A glossary of plant cell structures: Current insights and future questions

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Title: A Glossary of Plant Cell Structures: current insights and future questions

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Abstract

In this glossary of plant cell structures, we asked experts to summarize a present-day view of plant organelles and structures, including a discussion of outstanding questions. In the following short reviews, authors discuss the complexities of the plant cell endomembrane system, exciting connections between organelles, novel insights into peroxisome structure and function, dynamics of mitochondria, and the mysteries that need to be unlocked from the plant cell wall. These discussions are focused through a lens of new microscopy techniques. Advanced imaging has uncovered unexpected shapes, dynamics and intricate membrane formations. With a continued focus in the next decade, these imaging modalities coupled with functional studies are sure to begin to unravel mysteries of the plant cell.

Introduction

For the Cell Biology Special Focus Issue, we wanted readers to have a modern view of plant cell structures that are sure to come up in research articles and other reviews. We gathered experts in the field to share their striking images as well as their intellectual insights on how plant cell structures are viewed today. The journey through the plant cell begins at the nucleus, where new insights into nuclear connections with the cytoplasm are beginning to decipher how the nucleus is organized and linked to cytoplasmic status. The nucleus is also the site of many phase separated structures, making the plant nucleus an ideal place to study this exciting new cell biological phenomena. Continuous with the nuclear envelope, the endoplasmic reticulum (ER) in all of its spatial and temporal complexity holds many unresolved questions. The Golgi, of central importance in the polysaccharide biosynthesis for building the plant body, has several plant-specific features. The trans Golgi network and endosomes comprise a nexus of membrane intricate compartments with vastly different shaping mechanisms ultimately linking trafficking to the plasma membrane or the vacuole. The vacuole is the largest organelle in mature plant cells, playing multiple roles from cellular homeostasis, storage, development, to response against biotic/abiotic stresses. Long known to be a reservoir for lipids, lipid droplets are emerging as important for responding to environmental stress. New insights into the molecular mechanisms driving lipid droplet formation from the ER are discussed. Recent imaging of peroxisomes in developing seedlings revealed strikingly complex membrane topologies. Imaging of live mitochondria demonstrates how dynamic plant mitochondria are with many fusion and fission events occurring to generate a syncytial mitochondria network within cells. High resolution imaging of chloroplasts during developmental transitions underscores the structural complexity of these organelles and provides new models for populating the essential thylakoid membranes. Contact sites couple organelles to each other creating a mechanism to communicate status across different subcellular structures. Plasmodesmata connect cells to each other providing long-distance communication. Finally, the cell wall not only patterns the cell but builds the plant body and protects the plant from both abiotic and biotic stressors.

Plant nucleus: a giant in the organelle galaxy

The nucleus can be viewed as a gigantic organelle and is defined by a double-layered membrane structure called the nuclear envelope (NE). The NE sequesters the nuclear genome and spatially separates transcription from translation, an evolutionary invention that enables remarkable functions and regulations in the eukaryotic cell. Here, we briefly summarize current views in key aspects of the plant nucleus, including structure, composition, dynamics, and function, from the surface to the interior.

Nuclear envelope protein composition and function

The NE is thought to have evolved from the endoplasmic reticulum (ER) and coated vesicles and is composed of the outer nuclear membrane (ONM) and the inner nuclear membrane (INM), both of which harbor distinct collections of proteins that make the NE a platform for versatile functions and communications. Plant NE proteins have been reported to function in nuclear calcium signaling (Capoen et al., 2011; Charpentier et al., 2016), chromatin organization and dynamics (Pawar et al., 2016; Gumber et al., 2019), immune activation (Gu et al., 2016), cell cycle progression (Wang et al., 2019c), mechanical shielding (Goswami et al., 2020), and more. Among them, the linker of nucleoskeleton and cytoskeleton (LINC) complex is one of the best characterized. The LINC complex is composed of the INM-localized Sad1/UNC48 homology (SUN) protein and the ONM-localized Klarsicht/ANC-1/Syne Homology (KASH) protein, with the former associated with the nucleoskeleton and chromatin and the latter bound with cytoskeleton and motor proteins. SUN and KASH physically interact in the perinuclear region and establish a molecular structure that enables the translation of cytoplasmic mechanical forces into the nuclear movement and chromatin activities. The plant LINC complexes have been shown to play critical roles in stomatal development and responses to light and hormone signals (Gumber et al., 2019; Biel et al., 2020a, b), male gametophyte development (Tamura et al., 2013; Varas et al., 2015; Zhou et al., 2015; Moser et al., 2020), and plant-microbe interactions (Zhou et al., 2014; Newman-Griffis et al., 2019). Nonetheless, compared with animals and yeast, we still lack a comprehensive understanding of the NE proteome and function in plants. Recent applications of advanced proteomic tools (e.g. proximity labeling proteomics) empowered the identification of novel NE components (Goto et al., 2019; Tang et al., 2020) and NE-specific biological processes in plants (e.g. INM-associated membrane protein degradation (Huang et al., 2020), opening brand new avenues to greatly expand our view of the global protein landscape of the plant NE and to unravel both eukaryote-conserved and plant-specific NE functions.

Nuclear pore complex, more than a conduit for nucleocytoplasmic transport

As a special membrane compartment, the nucleus evolved a sophisticated communication system that allows the remarkably efficient but highly selective exchange of materials across the NE. The ONM and the INM fuse at numerous sites to form physical openings, ~120 nm each in diameter, termed nuclear pores. The surface of individual plant nuclear pores is covered by ~1,000 nucleoporin proteins of ~40 different kinds, which are assembled into a structurally conserved mega protein complex named the nuclear pore complex (NPC) (Tamura et al., 2010; Mosalaganti et al., 2018). The central channel of the NPC is filled with a protein meshwork made by intrinsically disordered phenylalanine-glycine (FG)-rich nucleoporins, which are capable of interacting with nuclear transport receptors (importin and exportin) and mediate selective transport of cargo molecules. Besides a conserved role in mediating nucleocytoplasmic transport, individual plant nucleoporins have been reported to play specific roles in regulating flowering time, hormone signaling, and activation of abiotic and biotic stress responses, suggesting that the NPC may function as a versatile signaling platform in addition to a conserved trafficking apparatus in plants (Meier et al., 2017; Gu, 2018; Li and Gu, 2020).

Nucleoskeleton

Underneath the INM deploys the plant nucleoskeleton assembled by long coiled-coil lamin-like proteins (e.g. CRWNs) and CRWN-associated proteins (e.g. KAKU4), which bear no sequence homology with animal lamin proteins. They are required for proper nuclear morphology (Wang et al., 2013; Goto et al., 2014; McKenna et al., 2021) and potentially interact extensively with membrane-bound INM proteins to form the plant nuclear lamina (PNL). CRWNs were recently shown to interact with histone modifiers and necessary for tethering chromatin to the INM to suppress stress-related gene expression (Hu et al., 2019; Mikulski et al., 2019; Choi and Richards, 2020; Sakamoto et al., 2020; Wang et al., 2021). These studies suggest a critical role of the PNL in maintaining heterochromatin organization and repression at the nuclear rim, similar to what was found in animals.

However, it remains to be determined whether other PNL components, such as INM proteins, also contribute to this process.

Nuclear interior organization

Within the nucleus, the genome is organized three-dimensionally with chromosomes occupying specific territories and active and inactive chromatin regions separated from each other. Most heterochromatic regions and chromocenters are typically positioned near the nuclear periphery. However, the distribution of telomeres and some other transcriptionally quiescent regions varies between plant species. For example, most telomeres are attached to the nuclear surface in wheat and barley but are associated with the nucleolus in Arabidopsis and maize (Pontvianne et al., 2016). Recent genome-wide high throughput chromosome conformation capture (Hi-C) analyses in both diploid and polyploid plant species revealed extensive inter- and intra-chromosomal interactions that define higher-order chromosomal packing during interphase (Bi et al., 2017; Liu et al., 2017a; Dong et al., 2018; Concia et al., 2020). Both the spatial positioning (NE tethering) and the three-dimensional organization of chromatin are tightly linked to local epigenetic states and can profoundly influence chromatin activities, such as transcription regulation and timing of DNA replication (Grob et al., 2014; Wear et al., 2017; Karaaslan et al., 2020; Sakamoto et al., 2020; Bishop et al., 2021).

Like chromatin, many other biomolecules are also organized in a dynamic and heterogeneous manner in the nucleus. Spontaneous nucleation of biomolecules drives the formation of many membrane-less droplets observed in plant nuclei, including nucleoli, Cajal bodies, photobodies, dicing bodies, splicing speckles, DNA damage foci, and immune-activated condensates (Emenecker et al., 2020; Zavaliev et al., 2020; Huang et al., 2021b). In these nuclear bodies, multivalent proteins/nucleic acids capable of forming extensive inter- and intra-molecular interactions undergo liquid-liquid phase separation (LLPS) to concentrate functionally relevant molecules and create a specific subnuclear environment that is integral to nuclear functions such as ribosome biogenesis, mRNA and miRNA processing, transcription activation, and signaling (Liu et al., 2012; Van Buskirk et al., 2012; Fang et al., 2019; Powers et al., 2019; Jung et al., 2020; Zavaliev et al., 2020; Huang et al., 2021a; Huang et al., 2021b). Further exploring the role of LLPS-promoted condensates in plants and elucidating how phase separation may be regulated by internal and external signals represent an exciting new research area for plant science in the next decade.

Movement and dynamics of the nucleus

Like most other organelles, the entire nucleus is capable of directional movement (e.g. towards pathogen invading loci or with rapid elongation of pollen tubes) triggered by environmental and developmental cues (Griffis et al., 2014) and can establish connections with other organelles (e.g. chloroplast stromules) for signal exchange (Caplan et al., 2015; Gu and Dong, 2015). Plant nuclei also exhibit distinct morphology in different cell types and membrane dynamics during cell cycle progression. As an extreme example, the NE undergoes a complete breakdown and subsequent reformation during mitosis. These aspects of plant nuclear dynamics have been extensively reviewed elsewhere (Meier et al., 2016; Meier et al., 2017; Groves et al., 2018; Groves et al., 2020; Goto et al., 2021), and mechanisms that regulate plant nuclear movement, NE dynamics, inter-organellar communication, and their functional importance are currently under active investigation

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Open questions on the network structure of the plant endoplasmic reticulum

The plant ER network is composed of interconnected tubules and cisternae that form a highly dynamic membrane network, which is anchored to the plasma membrane (PM), similar to a spider web hanging off surfaces (Figure 2). ER tubules connect with other tubules and cisternae forming small, triangular sheets that are called “three-way junctions” (Shemesh et al., 2014). The bulk of the plant ER is distributed at the cell cortex where it is sandwiched between the PM and the tonoplast, in continuum with the nuclear envelope and the transvacuolar strands (TVSs). TVSs form a tightly packed meshwork of ER tubules and cisternae that connect distal portions of the ER across the cell through tonoplast invaginations. The nature of the plant ER cisternae is unknown: they may be continuous membrane sheets and tightly packed tubules or perforated sheets of membranes, as described in non-plant species (Nixon-Abell et al., 2016; Schroeder et al., 2019).

The ER network undergoes continuous remodeling, through processes that include homotypic fusion of ER tubules and interconversion of ER tubule and cisternae, due to the action of ER shapers, cytoskeleton and associated motors, and ER-cytoskeleton connectors (Brandizzi, 2021). Together, these processes and ER shapers contribute to the overall movement or streaming of the ER, which is distinct from the movement of other organelles (e.g., peroxisomes, mitochondria, endosomes), which translocate across the cytoplasm. The relative abundance of ER tubules and cisternae varies during cell growth. As cells expand, the ER shape transitions from a more predominantly cisternal form, typical of non-expanded cells, to a more tubular form that is visible in mature cells (Ridge et al., 1999; Stefano et al., 2014), through mechanisms that are yet to be established.

In vitro and *in vivo* experiments have demonstrated that the ER membrane-associated GTPase Root Hair Defective 3 (RHD3) is responsible for the homotypic fusion of the ER membrane (Chen et al., 2011; Stefano et al., 2012; Zhang et al., 2013; Ueda et al., 2016), similarly to the mammalian and yeast homologs: atlastins and Sey1p, respectively (McNew et al., 2013); however, the mechanisms underlying the fast and dynamic interconversion of ER tubules and cisternae are yet to be discovered. A redistribution of membrane curvature-inducing proteins, such as the conserved membrane-inducing reticulons (Tolley et al., 2008; Sparkes et al., 2009b) and the three-way junction-stabilizing Lunapark proteins (Lnp1 and Lnp2) (Kriechbaumer et al., 2018; Ueda et al., 2018; Sun et al., 2020a), is likely responsible for the dynamic interconversion of ER forms, but the underlying regulatory mechanisms are yet largely unknown.

The biological function of the reshaping of the plant ER is still unclear. Confocal microscopy analyses have demonstrated that the ER movement increases during cell growth concomitant with an increase in the streaming of other organelles with whom the ER is in close association, such as Golgi stacks, mitochondria, peroxisomes, and endosomes. Furthermore, defects in ER network structure due to the loss of RHD3 compromise cell expansion as well as the streaming of the ER and closely associated organelles (Stefano et al., 2014; Stefano et al., 2015). Therefore, the ER contributes to the dynamics and spatial organization of other organelles, possibly through ER-organelle contact sites, and this may be necessary for organelles’ function. This is supported by the evidence that in an *rhd3* loss-of-function mutant, the streaming of endosomes is reduced and clathrin-mediated endocytosis is compromised (Stefano et al., 2015). These results support the conceivable hypothesis that the streaming of the ER and closely associated organelles is ultimately important for cell growth, but this has yet to be experimentally demonstrated.

A double loss-of-function mutant of the two Arabidopsis *Lnps* shows an increased abundance of ER sheets with dense fenestration and ER conglomerates (Kriechbaumer et al., 2018; Ueda et al., 2018; Sun et al., 2020a). Combined, the evidence that the localized distribution of Lnps in the ER depends on the cellular availability of their interacting protein RHD3, and that Lnps antagonize the ER shaping role of RHD3 and induce RHD3 degradation via the proteasome pathway (Sun et al., 2020a) mechanistically support a dependence of certain ER shapers onto the abundance of other ER shapers for their distribution and function in the ER. Curiously, the loss of RHD3 alone is viable and causes only limited phenotypic defects in plant growth (Stefano et al., 2012); however, the loss of RHD3 with either member of the RHD3 family of proteins, RHD3-like 1 or RHD3-like 2, is either lethal or causes reproductive defects (Zhang et al., 2013). Conversely, the loss of both Lnps is viable, and causes only minor defects in plant growth (Sun et al., 2020a). Therefore, certain ER shapers may have a more relevant role in the life of the cell compared to others, either because associated ER shaping events are essential compared to others or because the shapers carry out other functions, in

addition to ER reshaping. For example, it has been demonstrated that maize reticulons 1 and 2 function in shaping the ER but also as autophagy receptors, and are involved in degradation of the ER through the regulated process known as ER-phagy (Zhang et al., 2020). Furthermore, RHD3 has been found to interact with Ark1, an armadillo-repeat containing kinesin, which has been suggested to pull an ER tubule toward another tubule (Sun et al., 2020b). While these findings support earlier discovery that the remodeling of a subset of ER tubules depends on their sliding on pre-existing microtubules (Hamada et al., 2014), they also highlight additional functions of RHD3 besides a fusogenic activity of the plant ER membranes.

Future characterization of the broader roles of the plant ER shapers may provide opportunities to establish how physiologically and developmentally relevant processes are connected to ER network integrity. For example, the loss of RHD3 leads to an attenuation of signaling in the unfolded protein response (Lai et al., 2014), a conserved cytoprotective pathway that is designed to attenuate proteotoxic stress in the ER (Pastor-Cantizano et al., 2020). While these results support that the homeostasis of the ER network structure is critical for cell health, a challenge for the future is to establish a mechanistic framework to connect ER shape integrity with essential signaling pathways.

