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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.

85 **Plant nucleus: a giant in the organelle galaxy**

86
87 The nucleus can be viewed as a gigantic organelle and is defined by a double-layered membrane
88 structure called the nuclear envelope (NE). The NE sequesters the nuclear genome and spatially
89 separates transcription from translation, an evolutionary invention that enables remarkable functions
90 and regulations in the eukaryotic cell. Here, we briefly summarize current views in key aspects of the
91 plant nucleus, including structure, composition, dynamics, and function, from the surface to the
92 interior.

93 94 *Nuclear envelope protein composition and function*

95 The NE is thought to have evolved from the endoplasmic reticulum (ER) and coated vesicles and is
96 composed of the outer nuclear membrane (ONM) and the inner nuclear membrane (INM), both of
97 which harbor distinct collections of proteins that make the NE a platform for versatile functions and
98 communications. Plant NE proteins have been reported to function in nuclear calcium signaling
99 (Capoen et al., 2011; Charpentier et al., 2016), chromatin organization and dynamics (Pawar et al.,
100 2016; Gumber et al., 2019), immune activation (Gu et al., 2016), cell cycle progression (Wang et al.,
101 2019c), mechanical shielding (Goswami et al., 2020), and more. Among them, the linker of
102 nucleoskeleton and cytoskeleton (LINC) complex is one of the best characterized. The LINC complex
103 is composed of the INM-localized Sad1/UNC48 homology (SUN) protein and the ONM-localized
104 Klarsicht/ANC-1/Syne Homology (KASH) protein, with the former associated with the nucleoskeleton
105 and chromatin and the latter bound with cytoskeleton and motor proteins. SUN and KASH physically
106 interact in the perinuclear region and establish a molecular structure that enables the translation of
107 cytoplasmic mechanical forces into the nuclear movement and chromatin activities. The plant LINC
108 complexes have been shown to play critical roles in stomatal development and responses to light and
109 hormone signals (Gumber et al., 2019; Biel et al., 2020a, b), male gametophyte development (Tamura
110 et al., 2013; Varas et al., 2015; Zhou et al., 2015; Moser et al., 2020), and plant-microbe interactions
111 (Zhou et al., 2014; Newman-Griffis et al., 2019). Nonetheless, compared with animals and yeast, we
112 still lack a comprehensive understanding of the NE proteome and function in plants. Recent
113 applications of advanced proteomic tools (e.g. proximity labeling proteomics) empowered the
114 identification of novel NE components (Goto et al., 2019; Tang et al., 2020) and NE-specific biological
115 processes in plants (e.g. INM-associated membrane protein degradation (Huang et al., 2020),
116 opening brand new avenues to greatly expand our view of the global protein landscape of the plant
117 NE and to unravel both eukaryote-conserved and plant-specific NE functions.

118 119 *Nuclear pore complex, more than a conduit for nucleocytoplasmic transport*

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

133 134 *Nucleoskeleton*

135 Underneath the INM deploys the plant nucleoskeleton assembled by long coiled-coil lamin-like
136 proteins (e.g. CRWNs) and CRWN-associated proteins (e.g. KAKU4), which bear no sequence
137 homology with animal lamin proteins. They are required for proper nuclear morphology (Wang et al.,
138 2013; Goto et al., 2014; McKenna et al., 2021) and potentially interact extensively with membrane-
139 bound INM proteins to form the plant nuclear lamina (PNL). CRWNs were recently shown to interact
140 with histone modifiers and necessary for tethering chromatin to the INM to suppress stress-related
141 gene expression (Hu et al., 2019; Mikulski et al., 2019; Choi and Richards, 2020; Sakamoto et al.,
142 2020; Wang et al., 2021). These studies suggest a critical role of the PNL in maintaining
143 heterochromatin organization and repression at the nuclear rim, similar to what was found in animals.

