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Chapter

Reorganization of the Endomembrane System and Protein Transport Pathways under Abiotic Stress

Miguel Sampaio, João Neves, Tatiana Cardoso, José Pissarra, Susana Pereira and Cláudia Pereira

Abstract

Stress compromises protein trafficking in plants, which often results in modifications to the endomembrane system and trafficking pathways. Proteins travel in unexpected ways during stress, and cell compartments alter their appearance, activity, and content to cope with the difficulties that stress brings. We will piece together material on the issue in this chapter, emphasizing how the endomembrane system processes such changes and how it reacts to a dynamic environment. The intricate dynamics of protein transport pathways and how they maintain cellular homeostasis under challenging circumstances is illustrated.

Keywords: abiotic stress, endomembranes, protein trafficking, vacuolar routes, endoplasmic reticulum

1. Introduction

Diverse environmental stresses frequently trigger signals and pathways that lead to cellular responses, such as increased antioxidant expression, solute accumulation, altered protein transport, and endomembrane remodeling [1–4]. In fact, nowadays, crop failures caused by climate change and human action pose the biggest hazard to human and environmental health through food safety declining [5]. Trying to face this everchanging environment, plants have developed the capacity to adapt to and benefit from changes in their surroundings, activating stress defense mechanisms [6]. The processes behind the stress response are only partially understood, and alterations in the transcriptome are still the outcome of a complex chain of circumstances. One of the most important mechanisms, especially concerning interorganellar connections, occurs at the endomembrane level [7, 8], from which new markers for the assisted selection of stress-resistant crop types can be found. Since the plants' successful adaptation likely relies on balanced interactions and synergistic effects among ordinarily unrelated proteins, defining each participant's precise roles in the game is a crucial aspect of plant genetic improvement [9]. Recent experimental

evidence [10] points to a variety of protein classes (including aquaporins, soluble N-ethylmaleimide-sensitive factor attachment protein receptors (SNAREs), ATPase pumps, or channels) that regulate particular membrane transport events, resulting in significant cell reorganization events in challenging environmental conditions. As an example, the AKT1/KC1, a shaker-like potassium channel, was selectively accumulated on small vacuoles [11] and is sufficient to confer stress tolerance when overexpressed. Several research groups discovered intriguing connections between stress tolerance and previously unrecognized membrane rearrangements. However, the relationship between the architecture of membranous structures and their ability to withstand stress has only recently gained the attention of researchers. Numerous research items have supported the notion that endomembrane trafficking is closely related to stress signaling pathways; nevertheless, these studies lack a better understanding of the underlying mechanisms. In the last several years, there has been a notable advancement in our understanding of the mechanisms behind protein sorting. Due to their significance in maintaining the homeostasis of plant cells, particular attention has been paid to the study of proteins that are directed toward the vacuole and the inherent sorting mechanisms. Regarding this matter, recent results imply that alternative routes may challenge the orthodox concept of protein transport to the vacuole [12–14]. These alternative routes are regarded as one of the plant's adaptations to challenging circumstances. As a result, it is believed that certain conditions may cause the vacuolar trafficking pathways to change to better serve the demands of the plant. Alongside the vacuole, the endoplasmic reticulum, as the entrance to the endomembrane trafficking routes, also plays an important role in the folding, quality control, and sorting of newly produced proteins [15–17]. Additionally, as the link between the actin cytoskeleton and the endomembrane system is essential to maintaining many aspects of plant cell function and development, the cell cytoskeleton also plays a significant role in the response and adaptation to stress [18]. This chapter aims at describing the more recent findings on the effects of abiotic stress in the endomembrane system, alterations in vacuolar trafficking routes, and the importance of the cell cytoskeleton in these processes. Also, examples of proteins and endomembrane effectors with altered expression/localization were depicted from the available literature that can represent a collection of putative markers for abiotic stress studies (**Table 1**).