Despite a functional conservation of shapers, such as RHD3, reticulons and Lnps, the plant ER structure depends on plant-unique factors. For example, a minor role of microtubules in ER reshaping is consistent with a predominant role of actin in this process (Sparkes et al., 2009a); this is markedly different from the dependence of the ER network shaping on microtubules in mammalian cells (Waterman-Storer and Salmon, 1998; English et al., 2009). The existence of plant-unique ER-actin interactors (i.e., SYP73 and NETWORKED 3B; (Cao et al., 2016; Wang and Hussey, 2017), plant-specific molecular motors (i.e. Myosin XI family) (Peremyslov et al., 2010; Ueda et al., 2010), and the absence in the plant genome of CLIMP63, the connector of the mammalian ER to microtubules and a spacer of the cisternal lumen (Klopfenstein et al., 2001; Shibata et al., 2010), further support that plants have developed specific mechanisms of ER shaping across kingdoms. An obvious challenge for the future is to determine the nature or such mechanisms through the identification of additional players. For example, proteomics of cellular compartments or targeted proteomics based on pull-downs of ER shapers have yielded opportunities to identify proteins making up the plant ER (Dunkley et al., 2006; Kriechbaumer et al., 2018), but the challenge ahead is to define a functional pipeline to identify proteins specifically involved in ER structure. Forward genetics screen based on confocal microscopy analyses of Arabidopsis seedlings expressing fluorescent markers to identify mutants with defective organization of secretory organelles (Faso et al., 2009; Nakano et al., 2009; Takagi et al., 2013) offer a realistic opportunity to identify mutations that compromise the ER, although an innate limitation of these screens is their labor-intensive nature. Automation of this type of screens alongside the implementation of software capable to quantitatively analyze the dynamics of the ER (Pain et al., 2019) is likely to offer a platform for the fast identification of modifiers of the ER shape and dynamics.

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Plant Golgi stacks – Versatile glycosylation factories on the move

The Golgi lies at the center of the secretory pathway, importing cargoes from the endoplasmic reticulum (ER), adding glycosyl groups, and exporting to the post-Golgi compartments or to the extracellular space (Alberts et al., 2014). Its role as a processing trader is illustrated in its polarized stack architecture where entry (*cis*) and exit (*trans*) sides are discerned (Figure 3 A-C) (Farquhar and Palade, 1981; Moore et al., 1991). The plant Golgi also synthesizes non-cellulosic cell wall polysaccharides (Zhang and Staehelin, 1992; Carpita and McCann, 2000). The Golgi in plant cells consists of many discrete stacks (Figure 3B) and each stack is thought to function independently (Nebenfuhr and Staehelin, 2001). The stacks travel in the cytosol at speeds up to several microns per second and the movement is dependent on myosin motors (Boevink et al., 1998; Madison et al., 2015). The decentralized organization contrasts with the mammalian Golgi in which stacks are stitched to form a ribbon or a complex next to the nucleus (Marsh et al., 2001). Therefore, ER-to-Golgi transport and post-Golgi secretion requires long-distance vesicular trafficking to and from the Golgi (Gillingham and Munro, 2016). Mobile Golgi stacks in plants, instead, can visit ER export sites (ERESs), concentrate to sites of secretion, and redistribute for cell division (Nebenfuhr et al., 2000; Yang et al., 2005; Ndinyanka Fabrice et al., 2017).

Transport through the plant Golgi

Golgi stacks move slowly when they become associated with ERES and the ER-to-Golgi transport is mediated by COPII-type vesicles (Nebenfuhr et al., 1999)](Yang et al., 2005) (Kang and Staehelin, 2008). In mammalian cells, the ER-to-Golgi intermediate compartment (ERGIC) assembles at ERES and ER-resident proteins are retrieved from ERGIC before they reach the perinuclear Golgi complex (Appenzeller-Herzog and Hauri, 2006). The plant Golgi lacks ERGIC compartments as COPII vesicles are directly transferred to the cis-Golgi. It was demonstrated that biosynthetic enzymes are localized to the medial Golgi after recycling of ER proteins is finished in the cis-Golgi (Donohoe et al., 2013), suggesting that the cis cisternae functionally replaces ERGIC in plants (Ito and Boutte, 2020).

Among the models explaining the intra-Golgi transport, the cisternal progression/maturation model has been supported by transmission electron microscopy (TEM) studies of the plant Golgi (Robinson, 2020). It is evident from electron micrographs of plant Golgi stacks that Golgi cisternae are peeled off from the trans-side, indicating that Golgi cisternae are transient entities, disposed of from the stack once they reach the trans-end (Day et al., 2013). Electron tomography (ET) analysis has shown assembly intermediates of new cisternae on the *cis*-side that exhibit highly varying sizes and shapes (Donohoe et al., 2013). Cell wall polysaccharides were detected in the cisternal lumen but not in COPI-type vesicles at the cisternal margins that are thought to retain Golgi resident proteins against the cisternal membrane flux (Donohoe et al., 2007). On the trans-side, trans-Golgi network (TGN) compartments arise from the trans-most cisternae. The transformation involves a significant reduction in the membrane amounts, suggesting that Golgi resident proteins are retrieved from the TGN (Kang, 2011; Kang et al., 2011).

The aforementioned transports occur within a ribosome-excluding matrix that encloses COPII vesicles to TGN cisternae (Figure 3D) (Staehelin and Kang, 2008). They probably correspond to a dense network of proteins involved in Golgi membrane assembly, maturation, TGN formation, and fastening cisternae into a stack. Golgins are Golgi-localized long coiled-coil proteins and some of them are tethering factors (Latijnhouwers et al., 2005) and; given their rod-like shape, they constitute scaffolds for the matrix. Mammalian Golgins are required for the Golgi integrity, vesicular trafficking to the Golgi, and protein glycosylation (Wong and Munro, 2014), (Liu et al., 2017b) (Witkos et al., 2019). Arabidopsis Golgins have been shown to play roles in COPII vesicular transport (Kang and Staehelin, 2008) and interaction of the cis-Golgi with ERES (Osterrieder et al., 2017).

Biosynthesis in the plant Golgi

Production and export of cell wall matrix polysaccharides distinguish the plant Golgi from its animal counterpart. It has been shown that the reaction cascades for polysaccharide synthesis are arranged sequentially over the stack from the *cis*-to-*trans* direction. As amounts of glycosyltransferases and sugar transporters are small per stack, their localization within the Golgi has been investigated with overexpressor lines or by localizing reaction products (Chevalier et al., 2010; Meents et al., 2019). Cell wall polysaccharides secreted constitutively and several mechanisms for retaining Golgi proteins from the bulk flow have been characterized (Brandizzi, 2002; Schoberer et al., 2019).

TGN cisternae consist of distinct domains where secretory and vacuolar cargoes are separately packaged (Shimizu et al., 2021). Electron tomography imaging of Golgi/TGN complexes revealed that varying ratios of different vesicle buds in a TGN cisterna, suggesting that biosynthetic functions of

each Golgi stack are not uniform in a plant cell (Staehelin and Kang, 2008). Golgi stacks appear to be versatile factories of which activities are determined by the protein that they received from the ERES. Golgi stacks enriched with enzymes for synthesizing cell wall polysaccharides would give rise to more secretory vesicles than those that received proteins destined for the vacuole.

Future research perspectives

The structure of plant Golgi varies in different cell types (Staehelin et al., 1990) but the molecular mechanisms governing the remodeling remain elusive. For example, small Golgi stacks in root meristem cells exhibit structural-functional modifications in parallel with the differentiation of the meristem cells into columella and eventually into peripheral/border cells in the root cap (Wang et al., 2017c). Since several cell-specific markers for the Arabidopsis root cap have been identified (Kamiya et al., 2016), it would be possible to identify genes involved in Golgi-mediated secretion or glycosylation in columella or peripheral/border cells after single-cell sequencing of root cap isolates (Shaw et al., 2021).

Correlative light and electron microscopy refers to protocols in which macromolecules are first localized with fluorescence microscopy and the volume enclosing the macromolecules is imaged with EM. The correlative approach will be useful for analyzing organelles composed of heterogeneous members (Wang et al., 2019a). After classifying Golgi stacks associated with specific markers, each group could be investigated for characterizing its nanoscale architectures and interaction with other organelles. The dynamics of Golgi subpopulations under stress conditions will help understanding how the secretory pathway reorganizes in response to threats from outside. As the export from the Golgi is mediated by the trans-Golgi network, this study should be combined with TGN dynamics (Uemura et al., 2019).

Advances in cryo-electron microscopy and sample processing technology allowed for ET analysis of frozen-hydrated cells to visualize macromolecular complexes *in situ* (Otegui and Pennington, 2018). Due to the limitation in section thickness for EM, frozen cells need to be either sliced or thinned with focused ion beam milling (FIB). Golgi vesicles and intraluminal filaments were delineated in Chlamydomonas cells by cryo-ET (Engel et al., 2015). Although intact plant tissues are too thick for FIB, *in vitro* germinated pollen tube tips are amenable to FIB thinning (Liu et al., 2021b). As Golgi stacks produce numerous secretory vesicles to sustain pollen tube tip growth, it would be exciting to examine plant Golgi stacks with cryo-ET to uncover novel features not observed in plastic-embedded electron microscopy samples.

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Plant Endosomes: The protein sorting masters.

The ability to regulate the composition of the plasma membrane and the endomembrane system is critical for cell survival. Endosomes have a central role in this process by regulating protein and lipid (cargo) trafficking in the endomembrane system, both through the anterograde and retrograde pathways. As part of the anterograde pathways, that is, transport from the site of synthesis to the place of residence and function, proteins and lipids synthesized in the endoplasmic reticulum (ER) are typically transported in vesicles to the Golgi, to the Trans-Golgi Network (TGN), and from there, either to the plasma membrane (exocytosis) or to the vacuole. Retrograde pathways mediate the transport of cargo or trafficking factors in the opposite direction to the anterograde pathway, usually back to their original donor compartments. Proteins removed from the plasma membrane in vesicles through endocytosis are delivered to early endosomes, where they can be either recycled to the plasma membrane or carried to multivesicular endosomes (MVEs) for further sorting into intralumenal vesicles and subsequent degradation in the vacuolar lumen (Valencia et al., 2016). In plants, the TGN functions as the early endosome since it is the first compartment that receives endocytosed cargo (Dettmer et al., 2006; Lam et al., 2007). Thus, in contrast to animal cells, plant cells do not have separate early endosomes but combine both endocytic and biosynthetic sorting at the TGN (Viotti et al., 2010).

TGNs and MVEs, the two types of plant endosomes, arise, mature, and are consumed as part of their membrane trafficking function. Therefore, both types of organelles are in continuous flux and can be found as subpopulations at different maturation stages.

The TGN

As part of the endosomal pathway, the TGN receives plasma membrane cargo, which is either recycled back to the plasma membrane or retained for further sorting in MVEs and degradation in vacuoles. As part of the secretory pathway, the TGN produces both secretory vesicles carrying protein, membrane lipids, and cell wall polysaccharides to the plasma membrane and vesicles containing vacuolar cargo (Rosquete et al., 2018) and mediates retrograde recycling back to the Golgi and ER through COPI- (Bykov et al., 2017) and retromer-mediated traffic (Niemes et al., 2010).

The TGN forms largely through cisternal maturation of the trans-most Golgi cisterna (Golgi-associated TGN or GA-TGN) but eventually detaches from the Golgi becoming an independent organelle (free or also called Golgi-independent TGN or GI-TGN) that fragments into vesicles (Toyooka et al., 2009; Kang et al., 2011; Uemura et al., 2014; Uemura et al., 2019) (Figure 4). There are approximately 35 Golgi stacks and GA-TGNs in an interphase Arabidopsis meristematic cell (Segui-Simarro and Staehelin, 2006). In Arabidopsis root cells, as the *trans*-most cisterna matures into the TGN, it develops numerous vesicle buds, loses 30-35% of its total membrane surface area, and becomes enriched in the Rab GTPases RAB-A2a and RAB-A4b, the phosphatidylinositol 4-kinase PI4Kb1, the vacuolar V-ATPase subunit VHA1a, and the SNAREs (Soluble N-ethylmaleimide sensitive factor Attachment protein Receptor) SYP61, SYP43 , VAMP721, VAMP722, and VAMP727 (Dettmer et al., 2006; Chow et al., 2008; Kang et al., 2011; Zhang et al., 2011). As the GA-TGN detaches from the Golgi stacks to become free/GI-TGNs, the budding profiles become more abundant.

These GA- and GI-TGN subpopulations play distinct trafficking functions (Renna et al., 2018; Uemura et al., 2019; Ito and Boutte, 2020). For example, GA-TGN but not free/GI- TGNs label with the endocytic tracer FM4-64 (Uemura et al., 2019), suggesting that endosomal function is carried out by the GA-TGN whereas free GI/TGNs seem to be primarily involved in exocytosis. The different trafficking functions of the TGN are spatially separated in subdomains that differ both in their protein and membrane lipid composition (Wattelet-Boyer et al., 2016). Thus, within the GA-TGN, there are at least two “zones”, the secretory-trafficking zone that generates exocytic vesicles and is enriched in the SNARE VAMP721, the adaptor complex AP-1, the accessory protein EPSIN1, and clathrin and the vacuolar trafficking zone enriched in VAMP727, the adaptor complex AP-4, and accessory protein MODIFIED TRANSPORT TO THE VACUOLE1 (MTV1) (Heinze et al., 2020; Shimizu et al., 2021). In addition, a plant-specific TRAPPII complex has been hypothesized to mediate the recruitment/tethering of endocytosed vesicles to subdomains of the TGN (Rosquete et al., 2019).

The TGN not only has subdomains for exocytic, endocytic, and vacuolar trafficking, but also it associates with protein complexes that control the trafficking of specific cargo proteins. Thus, for example, the TGN-localized protein ECHIDNA controls the secretion of only a subset of plasma membrane proteins, such as the auxin influx carrier AUX1 (Boutte et al., 2013). In contrast, a module formed by seven transmembrane domain-containing proteins (7TM) and components of the guanine nucleotide-binding (G) protein signaling work together at the Golgi and TGN to regulate exocytosis of

cellulose synthases, but not endocytosis or general exocytosis of both soluble and plasma membrane cargo (McFarlane et al., 2021).

MVEs

MVEs arise from membranes derived from the TGN and are characterized by a rounded shape, the presence of intralumenal vesicles, and their association with RAB-F GTPases such as ARA6, ARA7, and RHA1 (Haas et al., 2007). There are approximately 17-20 MVEs in interphase meristematic cells and are usually found in close proximity to the GA-TGN (Segui-Simarro and Staehelin, 2006). Plasma membrane proteins targeted for degradation are usually ubiquitinated at the plasma membrane, internalized by endocytosis, and delivered first to the TGN and then to MVEs. At the MVE limiting membrane, the ESCRT (Endosomal Sorting Complex Required for Transport) machinery binds, clusters, and sorts the ubiquitinated cargo into membrane domains that bend away from the cytoplasm, that is membrane bending in the reverse (negative) topology of the better understood cases of vesiculation, such as clathrin-mediated endocytosis. Failure to properly sort plasma membrane components into intralumenal vesicles results in the accumulation of plasma membrane proteins in the vacuolar membrane (Figure 4), which leads to severe alterations in development and most frequently, to lethality. Although it has long been assumed that ESCRTs orchestrate the formation and release of one single endosomal vesicle at a time, studies performed in *Arabidopsis thaliana* have shown that at least in plants, these vesicles do not bud off individually but form in concatenated networks (Buono et al., 2017; Goodman et al., 2021).

In general, ESCRT proteins are well conserved across organisms, from Archaea (Makarova et al., 2010; Dobro et al., 2013; Pulschen et al., 2020) to Eukarya. In fungi and metazoans, five multimeric ESCRT complexes have been identified: ESCRT-0 to III and the triple AAA ATPase SKD1 (SUPPRESSOR OF K^+ TRANSPORT GROWTH DEFECT 1) with its activator LIP5. Plants contain putative orthologs for most of the ESCRT proteins originally identified in metazoans and fungi (Spitzer et al., 2006; Haas et al., 2007; Spitzer et al., 2009; Kalinowska et al., 2015; Buono et al., 2016; Yu et al., 2016; Wang et al., 2017a) with the exception of ESCRT-0 (Winter and Hauser, 2006), which is an early acting complex that binds phophoinositide-3-phosphate (PI3P), a lipid enriched in endosomal membranes and critical for recruitment of ESCRT proteins to endosomes. However, a group of proteins called TOL (TOML1-LIKE) are likely to play the role of ESCRT-0 in plants (Korbei et al., 2013; Moulinier-Anzola et al., 2020).

