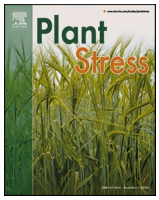
Plant Stress 16 (2025) 100810

Contents lists available at ScienceDirect

Plant Stress

journal homepage: www.sciencedirect.com/journal/plant-stress



Review

The role of membrane-biomolecular condensate interactions in stress

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ARTICLE INFO

Keywords:
LLPS
Biomolecular condensates
Stress
Membrane wetting
Membrane trafficking

ABSTRACT

Biomolecules can be condensed through liquid-liquid phase separation (LLPS) or other material states. The resulting biomolecular condensates can play key roles in cellular organisation and stress responses. While often regarded as membrane-less structures, some biomolecular condensates interact with cellular membranes. Despite their potential importance, these interactions remain largely unexplored, primarily due to their dynamic nature. We focus here on membrane-biomolecular condensate interactions that have significant functions in stress responses, suggesting their link with long-term stress adaption.

Introduction

Cells constantly monitor their surroundings for changes that could disrupt their normal function. When a cell encounters environmental stress, such as extreme temperatures (heat or cold), drought, or the presence of harmful organisms, it initiates a complex response to survive. This process begins with specialised sensor molecules, known as receptors, strategically positioned on the cell's surface, within its cytoplasm, or in other cellular compartments (Wang et al., 2024b). These receptors act like sentinels, detecting the specific stressor and triggering a cascade of molecular events (Jiang et al., 2019). This cascade often involves intricate protein-protein interactions, chemical modifications like phosphorylation, and the release or activation of signalling molecules called secondary messengers (e.g., calcium and reactive oxygen species). These signalling events ultimately converge on key cellular players, including transcription factors, enzymes, and other regulatory proteins. By modulating the activity of these proteins, the cell orchestrates a coordinated stress response aimed at mitigating the damage, restoring homeostasis, and ensuring survival.

Environmental stress profoundly impacts the cellular organisation, affecting both traditional organelles and the more recently discovered membrane-less organelles, known as biomolecular condensates (Wang et al., 2020b). Biomolecular condensates usually form through liquid-liquid phase separation (LLPS) (Holehouse and Alberti, 2025). These condensates, composed of proteins, RNA, and other biomolecules, were initially thought to exist primarily within the cytoplasm and nucleoplasm. However, they frequently interact with cellular membranes, membranous vesicles, and lipids, expanding the complexity of their functional roles (Mangiarotti et al., 2023; Dumelie et al., 2024).

One of the most well-characterized examples of a membrane-bound condensate in a stress context is the mammalian T-cell receptor (TCR) signalling, a critical component of the adaptive immune response (Huang et al., 2019). Upon encountering an antigen, the T-cell receptor initiates a signalling cascade leading to T-cell activation. This process involves the formation of a condensate at the plasma membrane, consisting of the transmembrane protein Linker of Activation of T cells (LAT) and the cytoplasmic adaptor proteins Growth factor receptor-bound 2 (Grb2) and Son of Sevenless 1 (Sos1). This LAT/Grb2/Sos1 condensate acts as a specialised microenvironment, concentrating the signalling components necessary for efficient TCR signalling. Within this condensate, proteins are brought into proximity, facilitating phosphorylation and thus downstream signalling pathways. This precise spatiotemporal signalling is crucial for fine-tuning the immune response.

Although many biomolecular condensates have been identified in plants, a significant gap remains in our understanding of their interactions with membranes and how they behave and function there, particularly under stress conditions. The broader landscape of plant biomolecular condensates, including their diverse types and functions, has been extensively reviewed (Liu et al., 2024b; Fang and Li, 2024). Here, we will specifically focus on those condensates that exhibit a clear functional connection to membranes, especially in cellular stress responses.

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https://doi.org/10.1016/j.stress.2025.100810
Received 3 February 2025; Received in revised form 11 March 2025; Accepted 13 March 2025
Available online 13 March 2025

The basics of membrane trafficking in plants

Before exploring the interplay between biomolecular condensates and membranes, it is essential to understand the fundamental process of membrane dynamics, known as membrane trafficking. This process governs the movement of membrane-bound vesicles and organelles, facilitating the targeted delivery of molecules within the cell. This dynamic process is particularly crucial during stress responses, enabling the recycling of damaged molecules and the transport of both intracellular and extracellular materials. Below, we provide a concise overview of membrane trafficking in plants. For a more in-depth exploration, we refer the reader to (Aniento et al., 2022). In plants, two primary pathways orchestrate membrane trafficking:

The Secretory Pathway: This pathway originates in the ER, the central hub for protein synthesis, folding, and initial packaging. Proteins destined for secretion or integration into cellular membranes are processed within the ER and transported to the Golgi apparatus. Here, further modifications, such as glycosylation and phosphorylation, occur, and the proteins are sorted and packaged into transport vesicles. These vesicles then bud off from the Golgi and are targeted to their final destinations, including the plasma membrane, the vacuole, or the cell wall.

The Endocytic Pathway: This pathway mediates the internalisation of molecules from the plasma membrane (or elsewhere), encompassing a diverse array of cargo, including signalling molecules, ion channels, and receptors. Endocytosis involves plasma membrane invagination to form vesicles that bud inward and undergoing scission, encapsulating the target molecules. These vesicles then fuse with early endosomes (EEs)/ *trans*-Golgi network (TGN), a complex assembly of interconnected membranes. From these intermediate compartments, cargo can be recycled back to the plasma membrane, directed to the vacuole, or transported to other specific cellular locations.