2. Endoplasmic reticulum and stress

A network of tubules and cisternae that extends across the entire cell and links with several other organelles, the endoplasmic reticulum (ER), is crucial for maintaining cellular homeostasis as well as for detecting and disseminating external signals [7]. The ER is one of the main organelles that mediate the stress response in both plants and animals [15–17]. Protein misfolding and accumulation following adverse environmental conditions can lead to ER stress [19–21]. In response, the cell activates various mechanisms to maintain the homeostasis of the ER, such as the expression of genes encoding chaperones and other proteins with the ability to fold proteins, degradation linked to the ER, or a reduction in the amount of protein translation loaded into the ER [19, 22]. As an example, unfolded proteins can bind to BIP proteins (binding proteins), which activate bZIP transcription factors like bZIP17/bZIP28 that are transported to the Golgi to be cleaved (**Figure 1**) [17, 19]. To regain ER equilibrium, this transport will upregulate genes related to the ER stress pathway [17]. The

	Protein	Stress-related response	Refs
ER-related	bZIP28	Involved in the activation of heat stress response genes	[17, 19]
	bZIP17	Participates in the activation of salt stress response genes	[20, 21]
	IRE1	Responsible for the splicing of bZIP60 mRNA, required for the activation of genes involved in the ER stress reaction; regulates the stress transcriptome by degrading several mRNAs	[22–25]
	NPR1	Suppresses the transcriptional role of bZIP28 and bZIP60 in ER stress responses triggered during pathogen attack	[26, 27]
	ATG8	Following ER stress, many ER components are delivered for degradation *via* autophagy, forming ER-derived autophagic bodies	[28–30]
Vacuole-related	CBL–CIPK	Important role in the detoxification of $Mg2^{+}$ in the vacuole during salt stress conditions	[31]
	VPEs	Hydrolytic enzymes, such as proteases and antimicrobial compounds, are released to the cytosolic environment, or extracellularly, to fight pathogen attacks.	[32–34]
Cytoskeleton-related	CesA	Osmotic stress induces endocytosis of cellulose synthase complex and their interaction with cortical microtubules	[35, 36]
	CSI1-dependent SmaCCs/ MASCs	During endocytosis, CSI1-dependent SmaCCs/MASCs are formed, allowing a quick regulation of cellulose synthesis under abiotic stress	[37]
	NET1A	Reacts to extracellular signals, such as stress related to pathogen infection	[38]
Vacuolar trafficking	RMR1; VSR1; SYP51; VTI12; VTI11; VSR2	Genes involved in the PSV sorting are positively regulated in plants under abiotic stress, while genes involved in the LV sorting downregulated	[4]
	VSR1	Important for the regulation of abscisic acid (ABA) biosynthesis, a signaling molecule in several stress conditions	[39]
	RabG3e	Arabidopsis plants overexpressing AtRabG3e showed increased tolerance to salt and osmotic stress along with a reduction in the accumulation of reactive oxygen species	[40]
	VAMP7C	Suppression of the v-SNARE AtVAMP7C had a positive impact in improving plant salt tolerance by inhibiting the fusion of H_2O_2-containing vesicles with the vacuole	[41]
Unconventional vacuolar routes	PSIB	Overexpression of PSIB in *Arabidopsis thaliana* correlates with salt and osmotic stress conditions, in some cases improving plant fitness	[42]
	Cysteine Proteinases	Cysteine proteinases accumulate in long ER bodies, whose fusion with the PSV may be triggered by stress	[43]
	PR1 PDF1.2	ER bodies filled with defense proteins are formed and eventually fuse with the plasma membrane or with the vacuole in a Golgi-independent manner	[44]

Table 1.
Endomembrane-associated proteins with responses to adverse abiotic conditions.

upregulation of genes implicated in stress response, such as bZIP28, which activates heat stress response genes [17, 23] and bZIP17, which activates salt stress responses [20, 24], may also be mediated *via* this transport. As so, it is easy to see that ER stress responses are frequently triggered in scenarios of heat and salt stress [17, 23, 24]. However, other significant proteins, such as the ER-resident transmembrane protein inositol-requiring enzyme-1 (IRE1), are implicated in the unfolded protein responses (UPR) that react to unfavorable environmental conditions (**Figure 1**) [17, 25]. The heat stress response is said to be mediated by this protein. It is necessary for the activation of the genes involved in the ER's stress response because bZIP60 mRNA, which is spliced by the heat-activated enzyme IRE1 [26], is present. By destroying several mRNAs, this protein also controls the stress transcriptome [27, 28]. Other UPRs are triggered in this sort of stress in addition to the previously reported mechanism, but their overexpression is irrelevant, suggesting that salt stress can merely increase the misfolding of a new group of proteins [17, 24, 29, 30]. Another transcriptional component that affects plant UPR has recently been discovered. It has been shown that the nonexpressor of PR1 gene 1 (NPR1) inhibits the transcriptional function of bZIP28 and bZIP60 in ER stress responses (**Figure 1**). NPR1 is a critical redox-regulated master regulator of salicylic acid (SA)-dependent responses to pathogens. NPR1 is translocated to the nucleus and physically interacts with bZIP28 and bZIP60, acting as an antagonist of such UPR proteins to maximize their cytoprotective function in the UPR (**Figure 1**). This occurs when ER stress causes the cytosolic redox potential to decrease. A negative feedback loop that is crucial for regulating energy consumption and preserving basal cellular homeostasis during ER stress signaling may be