How do ESCRT proteins mediate intralumenal vesicle formation and sequestration of cargo proteins? ESCRT-0, -I, and -II contain ubiquitin-binding domains and contribute to the clustering of ubiquitinated cargo on the endosomal membrane and to membrane deformation (Liese et al., 2020). De-ubiquitinating enzymes remove the ubiquitin on cargo before their final sequestration into intralumenal vesicles. Critical for the final steps in vesicle formation are the presence of membrane cargo (Chiaruttini et al., 2015) as well as ESCRT-III and ESCRT-III-associated proteins, which are able to trigger membrane deformation and neck constriction (Hanson et al., 2008; Fyfe et al., 2011; McCullough et al., 2013; Chiaruttini et al., 2015).

Plants commonly contain several isoforms for each ESCRT subunits and even have evolved plant-specific ESCRT proteins, such as PROS (Positive Regulator of SKD1) that enhances SKD1 activity (Reyes et al., 2014), FREE1/FYVE1(Gao et al., 2014), and FYVE4 (Liu et al., 2021a). Interestingly, both proteins contain FYVE domains able to bind PI3P. FREE1 interacts with ESCRT-I subunits and is essential for endosomal sorting (Gao et al., 2014) whereas FYVE4 is necessary for the recruitment of ESCRT-III subunits (Liu et al., 2021a).

Future perspectives

Our understanding of endosomal biogenesis and the molecular machinery mediating its multiple sorting functions have increased dramatically during the past decades. However, new regulatory and sorting components are being discovered and many more remain elusive, making it still challenging to comprehend how sorting functions are both segregated and integrated in TGNs and MVEs. The plant endosomes have many distinct features that make them different from their counterparts in other organisms. For example, whether the concatenation of MVE intralumenal vesicles in complex networks is unique to plants or is a universal mechanism in all eukaryotes is presently unknown. It is tempting to speculate that the evolution of unique ESCRT components and the drastic diversification of some ESCRT isoforms may have contributed to the unique features of intralumenal vesicle formation in plants.

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Lipid Droplets: Specialized Subcellular Hydrophobic Compartments

Like all cells, plant cells accumulate storage lipids in their cytoplasm as discrete lipid droplets (LDs), most often consisting of a hydrophobic core of non-bilayer forming lipids such as triacylglycerols (TAGs) or sterol esters surrounded by an emulsifying monolayer of phospholipids (Pyc et al., 2017a; Huang, 2018; Ischebeck et al., 2020). Although less commonly considered, rubber particles of rubber-producing plant species with a polyisoprenoid hydrophobic core, share the same overall structure (Yamashita and Takahashi, 2020). This thermodynamically stable structure was originally observed in TEM micrographs, and described by various terms as lipid bodies, oil bodies, spherosomes or oleosomes (Wanner and Theimer, 1978). However, the contemporary, unifying terminology of "lipid droplets" emphasizes the evolutionary conservation of this compartment across kingdoms of life where there are increasing reports of functions beyond the efficient storage of carbon (Lundquist et al., 2020).

In plants, LDs are most commonly associated with oilseeds and oleaginous fruits where they compartmentalize the well-known "vegetable oils" (Chapman et al., 2012). However LDs are present in essentially all cell types in plants. Because the most abundant LD proteins in seeds—oleosins—are not produced in most plant cell types, recent efforts to identify LD proteins in non-seed tissues (Horn et al., 2013; Brocard et al., 2017; Kretzschmar et al., 2018; Fernandez-Santos et al., 2020) have expanded the inventory of LD proteins in plant cells. These new proteins and their partners have begun to suggest previously unrecognized participants in LD formation, stability, turnover and functions.

Among the recently-recognized LD proteins are the so-called LDAPs (LIPID DROPLET-ASSOCIATED PROTEINs), which share homology with small rubber particle proteins from rubber producing plants. LDAPs were identified as prominent proteins in purified LDs isolated from avocado mesocarp (Horn et al., 2013), and have since become appreciated for their widespread occurrence throughout the plant kingdom (Gidda et al., 2016; Brocard et al., 2017; de Vries and Ischebeck, 2020) as well as for their induction by drought stress (Kim et al., 2016). The LDAPs are relatively small proteins without extended hydrophobic regions, and they have been shown to localize specifically to the LD surface perhaps through their extensive amphipathic helices. Screens for potential protein interactors, that might serve as protein recognition sites for LDAPs on the organelle surface, identified the protein LDIP (LDAP-INTERACTING PROTEIN), which also is widely- distributed in the plant kingdom (Pyc et al., 2017b; Coulon et al., 2020) (de Vries and Ischebeck, 2020). LDAPs and LDIP are expressed in *both* seed and non-seed tissues of plants, and are suspected in playing broader roles in compartmentalization of neutral lipids in cells beyond those found in seed tissues.

Another recently-identified LD protein is the PLANT UBX DOMAIN-CONTAINING PROTEIN10 (PUX10). PUX10 localizes to LDs through a hydrophobic polypeptide sequence and recruits an AAA-type ATPase CELL DIVISION CYCLE48 (CDC48) protein to the LD surface (Deruyffelaere et al., 2018; Kretzschmar et al., 2018). This interaction is believed to support the selective extraction of LD surface proteins, like oleosins and LDAPs, for their ubiquitin-mediated protein degradation. This LD-associated degradation pathway likely operates in all cells of plants to repurpose the surface and/or contents of the LD compartment during development or in response to environmental stresses.

LD formation at the ER

Like in most eukaryotes, LD formation in plant cells originates in the ER where the enzymes for storage lipid assembly are present. Ultrastructural studies frequently reveal intimate connections of LDs with the ER (Herman, 2009; Brocard et al., 2017) which can also be captured by confocal fluorescence laser scanning microscopy (Figure 6A). The process of LD proliferation can be capitulated at the subcellular level in *Nicotiana benthamiana* cells, where LDs are normally low in abundance, and transient expression of cDNAs encoding proteins suspected in LD formation can be readily studied (Figure. 6). A transient system for LD studies also has been developed with tobacco pollen tubes (Muller et al., 2017), and this has been particularly useful for protein localization studies due to the large number of LDs normally present in these cells.

Existing models for LD formation suggest that newly-synthesized TAGs aggregate and form foci or "lipid lens" structures between the two leaflets of the ER bilayer (Figure 6B) (Pyc et al., 2017a). An oligomeric protein complex comprised of SEIPIN subunits in the ER bilayer coordinates these TAG foci as they grow (Chapman et al., 2019). SEIPIN proteins direct a bulge of newly accumulating neutral lipids to emerge into the cytoplasm covered with a monolayer of ER-derived phospholipid. Unlike fungi and metazoans, plants have multiple genes encoding SEIPIN isoforms (Cai et al., 2015). In Arabidopsis *SEIPIN 1* is expressed mostly in seed and seedling tissues, whereas *SEIPIN 2* and *SEIPIN 3* are expressed in essentially all issues. While loss-of-function mutants in a

single *SEIPIN* gene in Arabidopsis resulted in negligible phenotypes, double and especially triple *seipin* mutants showed dramatic cellular disruptions in normal LD formation (Taurino et al., 2018). Seeds and pollen of *sei1/sei2/sei3* mutants accumulated large aberrant-shaped LDs, sometimes observable in the nucleus and ER lumen in addition to the cytoplasm. These results indicate that SEIPINs play a critical and partially redundant role in the normal formation of LDs in plant cells. Structural models based on homology with known structures of Drosophila and human SEIPIN, suggests that the three Arabidopsis SEIPINS can form homo-oligomeric structures with different numbers of subunits (Chapman et al., 2019), but future work is required to understand the functional interactions of the three SEIPIN proteins in plant cells, their potential for hetero-oligomeric interactions and their partners in LD biogenesis.

The loss-of-function of two other Arabidopsis genes revealed similar, large and aberrant LD phenotypes in seeds, reminiscent of *seipin* mutants. These two genes encode the VESICLE-ASSOCIATED MEMBRANE PROTEIN-ASSOCIATED PROTEIN 27-1 (VAP27-1) and LDIP proteins, respectively, which were shown to interact with SEIPINs and with LDs (Pyc et al., 2017b; Greer et al., 2020). In other work, higher order oleosin mutants also displayed aberrant formation of LDs during early seed development, and this was reported to result from alteration of fusion dynamics of very small LDs, not necessarily during LD formation at the ER (Miquel et al., 2014). LDAPs also occur in seeds but at lower amounts than oleosins (Kretzschmar et al., 2018). And while LDAPs are interactors of LDIP (Pyc et al., 2017b), their loss-of-function in *ldap* mutants did not result in dramatic alterations of LD morphology in seeds (Gidda et al., 2016), although there may be some increase in LD size in leaves of *ldap* knockdowns (Brocard et al., 2017). Future work will be required to piece together the mechanistic associations between SEIPINs, LDIP, VAP27-1, oleosins, LDAPs and other LD proteins; nevertheless, results to date support cooperative roles for these proteins in the cellular process of LD formation in plant cells.

Engineering the LD compartment

Because of their high energy density and caloric value, LDs have become a target compartment for metabolic engineering strategies to overproduce storage lipids in vegetative parts of plants. This process has met with remarkable success, leading to tobacco plants with lipid yields from their leaves equivalent to oil yields from oilseed crops. This overall engineering process has been described as the “push, pull and protect” concept for the efficient production and packaging of storage lipids in plant tissues (Vanhercke et al., 2017; Vanhercke et al., 2019). Apparently the accumulation of lipids in leaves is at the expense of transient starch (Chu et al., 2020), illustrating a plasticity in leaves for carbon storage that may ultimately be exploited for bioenergy and/or feed energy-densification applications.

In addition to bioenergy applications, LDs offer a stable compartment for sequestration of various hydrophobic compounds. As such, several recent reports indicated that manipulation of LD machinery can be exploited for the subcellular storage of secondary metabolites. For example, (Sadre et al., 2019) engineered the accumulation of sesquiterpenes (patchoulol) and diterpenes (abetadiene) into cytoplasmic LDs. Elsewhere, the expression of lipogenic proteins from mouse elevated LDs dramatically in leaves, and supported the increased accumulation of the sesquiterpene phytoalexin, capsidiol, along with TAGs (Cai et al., 2019). With the preponderance of bioactive hydrophobic secondary metabolites, these studies illustrate the utility of engineering the cytoplasmic LD compartment in plants as a repository for high value isoprenoids in the future.

Future prospects for LD biology

In the last decade, increasing attention on cytoplasmic LDs has revealed an increasing inventory of proteins that support the formation, stability and turnover of this compartment in plant cells. Some proteins appear to have specific plant lineages, while others are conserved across kingdoms. The identification of this LD machinery will support a mechanistic examination of the interplay of these and other proteins in LD biogenesis, both in oilseeds and in non-seed tissues of plants. In addition, functions beyond neutral lipid storage continue to be revealed for LDs in different plant cell types including as a reservoir for membrane lipid remodeling (Xu and Shanklin, 2016), a platform for the production of lipophilic signals (Shimada et al., 2014; Fernandez-Santos et al., 2020), and responses to environmental stress (Yang and Benning, 2018) (Lu et al., 2020). Further, an improved understanding of the cellular processes for LD formation, neutral lipid deposition and LD stability will accelerate and expand promising applications for lipid engineering.

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The dynamic nature of peroxisome structures, abundance, and subcellular interactions

Peroxisomes compartmentalize diverse oxidative reactions, allowing metabolic, signaling, and detoxification roles while limiting the potential for damage (Kao et al., 2018; Pan et al., 2020). Peroxisomes are a closed system, permeable only to small (300-400 Da) molecules (Charton et al., 2019; Plett et al., 2020). Lipid substrates and ATP, NAD^+, and CoA cofactors are imported via membrane transporters (Charton et al., 2019; Plett et al., 2020), whereas enzymes are imported by cytosolic receptors that recognize a peroxisomal targeting signal (PTS1/PTS2; (Reumann and Chowdhary, 2018; Pan et al., 2020)). Plant peroxisomes are indispensable during early development, when seedlings rely on lipid breakdown prior to photosynthetic initiation (Graham, 2008) for photorespiration in leaf cells, and reactive oxygen (ROS) and nitrogen species (RNS) metabolism throughout development and under changing conditions (Del Rio and Lopez-Huertas, 2016; Kao et al., 2018; Corpas et al., 2020; Pan et al., 2020; Su et al., 2020).

Peroxisome abundance varies based on cell type, developmental stage, and environmental conditions. Peroxisome numbers increase in response to stress, including salt (Mitsuya et al., 2010; Fahy et al., 2017; Frick and Strader, 2018), light (Desai and Hu, 2008), and cadmium (Rodriguez-Serrano et al., 2016; Terron-Camero et al., 2020), and prior to cell division (Lingard et al., 2008). Peroxisome division occurs via fission or the budding of pre-peroxisomes from the ER (Agrawal and Subramani, 2016; Kao et al., 2018; Pan et al., 2020; Su et al., 2020). Peroxisomes can be degraded via pexophagy, an organelle-specific autophagy (Young and Bartel, 2016; Su et al., 2019), as part of a natural turnover ((Kao et al., 2018; Yamauchi et al., 2019) or when excess organelles are not necessary following stress (Calero-Munoz et al., 2019) or developmental transitions (Kim et al., 2013).

Peroxisomes are small, measuring 1-2 μm in Arabidopsis (Rinaldi et al., 2016) but with notable variability. Larger structures can be visualized 3-4 days post imbibition (Rinaldi et al., 2016), with some peroxisomes over 10 μm in 4-day-old seedlings. This expansion is temporary, hypothesized to occur following an influx of seed-storage lipids (Rinaldi et al., 2016). Although morphology can differ, peroxisomes are primarily spherical.

Since their identification, peroxisomes have been considered simple organelles, with typical definitions highlighting their small size, lack of a genome, and a single membrane surrounding a defined matrix. However, recent investigations by Wright and Bartel (2020) have led to an enhanced description of peroxisomes, one in which extensive internal membranes are present. The authors combined two high-sensitivity fluorescence reporters: an mRuby3-PTS to visualize the peroxisome interior and mNeonGreen tagged with an mPTS membrane peroxisomal targeting signal to label the membrane (Wright and Bartel, 2020). This combination revealed the unexpected presence of internal structures, coined intralumenal vesicles (ILVs).

In 3-4 day-old samples, membrane reporters localized around the structures, but also within the interior of the organelles (Wright and Bartel, 2020). Many peroxisomes contained numerous internal vesicles, which varied in size (Figure 7). As introduced above, 5-day-old seedlings showed expanded organelles that rapidly decreased in size. These size changes were concurrent with increasing ILVs and internalized membrane content. By 8 days, seedlings continued to show membrane reporters within the peroxisome lumen, with some images showing membrane signals throughout the entire structure. Watching this process suggested dense packing over time that precluded observation of individual vesicles, such that the membrane reporter appeared uniform within the lumen at this age (Wright and Bartel, 2020). These seedling experiments suggest how peroxisomes mature, starting as larger, variable structures, but stabilizing at a smaller size as membranes are internalized and lipid metabolism slows.

These microscopic images led to an enhanced understanding of peroxisomal structures: peroxisomes have an outer membrane surrounding lumenal space that contains imported matrix proteins, as well as a dynamic number of membrane-bound vesicles clear of matrix proteins (Figure 7) (Wright and Bartel, 2020). Further, two proteins with unique peroxisomal localization (SCO3/UP9; (Albrecht et al., 2010; Quan et al., 2013) accumulated within a subset of ILVs that lacked matrix proteins. This apparent segregation yields at least three distinct spaces within peroxisomes, potentially housing unique proteins, substrates, cofactors, and/or environments.

Mutants disrupting β-oxidation showed alterations in ILV number, size, composition, and orientation, suggesting β-oxidation activity is required for inner membrane formation (Wright and Bartel, 2020).

Long-chain seed storage lipids are insoluble; Wright and Bartel (2020) hypothesize membrane internalization may reduce the solubility challenges associated with lipid mobilization in an aqueous matrix. Lipids could be degraded from the membrane, with subsequent release and degradation of the shorter, more soluble substrates, leading to the reduced organelle size common in older seedlings.