Vesicle formation, movement, and targeted fusion are regulated by a diverse array of molecular machinery. Key players in this dynamic system are the RAS-RELATED IN BRAIN (RAB) GTPases. These small proteins exhibit remarkable specificity, localising to distinct membrane compartments and recruiting effector proteins that orchestrate vesicle transport and fusion. Vesicle formation is driven by the assembly of coat proteins on the membrane surface. Three major types of coat proteins exist: COAT PROTEIN COMPLEX I (COPI), COPII, and CLATHRIN. COPI plays a crucial role in retrograde transport, which is shuttling cargo from the Golgi apparatus back to the ER, a process facilitated by ADP RIBOSYLATION FACTOR 1 (ARF1) (Snead et al., 2017). Conversely, COPII drives anterograde transport, carrying nascent proteins from the ER to the Golgi. CLATHRIN-coated vesicles (CCVs) mediate vesicular transport, including both Golgi-to-endosome/plasma membrane trafficking and endocytosis. CLATHRIN-coated vesicles (CCVs) mediate transport from the Golgi to the endosomes and plasma membrane. At the plasma membrane, CLATHRIN is essential for receptor-mediated endocytosis, forming CLATHRIN-coated pits that invaginate and bud off as vesicles (Gollapudi et al., 2023). Yet, as discussed later, other types of endocytosis exist.

The family of N-ETHYLMALEIMIDE-SENSITIVE FACTOR ATTACHMENT PROTEIN RECEPTOR (SNARE) proteins ensures vesicular fusion specificity (Park et al., 2023). v-SNAREs reside on the vesicle membrane, while t-SNAREs are on the target membrane. The interaction between complementary v-SNAREs and t-SNAREs brings the vesicle and target membrane into close proximity, enabling membrane fusion. In addition to SNAREs, the HOMOTYPIC FUSION AND PROTEIN SORTING (HOPS) and the EXOCYST complexes act as crucial tethering factors (Takemoto et al., 2018; Synek et al., 2021; Michalopoulou et al., 2022). Composed of six subunits (VACUOLAR PROTEIN SORTING ASSOCIATED11, VPS16, VPS18, VPS33, VPS39, and VPS41), HOPS bridges the vesicle and target membrane, bringing them close enough for SNARE-mediated fusion. The EXOCYST complex is composed of eight subunits: SEC3, SEC5, SEC6, SEC8, SEC10, SEC15, EXO70, and EXO84, which also facilitate fusion. Finally, the intracellular transport of vesicles relies on actin filaments and microtubules, which, in conjunction with motor proteins like myosin and kinesin, provide the tracks along which vesicles are transported (Ruan et al., 2018; Liu et al., 2023b).

Both endocytosis and the secretory pathway play crucial roles in regulating the composition of the plasma membrane and influencing cellular signalling. They achieve this by modulating the trafficking of receptors, channels, and hormone-receptor complexes to and from the cell surface. This dynamic regulation directly impacts the initiation and strength of cellular responses during stress (Dragwidge et al., 2024). Beyond signalling components, these pathways also manage the delivery of stress-related proteins, such as antioxidant enzymes and heat shock proteins, equipping the cell to respond to environmental challenges (Driedonks et al., 2015). Endocytosis further contributes to cellular homeostasis by removing damaged or modified proteins from the plasma membrane, such as oxidised proteins, ensuring proper receptor function and preventing aberrant signalling. In addition to these functions, the secretory pathway is essential for delivering key structural components to the cell's exterior, including cell wall components like cellulose synthase complexes (CESA), and polysaccharides, such as pectin (Sinclair et al., 2018).

Another regulator of membrane trafficking involves the Endosomal Sorting Complex Required for Transport (ESCRT) (Mosesso et al., 2024; Liu et al., 2024a; Liu et al., 2023a). This machinery comprises several cytosolic protein complexes, including ESCRT-0, -I, -II, and -III, along with accessory proteins like VPS4, LYSOSOMAL TRAFFICKING REGULATOR INTERACTING PROTEIN-5 (LIP5), and ALG2-INTERACTING PROTEIN X (ALIX) (Hu et al., 2022). While plants possess most ESCRT components (ESCRT-I, -II, -III, and VPS4/ SUPPRESSOR OF K+ TRANSPORT GROWTH DEFECT 1), they lack canonical ESCRT-0 subunits. However, they compensate for ESCRT-0 lack with a plant-specific ESCRT protein, FYVE DOMAIN PROTEIN REQUIRED FOR ENDOSOMAL SORTING 1 (FREE1). ESCRT-I complex assembly initiates with interactions between VPS23, VPS37, and VPS28. VPS28 is crucial for binding to protein cargo that has been tagged with ubiquitin and its associated adaptor proteins. This interaction effectively links the ubiquitinated cargo destined for degradation with the ESCRT machinery. Following cargo binding, the ESCRT-I complex undergoes further assembly, involving the association of additional subunits like VPS46. These components contribute to stabilising the complex and enhancing its interaction with membranes. Furthermore, the ESCRT-I complex interacts with other ESCRT complexes, particularly ESCRT-II (VPS36, VPS22, VPS25) and ESCRT-III (SNF7, VPS20), to coordinate the cargo sorting process (Christ et al., 2016).

The ESCRT assembly is key in membrane remodelling, a process crucial for various cellular events, including the formation of multivesicular bodies (MVBs). MVBs function as sorting stations that deliver cargo to the vacuole for degradation or storage (Simon et al., 2016). MVBs are enclosed by a single membrane that originates from endosomes and contains numerous smaller vesicles, known as intraluminal vesicles (ILVs), within their lumen. IVLs contain proteins and other molecules; this cargo is often ubiquitinated. MVBs mature into late endosomes (LE), also known as pre-vacuolar compartments (PVCs). FREE1, a plant-specific ESCRT protein, collaborates with ESCRT-I to regulate the sorting of endosomes to MVBs and the subsequent formation of ILVs, and, ultimately, MVB delivery to the vacuole (Wang et al., 2024a). ILV formation depends on membrane scission, mediated by membrane-bound ESCRT-III, which results in ILV release into the MVB lumen (Pfitzner et al., 2021).