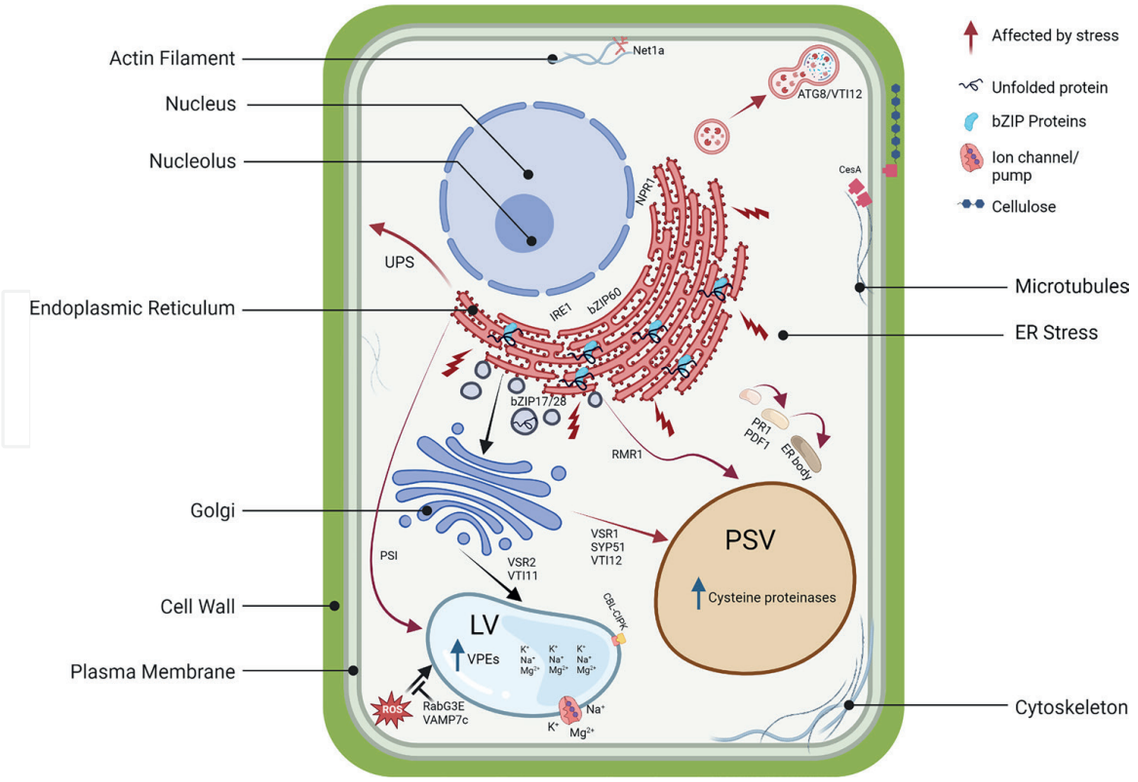

Figure 1.
Diagram showing the modifications in endomembrane trafficking and related protein effectors under abiotic stress conditions. LV—Lytic Vacuole; PSI—Plant Specific Insert; PSV—Protein Storage Vacuole; ROS—Reactive Oxygen Species; UPS—Unconventional Protein Secretion; VPEs—Vacuolar Processing Enzymes. Image created with BioRender.com, accessed on 21 November 2022.

promoted by NPR1 roles in plant UPR monitoring [31]. The intercellular mobility of bZIP60, which promotes systemic UPR signaling, has been shown to govern a non-cell-autonomous component in addition to cell-intrinsic UPR signaling. Evidence suggests that the sbZIP60 protein can move between cells and activate a target gene's promoter, thus promoting UPR gene expression in cells far from the region of ER stress. Such findings imply that ER stress systemic signaling may represent a mode of anticipation of a potentially imminent ER stress, as the cells of tissues that have not yet been subjected to ER stress are prepared by triggering the accumulation of ER stress attenuating protein transcripts [32].