Beyond structures, imaging and biochemical studies have revealed the physical association of peroxisomes with lipid bodies, plastids, mitochondria, and the ER (Figure 7); (Shai et al., 2016) (Oikawa et al., 2019). Peroxisomal enzymes catalyze specific reactions within metabolic pathways, which often extend to two (or more) subcellular spaces. These organelle interactions are dynamic: peroxisomes in seedlings associate with oil bodies, for instance, whereas peroxisomes in leaves associate with chloroplasts and mitochondria (Oikawa et al., 2019). Interaction points would enhance the transfer efficiency of pathway intermediates. These sites also may facilitate transferring hydrogen peroxide and other reactive species from other organelles to peroxisomes for sequestration and degradation (Shai et al., 2016; Su et al., 2019).

Many plant species contain oil bodies (also known as lipid droplets or lipid bodies) that store triacylglycerols for energy reserves (Esnay et al., 2020). Peroxisome-oil body association facilitates the efficient transfer of stored material for metabolism via fatty acid β-oxidation and the glyoxylate cycle. Extended interactions and peroxisomal clusters in proximity to oil bodies occur in β-oxidation mutants (Hayashi et al., 2001; Rinaldi et al., 2016), while exogenous sucrose reduces the association (Cui et al., 2016), suggesting this interaction is mediated by cellular requirements for lipid mobilization.

Peroxisomes and chloroplasts can form specific pairs that remain intact over time (Oikawa et al., 2015). Peroxisome shape alterations expand the surface area to increase chloroplast interactions. In the light, peroxisomes extend into an elliptical shape, versus a spherical shape in darkness. Tethering factors connecting peroxisomes and chloroplasts may facilitate this interaction (Oikawa et al., 2015; Gao et al., 2016), potentially including the PEX10 RING finger protein (Schumann et al., 2003; Sparkes et al., 2003; Schumann et al., 2007). A dominant-negative PEX10 line had clustered peroxisomes that did not associate with chloroplasts; this line had phenotypes similar to photorespiration mutants (Schumann et al., 2007), consistent with a role for organelle association in efficient metabolic transfer.

Mitochondria also appear in close proximity to both peroxisomes and chloroplasts in the light, consistent with their interactive metabolic roles (Oikawa et al., 2015). Peroxisomes associate with mitochondria in stress conditions as well; increasing interactions are seen in cells exposed to high ROS and might be important for ROS neutralization (Jaipargas et al., 2016; Mathur, 2021).

Finally, peroxisomes show a close proximity with the ER (Barton et al., 2013; Oikawa et al., 2019). Interestingly, one of the two mPTS signals used by Wright and Bartel (2020) revealed accumulation in peroxisomes and reticular membranes thought to be ER. This finding is consistent with a hypothesis that the membrane protein was trafficked through the ER or has a dual function at both sites (Wright and Bartel, 2020).

Another shape alteration to peroxisomes are thin organelle protrusions known as peroxules (Mathur, 2021). These structures are up to 15 μm, dramatically increasing the surface area (Sinclair et al., 2009; Barton et al., 2013). Formation of these organelle extensions is transient and dynamic (Mathur, 2021). The interactions between organelles described above may be mediated by peroxules, including proposed interactions with oil bodies (Thazar-Poulot et al., 2015), chloroplasts (Schumann et al., 2007), mitochondria (Jaipargas et al., 2016), and ER (Sinclair et al., 2009). Extended structures are seen following H_2O_2, UV-A, and hydroxyl radical stress, but retract when stress is minimized (Sinclair et al., 2009). In addition, elongations are common during the constriction and fission steps of peroxisome division (Sinclair et al., 2009; Barton et al., 2013). Cadmium induces ROS and similarly leads to peroxule formation that results in division to increase peroxisome numbers (Rodriguez-Serrano et al., 2016). Increased peroxule frequency in cells exposed to ROS leads to a hypothesis that extensions facilitate neutralization to prevent or reduce damage (Sinclair et al., 2009; Barton et al., 2013; Rodriguez-Serrano et al., 2016). Separately, peroxule-mediated contacts might assist in protein localization. The SDP1 lipase (Eastmond, 2006) localizes to peroxisomal membranes and then the oil body, a transition concurrent with peroxule development (Thazar-Poulot et al., 2015)

The refined visualization of peroxisome structures and our increasing understanding of organelle interactions has led to an enhanced view of peroxisomes compared to a previously simple model.

Many open questions about peroxisome biology remain. What is the mechanism of and importance for dynamic membrane changes for peroxisomes in adult tissues and under changing environmental conditions? How do peroxisome substructures form and how are membrane and matrix proteins sorted to create unique environments or provide specific functionality? Understanding such details about peroxisome structures, as well as the factors promoting and mediating peroxisome interactions with other organelles, will continue to increase our understanding of these dynamic organelles.

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Plant mitochondria

In plants, mitochondria provide a large portion of the ATP in the cytosol through oxidative phosphorylation, and are the sites of some amino acids, nucleic acids, lipids, and plant hormone metabolism. Plant mitochondria also control redox balances when photosynthesis is on or off or fluctuating (Noguchi and Yoshida, 2008; Finkemeier and Schwarzlander, 2018), have roles in cellular signaling (Huang et al., 2016; Welchen et al., 2021) et al., 2021), and in resistance to diseases (Fuchs et al., 2020). In agriculture, cytoplasmic male sterility, which is caused by genes encoded in the mitochondrial genome, is used for production of F1 hybrid seeds in diverse crops and vegetables. The fine structure and dynamics of plant mitochondria are briefly reviewed here.

Mitochondria have two lipid bilayers that form the outer and inner membrane (Figure 8). Some parts of the inner membrane are invaginated to form sacs, called cristae, that increase the area of oxidative phosphorylation complexes. Five diverse eukaryotic-conserved complexes are embedded in the cristae membrane. In contrast, plant-specific proteins (alternative oxidases and extra NDH and NDPH dehydrogenases) for alternative respiration pathways mainly reside in the non-cristae parts of the inner-membrane (Schwarzlander and Fuchs, 2017). Plant ATP synthase dimers (complex V) are in the cristae membrane, where they contribute to its curvature (Zancani et al., 2020. Complexes I to V have roles in oxidative phosphorylation. Some of them form super-complexes for functional efficiency and to regulate oxidative phosphorylation [Braun, 2020 #2342. Protein-protein interactions and metabolite channeling are observed also in the TCA cycle in the matrix [Zhang, 2017 #2382). Additionally, glycolysis enzymes in the cytosol dynamically associate on the outer surface of mitochondria (Giege et al., 2003; Graham et al., 2007), probably to more efficiently transport metabolites.
The mitochondrial outer membrane has the most abundant protein in plant mitochondria, the Voltage-Dependent Anion Channel (VDAC1). A single mitochondrion contains 40,000 VDACs out of a total of 1.4 million proteins (Fuchs et al., 2020). The outer membrane does not just encapsulate the inner membrane but also sometimes extends into the cytosol and other organelles (without extending the inner-membrane), and occasionally the extensions are pinched off to form small vesicle-like structures (Yamashita et al., 2016); Figure 8D). In mammals, mitochondria-derived vesicles which do not contain inner membranes are reported to be involved in the transport of specific proteins to peroxisomes, endosomes, and multivesicular bodies (Sugiura et al., 2014), and in the biogenesis of peroxisomes [Sugiura, 2017 #2376.

Each Arabidopsis leaf cell contains 300-450 mitochondria. Many plant mitochondria move along microfilaments at 0.05 - 3 μm/sec [Doniwa, 2007 #2344](Oikawa et al., 2021), which is about an order of magnitude faster than mammalian and yeast mitochondria, which mainly move along microtubules. Some plant mitochondria stop and wiggle, as if they were anchored to the cytoskeleton or other organelles, such as plastids and peroxisomes (Jaipargas et al., 2016; Oikawa et al., 2021) et al., 2016). Moving plant mitochondria can change their speed and also can change their shapes from granular to linear to attach to other organelles in response to the presence of sucrose or light (Jaipargas et al., 2016). A single plant cell can have mitochondria with different shapes (Jaipargas et al., 2015), different DNA contents (Arimura et al., 2004b; Preuten et al., 2010), (Figure 8E) and transiently fluctuating membrane potentials (Schwarzlander et al., 2012). In addition, as shown in Figure 8B, differently colored groups of mitochondria in a cell achieve a unified color in two hours, indicating that mitochondria undergo frequent fusion and fission, resulting in the sharing of internal proteins. Mitochondria involved in such dynamic sharing of materials in a plant cell are referred to as a dynamic syncytium (Lonsdale et al., 1988), and the collective mitochondria in a cell are thought to exist as a discontinuous whole (Logan, 2017). Fusion of mitochondria results in the formation of elongated and/or branched mitochondria in some meristematic tissues, such as shoot apical apices (Segui-Simarro and Staehelin, 2006), germinating seeds (Paszkiewicz et al., 2017), and dedifferentiating protoplasts (Sheahan et al., 2005; Rose and McCurdy, 2017).

Mitochondrial fission is achieved by dynamin-related proteins that are well-conserved in eukaryotes (e.g. DRP3A and 3B in Arabidopsis (Arimura and Tsutsumi, 2002; Arimura et al., 2004a; Arimura et al., 2004b; Fujimoto et al., 2009), Figure 8A), which polymerize to form ring-like structures outside mitochondria (Ingerman et al., 2005). Plant-specific ELM1, an outer surface protein, localizes DRP3s from the cytosol (Arimura et al., 2008). An outer-membrane embedded protein that is conserved in eukaryotes (Fis1) functions as a molecular adapter for DRP in budding yeast (Okamoto and Shaw, 2005). Fis1 had been thought to carry out the similar functions but is now thought to have only a

rather minor and indirect role in mitochondrial fission in both mammals (Otera et al., 2010; Giacomello et al., 2020) and plants (Nagaoka et al., 2017; Arimura, 2018). Other factors may be involved in plant mitochondrial fission, such as factors involved in cold-induced fission (Arimura et al., 2017) or factors that are independent of DRP and specific to Brassicaceae (Aung and Hu, 2011). On the other hand, no orthologues, factors or molecular mechanisms are known with certainty to be involved in mitochondrial fusion in plants. However, Friendly (FMT) is suggested to mediate inter-mitochondrial association before mitochondrial fusion because in *fmt* mutants, mitochondria gather together (Logan et al., 2003) but do not fuse (El Zawily et al., 2014).

Mitochondrial-specific autophagy (mitophagy) has been extensively studied in mammals and yeasts (Onishi et al., 2021), in which it is involved in mitochondrial quality control. In these organisms, degraded mitochondria with low membrane potential could not fuse with other “healthy” mitochondria, but they are specifically recognized, captured and engulfed by autophagosome membranes (Figure 8C). The engulfed mitochondria are transported to the vacuole to be digested to prevent accidental ROS generation and/or other negative effects. Therefore, mitophagy, fission, and fusion are thought to function as a quality control system for all the mitochondria in a cell (Twig et al., 2008). Mitochondrial-specific degradation in *Arabidopsis* has also been observed in several situations, including during leaf senescence (Broda et al., 2018) greening of cotyledons (Ma et al., 2021), after UV-irradiation (Nakamura et al., 2021) and after treating the inner membrane with ionophores (Ma et al., 2021). Orthologues of factors specific to mitophagy in mammals and yeasts have not yet been found in plant genomes, although FMT was recently reported to be involved in mitophagy in Arabidopsis (Ma et al., 2021).

Super resolution microscopy is a promising new technique that can clarify the internal structures of mitochondria in more detail with their diverse physiology and functions. In addition, recent trials to understand molecular numbers of averaged single mitochondrion (Fuchs et al., 2020) or estimated single mitochondrion (Moller, 2016) will hopefully develop to the next stage of analysis of the exact individual mitochondria to answer the actual quantitative dynamics of molecules (or “factfulness”) of diverse mitochondria. Until recently, transformation of mitochondrial genomes in multicellular plants has been impossible, but new genome editing methods (Kazama et al., 2019; Arimura et al., 2020) have opened the door to analyzing the functions of mitochondrial genes, as well as to regulate their expressions to breed crops with agriculturally important characteristics.

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Chloroplast – A Plant's Powerhouse with Tunable Performance

A unique endosymbiotic event more than 900 Ma ago was the starting point for the evolution of the chloroplast from a free-living cyanobacterial precursor (Sibbald and Archibald, 2020). Every second, the thylakoid membrane system of a modern chloroplast in *Viridiplantae* can convert energy from the sun in up to 80 million ATP and NADPH + H^+ molecules which fuels a number of anabolic reactions localized in the chloroplast stroma, like syntheses of sugars, lipids/fatty acids, amino acids, nucleotides, pigments, alkaloids, hormones, and vitamins (Kirchhoff, 2019). Furthermore, a battery of membrane-embedded chloroplast envelope transporters makes the competency for photosynthetic energy transforming available to the entire cell and beyond (Weber and Linka, 2011).

Chloroplast Lifecycle

During the last decade, electron tomography has provided detailed structural insights in the morphological transitions from an undifferentiated, non-photosynthetic proplastid to a mature chloroplast in the plant shoot apical meristem for illuminated shoots (Adam et al., 2011; Charuvi et al., 2012) or via the etioplast with its characteristic para-crystalline prolamellar body (Kowalewska et al., 2016). The correlation between the sequential appearance of proteins like photosystem I and II, light-harvesting complex II, CURT1 proteins, ATPase, protochlorophyllide oxidoreductase, and plastidial ribosomes on the one hand and structural developments of the plastid, on the other hand, provides insights on the role of particular proteins for the proplastid-chloroplast differentiation (Kowalewska et al., 2016; Liang et al., 2018a; Floris and Kuehlbrandt, 2021). Proplastid development requires a massive protein import from the cytoplasm into the chloroplast mainly by the TOC/TIC translocase system (Aronsson and Jarvis, 2008; Ling et al., 2012) since ~95% of chloroplast proteins are nuclear-encoded. Currently, two non-exclusive models are mainly discussed as to how hydrophobic nuclear-encoded proteins along with lipids and pigments, that are synthesized at the plastid envelope membranes, are transported through the aqueous stroma to reach their thylakoid membrane destination: (1) invaginations of the inner envelope membrane/direct contact sites with thylakoids and (2) vesicle transport (Lindquist and Aronsson, 2018; Mechela et al., 2019). Evidence exists that the invagination/direct contact site pathway is realized only in the proplastid-to-chloroplast transition whereas vesicle transport seems dominant in mature chloroplasts (Vothknecht and Westhoff, 2001; Andersson and D'ormann, 2008; Lindquist and Aronsson, 2018). For the latter, the role of typical vesicle forming proteins like COPI, COPII, SNARE, or VIPP1 for plastid biogenesis has still to be determined (Mechela et al., 2019). However, for cyanobacterial VIPP1 a structure-based molecular understanding was recently achieved (Gupta et al., 2021). In contrast to proplastids, mature chloroplasts propagate by binary fission (Osteryoung and Pyke, 2014; Yoshida, 2018). The plastid division machinery is made of four physically connected supramolecular ring structures, two outside (an outer polyglucan plastid-dividing ring and a dynamin-related ring) and two inside the chloroplast (an inner plastid-dividing ring and a tubulin-like FtsZ-ring beneath the inner envelope membrane). In a concerted mechanism, the rings generate the mechanical force for plastid constriction and eventually division. An example for the crucial role of regulatory proteins for plastid morphogenesis is visualized in Fig. 1. Open questions in the field are the composition of the inner plastid-dividing ring, how thylakoid membranes divide, and how chloroplast division is coordinated with cell and other organelle divisions (Osteryoung and Pyke, 2014; Yoshida, 2018). At the end of their life span, chloroplasts enter highly coordinated dismantling processes with the goal to minimize reactive oxygen production (ROS) and recycling of their abundant macromolecules to sink tissues of the plant (Avila-Ospina et al., 2014).,Strikingly chloroplasts hold ~80% of leaf nitrogen (Makino and Osmond, 1991). It seems that ROS-dependent retrograde signaling plays a key role for coordinating chloroplast degradation via multiple breakdown pathways including chlorophagy (Woodson, 2019; Dominguez and Cejudo, 2021). Current research focuses on elucidating how particular environmental conditions trigger specific dismantling pathways and deciphering the corresponding signal cascades.