Beyond the well-established mechanism of vesicular transport, membrane trafficking also relies on direct and dynamic connections between organelles (Perez-Sancho et al., 2015; Scorrano et al., 2019). The contact sites where organelle membranes come into proximity are not merely points of physical contact but rather functional hubs. Specific proteins and lipids localize to these regions, creating microenvironments that facilitate the exchange of molecules and signals between the interacting organelles. This direct communication plays a crucial role in

coordinating cellular processes and maintaining organelle homeostasis.

The basics of biomolecular condensates

Partitioning biomolecules into distinct compartments (e.g., membranous organelles) is crucial for the cellular stress response, impacting key processes such as protein synthesis, RNA processing, and signal transduction. Biomolecular condensates also form in various cell compartments, carrying various biomolecules (Fig. 1**A**). These condensates can be categorised as constitutive (always present, like nucleoli (Feric et al., 2016)) or inducible (formed in response to stress, like the condensates known as stress granules (Solis-Miranda et al., 2023)). Biomolecular condensation is often driven by Liquid-Liquid Phase Separation (LLPS), a physical process where a homogeneous solution separates into two distinct phases: a dense, solute-rich phase (the condensate) and a dilute, solute-poor phase (the surrounding cytoplasm, organellar lumen, or apoplast) (Fig. 1**B**) (Holehouse and Alberti, 2025). In cellular condensates, the solutes are typically proteins and sometimes include RNA, ions, small molecules, cell wall polymers, and even lipids. Several factors influence LLPS, including the concentration of the participating polymers (like proteins), their valency (the number of binding sites on each polymer), and the binding affinities between them. Intriguingly, despite lacking a traditional membrane boundary, condensates often behave like membrane-bound organelles undergoing fusion or fission, also exhibiting dynamic material properties ranging from liquid-like (droplet fusion, fission) to gel-like or even solid-like (Yeong et al., 2022).

As previously mentioned, many biomolecular condensates exhibit liquid-like properties at certain length and time scales, although it is important to note that liquidity is not essential for their function. While often initially liquid-like, condensates are dynamic structures that can evolve over time, acquiring a range of material properties (Liu et al.,