Under stress, the ER's other compartmentalization mechanisms, such as autophagy, are also engaged in addition to ER stress responses. The sequestration of cytosolic components by a newly generated, double-membrane vesicle known as an autophagosome, which is subsequently directed to the plant vacuole, is known as macroautophagy [33, 34]. Notably, it was also claimed that selective autophagy delivered vacuolar resident proteins to this organelle *via* specific trafficking channels. The degradative aspect that autophagy is typically associated with contrasts with its role in the biogenesis-mediating process. It was demonstrated that triggering ER stress in Arabidopsis causes the transfer of ER components, like the ribosome-decorated ER membrane, to vacuoles *via* autophagy [34], supporting the idea that autophagy may be involved in the trafficking of storage proteins. Additionally, it is now understood that both yeast and mammalian cells use autophagy to transfer ER components for destruction during ER stress [35–37]. Plants share many similarities with other eukaryotes in this regard, and the accumulation of Atg8-positive bodies that co-localized with the ER marker GFP-HDEL was found after ER stress. In the vacuoles of ER-stressed plants, the presence of autophagic structures, including ER membranes, was also discovered by electron microscopy [34]. IRE1b has been linked to this kind of response, according to a different study conducted by Bao and colleagues [38]. This pathway, however, is not related to BZIP60, but instead to the regulated IRE1-dependent decay of messenger RNA (RIDD), in which IRE1 degrades the mRNAs of factors encoded by genes that prevent the activation of autophagy processes in response to ER stress [39], such as BGLU21, a member of the β-glucosidase family and one of the main elements of ER bodies.

The ER is in a unique position to identify extracellular stimuli and coordinate the cellular response to adverse and demanding situations in the cell because it is the origin of the endomembrane system. Its central network-like structure, which permeates the entire cell, enables it to interact with other organelles at several points, demonstrating the high complexity of the ER mechanisms that are crucial to preserving the functionality of cellular homeostasis and signaling cascades.

3. The vacuole as a major player in cell homeostasis

Vacuoles perform physical and metabolic tasks, can occupy up to 80% of the volume of a cell, and are crucial for cellular responses to abiotic and biotic stimuli as well as to general cell homeostasis [40, 41]. These organelles often house water, nutrients, ions, and secondary metabolites, but they can also act as a deposition location for waste materials, excess solutes, and toxic cell remnants [42–45]. They also play a role in programmed cell death [46]. The protein storage vacuole (PSV) and the lytic vacuole (LV) are the two main forms of vacuoles found in plant cells. Proteins predominate in storage tissues (such as cotyledons, endosperm, and tubers) and

vegetative tissues (bark, leaves, and pods) of adult plants, and they often accumulate in the PSVs because of their higher pH and lower hydrolytic activity when compared to the LVs [47, 48]. LVs, on the other hand, are mostly present in vegetative tissues and are employed for storing and depositing undesirable substances. This form of vacuole controls the breakdown of a wide range of macromolecules and other chemicals because of its high hydrolytic activity and acidic pH [49, 50]. Initially, it was not expected to find both forms of vacuoles in the same cell; however, research done in root tip cells of barley and pea seedlings proved this was not the case [51, 52]. In addition, a study employing the model plant Arabidopsis thaliana found that, rather than being created from scratch, the LV is embedded in the PSV during germination [53]. Two distinct types of vacuoles suggest that plants have unique trafficking processes and pathways for various proteins. Additionally, it has been suggested that the coexistence of LVs and PSVs in a single cell may function as a plant flexibility mechanism in response to shifting environmental conditions [54–57].