Structural membrane dynamics as a means to control energy conversion

The fact that photosynthetic energy conversion has to integrate and balance significant fluctuations in both cell metabolism (including CO_2 availability) and energy input by sunlight in an oxidizing environment, calls for its strict regulation to minimize toxic ROS production. In the last decade, it turns out that a central regulatory element for tuning photosynthetic performance in plants is the dynamic adjustment of lateral and transversal geometric (grana) thylakoid dimensions that regulate electron transport, light-harvesting, and protein repair (Kirchhoff et al., 2011; Puthiyaveetil et al., 2014; Hepworth et al., 2021). It is an open question how reversible protein phosphorylation,

physicochemical membrane properties, and protein composition dynamics work together to control architectural thylakoid features and further on energy conversion.

Future perspectives: For the next five to ten years, the fast methodical and technological development in (cryo-)electron tomography is expected to provide detailed new insights into chloroplast structure-function relationships not only for the mature plastid but also for its biogenesis and dismantling. Furthermore, studying chloroplast diversity in non-model, more exotic species as well as in specialized plant tissues and organs (including transitions between different plastid types) gains increasing attention because it will uncover the metabolic plasticity and diversity of this organelle. Along these lines, current and future bioengineering tools for chloroplasts offer potential for improving crop plants by tuning for example non-photochemical quenching or photorespiratory pathways or for using the anabolic competence of the plastid to employ them as metabolic factory for valuable chemicals.

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Plant Membrane Contact Sites – Questions from the membrane interface.

Membrane Contact sites: Does one definition fit all?

Membrane Contact Sites (MCS) are evolutionarily conserved structures where the close proximity between two or more membrane-bound organelles enables direct exchange of molecules and facilitates coordinated inter-organelle adaptive responses (Figure 10 A-B). Recent advances in plant cell imaging and the development of novel genetic and molecular tools have fueled an emerging field of research devoted to the investigation of their structural organization, dynamics, and physiological functions. This interest is uncovering plant-specific MCS structures and molecular mechanisms, but also exposing some limitations on the commonly accepted definitions and physiological functions inferred from different model organisms. As in yeast and animal cells, the plant endoplasmic reticulum (ER) is an interconnected organelle that establishes MCS with multiple cellular structures including the plasma membrane (PM), mitochondria, endosomes, peroxisomes, Golgi and trans-Golgi network (Barton et al., 2013; Stefano et al., 2014; Wang et al., 2014; Perez-Sancho et al., 2015; Wang et al., 2019b; Brandizzi, 2021). Unique to plants; however, are the functional interactions at ER-plastids MCS for lipid synthesis and transport (Liu and Li, 2019), the control of intercellular communication through plasmodesmata MCS–regulated intercellular bridges (Tilsner et al., 2016), and the MCS activities driven by a super-continuum that encompasses the cell wall, PM, ER, and cytoskeleton (Wang et al., 2014; Perez-Sancho et al., 2015; Zang et al., 2021). These plant-specific features are placing MCS research in plants at the forefront of discovery, broadening the MCS definition beyond yeast and animal systems.

In plants, MCS can be defined as environmentally and developmentally regulated microdomains with an intermembrane gap as small as 3 nm in plasmodesmata, and an arbitrarily defined upper limit of 80-100 nm. Plant MCS are enriched with a variety of protein-protein, and/or protein-cytoskeleton tethering assemblies that establish dynamic interactions with membrane phospholipids and/or the cell wall. Plant MCS carry out essential cellular functions including, but not restricted to maintenance of membrane lipid homeostasis, cell-to-cell communication, organelle biogenesis, autophagy, endocytosis, receptor kinase signaling, and the regulation of Ca^{2+}-dependent stress responses (Figure 10 C-D), reviews in (Perez-Sancho et al., 2016; Wang and Hussey, 2017; Liu and Li, 2019; Petit et al., 2020; Rosado and Bayer, 2021).

Lipid transfer at MCS: Is that what plant tethers do?

Due to their hydrophobicity the transport of lipids between organelles relies on either vesicle-mediated delivery mechanisms or MCS-localized lipid transport proteins (LTP) (Scorrano et al., 2019). Most MCS-localized LTPs contain an internal hydrophobic cavity adapted to solubilize water-insoluble molecules (Wong and Levine (Wong and Levine, 2016), 2016), are anchored to the ER by either transmembrane domains or stable interactions with ER- anchored proteins (Scorrano et al., 2019), and interact with the opposing membrane mainly through domains that bind anionic lipids (Perez-Lara and Jahn, 2015). In animal cells or yeast, direct lipid transport using MCS-localized LTPs may be one of the most notorious and documented MCS functions and lipid species transferred using this mechanism include sterols, ceramides, phosphatidylserine (PS), phosphatidylinositol 4-phosphate (PI4P), and diacylglycerol (DAG) (Wu et al., 2018). In plants, the emerging view is that MCS-localized LTPs similarly participate in the delivery of lipids between the ER and organelles not linked by vesicular traffic, (e.g. mitochondria and plastids) but also in the bulk transport of lipids between organelles connected by the secretory pathway. In a recent landmark study Ruiz-Lopez et al. showed that stress signals regulate the activity of two members of the Synaptotagmin (SYT) family of LTPs at ER-PM MCS (SYT1 and SYT3), and demonstrated their function as LTPs transferring DAG between the PM and the ER *in vivo* (Ruiz-Lopez et al., 2021). The authors propose a geometrical model where SYT activities counteract the stress-induced build-up of conically shaped DAG at the PM and prevent the generation of areas of negative membrane curvature that could disrupt the stability of the PM during stress episodes.

MCS in motion: Who controls MCS plasticity and dynamics?

The molecular composition, geometry, and plasticity of inter-organelle junctions determine their ability to integrate and respond to cellular signals. Recent studies provide an emerging picture where MCS tethers do not act in isolation but interact with anionic lipids, cytoskeletal elements, and regulate the plasticity, function and dynamics of these cellular microdomains.

Anionic phospholipids represent only a few percent of the total lipids but they are critical biochemical and biophysical landmarks of membrane identity (Noack and Jaillais, 2020). Within the

endomembrane system, they consist of the phosphoinositides (PIPs), phosphatidic acid (PA) and phosphatidylserine (PS), and determine the electrostatic potential of each membrane being highest at the PM, intermediate in endosomes and low in the ER (Platre et al., 2018; Dubois and Jaillais, 2021). *In vitro* or *in silico* data for MCS tethers such as the synaptotagmins (SYTs), Multiple C2 domains and transmembrane region (MCTPs), and Vesicle-associated membrane protein (VAMP)-associated proteins (VAPs) families, support the notion that anionic lipids profoundly impact the structure and function of MCSs by enabling protein-lipid interactions that regulate the association of the ER with the PM, TGN and early endosomes (Perez-Sancho et al., 2015; Stefano et al., 2018; Brault et al., 2019; Ruiz-Lopez et al., 2021). Interestingly, these interactions appear to be mostly non-specific, the primary determinants being the negative charge carried by the anionic lipids and, in some cases, the presence of Ca^{2+} (Schapire et al., 2008). Accordingly, electrostatic interactions between phosphatidylinositol-4-phosphate (PI4P) and SYT1/SYT3 underpin the localization of SYT1/SYT3 to ER-PM MCS (Ruiz-Lopez et al., 2021), MCTP4 to plasmodesmata-MCS, (Brault et al., 2019), and the remodelling of SYT1 ER-PM MCS in response to rare-earth elements (Lee et al., 2020). Similarly, the accumulation of phosphatidylinositol 4,5-biphosphate ($PI(4,5)P_2$) at the at the PM enables interactions with SYT1 and correlates with the rearrangement and expansion of ER-PM MCS in response to ionic stress (Lee et al., 2019).

MCS plasticity is also controlled by components that crosslink the actin cytoskeleton at MCS and create trapping mechanisms that influence MCS architecture and expansion. In plants, this cross-linking seems to be carried out by a plant-specific complex that includes the actin associated NET3C protein, and the microtubule associated Kinesin light chain related (KLCRs) and IQ67-Domain (IQD) proteins (Zang et al., 2021) (Figure 10E). Remarkably, in plants, the presence of cell walls underlies the formation of a plant-specific supramolecular assembly known as the MCS super-continuum. This super-continuum encompasses the cell wall, PM, ER, and cytoskeleton, and renders MCS with distinct kinetics, shapes, geometries, and functions (Rosado and Bayer, 2021; Zang et al., 2021). Recent studies propose that the MCS super-continuum serves as a nexus that limits the mobility of MCS tethering assemblies (Wang et al., 2016; Lee et al., 2019; Zang et al., 2021), and control their activities. Examples of regulation mediated by this continuum may include the activity of receptor like kinases in pollen and/or stomatal cells (Ho et al., 2016; Duckney et al., 2021), and the regulation of phospholipase C mediated stress signals at the PM (Ruiz-Lopez et al., 2021). Last, a unique type of regulation occurs at plasmodesmata MCS where the transfer of molecules is parallel to the membranes, as opposed to orthogonal to them. In those ER-PM MCS the intermembrane space may not be solely regulated by the tethers, lipids, and cytoskeleton elements in the super-continuum, but also by wall polymers (e.g. callose), which are locally synthesized around the PD structure (Petit et al., 2020).

Future MCS research: What's in the plant toolkit?

MCS are microdomains with an intermembrane distance below the resolution limit of conventional fluorescence microscopy, and with a dynamic behavior that requires the use of live-cell compatible techniques (McFarlane et al., 2017). In recent years, advances in super-resolution microscopy (e.g. Total Internal Reflection Fluorescence (TIRF), and Structure illumination microscopy (SIM), (Figure 10F), and electron tomography (Figure 10G) are providing for the first time detailed high-resolution visualizations and 3D reconstructions of the MCS ultrastructure in plants (Baillie et al., 2020). In parallel, the use of optical laser tweezers to manipulate plant MCS *in vivo* is facilitating the characterization of putative MCS components such as the AtCASP tether identified at ER-Golgi MCSs (Osterrieder et al., 2017) and the mitochondria-associated GTPase, Miro2 at ER-mitochondria contact sites (White et al., 2020). Plant MCS research is also adopting genetically encoded tools such as synthetic tethers that bridge apposed membranes (e.g. MAPPER-GFP, (Lee et al., 2019), or split-fluorescence systems (e.g. split super-folder (sp) GFP proteins, (Li et al., 2020) to visualize MCS contacts. These artificial systems, however, have limited application in functional studies as their expression could induce non-physiological changes in the MCS structure. Additional molecular tools with broad application such as inducible phosphoinositide depletion systems (Doumane et al., 2021), and phosphoinositide fluorescent markers (Simon et al., 2014) are being currently adopted for MCS research and represent promising avenues to elucidate the roles of anionic phospholipids in plant MCS function and dynamics.

We forecast that the combination of collaborative research, technical advances, and novel molecular tools in this quickly evolving field will provide breakthroughs that will transcend plant MCS research. In this context, we apologize to those whose important contributions to plant MCS research were not included in this brief review.

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Diversity in plasmodesmata form and function

General PD structure

Plasmodesmata (PD) evolved multiple times in the plant lineage and are present in some groups of algae and in all land plants (Brunkard et al., 2015; Azim and Burch-Smith, 2020), 2020). Generally, PD provide continuity of the plasma membranes (PMs) and cytoplasm across cell walls. In land plants and some algae, PD also include a central strand of endoplasmic reticulum (ER) (Botha, 1992),(Ding et al., 1992; Franceschi et al., 1994; Cook et al., 1997). The cytoplasmic and membrane connectivity provided by the PD is the route for intercellular trafficking of numerous biomolecules, effectively rendering the plant a symplast. PD are therefore essential for plant growth, development and environmental responses. Some molecules traffic through PD by passive diffusion, and movement depends on the size of the molecules and the trafficking capacity of the pores. Others are targeted to PD using the endomembrane system (Spiegelman et al., 2019). A typical cell wall is pervaded by hundreds or thousands of PD that are often clustered into groups (pitfields), and as such the continuity between adjacent cells can be extensive.

PD are nanopores with outer diameters, delimited by the PMs of connected cells, ranging from 25 to 50 nm depending on the tissue and species, and they extend for the length of cell wall thickness. Thus, much of what is known about PD structure is derived from TEM (Figure 11). The center of PD of land plants is occupied by a central structure called the desmotubule (DT). The DT was observed to be continuous with the cortical ER of connected cells and the DT is now recognized as an intercellular strand of modified ER. The DT diameter is constrained to approximately 15-20 nm (Ding et al., 1992; Schulz, 1995), and so the desmotubule comprises the most tightly curved biological membranes described to date (Tilsner et al., 2011). The DT does not include a typical ER lumen and instead the space is largely occupied by proteins (Tilney et al., 1991), whose likely function is to enable the tight curvature of the membranes, e.g. the ER tubulating reticulon proteins (Tilsner et al., 2011; Knox et al., 2015; Kriechbaumer et al., 2015). The DT is tightly connected to the PD PM by structures originally described as spokes (Ding et al., 1992). The cytosol-filled space between the DT and PM is called the cytoplasmic sleeve or annulus and it is likely the main route for PD trafficking although the spoke proteins divide it into nanochannels 2-3 nm wide.

Analysis of PD isolated from Arabidopsis suspension cell culture identified 1,341 proteins as the putative PD proteome (Fernandez-Calvino et al., 2011). Of those, 21% were membrane proteins and included proteins previously identified as PD resident, e.g. PDLP1 (Thomas et al., 2008) and ATBG_papp (Levy et al., 2007). In addition, several GPI-anchored proteins and proteins associated with the secretory pathway were identified. Further refinement of the PD proteome identified multiple C2 domains and transmembrane region proteins (MCTPs) as PD constituents and they have been designated as the likely spokes of PD (Brault et al., 2019). The spokes control spacing between the DT and PM and this distance is correlated with PD developmental states (Nicolas et al., 2017a). Interestingly, in Arabidopsis roots, PD lacking cytoplasmic sleeves apparently had a higher trafficking capacity than did PD with cytoplasmic sleeves (Nicolas et al., 2017a), raising questions about how trafficking via those PD is achieved. There are a few reports of trafficking through the DT lumen, although the DT membranes appear to provide a surface for cell-to-cell movement (Guenoune-Gelbart et al., 2008; Barton et al., 2011). The DT membranes are important conduits for transport of at least some viruses between cells (Guenoune-Gelbart et al., 2008).

The lipid composition of PD PMs is also distinct from the bulk PM. The PM of PD from Arabidopsis suspension cells is enriched in sterols and sphingolipids with saturated very long chain fatty acids (Grison et al., 2015), consistent with the presence of lipid microdomains akin to lipid rafts in PD (Raffaele et al., 2009; Tilsner et al., 2013) and GPI-anchored proteins in the PD proteome (Fernandez-Calvino et al., 2011). Further biochemical treatments revealed that PD protein composition was dependent on PM lipid composition (Grison et al., 2015). PD lipid composition is also important for PD function, as changes in lipids affect the ultrastructure and permeability of PD (Yan et al., 2019; Iswanto et al., 2020; Liu et al., 2020). A modern view of PD combines its unique lipid and protein composition to describe PD as specialized membrane contact sites (Brault et al., 2019; Petit et al., 2019; Ishikawa et al., 2020).

PD formation and distribution

PD are intrinsic components of the cell walls. Primary PD form at the end of cell division, during cytokinesis, when strands of ER become encased in the developing cell plate. The reticulon proteins, RTNLB3 and 6, and MCTPs are involved in this process (Knox et al., 2015; Brault et al., 2019). The presence of substructures like the DT in newly formed PD is uncertain, as revealed by TEM (Ehlers and van Bel, 2010). Secondary PD form across existing cell walls where cell division is not occurring.

The insertion of these new PD is likely necessary to establish or maintain symplastic connectivity as in graft unions or when cells divide and grow (Ehlers and Kollmann, 2001). Studies in Arabidopsis trichomes suggest that new secondary PD form in close proximity to existing PD, as described in the multiple twinning model (Faulkner et al., 2008). It is proposed that PD divide by fission, although a mechanism for this is unclear.

