polysaccharides, lipids and small RNAs. In combination with bioinformatic analysis, the developing techniques of plant proteomics, glycomics, and metabonomics could help to provide more information on putative stress related trafficking regulators. In addition, it will be necessary to pay more attention to the cellular responses to the crosstalk of multiple stresses, and to the crosstalk between environmental stresses and internal growth signals. It is because of this that plants might need to respond to different stresses at

Table 1. Endomembrane trafficking proteins in plant abiotic stress responses

Proteins		Functions in endomembrane trafficking	Participation in abiotic stresses	Mechanisms	References
Coat and adaptor proteins	Sec31a	Outer coat protein of COPII vesicles	ER stress	Unknown	Song et al. 2015; Chung et al. 2016
	Sec23a	Inner coat protein of COPII vesicles	ER stress	Forming a specific pair with Sar1a, and regulating the ER export of ER stress related transcription factor bZIP28	Zeng et al. 2015; Chung et al. 2016
	ECA4	Adaptor in CCV	Salt stress	Mediating the recycling of ABA transporter ABCG25 back to the PM	Nguyen et al. 2018
SNAREs	SYP61	TGN localized SNARE protein driving membrane fusion	Salt stress; osmotic stress; drought stress	Mediating the secretory trafficking of multiple cargoes related to stress responses	Zhu et al. 2002; Konno et al. 2008; Leucci et al. 2008; Drakakaki et al. 2012; Tenhaken 2014; Zhang et al. 2016
	SYP121	PM localized SNARE protein driving membrane fusion	Drought stress; K^+ stress	1. Delivering stress related cargoes to the PM such as aquaporin PIP2;7; 2. Interacting with K^+ channels and regulating the channel activity to promote K^+ uptake	Leyman et al. 1999; Honsbein et al. 2009; Besserer et al. 2012; Eisenach et al. 2012; Hachez et al. 2014; Lefoulon et al. 2018
	SYP42/SYP43	TGN localized SNAREs driving membrane fusion	Osmotic stress; salt stress	Unknown	Uemura et al. 2012
	VAMP711	TGN localized SNAREs driving membrane fusion	Drought stress	Interacting with PM localized H^+-ATPases and inhibiting their activities, thus	Xue et al. 2018

(Continued)

Table 1. Continued

Proteins		Functions in endomembrane trafficking	Participation in abiotic stresses	Mechanisms	References
				regulating stomatal movement in drought stress	
Small GTPases	Sar1a	Mediating the COPII vesicle formation	ER stress	Forming a specific pair with Sec23a, and regulating the ER export of ER stress related transcription factor bZIP28	Song et al. 2015; Zeng et al. 2015; Chung et al. 2016
	RABA1s	Regulating the vesicle trafficking between the TGN and the PM	Salt stress	Unknown	Asaoka et al. 2013
	RABF1/ARA6	Plant unique RAB5 protein localized on both endosomes and the PM, regulating endosomal trafficking	Salt stress	Regulating the specific SNARE complex formation on the PM and involved in salt stress response with a yet unclear mechanism	Ebine et al. 2011
	RabG3e	Tonoplast localized small GTPase functioning in vacuolar transport	Salt stress; osmotic stress	Unknown	Mazel et al. 2004
ESCRT complex	FREE1	Plant unique ESCRT-I component performing multiple functions in MVB biogenesis, endosomal sorting and autophagic pathways	Drought stress	1. Interacting with ABA receptor PYLs and mediating their vacuolar sorting and degradation; 2. Regulating the polarized PM localization of IRT1 with a yet unclear mechanism 3. Translocating into	Barberon et al. 2014; Belda-Palazon et al. 2016; Li et al. 2019

(Continued)

Table 1. Continued

Proteins	Functions in endomembrane trafficking	Participation in abiotic stresses	Mechanisms	References
			the nucleus after being phosphorylated by SnRK2s and repressing the transcriptional activities of ABF4 and ABI5	
VPS23a	Plant ESCRT-I component mediating the MVB biogenesis and endosomal sorting	Drought stress	Interacting with ABA receptor PYLs and mediating their vacuolar sorting and degradation	Yu et al. 2016
ALIX	Accessory protein mediating the MVB biogenesis and endosomal sorting	Drought stress	1. Interacting with ABA receptor PYLs and mediating their vacuolar sorting and degradation 2. Regulating the vacuolar degradation of high-affinity phosphate transporters PHT1 and maintaining the phosphate homeostasis in *Arabidopsis*	Cardona-Lopez et al. 2015; Garcia-Leon et al. 2019
LIP5	Accessory protein mediating the MVB biogenesis and endosomal sorting	Drought stress; heat stress; salt stress	1. Functioning as a positive regulator in ABA signaling with a yet-unknown mechanism; 2. Regulating the vacuolar degradation of ubiquitinated	Wang et al. 2015a; Xia et al. 2016

(Continued)

Table 1. Continued

Proteins		Functions in endomembrane trafficking	Participation in abiotic stresses	Mechanisms	References
				aggregated proteins under stress conditions	
	VPS4/SKD1	AAA-type ATPase mediating the MVB biogenesis and endosomal sorting	Salt stress	Maintaining the Na^+/K^+ homeostasis and salt tolerance with a yet-unknown mechanism	Ho et al. 2010
Vacuole sorting receptors	VSR1	Recognizing the soluble vacuolar cargo proteins and mediating the vacuolar transport	Osmotic stress	Affecting the expression of ABA synthesis gene and ABA level with a yet-unknown mechanism	Wang et al. 2015b

the same time in nature, with the coexistence of insects, bacteria, and pathogens, and need to fine-tune the balance between stress-related cargo delivery and housekeeping trafficking to maintain cell integrity and plant survival.

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AUTHOR CONTRIBUTIONS

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