According to a recent study by Neves and colleagues, Arabidopsis plants exposed to abiotic stress exhibit differential expression of genes involved in vacuolar trafficking, with the pathway to the PSV becoming enhanced [4]. In fact, under abiotic stress, plants are able to control their growth and development by changing cellular and morphological mechanisms, and cellular responses/adaptations to stress may affect the distribution and sorting of particular proteins and molecules. Additionally, numerous studies highlight the crucial function of the vacuole as a defense mechanism against abiotic stress. In fact, the vacuole appears to respond to stress through various processes, including the build-up of hazardous products and the maintenance of cell-turgor pressure. According to a study using suspension-cultured mangrove (*Bruguiera sexangula*) cells, when cells are exposed to salt stress, their vacuolar volume quickly increases at the expense of their cytoplasm volume in order to maintain turgor pressure, most likely due to an increase in the concentration of Na^+ in the vacuole [58]. Another study employing the Arabidopsis thaliana plant demonstrates the significance of the vacuole during oxidative stress. In fact, the vacuole developed large concentrations of GSSG (oxidized glutathione) as a defense mechanism against a too positive shift in the cytosolic glutathione redox potential [59]. In addition, the vacuole plays a role in systems that counteract environmental stress, such as lowering the cytoplasmic toxicity of high ion concentrations to prevent cell death. According to a study by Tang and colleagues [60], the excessive Mg^{2+} vacuolar sequestration that plants use to survive Mg^{2+} stress is a novel function of the Calcineurin B-like (CLB) interacting protein kinases' (CIPK) (CBL-CIPK) signaling network. A generic mechanism underpinning the detoxification of additional ions, such as Na^+, may be represented by the reported Mg^{2+} partitioning process in the vacuole controlled by the CBL-CIPK pathway (**Figure 1**). Contrary to abiotic stress, where the vacuole's integrity is crucial for maintaining the cell's homeostasis, pathogen infections necessitate the breakdown of the vacuole and the release of its contents (for a review on the subject, see [61]). The vacuole stores vast amounts of hydrolytic enzymes, such as proteases and antimicrobial substances as an innate defense mechanism, that are subsequently released under pathogen attack in a procedure that is not fully understood [62, 63]. The release of vacuolar contents has been attributed to two distinct mechanisms, including hypersensitive reaction and programmed cell death (PCD) [64]. The disruption of the tonoplast and involvement of vacuolar processing enzymes (VPEs) in one case, and the fusion of the tonoplast and plasma membrane (PM) in the other, were observed (**Figure 1**). Vacuolar contents are released as a consequence in both situations.

Alterations in vacuolar morphology, such as changes in vacuolar trafficking, are a crucial aspect of cell homeostasis under stress and also help maintain plant homeostasis. The actin cytoskeleton and SNARE proteins, which control these adaptations, allow the vacuolar network to be structurally reorganized while preserving its dynamics [65, 66].

4. The dynamic cytoskeleton concept

The notion of cytoskeleton has been transformed from a static, supporting structure to a dynamic mechanism in energetic balance that fine-tunes its time and space resolutions to adjust its functions to driving changes and stress reactions [67]. In plant cells, intracellular transport is primarily driven by myosin motors and actin filament bundles. Modifications in Golgi body motility show that changes in the pace of actin remodeling also have an impact on its functionality [68]. Depolymerization of actin inhibits both ER remodeling and Golgi movement, highlighting the significance of the actin cytoskeleton [69, 70]. Four members of the Myosin XI family (xi-k, xi-1, xi-2, and xi-i) were subjected to mutant knock-out studies, which revealed the importance of these proteins for normal cellular and whole-organism development as well as Golgi body dynamics [71]. However, microtubules are believed to be crucial at specific times in the formation of plant cells [72]. Given that stress is a condition that the cell finds to be quite difficult, it is necessary to test the idea that the cytoskeleton network will also have to adapt because its contact with membranes is essential for the cell's ability to self-organize. Reviewing the complexity of organelle movement within the plant secretory pathway, Brandizzi and Wasteneys [72] cast doubt on the actin-centric view of the motility of secretory organelles. They analyzed past studies and recent discoveries that support the critical function of microtubules in plant cell development, positioning of Golgi stacks, involvement in cellulose synthesis, and polar auxin transport.