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

146

147 *Nuclear interior organization*

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

161 Like chromatin, many other biomolecules are also organized in a dynamic and heterogeneous
162 manner in the nucleus. Spontaneous nucleation of biomolecules drives the formation of many
163 membrane-less droplets observed in plant nuclei, including nucleoli, Cajal bodies, photobodies, dicing
164 bodies, splicing speckles, DNA damage foci, and immune-activated condensates (Emenecker et al.,
165 2020; Zavaliev et al., 2020; Huang et al., 2021b). In these nuclear bodies, multivalent proteins/nucleic
166 acids capable of forming extensive inter- and intra-molecular interactions undergo liquid-liquid phase
167 separation (LLPS) to concentrate functionally relevant molecules and create a specific subnuclear
168 environment that is integral to nuclear functions such as ribosome biogenesis, mRNA and miRNA
169 processing, transcription activation, and signaling (Liu et al., 2012; Van Buskirk et al., 2012; Fang et
170 al., 2019; Powers et al., 2019; Jung et al., 2020; Zavaliev et al., 2020; Huang et al., 2021a; Huang et
171 al., 2021b). Further exploring the role of LLPS-promoted condensates in plants and elucidating how
172 phase separation may be regulated by internal and external signals represent an exciting new
173 research area for plant science in the next decade.

174

175 *Movement and dynamics of the nucleus*

176 Like most other organelles, the entire nucleus is capable of directional movement (e.g. towards
177 pathogen invading loci or with rapid elongation of pollen tubes) triggered by environmental and
178 developmental cues (Griffis et al., 2014) and can establish connections with other organelles (e.g.
179 chloroplast stromules) for signal exchange (Caplan et al., 2015; Gu and Dong, 2015). Plant nuclei
180 also exhibit distinct morphology in different cell types and membrane dynamics during cell cycle
181 progression. As an extreme example, the NE undergoes a complete breakdown and subsequent
182 reformation during mitosis. These aspects of plant nuclear dynamics have been extensively reviewed
183 elsewhere (Meier et al., 2016; Meier et al., 2017; Groves et al., 2018; Groves et al., 2020; Goto et al.,
184 2021), and mechanisms that regulate plant nuclear movement, NE dynamics, inter-organelle
185 communication, and their functional importance are currently under active investigation

186

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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

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

261
262 Future characterization of the broader roles of the plant ER shapers may provide opportunities to
263 establish how physiologically and developmentally relevant processes are connected to ER network
264 integrity. For example, the loss of RHD3 leads to an attenuation of signaling in the unfolded protein
265 response (Lai et al., 2014), a conserved cytoprotective pathway that is designed to attenuate
266 proteotoxic stress in the ER (Pastor-Cantizano et al., 2020). While these results support that the
267 homeostasis of the ER network structure is critical for cell health, a challenge for the future is to
268 establish a mechanistic framework to connect ER shape integrity with essential signaling pathways.

269
270 Despite a functional conservation of shapers, such as RHD3, reticulons and Lnps, the plant ER
271 structure depends on plant-unique factors. For example, a minor role of microtubules in ER reshaping
272 is consistent with a predominant role of actin in this process (Sparkes et al., 2009a); this is markedly
273 different from the dependence of the ER network shaping on microtubules in mammalian cells
274 (Waterman-Storer and Salmon, 1998; English et al., 2009). The existence of plant-unique ER-actin
275 interactors (i.e., SYP73 and NETWORKED 3B; (Cao et al., 2016; Wang and Hussey, 2017), plant-
276 specific molecular motors (i.e. Myosin XI family) (Peremyslov et al., 2010; Ueda et al., 2010), and the
277 absence in the plant genome of CLIMP63, the connector of the mammalian ER to microtubules and a
278 spacer of the cisternal lumen (Klopfenstein et al., 2001; Shibata et al., 2010), further support that
279 plants have developed specific mechanisms of ER shaping across kingdoms. An obvious challenge
280 for the future is to determine the nature of such mechanisms through the identification of additional
281 players. For example, proteomics of cellular compartments or targeted proteomics based on pull-
282 downs of ER shapers have yielded opportunities to identify proteins making up the plant ER (Dunkley
283 et al., 2006; Kriechbaumer et al., 2018), but the challenge ahead is to define a functional pipeline to
284 identify proteins specifically involved in ER structure. Forward genetics screen based on confocal
285 microscopy analyses of Arabidopsis seedlings expressing fluorescent markers to identify mutants with
286 defective organization of secretory organelles (Faso et al., 2009; Nakano et al., 2009; Takagi et al.,
287 2013) offer a realistic opportunity to identify mutations that compromise the ER, although an innate
288 limitation of these screens is their labor-intensive nature. Automation of this type of screens alongside
289 the implementation of software capable to quantitatively analyze the dynamics of the ER (Pain et al.,
290 2019) is likely to offer a platform for the fast identification of modifiers of the ER shape and dynamics.