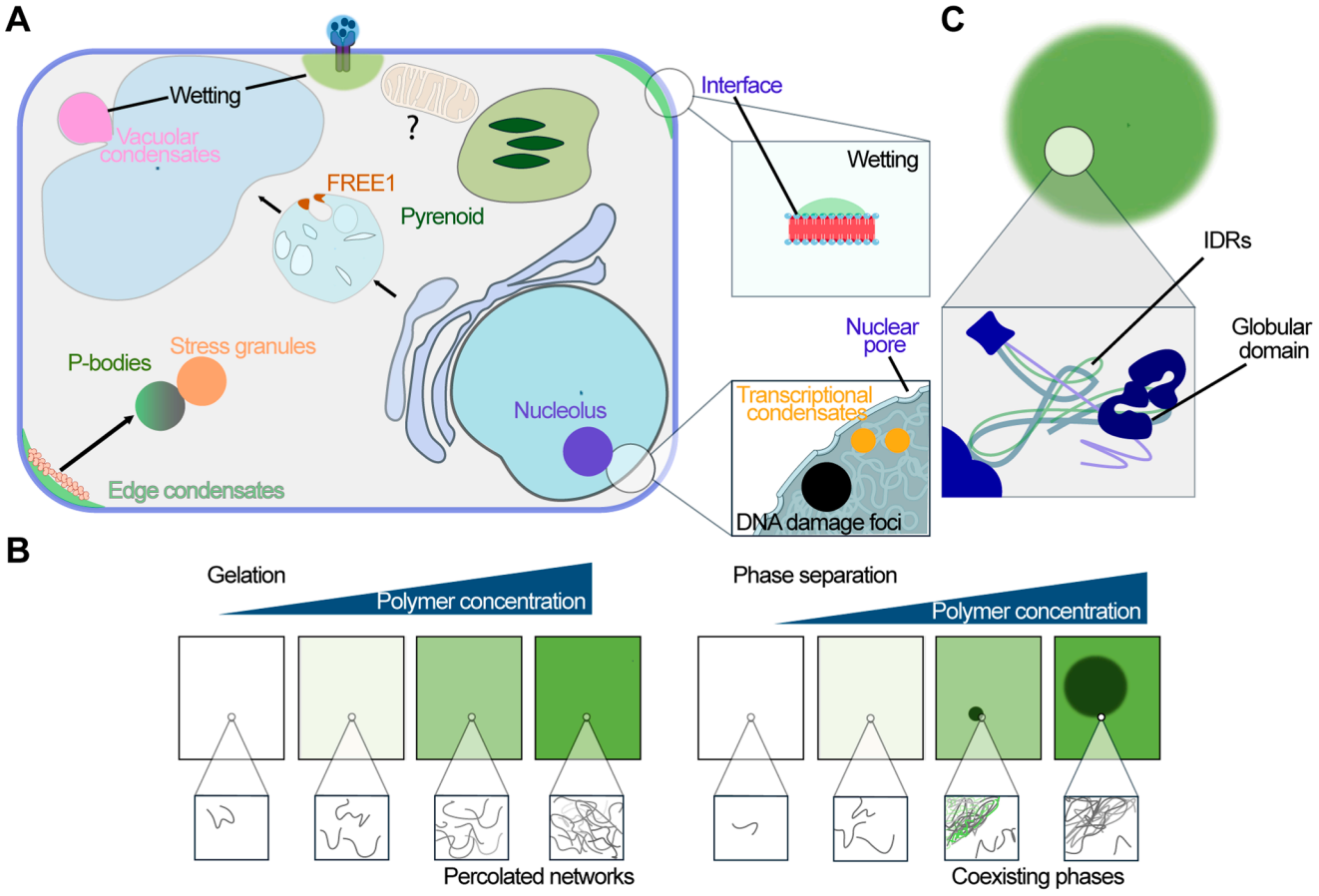

Fig. 1. Diverse forms and functions of biomolecular condensates in plants.
(A) Cellular Localization and Interactions. This schematic depicts a plant cell showcasing the diverse localisation of biomolecular condensates. Condensates, depicted in various colours and shapes, are shown in the cytoplasm (stress granules (Wang et al., 2024b; Gutierrez-Beltran et al., 2021), P-bodies (Lee et al., 2020), edge condensates (Liu et al., 2024b; Liu et al., 2023a), vacuolar condensates (e.g., LATE EMBRYOGENESIS ABUDANT (Belott et al., 2020)) interacting with the vacuole membrane via wetting), nucleus (nuclear pore (Celetti et al., 2019), nucleolus (Feric et al., 2016), transcriptional condensates (Feric et al., 2022), DNA damage foci (Fijen and Rothenberg, 2021), and chloroplast (pyrenoid (Wang et al., 2019a) or STT1/2 (Ouyang et al., 2020)). The ESCRT-I component FREE1 is shown localised to a membrane, illustrating a condensate-membrane interface (Zeng et al., 2023; Wang et al., 2024a). The question mark close to the mitochondrion indicates that biomolecular condensates have not been studied for this organelle in plants. However, many relevant condensates have been found in non-plants (for example (Long et al., 2021; Hou et al., 2023; Rey et al., 2020; Peng et al., 2021)).
(B) Material Properties and Phase Behavior. This panel illustrates the different material properties and phase behaviour observed in biomolecular condensates. The left series demonstrates the transition from a dilute solution (light green) to a percolated network (intermediate green; (Mittag and Pappu, 2022)) and, finally, a gel-like state (dark green; (Iserman et al., 2020; Fuller et al., 2020; Kato et al., 2012; Franzmann et al., 2018)) with increasing polymer concentration. The right series shows the process of phase separation, where increasing polymer concentration leads to the formation of coexisting phases: a dilute phase (light green) and a dense, condensate-rich phase (dark green droplet). The schematic representations below each graph depict the arrangement of molecules in each state.
(C) Domain Architecture of Condensate Components: Inset highlighting the modular domain architecture commonly found in proteins that form biomolecular condensates. These proteins often contain intrinsically disordered regions (IDRs), shown as flexible loops, interspersed with globular domains, shown as more structured shapes. IDRs facilitate phase separation, while globular domains provide specific functions or interactions.

2024b). This dynamic behaviour likely stems from the increasing confinement of proteins within low-energy conformations as the condensation process progresses (Kulkarni et al., 2022). As a result, condensates can transition through a spectrum of states, ranging from semifluid gels to more rigid glass-like or even solid-like states (Woodruff et al., 2018; Jawerth et al., 2020) (Fig. 1**B**). To encompass this dynamic nature and avoid potential ambiguities, we will use the term "phase separation" (and not LLPS) to describe the process that leads to the formation of these condensates (Musacchio, 2022).

Intrinsically disordered proteins (IDPs), characterised by significant conformational flexibility, play a prominent role in phase separation. These proteins contain intrinsically disordered regions (IDRs) that rapidly interconvert between multiple conformations, forming an ensemble of structures (Fig. 1**C**). This dynamic nature makes IDRs highly sensitive to environmental changes, such as those encountered during cellular stress, allowing proteins and other biomolecules to be entrapped in the low-energy conformations mentioned above. The stress-induced structural fluctuations of IDRs can promote interactions with other molecules, thereby promoting condensate formation. This ability suggests that IDPs act as stress sensors and thus can be considered as stress receptors (Wang et al., 2024b; Hsiao, 2022; Field et al., 2023; Riback et al., 2017).

While IDRs are often associated with low-complexity sequences, this is not always the case (Martin and Mittag, 2018). Although initially believed to be primarily driven by IDRs, recent evidence indicates that folded protein domains can also contribute to phase separation (Hess and Joseph, 2025). Computational analysis has further revealed distinct characteristics of IDRs and low-complexity regions in proteins that undergo phase separation. Proteins that can independently induce phase separation (without partner molecules) exhibit different IDR and low-complexity region profiles compared to the general proteome (Ozawa et al., 2023). Conversely, proteins that require partner proteins or other molecules for phase separation do not show such a clear difference in their IDR composition compared to the reference proteome. For example, the folded domains of some RNA-binding proteins, like the non-plant HETEROGENEOUS NUCLEAR RIBONUCLEOPROTEIN A1, can contribute to phase separation through multivalent interactions (Martin et al., 2021).

Basics of membranes-condensates interfaces

Membrane lipids, such as anionic lipids and sterols, can anchor and thus modulate condensate-associated molecules, influencing their spatiotemporal organisation, shape, and properties. These condensate-membrane interactions can selectively recruit or concentrate lipids and proteins (or RNA) into specific membrane domains, impacting cell polarity and signalling pathways (Snead et al., 2022). The increase in condensate research has resulted in a scenario where various definitions are often used interchangeably, obstructing precise communication. Acknowledging this issue, a recent initiative has aimed to establish a framework for classifying plasma membrane-associated condensates based on function, distinguishing nanodomains and polar domains (Jaillais et al., 2024).