The research of Ambrose and collaborators [73], which used hybrid and *in vivo* bimolecular fluorescence complementation techniques, was a turning point in understanding the relationship between endomembrane trafficking and microtubules. They found that the microtubule-associated protein CLASP interacts with the retromer, facilitating the association between TGN/early endosomes and cortical microtubules through interaction with sorting nexin1 (SNX1). The retromer protein complex, which SNX1 is a part of, recycles the plasma membrane auxin efflux carrier PIN2, hence regulating auxin transport.

Further investigations demonstrated the anchoring of compartments transporting cellulose synthase complexes to microtubules, confirming the importance of microtubules in organelle location and function. Cellulose is created at the plasma membrane by multi-enzyme complexes, in contrast to some cell wall polysaccharides made by glycosyl transferases and altered by Golgi-located enzymes [72]. This multi-enzyme complex must be delivered to the appropriate places at the PM. The trans-Golgi network (TGN) compartment is used to secrete cellulose synthase (CESA) complexes (CSCs) to the plasma membrane [74]. Through research on the intracellular trafficking of cellulose synthase complexes, small CesA-containing compartments (SmaCCs) [75] and microtubule-associated cellulose synthase compartments (MASCs) [76] were identified. Osmotic stress or the reduction of cellulose synthesis causes the endocytosis processes of the cellulose synthase complex, which causes the concentration of organelles containing CESA and their intense interaction

with cortical microtubules [75, 76]. The SmaCCs associated with CSC transport may constitute a specialized secretory route involved in cell wall production, according to a theory where microtubule-associated compartments constitute functional secretory vesicles when plants are under cellular stress (**Figure 1**) [74]. This is a result of the fact that, before releasing CSC to the PM, these organelles reduce osmotic stress [75]. The SmaCC/MASC-mediated fast recovery of CSCs after stress relief depends on the protein cellulose synthase interactive 1 (CSI1), which is connected to cortical microtubules and involved in the interaction between CSCs and these structures [77].

SmaCCs/MASCs are also formed as a result of AP2M, a part of clathrin-mediated endocytosis. Lei and colleagues [77] suggest a concept in which CSI1-dependent SmaCCs/MASCs are produced during endocytosis, enabling rapid modulation of cellulose synthesis in response to abiotic stress. All of these methods help to decipher a spatiotemporal model of trafficking processes in cell wall deposition under both stress-free and demanding circumstances. Actin-binding proteins from the NET super-family [18] are recruited to various membrane compartments *via* a C-terminal region and directly interact with F-actin. These proteins include NET1A, which labels the plasma membrane, NET4A, which labels the tonoplast, and NET3B, which labels the endoplasmic reticulum. The fact that NET1A is among the actin-associated endoplasmic reticulum-plasma membrane contact site (EPCSs) proteins and that they react to extracellular signals like stress brought on by pathogen infection is further evidence for this claim [78]. The protein complex composed by the membrane-anchored protein VAP27 (At3g60600) and the actin-binding protein NET3C (At2g47920), which has an affinity for microtubules, is indicated to define the contact points between the plasma membrane and the cortical endoplasmic reticulum network [79]. In conclusion, the coordination of endomembrane trafficking requires the precise control of endomembrane carriage in space and time, incorporating both actin- and microtubule-based processes.

Additionally, vesicle shuttles (also known as transport vesicles) are the primary means of moving cargo molecules across compartments, and the cytoskeleton plays a function in making this process easier [80]. When the plant is exposed to harsh conditions, the relevance of this "shuttle transport" may take on more substantial outlines in the context of cellular rearrangement.

5. Vacuolar transport under stress

A sophisticated network of receptors and vesicles controls the movement of proteins into the vacuole. Because of this, proteins can be sorted differently, arriving at various locations depending on the receptors and vesicles employed [81, 82]. The vacuolar sorting receptors (VSRs), which are in charge of cargo binding and release as well as traffic regulation from and to the prevacuolar compartment (PVC) [14, 83], are involved in the transport of soluble cargoes by the conventional pathway. In addition to these receptors, proteins with the receptor homology region-transmembrane domain-RING-H2 (RMR) have been found to be involved in the flow to the PSV. These receptors, however, cannot be regenerated again [81, 84, 85]. The type of vesicles is another distinguishing element for the eventual location of the vacuolar proteins. Clathrin-coated vesicles (CCVs), which are located in the trans-Golgi Network (TGN) and are engaged in post-Golgi transport, are in charge of transporting proteins to the LV [81, 84, 86]. Dense vesicles (DVs), which are larger carriers compared to CCVs, fuse with PVCs and go to the PSV [14, 87–89]. It is evident

that it is a flexible and well-coordinated network when all the information on protein trafficking to the vacuole is considered collectively [90]. Therefore, it is not surprising that this delicate balance can be disrupted in response to abiotic stress in order for the cell and, eventually, the plant, to meet their demands and survive.