PD may also be removed from existing cell walls by a still unknown process. Studies on cambial division and vascular differentiation have shown that PD numbers can increase and decrease over the lifespan of a given cell-cell interface, and this would necessarily involve the removal and insertion of PD at a given interface (Ehlers and van Bel, 2010; Fuchs et al., 2010). In other instances, PD can be drastically modified or even truncated to disrupt intercellular trafficking. For example, guard cell initials contain PD, and PD trafficking is critical for guard cell development (Guseman et al., 2010). As stomata develop, however, PD are lost from the guard-cells, rendering them symplastically isolated (Wille and Lucas, 1984). It may be that PD removal is a more common occurrence in plant cell development and differentiation than previously reported. This aspect of PD biology awaits further exploration using advanced imaging approaches.

Structure-function relationships in PD

PD are often depicted as simple linear structures traversing the cell wall but PD structure is much more diversified. PD are often branched, consisting of multiple pores that connect in the vicinity of the cell wall middle lamella (Figure 11). The formation and origins of branched PD are unclear, but they likely arise through modification of existing simple PD (Burch-Smith et al., 2011). This diversity in structure suggests diversity in function. Exemplary studies of PD in tobacco leaves undergoing the sink-source transition demonstrated that simple PD were converted to branched PD contemporaneously with decreased import of fluorescent dye (Oparka et al., 1999; Roberts et al., 2001). Another common variation of PD form is the dilation of PD pores away from the PD openings or the constriction of PD at their necks (region just below opening). This PD variation seems to correlate with PD maturation (Nicolas et al., 2017b) or with trafficking capacity (Ding et al., 1992). Mathematical modeling supports that dilation increases trafficking capacity as the cell wall thickens (Deinum et al., 2019), a correlation previously observed by TEM (Nicolas et al., 2017b). Another PD form that has a specialized role in trafficking is the 'funnel PD' in sink root tissue (Ross-Elliott et al., 2017). These PD have wide openings at the phloem sieve elements that narrows considerably as they cross the cell wall and open on the phloem-pole pericycle creating a 'funnel' shape. The specialized PD shape appears to facilitate the unloading of sucrose in the root phloem and mathematical modelling supports the need for this unusual PD form to allow phloem unloading at physiological sucrose concentrations. Specialized PD forms have also been reported at sites where sugars are loaded into the phloem in source tissues. For example, PD at the phloem parenchyma-companion cell interface in Arabidopsis leaf veins have many openings to the phloem parenchyma but only one to the companion cells (Haritatos et al., 2000). These distinct PD forms correlate with specialized functions, and raise the possibility of PD sub-functionalization between tissues and even at a given cell-interface. Despite the importance of PD to plants, many aspects of their formation, structure and function remain unknown. Undoubtedly, comprehensive understanding of PD will enable novel approaches to engineering solutions for challenges in plant growth and development.

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So much more than bricks and mortar: plant cell walls as dynamic extracellular "organelles"

Much as the skin is the largest organ in the human body, the plant cell wall can be thought of as the largest organelle in the plant cell, even though the wall is not bound by a membrane but instead encases the plasma membrane-delimited protoplast that contains the canonical organelles. Our understanding of cell wall composition, structure, and mechanics has expanded rapidly over the past decade due to advances in high-resolution imaging (Zeng et al., 2017; Rydahl et al., 2018; Voiniciuc et al., 2018; Zhao et al., 2019), biochemical and spectroscopic analyses of wall polymers and their interactions down to single-molecule and nanoscale levels (Voxeur et al., 2019; Zhao et al., 2020; Cai et al., 2021), and new computational modeling methods that relate wall mechanics to the deformations, movements, and interactions of individual wall polymers (Zhang et al., 2021). In contrast to its previous conception as simply "dead wood" that is the fossilized product of polysaccharide secretion by plant cells, the plant cell wall is now starting to be appreciated as a dynamic structure that changes over time and encompasses specialized metabolic processes, including wall polymer polymerization, coalescence, binding/unbinding, cleavage, and re-ligation that facilitate both plant growth and the processing of plant biomass for human use (Obro et al., 2011). The intercellular transport of nutrients, secreted peptides, hormones, and other metabolites across the wall (Ramakrishna and Barberon, 2019), the discovery of extracellular vesicles that can deliver small RNAs to silence virulence genes in plant pathogens (Cai et al., 2018) and the ability of plants to sense pathogen-generated wall fragments (Vaahtera et al., 2019) and other aspects of wall integrity (Rui and Dinneny, 2020) together highlight how the apoplast, the extracellular compartment in which the cell wall exists, might also allow for previously unappreciated forms of trafficking and act as a molecular frontier in the interactions between plants and their abiotic and biotic environments.

Cell wall assembly and structure

Consider the plant cell wall as a futuristic building that can grow (and sometimes shrink) and protects and shapes its occupant, in this case the protoplast, and also helps sense and transduce important environmental and mechanical information. Cellulose, the most abundant biopolymer on Earth, forms the "girders" of the cell wall as its primary load-bearing component, and coincidentally has a tensile strength similar to that of steel. Cellulose is extruded directly into the apoplast by multi-subunit Cellulose Synthase Complexes (Wilson et al., 2021), which move through the plasma membrane along trajectories that are likely driven by the force of polymerization and are guided by either cortical microtubules or existing wall patterning (Chan and Coen, 2020). The estimated 18 catalytic subunits in each Cellulose Synthase Complex (Nixon et al., 2016) produce strands of β-1,4-linked glucose that coalesce into cable-like microfibrils that are predicted to have 18-24 chains (Yang and Kubicki, 2020). Forming the "cross-beams" and "insulation" between the cellulose "girders" are matrix polysaccharides that include pectins and hemicelluloses. Pectins are acidic polysaccharides that are composed of homogalacturonan, rhamnogalacturonan-I, and rhamnogalacturonan-II domains (Anderson, 2019), whereas hemicelluloses contain mostly neutral sugars and include xyloglucans, xylans, and mannans (Scheller and Ulvskov, 2010). In growing cells, matrix polysaccharides initially interact with cellulose upon their secretion at the cell surface, following polymerization in the Golgi lumen and post-Golgi trafficking (Hoffmann et al., 2021) (Figure 12). Both pectins and hemicelluloses can associate with the surfaces of cellulose microfibrils, potentially preventing cellulose agglomeration and thus assembling a strong but deformable wall that also contains glycoproteins, enzymes, metabolites, ions, and water (Cosgrove, 2018). In the secondary walls produced by certain cell types, a polyphenolic, hydrophobic compound called lignin is also deposited (Dixon and Barros, 2019). In many cell types, the wall is deposited in layers with differing cellulose orientations, conferring multidirectional resistance to mechanical failure.

Dynamics and functions of plant cell walls

What happens to the strong but flexible wall as a plant cell grows? Atomic force microscopy (Zhang et al., 2017) and coarse-grained modeling (Zhang et al., 2021) indicate that cellulose microfibrils bend, bundle, unbundle, and slide during experimentally imposed or computationally simulated wall deformation, respectively; one remaining question is exactly how these processes occur in the growing cells of living plants, where wall deposition is typically ongoing, matrix polysaccharides also undergo reorganization (Anderson et al., 2012), and wall-modifying enzymes can modulate cell growth (Xiao et al., 2014). Also unclear is the extent to which extracellular ATP and other energetic compounds might be used in wall metabolism, in addition to their functions as signaling molecules (Pietrowska-Borek et al., 2020). Cell walls are highly diverse across plant tissues and taxa (Hoffmann

et al., 2021) and allow cells to adopt myriad shapes and perform specialized functions that include nutrient and water absorption (e.g., root epidermal cells), transport (e.g., xylem and phloem), and secretion (e.g., aerial epidermal and nectary cells). Autodegradation of the plant cell wall allows for developmental processes that include organ abscission and pollen dehiscence, and might allow for recycling of some wall components to produce new wall polymers (Barnes and Anderson, 2018). Overall, the plant cell wall is a fascinating biological environment, one for which we are only beginning to be able to understand well enough to be able to engineer ourselves.

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Figures

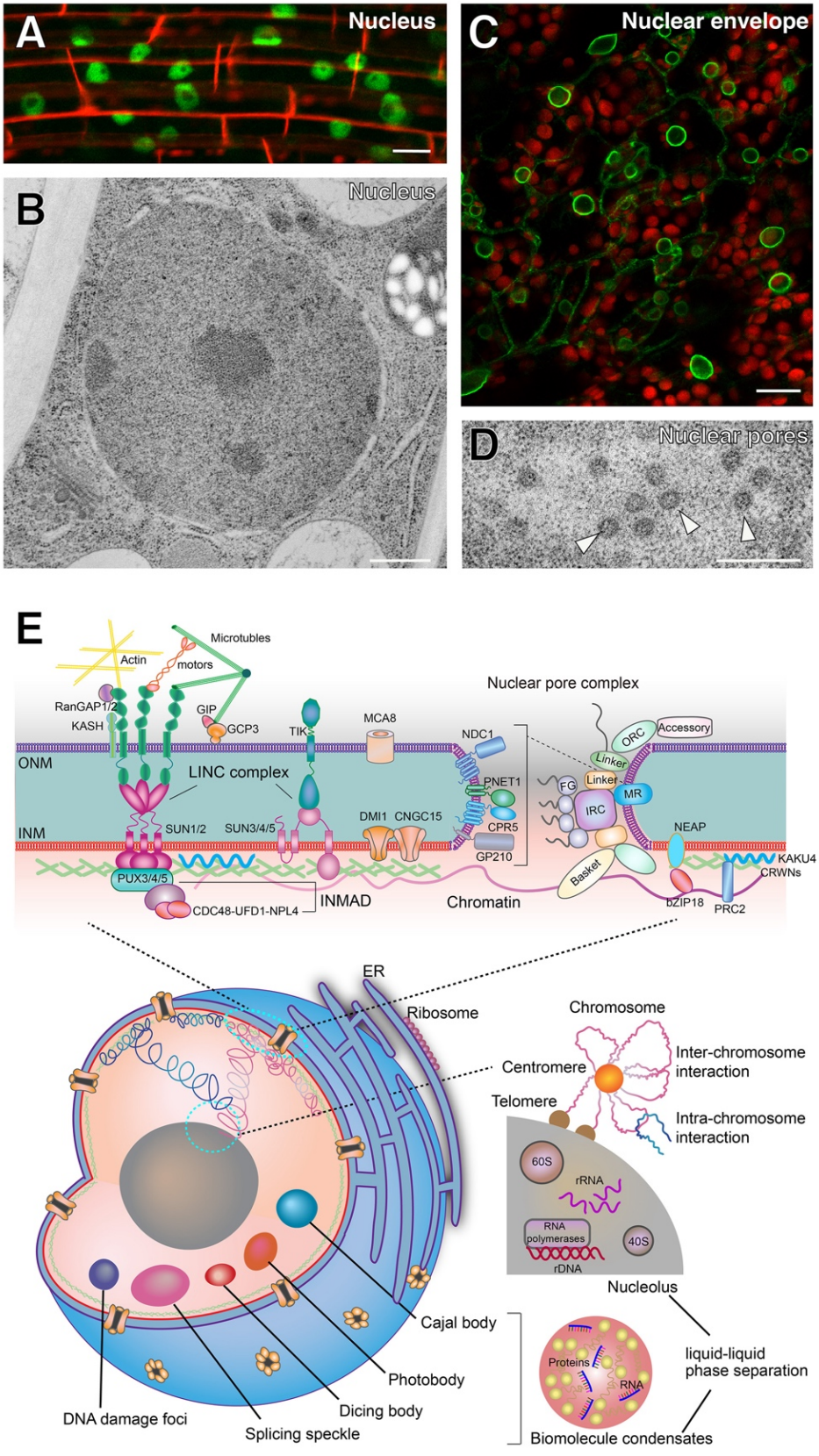
A
Nucleus
B
Nucleus
C
Nuclear envelope
D
Nuclear pores
E
Microtubules
Actin
motors
RanGAP1/2
KASH
GIP
GCP3
TIK
MCA8
Nuclear pore complex
NDC1
ONM
LINC complex
PNET1
ORC
Accessory
Linker
FG
Linker
MR
IRC
INM
SUN1/2
SUN3/4/5
DMI1
CNGC15
CPR5
GP210
NEAP
KAKU4
CRWNs
PUX3/4/5
CDC48-UFD1-NPL4
INMAD
Chromatin
Basket
bZIP18
PRC2
ER
Ribosome
Chromosome
Centromere
Inter-chromosome interaction
Telomere
Intra-chromosome interaction
60S
rRNA
RNA polymerases
40S
rDNA
Nucleolus
Cajal body
Photobody
Dicing body
Splicing speckle
DNA damage foci
Proteins
RNA
liquid-liquid phase separation
Biomolecule condensates

Figure 1. The nucleus and its constituents (A-B) Fluorescence **(A)** and electron **(B)** micrographs of nuclei in Arabidopsis root cells. Nuclei and the plasma membrane were labeled in (A) with NPR1-GFP and FM4-64, respectively. **(C)** Nuclear envelope of Arabidopsis leaf epidermal cells expressing GFP tagged KAHS protein WIP1. Chlorophyll autofluorescence was overlaid. **(D)** Nuclear pore complexes in an Arabidopsis root cell. The electron micrograph shows a tangential section through the nuclear envelope. Scale bars in B and D: 500 nm. **(E)** The nucleus is defined by the double-layered nuclear envelope composed of the ONM and the INM, which join at the nuclear pore membrane. The NE hosts a specific population of proteins. SUN and KASH proteins comprise the LINC complex and function in various aspects of plant cell biology and physiology. CPR5, PNET1, GP210, and NDC1 are structural components of the plant NPC membrane ring (MR). CNGC15, DMI1, and MCA8 regulate nuclear calcium transport and signaling and affect symbiotic interaction with arbuscular mycorrhiza. GCP3 and GIP proteins are part of the microtubule nucleation complex and regulate nuclear stiffness. CRWN and KAKU4 proteins assemble the plant nuclear skeleton and also function as a platform to interact with INM proteins and regulate chromatin organization through binding chromatin-associating proteins (such as the PRC2 complex). NEAP proteins bind transcription factor bZIP18 and may also influence chromatin organization. The CDC48-UFD1-NPL4 trimeric complex and PUX3/4/5 proteins mediate plant INM-associated protein degradation (INMAD). The nuclear interior is organized heterogeneously. Typically, heterochromatic regions and chromocenters are associated with near the nuclear periphery and the nucleolus. Other multivalent biomolecules (e.g., proteins and RNAs) aggregate to form various types of membrane-less condensates through the liquid-liquid phase separation mechanism.

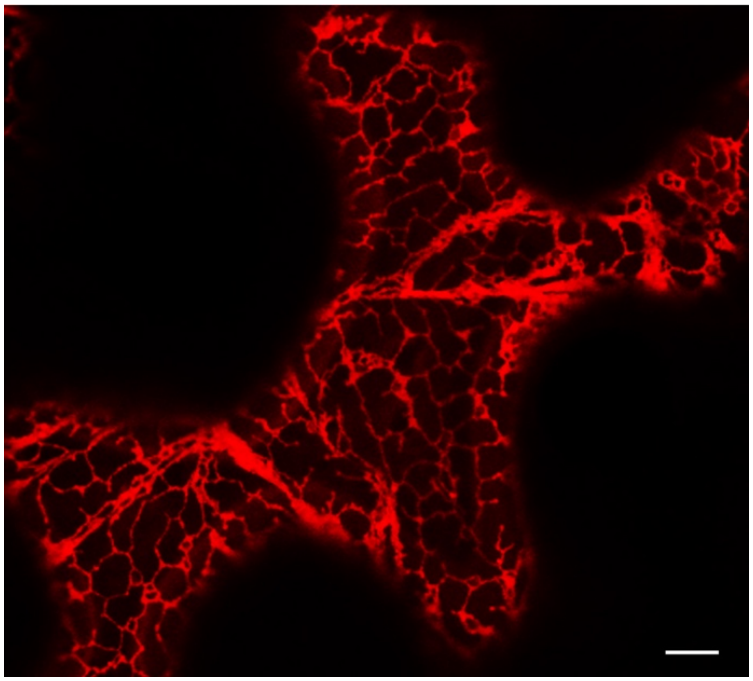

Figure 2. The plant ER forms a distinctive network of membranes at the cell cortex. Confocal microscopy image of a tobacco leaf epidermal cell transiently expressing the fluorescent lumenal marker, ER-mCherry (Nelson et al., 2007), which labels the lumen of the bulk ER network. Scale bar = 40 μm.