Collectively, the phenomenon of biomolecular condensation on membranes is known as wetting (Kusumaatmaja et al., 2021b; Kusumaatmaja et al., 2021a). The interactions that underpin wetting suggest stereospecific binding between chemical groups within the condensates and the lipids. For instance, in animals, the ARGONAUTE proteins (AGOs) phase separate atop phosphatidylinositol lipids of the ER (Gao et al., 2022), whereas the human condensate known as TIS granule interacts with ER lipids through RNA bridges (Ma and Mayr, 2018). Notably, our research provided the first evidence of a specific plant condensate, the SFH8 (SEC14 HOMOLOG LIKE 8), binding to anionic membrane lipids, revealing also that these interactions modulate the condensate's properties (Liu et al., 2023b).

As condensate wetting can also influence the lipid composition of membrane nanodomains, this process could impact regions beyond these localised areas. This phenomenon can lead to alterations in membrane dynamics (i.e., tension and elasticity (Kusumaatmaja et al., 2021b)). In some cases, external mechanical forces, such as those generated by the cytoskeleton, can contribute to the spreading of the condensate. Given the critical dependence of plant cell membrane function on fluidity and its dynamics, which is itself influenced by factors like lipid composition (e.g., fatty acid saturation), protein composition, and overall lipid content (Mangiarotti and Dimova, 2024), condensate wetting has the potential to significantly modulate stress signalling. Yet, this hypothesis remains to be experimentally validated in stress scenarios where membrane composition, damage, and other dynamic properties (e.g., tension) are important (e.g., wounding or cold stress).

Membrane-condensate interfaces in plant stress

Environmental stresses like drought, salinity, extreme temperatures, and pathogen attacks can significantly compromise both membrane integrity and the function of biomolecular condensates (reviewed in (Solis-Miranda et al., 2023)), potentially disrupting the crucial interface between them and consequently affecting stress signalling. The following sections will explore specific examples of membrane-condensate interfaces with established roles in plant stress responses.

Endoplasmic reticulum

As the central hub of the endomembrane system, and due to its extensive connections with the plasma membrane, the ER acts as a primary sensor of extracellular cues and plays a crucial role in coordinating cellular responses to adverse conditions. The ER integrates a multitude of environmental stimuli and can itself experience stress. ER stress arises when the ER's protein folding and modification capacity is overwhelmed. In response to this stress, cells activate a signalling pathway known as the unfolded protein response (UPR) (reviewed in (Strasser, 2018)).

In plants, ER stress comprises two major pathways: IRE-bZIP60 and bZIP17/bZIP28. Like in animals, the plant IRE1-bZIP60 pathway uses the endoribonuclease INOSITOL-REQUIRING ENZYME 1 (IRE1) that splices the mRNA of bZIP60, a transcription factor. This unconventional splicing event generates an active transcription factor that translocates to the nucleus and regulates the expression of genes involved in protein folding (e.g., by chaperones such as BiP, calnexin, calreticulin), protein modifications (e.g., by folding enzymes such as protein disulfide isomerase), and ER-associated degradation (ERAD) of misfolded proteins (Shin et al., 2018; Van Hoewyk, 2018; Cui et al., 2019; Ling et al., 2019; Wang et al., 2019c; Zhang et al., 2022; Tang et al., 2023; Liu et al., 2024a). In bZIP17/bZIP28 pathway, plant-specific membrane-bound transcription factors, bZIP17 and bZIP28, are activated in response to ER stress and translocate to the nucleus to regulate gene expression. Beyond splicing bZIP60 mRNA, IRE1 also performs Regulated IRE1-Dependent Decay (RIDD) (Srivastava et al., 2018; Park and Horton, 2019). RIDD entails the degradation of specific mRNAs through IRE1's endoribonuclease activity. This mechanism assists in alleviating the overall protein synthesis burden on the ER.

Despite the ER's critical role in stress responses, our understanding of condensate-membrane interfacing at the ER remains limited. In Arabidopsis dry seeds, metacaspases (a class of proteases) form condensate-like structures on both the ER and the ER-associated organelles known as lipid droplets (Liu et al., 2024a). However, the mechanisms underlying the specific recruitment of metacaspases to the ER remain elusive, although functional interactions between metacaspases and ERAD components were reported in the same study. In animal cells, processing bodies (P-bodies), conserved mRNA regulatory condensates, interact with the ER and influence P-bodies' fission (Lee et al., 2020). While the

functional significance of this interaction is not fully understood, recent evidence suggests that ER stress induced by pathogens can modulate P-body dynamics in plants (González-Fuente et al., 2025). Given the role of P-bodies and RIDD in mRNA turnover regulation, the P-body-ER interaction raises the possibility of P-body/RIDD cooperation in stress-induced mRNA degradation. Furthermore, ER membrane domains may also host other signalling protein condensates (e.g., kinases, phosphatases) for signal transduction through condensates produced by P-bodies or other condensates.