Few studies have focused on this topic, and the changes in vacuolar trafficking that occur as a result of stress in cells have not yet been fully defined. Nevertheless, a few singular observations and reports are noteworthy because they might pave the way for further focused investigation. In recent work, Neves and colleagues [4] examined the expression of multiple endomembrane system effectors to assess how various abiotic stresses affect the endomembrane system in *A. thaliana*. The authors demonstrate that during abiotic stress, the PSV sorting genes AtRMR1, AtVSR1, AtSYP51, and AtVTI12 are positively regulated, whereas the LV sorting genes AtVTI11 and AtVSR2 are negatively regulated. The authors' theory, which is based on these observations, is that under abiotic stress circumstances, the PSV route would be strengthened at the expense of the LV pathway. Despite being very preliminary, this research identifies several crucial genes that are involved in the vacuolar route that may help understand how the cell responds to challenging circumstances. One example is the v-SNAREs VTI12 and its homolog VTI11, which work in several vesicle transport routes and mediate the transport to various vacuolar types [88]. VTI12, however, performs different activities, including helping autophagic vesicle binding and fusion [91]. Along with SYP61 and SYP41, it is a protein complex component located at the TGN. SYP61 has been linked to osmotic stress reactions [92], and it is hypothesized that it may also be a part of stress-responsive transport pathways, as that SYP121 at the plasma membrane has been linked to [10]. As a member of the same complex as SYP61, VTI12 might possibly take part in this mechanism. In fact, it has been demonstrated that VTI12 expression is 20–30 times higher in Arabidopsis plants grown under abiotic stress than in control circumstances [4], which is suggestive of a probable function in cells' adaptation or stress response. Additionally, the VSRs implicated in the trafficking of the PSV appear to react to stress. A unique role for AtVSR1 in osmotic stress tolerance and the control of abscisic acid (ABA) production, which is a key regulator of the signaling pathways generated by osmotic stressors, was recently proposed by Wang and collaborators [93]. With the aid of a vsr mutant, the authors demonstrated that vacuolar trafficking, which is mediated by VSR1, was essential for ABA production and osmotic stress tolerance. A different study found that Arabidopsis plants overexpressing AtRabG3e were more tolerant to salt and osmotic stress and produced fewer reactive oxygen species [94]. AtRabG3e engages in membrane fusion between the PVC and the vacuole, highlighting the importance of this pathway in stress response (**Figure 1**). The Rab GTPases are a broad family of proteins that regulate vesicle targeting and specificity [95]. In addition to the traditional pathway, the endocytic route to the vacuole has also been linked to plant tolerance to salt stress. This was demonstrated in a study by Leshem and colleagues [96], who found that suppressing the v-SNARE AtVAMP7C, which is necessary for endosomal vesicle fusion with the tonoplast, had a favorable effect on enhancing plant salt tolerance. Overall, the SNARE proteins are essential for protein trafficking to the vacuole, which is critical for both responses to stress and adaptations to it (See [97] for a review on SNAREs in plant stress responses). As with Adaptor protein 3 (AP-3) and the adaptor complex that interacts with VTI12 in the TGN, it is also important to investigate the role of other post-Golgi pathways [98]. This system interacts with the traditional pathway in a way that appears to affect how plants respond to stress circumstances while enabling a quicker supply of vital proteins for the vacuole's biogenesis. In addition,

DVs-mediated transport, which still has to be studied, is a good substitute for conventional transport in these challenging circumstances.