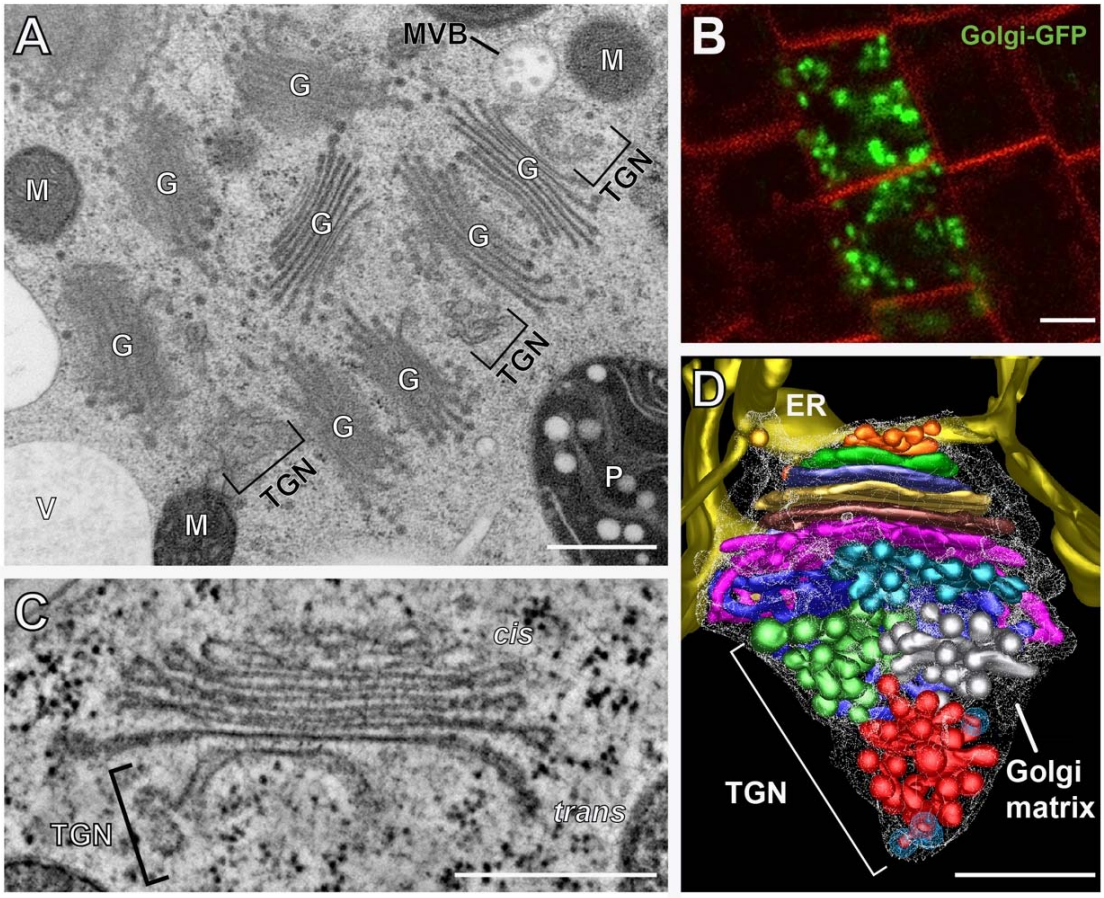

Figure 3. Structure and distribution of Golgi stacks in plant cells. (A) TEM micrograph showing a cluster of Golgi stacks in an Arabidopsis root tip cell. Golgi stack (G), trans-Golgi network (TGN), plastids (P), mitochondrion (M), multivesicular body (MVB), and vacuoles (V) are marked. (**B)** Confocal laser scanning micrograph of Arabidopsis root tip cells expressing a Golgi-localized green fluorescent protein. The cell wall is counterstained. (**C)** ET slice image of a Golgi stack. *Cis*-side, *trans*-side and TGN cisterna are marked. (**D)** ET model of an Arabidopsis Golgi stack associated with the endoplasmic reticulum (ER). The entire Golgi and TGN are encompassed by a ribosome-ribosome excluding matrix (Golgi matrix). Scale bars in A, C, and D: 500 nm. Scale bar in B: 10 μm.

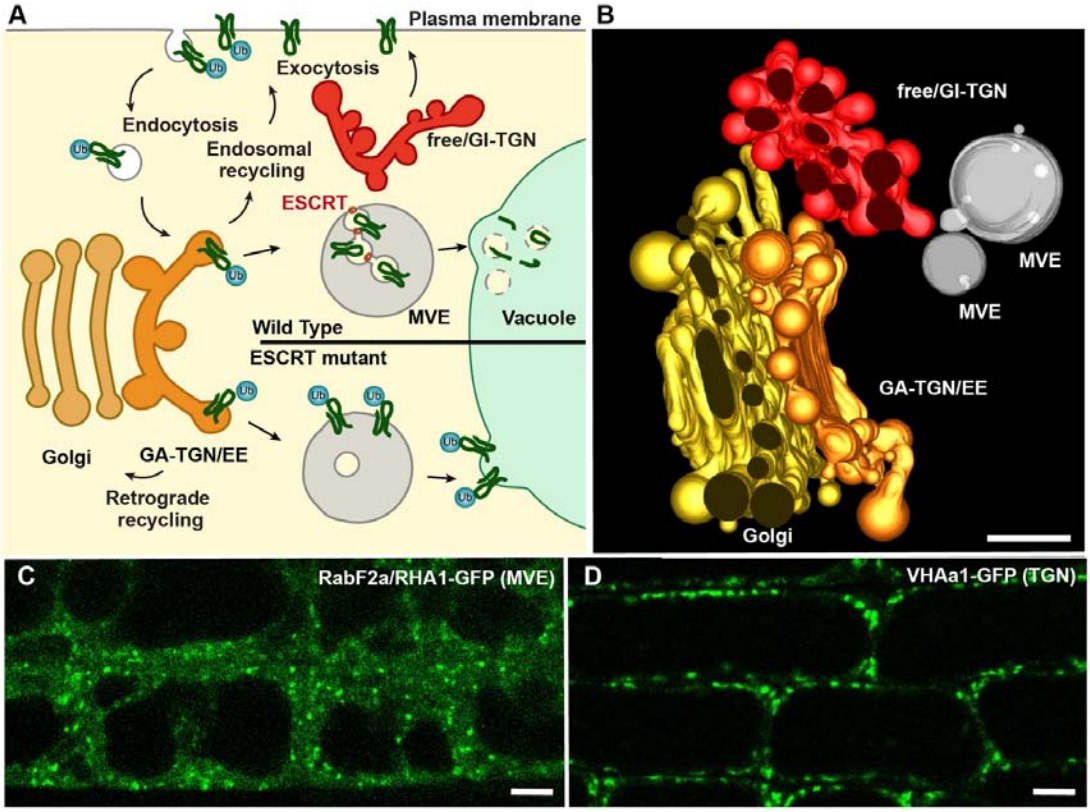

Figure 4. Plant endosomes. (A) Diagram of plant endosomes and main associated pathways, highlighting the effects on MVE mis-sorting in ESCRT mutants. **(B)** Tomographic reconstructions of a Golgi, Golgi-associated TGN (GA-TGN), and free/Golgi independent (GI-TGN) in an *Arabidopsis* embryo cells. **(C-D)** Confocal images of the MVE-localized RabF2a/RHA1-GFP (C) and the TGN-localized VHAa1-GFP in Arabidopsis root cells. Scale bar = 200 nm in (B) and 5 mm in (C) and (D).

Figure 5. The plant vacuole (A)

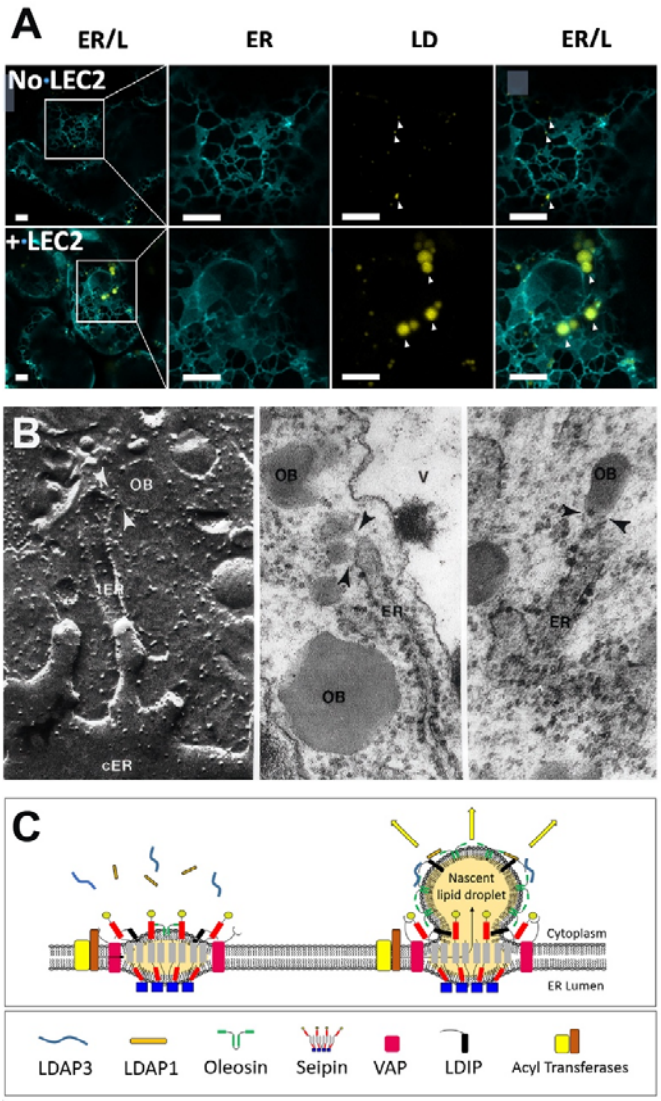

Figure 6. Spatial association of LD with ER and a model of LD biogenesis (A) Enhanced-resolution fluorescence imaging of the relationship of ER to LDs in leaf mesophyll cells of *N. benthamiana* infiltrated with ER marker and stained with LD-specific fluorescent dye BODIPY 493/503. The ER network was visualized as cyan color with the ER-lumen marker protein Kar2-CFP-HDEL and LDs are false-colored as yellow (white arrows). Normally in leaves, small LDs are observed associated with the ER (top row). In this system, LDs were induced to proliferate by expression of lipogenic factors to study LD proteins and their roles in LD formation (second row). Here this process is illustrated by expression in these leaves of the seed transcription factor LEAFY COTYLEDON 2 (LEC2) that promotes storage lipid synthesis and LD formation. Under semi-normal conditions the LD phenotype of tobacco shows few small LD's intimately connected to the ER. The CFP fluorophore was excited with a 405-nm laser with emission spectrum collected between 450 to 500 nm. LDs were visualized by excitation with a 488-nm laser, with emission spectra collected between 500 to 540 nm. Scale bars: 5µm.
(B) TEM micrographs showing LDs emerging from the ER. Left to right- freeze-fracture; cryofixation; chemical fixation. Arrows mark ER-LD junctions. For scale, ribosomes on the ER membrane are approximately 20 nm in diameter. Electron micrographs are courtesy of Dr. Eliot Herman, University of Arizona. **(C)** Diagram illustrating the current, general model for LD biogenesis. Initial LD formation begins with the coalescence of the "lipid lens" within the ER bilayer. Recruitment of various LD associated proteins such as SEIPINs, LDIP, LDAPs, VAP27-1, oleosins (in seeds) and LDIP, which together facilitate the formation and stabilization of nascent LD as it emerges into the cytoplasm. Adapted in part from model presented in Greer et al. (2020).

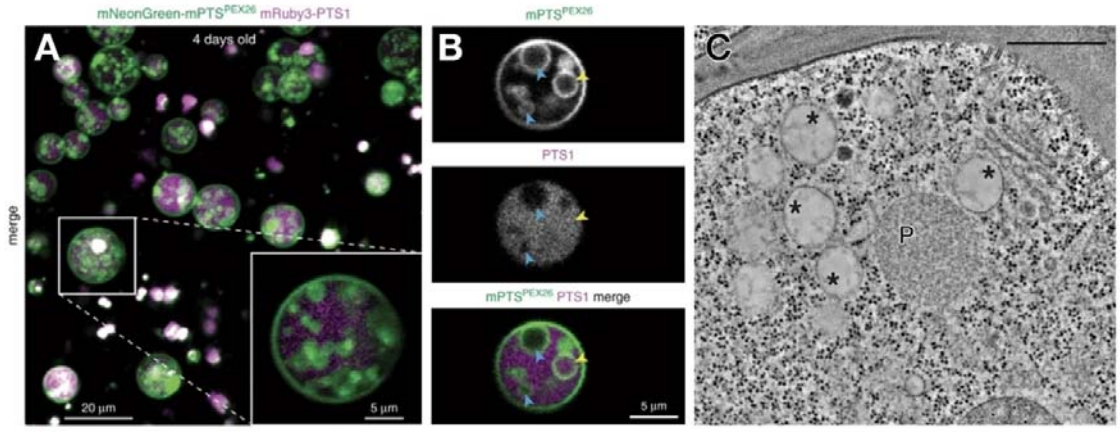

Figure 7. Microscopic images of peroxisomal structures in Arabidopsis cells. (A) Microscopic image of 4-day-old Arabidopsis cotyledons expressing mNeonGreen with a membrane peroxisomal targeting signal (mNeonGree-mPTSPEX26; green) and mRuby with a matrix-bound peroxisomal targeting signal (mRuby3-PTS1; magenta) show the presence of ILVs in peroxisomes. The close-up image highlights the variable sizes of the vesicles. (B) Separate images of the membrane (green) and matrix (magenta) fluorescent molecules highlights the different substructures within the peroxisome, including ILVs with (yellow) or without (blue) matrix proteins and a separate area with denser membrane accumulation. Images in parts A and B are from Wright and Bartel (2020). (C) ET slice image of a young root cell detailing a peroxisome (P), lipid bodies (*), and other organelles in its proximity. Scale bar: 500 nm.