Plasma membrane and cell wall

The plasma membrane and the cell wall are critical players in a cell's ability to sense and respond to stress. Acting as the first line of defence, they detect changes in the external environment and trigger intracellular signalling pathways that promote adaptation and survival. Similar to the phase separation observed in biomolecular condensates, cell wall components and lipids within biological membranes can also undergo a form of phase separation (Zhao and Zhang, 2020). This results in the clustering and lateral segregation of lipids and proteins into distinct, receptor-rich domains. These nano- and polar domains can be enriched in sphingolipids, cholesterol, and/or saturated lipids, exhibiting tighter lipid packing (Agarwal et al., 2024; Liu et al., 2023b; Dragwidge et al., 2024; Wang et al., 2023; Ma et al., 2022b; Chen et al., 2023; Yuan et al., 2021; Sun et al., 2021; Day et al., 2021; Su et al., 2020; Kulich et al., 2020). Nano- and polar domains may also be rich in phosphatidylinositol lipids. Although these lipids usually constitute <1 % of the membrane, they exhibit a high affinity for certain molecules which are concentrated on them, facilitating the formation of condensates (Gao et al., 2022; Jaqaman and Ditlev, 2021).

Emerging evidence suggests that interactions between membrane nano- or polar domains and specific molecules facilitate the formation of condensates, which coordinate signal transduction. Within these domains, membrane-bound receptors, such as pattern recognition receptors (PRRs), can perceive various signals. For instance, the perception of extracellular signals by receptor-like kinases (RLKs) can initiate intracellular signalling that leads to stress adaptation (Elliott et al., 2024; Chen et al., 2024). A key element of these signalling cascades is phosphorylation, catalysed by PRRs or associated kinases, along with the generation of secondary messengers (Yu et al., 2023; Li et al., 2022; Zhou et al., 2020; Yu et al., 2019). Usually, PRRs perceive extracellularly secreted peptides, like the RAPID ALKALINIZATION FACTOR1 (RALF1). RALF1 can undergo phase separation with pectin. This phase separation concentrates RALF1, which then binds to the FERONIA (FER) receptor and its coreceptor LORELEI-LIKE glycosylphosphatidylinositol-anchored protein 1 (LLG1) complex, further promoting their phase separation (Liu et al., 2024c). The pectin-RALF1-FER-LLG1 condensates lead to receptor clustering and trigger endocytosis. Environmental stressors, such as salt and high temperature, enhance the RALF1-pectin condensation, amplifying receptor clustering. RALF can also condense pectin by interacting with the cell wall-anchored LEUCINE-RICH REPEAT EXTENSIN (LRX) (Dunser et al., 2019; Moussu et al., 2023), suggesting the potential participation of LRX in the condensation process.

Intriguingly, Lee et al. demonstrated that protein phase separation on one side of a membrane can induce lipid phase separation on the opposite side (Lee et al., 2023). This "cross bilayer coupling" suggests a potential mechanism for signal transduction across membranes. These findings raise the compelling question of whether extracellular condensates, like pectin-RALF-FER-LLG1, are coupled with cytosolic condensates, such as stress granules or P-bodies, to regulate cell signalling. This line of inquiry is further supported by the reported links between cellular condensates formed by GLYCINE-RICH RNA BINDING PROTEIN 7 (GRP7), a component of both stress granules and P-bodies, and FER (Wang et al., 2020a; Ma et al., 2022a). The RALF1-FER-GRP7 module regulates RNA splicing upon stress, by promoting the relocation of GRP7 to the nucleus. Hence, it is tempting to speculate that condensates are coupled across membranes to orchestrate stress responses.

The plant-specific REMORIN protein provides another example of how membrane domains and protein condensates can be linked. REMORIN possesses a C-terminal membrane anchor domain, a homo-oligomerization domain, and an N-terminal IDR, allowing it to function as a tether (Xu et al., 2024) (Fig. 1). Upon membrane association, REMORINs recruit specific lipids, like sterols and anionic phospholipids, to form membrane nanodomains. In Arabidopsis, the IDR of REMORIN interacts with type-I FORMINS, which are actin nucleators. This interaction allows REMORIN nanodomains to gradually recruit and condense type-I FORMINS into the same nanoclusters, enhancing actin nucleation and polymerisation during immune responses (Ma et al., 2022b).

Polar plasma membrane domains are characterised by the asymmetric distribution of cellular components, such as proteins and lipids with functional implications (Jaillais et al., 2024). For instance, the SFH8 condensate mentioned above forms large domains at the plasma membrane of Arabidopsis root cells, playing a key role in exocytosis (Liu et al., 2023b). An important open question is how this pathway is specifically modulated under different stress conditions. Furthermore, it remains unclear how SFH8 condensates, as has been reported, promote exocytosis through fusion. A potential mechanism involves SFH8-induced localised modifications to membrane dynamics or composition. Accordingly, others have shown that phase separation can induce membrane curvature, a process crucial for membrane fusion (Yuan et al., 2021). The formation of protein-rich condensates can deform the membrane, bringing vesicle and target membranes into close proximity, which is a prerequisite for fusion (Liu et al., 2023b).

MVBs and vacuole

As mentioned earlier, MVBs are essential sorting organelles that mainly direct cargo to the vacuole. The plant-specific ESCRT-I subunit FREE1, which contains an IDR, undergoes phase separation to form condensates on the MVB surface. This phase separation is critical for efficient ILV formation within MVBs (Mosesso et al., 2024; Wang et al., 2024a). Plants expressing a FREE1 mutant lacking this specific IDR show hypersensitivity to the stress hormone abscisic acid (ABA), suggesting that FREE1-mediated phase separation plays a vital role in ABA homeostasis. This hypersensitivity likely results from impaired MVB-dependent degradation of ABA-related signalling components. In addition to driving its own condensation, FREE1 acts as a scaffold within the MVB pathway, recruiting binding partners such as soluble cargo proteins and other ESCRT proteins. This proposed mechanism of ILV scission may provide insights into the evolution of cellular compartmentalisation and the interplay between traditional, machinery-dependent (regular endocytosis) and condensate-mediated membrane scission (Rangachari, 2023).