6. Taking a shortcut to the vacuole

Studies have described proteins and vacuolar signals that do not follow the mainstream route to the vacuole. The Golgi apparatus is required for some alternative sorting routes, like AP-3 and dense vesicle sorting, although other pathways also seem to be Golgi-independent [14]. Stress may activate these alternative sorting routes to better meet the plant's unique needs at the cellular level, but the relationship between stress and unorthodox sorting routes is largely unknown. In fact, autophagy-related processes, which can be triggered by a variety of environmental perturbations, seem to be connected to direct ER-to-vacuole pathways. A different pathway from the ER to the vacuole has been described for a variety of proteins or vacuolar sorting determinants in recent years [99–101]. Cardosin, a Plant Specific Insert (PSI), stands out among them because other similar domains lack this capability [13].

It is thought that additional unidentified, unconventional routes operate identically to the PSI-mediated vacuolar transport when plants are under stress, providing plants the option to sort proteins by the conventional approach or by a direct ER-to-vacuole transfer. In fact, a recent exploratory study [102] showed that Arabidopsis thaliana overexpression of PSIB correlates with conditions of salt and osmotic stress, occasionally improving plant fitness. A distinct family of proteins known as cysteine proteases also appears to be connected to salt stress. In both seedlings (as demonstrated in Vigna mungo [103] and Ricinus communis [104]) and the epidermis of vegetative tissues (Arabidopsis thaliana [105]), these proteins accumulate in lengthy ER bodies that eventually merge with the vacuole. Recent evidence suggests that direct ER body fusion with the vacuole might well be induced by stress, which sheds fresh light on the relevance of this kind of transport. The breakdown of storage proteins during plant growth is brought on by these proteins and the vacuolar processing enzymes.

The formation of ER bodies filled with defense proteins like pathogenesis-related 1 (PR1) or plant defensin 1.2 (PDF1.2) in response to pathogen attacks has been described in a similar way (for a review, see [61]) (**Figure 1**). These ER bodies then fuse with the plasma membrane or the vacuole in a way that is Golgi-independent. Additionally, autophagy markers are regularly seen in the ER and vacuole membranes [93], and stress frequently induces autophagic compartments [3, 106]. It is yet unclear how autophagy in and of itself can aid in vacuolar sorting, and additional mechanisms or regulators undoubtedly need to be engaged. An intriguing example of unusual trafficking involves the exocyst pathway, which plays a role in autophagy and plant defense, and anthocyanins that are imported to the vacuole during cycles of stress and famine [107, 108]. After reviewing all the available instances, it is critical to research the direct ER-to-vacuole transfer in stressed plants. In fact, defining atypical sorting routes along with stress responses would offer fresh perspectives on the scant knowledge that has previously been known. Given that it speeds up and increases the dynamic of protein transport to the vacuole, the Golgi bypass may significantly impact stress responses. As a matter of fact, a number of unconventional pathways are triggered by modifications in the cell environment rather than being constitutive.

7. Conclusions

For many years, studies and discussions on the effects of stress on plants have dominated the headlines. However, because of the discussion's main emphasis on the physiology and antioxidant system of plants, essential cell activities are frequently overlooked. However, given that a significant number of genes and proteins are *de novo* generated in response to stress and must be transported to their correct locations, this is a crucial problem to investigate. Understanding trafficking processes and proteins linked with transport is crucial in this situation. The major "sensor" for stress is thought to be the ER, where the stress responses begin and from which proteins and signals are either transported to other parts of the cell or destroyed. Given its various dimensions and functions, the vacuole is also crucial to this process. As a result, one of the key mechanisms in plant defense and cellular homeostasis is the transit of vesicles between the ER and the vacuole. According to a recent study, in which it was demonstrated that the Golgi is hypertrophied and associated with high vesiculation in plants under stress using Transmission Electron Microscopy [4], the high amount of proteins and molecules newly produced will likely cause saturation of the Golgi trafficking pathways. In this case, the ER is directly connected to the vacuole, which is a speedier path and can be thought of as an escape from the gridlock that started between the ER, Golgi, and prevacuolar compartments. In fact, it appears that stress or other challenging conditions are connected to these atypical pathways to the vacuole or the plasma membrane. We still have a long way to go before we fully understand the mechanisms underlying these pathways and how they are regulated, but the first steps are being made, and in the near future, we anticipate having a clearer picture of the process and a better understanding of the mechanisms underlying plant tolerance and adaptation to stress.

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Conflict of interest

The authors declare no conflict of interest.

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