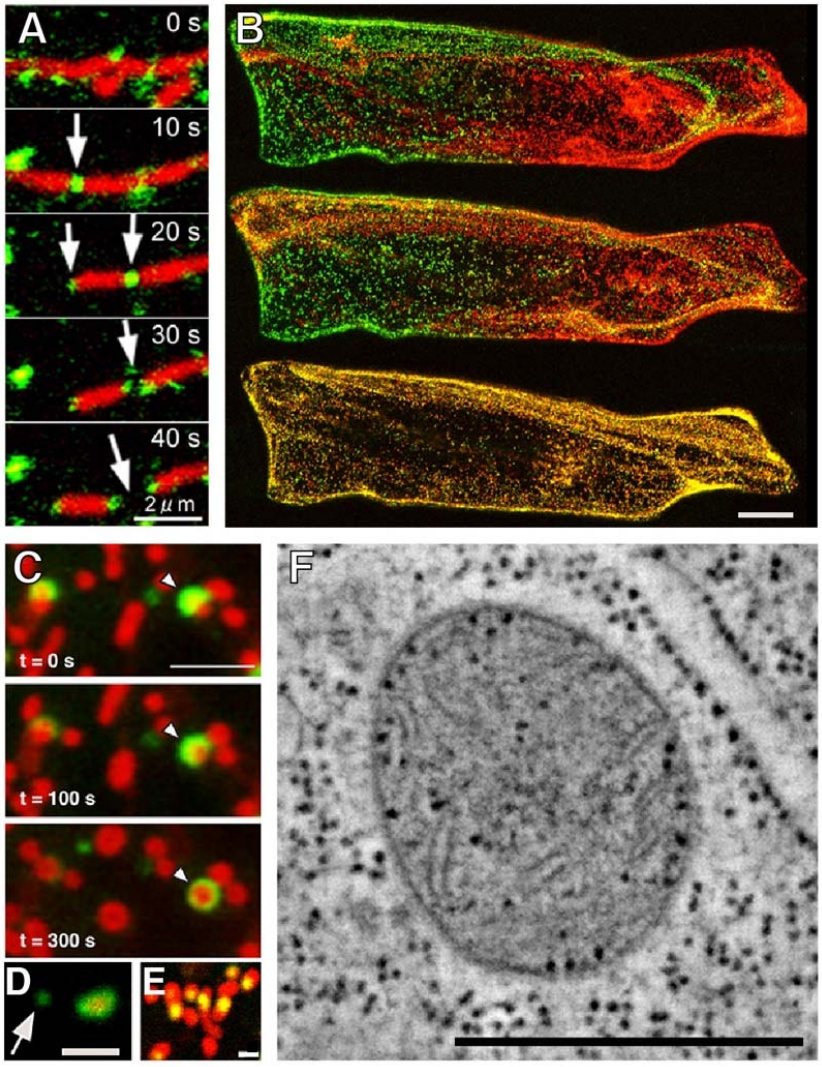

Figure 8. Microscopy imaging of plant mitochondria dynamics. (A) Five consecutive frames showing mitochondria fission in a tobacco BY-2 cell. The mitochondria are stained red and dynamin-related protein 3A is labeled with GFP (Arimura 2018). **(B)** Fusion of mitochondria in an onion bulb epidermal cell. The cell contains thousands of mitochondria. The mitochondria on the left and right sides of the cell were labeled green and red, respectively. The photos show the movement and mixing of the mitochondria after of 10 minutes (upper), one hour (middle), and two hours (bottom). Yellow mitochondria are the result of fusion between green and red mitochondria. **(C)** Progression of mitophagy in an Arabidopsis cell, in which the mitochondria were stained with MitoTracker Red and autophagosomes were visualized by expression of YFP-ATG8e. The autophagosome on the right (arrowhead) is shown engulfing a mitochondrion over a 300 s interval (Ma et al., 2021). **(D)** An apparent mitochondrial outer-membrane derived vesicle (MDV) (arrow) in an Arabidopsis cell. At right is a mitochondrion whose outer-membrane was stained with ELM1-GFP and whose matrix was stained with RFP. The MDV has only the outer membranes and no matrix (Yamashita et al., 2016). E. Heterogeneity of DNA contents in mitochondria. Mitochondria are stained red by MitoTracker Red and DNA stained by SYBR Green I. Green signals in red are shown in yellow. So red particles with yellow dots mean mitochondria having DNA, and red mitochondria without yellow mean having no DNA (Arimura et al., 2004). F. ET image of a mitochondrion in an Arabidopsis root meristematic cell. Scale bars. A, C, and D, 2μm; B, 40μm; E, 1μm; F, 500nm

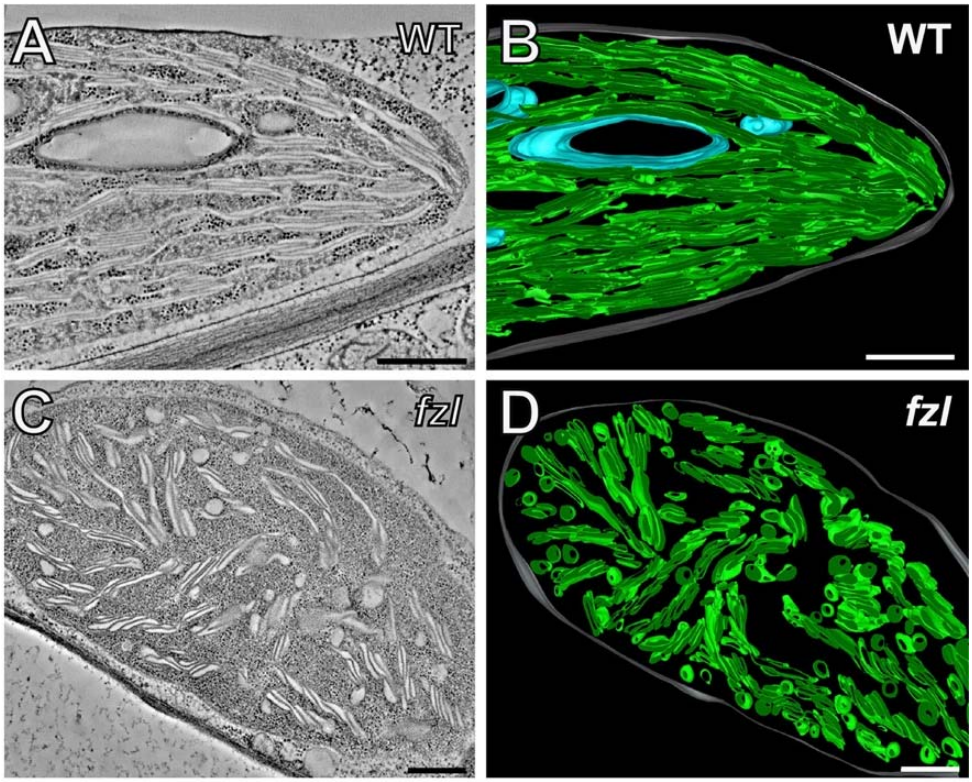

Figure 9. Chloroplast morphogenesis is a highly regulated process. (A) ET slice image of a normal-sized wild-type (WT) chloroplast with typical thylakoid differentiation into stacked (grana) and unstacked domains. **(B)** 3D model based on the chloroplast in A. **(C)** ET slice image of an oversized chloroplast (compare scale bars) with aberrant thylakoid membrane organization in a *flz* mutant (Liang et al., 2018b). FLZ is a dynamin-like protein in which thylakoid fusion is inhibited (Gao et al., 2006; Findinier et al., 2019). Instead of a stroma-wide network, thylakoids form discrete spirals in the mutant. (**D)** 3D model based on the chloroplast in C. Scale bars: 500 nm.

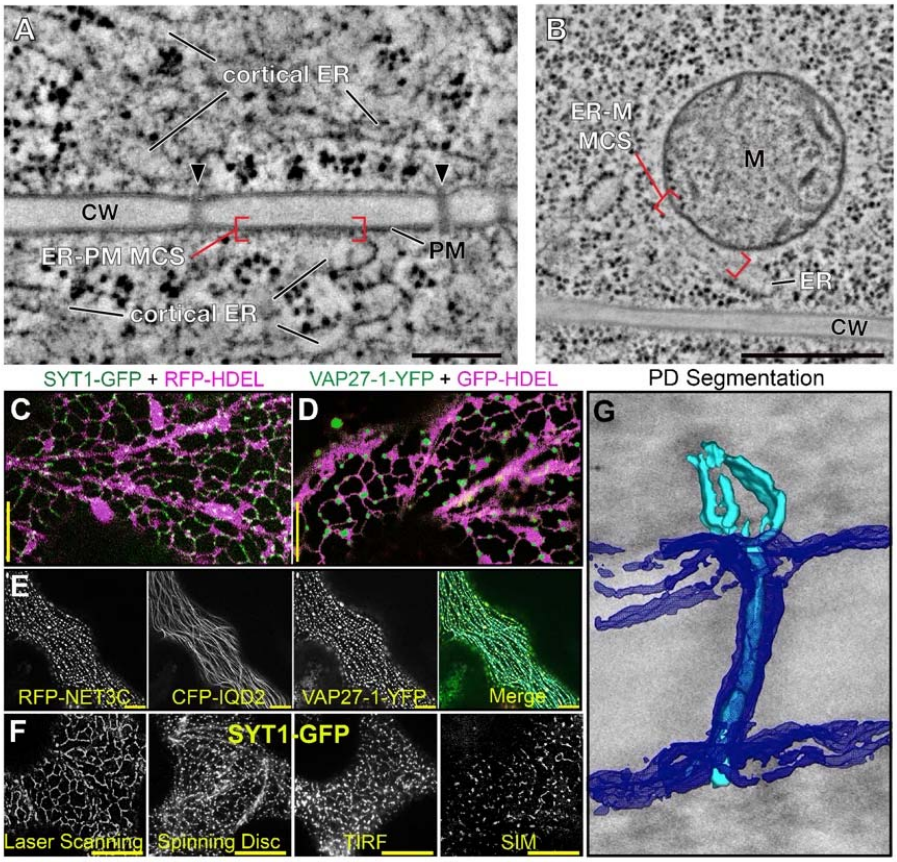

Figure 10. Examples of Membrane Contact Sites in Plants. **(A-B)** ET slice images showing different MCS present in plant cells. an ER-PM contact site (A) and an ER-mitochondrion contact site (B) are shown. Arrowheads mark plasmodesmata. CW: cell wall, M: mitochondrion. Scale bars: 500 nm. **(C-D)** Co-localization of SYT1-GFP and VAP27-1-YFP with ER markers (RFP-HDEL or GFP-HDEL) highlights the presence of spatially separated and functionally distinct ER-PM MCS within the cortical ER. **(E)** Co-expression of NET3C, IQD2 and VAP27-1 highlights the interaction of plant ER-PM MCS with the cortical cytoskeleton. **(F)** The intermembrane distances at MCS are below the light diffraction limit which limits the information provided by conventional confocal microscopes (Laser Scanning / Spinning Disc), and requires the use of super-resolution techniques (TIRF /SIM). **(G)** Advances in electron tomography techniques are enabling accurate 3D reconstructions of PD MCS. In current functional models, the cytosolic space between the ER and the PM inside PD serves as a trafficking conduit for mobile molecules and the adjustment of its width is believed to regulate their flow rate, effectively controlling inter-cellular trafficking.

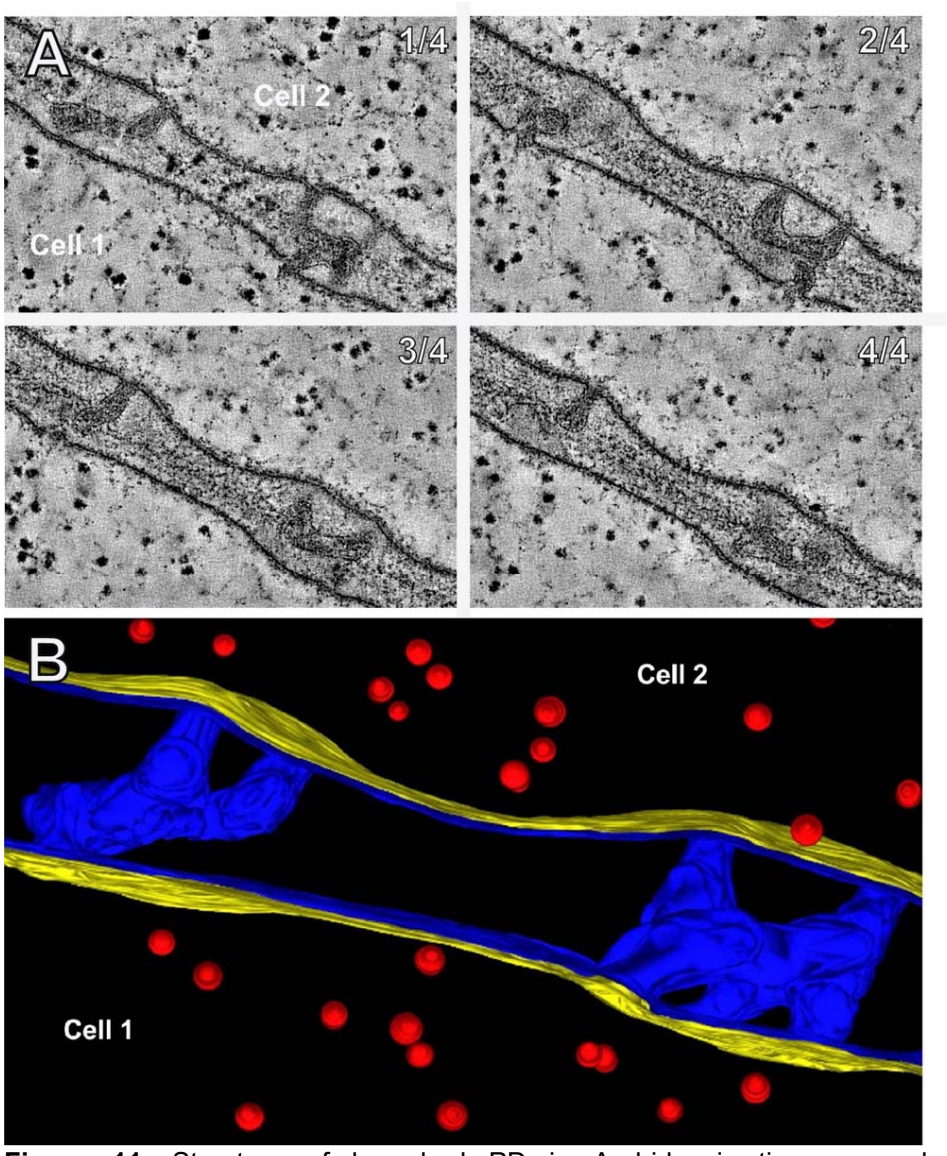

Figure 11. Structure of branched PD in Arabidopsis tissue revealed by ET. (**A)** Representative four individual frames from a tomogram (1/4 - 4/4). While the PM is readily visible in these images the desmotubule is difficult to discern. Central cavities are found in the vicinity of the middle lamella. **(B)** 3D models of PD generated by tracing the inner (yellow) and outer (blue) leaflets of the PM in the tomogram in A. The PD on the left consists of two pores in Cell 2 and one in Cell 1. The PD on the left has two openings to Cell 2 but three to Cell 1. Ribosomes (red) are shown for scale.

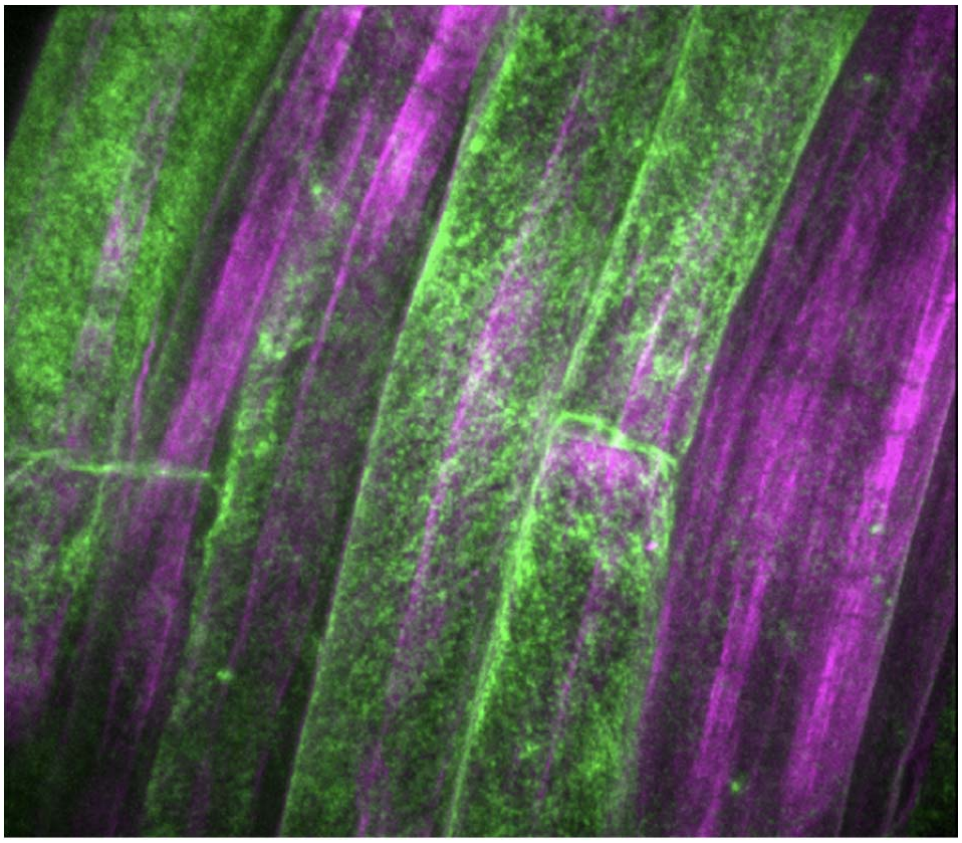

Figure 12. Cellulose labeled with Pontamine Fast Scarlet 4B (S4B, magenta) and newly synthesized pectin labeled with fucose-alkyne and Alexa488-azide (green) in epidermal cells of the root differentiation zone in 5-day-old Arabidopsis seedling. Note oblique, punctate labeling of Alexa488 signal and predominantly longitudinal labeling of S4B signal, and variation in intensity of Alexa488 signal between different cells.

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