Further examples where condensates are involved in membrane fission are the endocytic machinery condensates on yeast and plant plasma membranes that can support endocytosis (Dragwidge et al., 2024) and vacuolar fission (Kusumaatmaja et al., 2021b). Apart from lytic vacuoles (LVs) involved in degradation, vacuoles are categorised as protein storage vacuoles (PSVs) (Takemoto et al., 2018). Vacuolar degradation in LVs, which are more abundant in vegetative tissues, is essential for maintaining cellular homeostasis by recycling non-functional or misfolded proteins and ensuring proper cell signalling. PSVs, on the other hand, are prevalent in storage tissues, showing higher pH and lower hydrolytic activity compared to LVs. Both types can coexist within a single cell, with LVs potentially arising from PSVs. PSVs form through specific trafficking to the vacuole, while abiotic stress alters vacuolar trafficking pathways, favouring protein delivery to PSVs (Ren et al., 2020).

The PSV pathway's delivery of high concentrations of storage proteins (e.g., globulins) can promote weak, multivalent protein-protein interactions, potentially driving the formation of protein-rich

biomolecular condensates and contributing to vacuolar compartmentalisation and fission (Fig. 1) (Kusumaatmaja et al., 2021a). Detoxification compounds and high calcium levels within the vacuole could contribute to this phase separation. Cytoplasmic condensates may also contribute to vacuole fission by deforming the vacuolar membrane from the cytoplasmic side. Yet, we know little about the role of this pathway in stress responses, although it seems likely to regulate PSVs.

Autophagy

Apart from MVBs, autophagy is another crucial cellular process that plays a central role in delivering cellular components to vacuoles. Often induced by stress, autophagy helps the cell eliminate unwanted or damaged components (Zhou et al., 2024; Zou et al., 2025). Macroautophagy, a highly conserved process, involves the formation of vesicles called autophagosomes. These autophagosomes engulf cytoplasmic components, including organelles and macromolecules, and then deliver them to LVs. In contrast to macroautophagy, microautophagy bypasses the formation of autophagosomes. Instead, microautophagy directly engulfs cargo by inward folding or invagination of the vacuolar membrane. Microautophagy is often associated with the formation of PSVs, as it delivers cargo to these storage compartments, thus potentially playing a role in PSV biogenesis (Plott et al., 2025). It is important to note that while microautophagy has been extensively studied in yeast and mammalian cells, the mechanisms of microautophagy in plants remain largely unexplored.

Macroautophagy critically depends on AUTOPHAGY-RELATED (ATG) proteins for autophagosome formation. Among these, the ubiquitin-like ATG8 proteins are essential for autophagosome expansion and closure (reviewed in (Minina et al., 2017)). FREE1, the plant-specific ESCRT-I subunit, interacts with ATG8 proteins and other ATG proteins, such as the ATG12-ATG5-ATG16 complex, and is itself a cargo for autophagosomes (Liu et al., 2023a). Similar to its role in MVB formation, FREE1 incorporation into autophagosomal membranes promotes autophagosome membrane fission (Mosesso et al., 2024; Wang et al., 2024a), demonstrating the broader importance of FREE1 condensates. Biochemical analyses have shown that FREE1 forms a complex with other ESCRT-III components (Zeng et al., 2023), suggesting a more general link between ESCRT and autophagy, and likely condensates. Accordingly, upon autophagy induction during nutrient starvation, unsealed autophagosomes (open vesicles) accumulate in the cytoplasm of both autophagy and ESCRT-III mutants.

FREE1 shuttles from MVBs to autophagosomes, likely through modulation by the stress-related kinase KIN10 (SnRK1α1, Sucrose Non-Fermenting 1-Related Kinase 1) (Gutierrez-Beltran et al., 2021; Mountourakis et al., 2023). KIN10 directly interacts with and phosphorylates FREE1, suggesting that KIN10 might act as a molecular switch, redirecting FREE1 from its MVB function to a role in autophagy under stress conditions. Further research is needed to fully elucidate the dynamic interplay between FREE1, ESCRT-III components, ATG proteins, and kinases like KIN10 in MVB biogenesis and autophagy.

FREE1 has also been shown to interact with the retromer complex under autophagy-inducing starvation conditions (Schepetilnikov et al., 2017; Henriques et al., 2022). The retromer plays a crucial role in retrieving specific cargo proteins from endosomes and redirecting them to the TGN or the plasma membrane. This interaction, along with the presence of KIN10 in other condensates like stress granules (Gutierrez-Beltran et al., 2021), suggests that FREE1 may have additional functions beyond its roles in MVB and autophagosome formation. Beyond FREE1, the endocytic TPLATE complex has also been implicated in autophagy initiation at membrane contact sites (Wang et al., 2019b). Given that the TPLATE complex has recently been shown to form membrane-bound condensates (Dragwidge et al., 2024; Arora et al., 2020), it is tempting to explore its potential connection to stress perception and adaptation.

Interestingly, our recent findings on P-body composition reveal their enrichment of FREE1, along with numerous other components of the ESCRT machinery and the TPLATE complex (Liu et al., 2023a). This suggests that FREE1 may dynamically shuttle between different fission-related machineries in the cell, including those potentially operating within P-bodies (Liu et al., 2021). This dynamic partitioning of FREE1 could enable the cell to rapidly reconfigure membrane trafficking pathways in response to stress conditions.

Further research is needed to explore the role of condensates in autophagy, particularly their potential involvement in the initial assembly of ATG complexes, as has been observed in other organisms (Licheva et al., 2025). Recent evidence indicates that VPS41, a component of the Arabidopsis HOPS complex, undergoes a dynamic transformation upon autophagy induction (Jiang et al., 2024). VPS41 transitions from biomolecular condensates to puncta and then to ring-like structures called VPS41-associated phagic vacuoles (VAPVs). These VAPVs then enclose ATG8 s for delivery to LVs. This process is initiated by ARF-like GTPases (ARLs), specifically ARLA1, and occurs in concert with autophagy progression coupled with SNARE proteins. Under starvation conditions, this VAPV pathway protects plants. This study further elucidates the complexity of autophagy, particularly the role of VAPV condensate material transitions. However, the broader role of VAPVs in stress responses remains to be determined. It is also unclear whether EXOCYST, a parallel tethering complex to HOPS, is also undergoing phase separation.

A cytoplasm-to-membrane condensate shuttling mechanism could regulate rapid stress responses and adaptation

The evidence presented so far points to a dynamic interplay between biomolecular condensates, including their ability to shuttle between different types of condensates and interact with cellular membranes (e.g., FREE1). Besides, DECAPPING PROTEIN 1 (DCP1), a major component of P-bodies, dynamically shuttles between P-bodies and the plasma membrane (Liu et al., 2024b; Liu et al., 2023a). This shuttling has a regulatory effect: DCP1 localisation at the plasma membrane disrupts its interaction with DCP2. This interaction is important for the formation of the DCP1-DCP2 complex, which is responsible for RNA degradation by initiating, with other effector proteins, RNA decapping. Hence, this decapping has downstream consequences for RNA turnover and storability in P-bodies.

Furthermore, at the plasma membrane, DCP1 preferentially localises to apical or basal polar domains, often concentrating at the cell edge or vertex. At these locations, DCP1 colocalises with actin nucleators (Papalazarou and Machesky, 2021) in specific condensates. This condensation likely facilitates actin nucleation, as was suggested for REMORIN. However, direct in vitro evidence of actin polymerisation by this complex, like the proposed mechanism for REMORIN, is currently lacking.

Interestingly, heat stress triggers a decrease in DCP1 levels at the plasma membrane, coinciding with an increase in P-body formation. Given that DCP1 is a key protein for P-body assembly, some of these newly formed, stress-induced P-bodies sequester proteins and RNAs, likely for long-term storage (Liu et al., 2024b). Notably, these heat-induced P-bodies exhibit a more solid-like material state compared to P-bodies under normal conditions. This increased solidity may be attributed to a higher abundance of IDPs in P-bodies under stress, which facilitate stronger and more frequent interactions with various RNAs and proteins (Liu et al., 2024b). Hence, such new interactions would effectively increase the storage capacity of these stress-induced P-bodies.

Conversely, when the stress signal subsides, P-bodies dissolve, with DCP1 shuttling back to the plasma membrane. The released RNAs are then available for translation, promoting cellular recovery (Solis-Miranda et al., 2023; Liu et al., 2024b). However, this pathway of transcriptional reprogramming at the cellular level is not well understood, and it remains unclear whether it can be manipulated to enhance

stress tolerance. Given that heat stress increases the number of P-bodies and other condensates, such as stress granules (Gutierrez-Beltran et al., 2015), we propose that these condensates may serve as storage sites, sequestering RNAs and other molecules involved in long-term cellular memory.

These findings collectively suggest that condensate dynamics, modulated by changes in material properties coupled with membrane domain-specific interactions, play a significant role in stress signalling and adaptive responses. For example, Arabidopsis mutants with impaired P-body dissolution show altered long-term responses to the stress hormone ethylene (Liu et al., 2024b; Di Fino et al., 2025). Considering the complex interplay and feedback mechanisms often observed between the plasma membrane and the cell wall, it is crucial to investigate how these domains might amplify or stabilise condensate-mediated interactions. Nevertheless, DCP1 shuttling may also affect FREE1 release from P-bodies and, thus, its cytoplasmic levels. FREE1 release may, in turn, modulate autophagy, MVB formation, and PSVs.

Outstanding questions

Recent studies have shed light on the role of membrane-bound condensates in stress. However, many critical questions remain unanswered, including: How widespread are membrane-bound condensates in plant signalling pathways? How do cells specifically orchestrate the formation of distinct condensates-whether extracellular, intracellular, or transmembrane-coupled-at the plasma membrane to transduce specific signals? How do cells modulate the biophysical forces generated by condensate-membrane interactions to regulate signalling outcomes? How is phase separation involved in cargo sorting? The insights gained from such research could provide novel strategies for manipulating cellular signalling and improving plant stress tolerance.

Funding sources

Our studies on biomolecular condensates are supported by grants from Horizon Europe European Research Council (ERC 101,126,019 to P.N.M.), Fodation Sante (to P.N.M.), Swedish Research Council (Vetenskapsrådet, 2024–05,707 to P.N.M.), and Knut and Alice Wallenberg Foundation (KAW 2018.0026 to P.N.M.). Views and opinions expressed are those of the authors only and do not necessarily reflect those of the European Union or the European Research Council Executive Agency. Neither the European Union nor the granting authority can be held responsible for them.

Declaration of generative AI in scientific writing

During the preparation of this work, the authors used Gemini in order to improve text clarity. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

CRediT authorship contribution statement

Konstantin Kutashev: Writing – review & editing. **Panagiotis Nikolaou Moschou:** Writing – review & editing, Writing – original draft.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Panagiotis N. Moschou is an Editorial Board Member/Editor-in-Chief/Associate Editor/Guest Editor for this journal and was not involved in the editorial review or the decision to publish this article.

Acknowledgements

The authors thank the members of the Moschou lab for their valuable insights and the anonymous reviewers for their critical feedback.

Data availability

No data was used for the research described in the article.

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