291
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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

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

363

364 *Future research perspectives*

365 The structure of plant Golgi varies in different cell types (Staehein et al., 1990) but the molecular
366 mechanisms governing the remodeling remain elusive. For example, small Golgi stacks in root
367 meristem cells exhibit structural-functional modifications in parallel with the differentiation of the
368 meristem cells into columella and eventually into peripheral/border cells in the root cap (Wang et al.,
369 2017c). Since several cell-specific markers for the Arabidopsis root cap have been identified (Kamiya
370 et al., 2016), it would be possible to identify genes involved in Golgi-mediated secretion or
371 glycosylation in columella or peripheral/border cells after single-cell sequencing of root cap isolates
372 (Shaw et al., 2021).

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

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

391

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397

398 **Plant Endosomes: The protein sorting masters.**

399

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

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

419

420 *The TGN*

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

427 The TGN forms largely through cisternal maturation of the trans-most Golgi cisterna (Golgi-associated
428 TGN or GA-TGN) but eventually detaches from the Golgi becoming an independent organelle (free or
429 also called Golgi-independent TGN or GI-TGN) that fragments into vesicles (Toyooka et al., 2009;
430 Kang et al., 2011; Uemura et al., 2014; Uemura et al., 2019) (Figure 4). There are approximately 35
431 Golgi stacks and GA-TGNs in an interphase Arabidopsis meristematic cell (Segui-Simarro and
432 Staehelin, 2006). In Arabidopsis root cells, as the *trans*-most cisterna matures into the TGN, it
433 develops numerous vesicle buds, loses 30-35% of its total membrane surface area, and becomes
434 enriched in the Rab GTPases RAB-A2a and RAB-A4b, the phosphatidylinositol 4-kinase PI4Kb1, the
435 vacuolar V-ATPase subunit VHA1a, and the SNAREs (Soluble N-ethylmaleimide sensitive factor
436 Attachment protein Receptor) SYP61, SYP43, VAMP721, VAMP722, and VAMP727 (Dettmer et al.,
437 2006; Chow et al., 2008; Kang et al., 2011; Zhang et al., 2011). As the GA-TGN detaches from the
438 Golgi stacks to become free/GI-TGNs, the budding profiles become more abundant.

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

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

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

459

460 *MVEs*

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

477 In general, ESCRT proteins are well conserved across organisms, from Archaea (Makarova et al.,
478 2010; Dobro et al., 2013; Pulschen et al., 2020) to Eukarya. In fungi and metazoans, five multimeric
479 ESCRT complexes have been identified: ESCRT-0 to III and the triple AAA ATPase SKD1
480 (SUPPRESSOR OF K⁺ TRANSPORT GROWTH DEFECT 1) with its activator LIP5. Plants contain
481 putative orthologs for most of the ESCRT proteins originally identified in metazoans and fungi (Spitzer
482 et al., 2006; Haas et al., 2007; Spitzer et al., 2009; Kalinowska et al., 2015; Buono et al., 2016; Yu et
483 al., 2016; Wang et al., 2017a) with the exception of ESCRT-0 (Winter and Hauser, 2006), which is an
484 early acting complex that binds phosphoinositide-3-phosphate (PI3P), a lipid enriched in endosomal
485 membranes and critical for recruitment of ESCRT proteins to endosomes. However, a group of
486 proteins called TOL (TOML1-LIKE) are likely to play the role of ESCRT-0 in plants (Korbei et al., 2013;
487 Moulinier-Anzola et al., 2020).

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

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

502

503 *Future perspectives*

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

514

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518
519

520 Lipid Droplets: Specialized Subcellular Hydrophobic Compartments

521
522 Like all cells, plant cells accumulate storage lipids in their cytoplasm as discrete lipid droplets (LDs),
523 most often consisting of a hydrophobic core of non-bilayer forming lipids such as triacylglycerols
524 (TAGs) or sterol esters surrounded by an emulsifying monolayer of phospholipids (Pyc et al., 2017a;
525 Huang, 2018; Ischebeck et al., 2020). Although less commonly considered, rubber particles of rubber-
526 producing plant species with a polyisoprenoid hydrophobic core, share the same overall structure
527 (Yamashita and Takahashi, 2020). This thermodynamically stable structure was originally observed in
528 TEM micrographs, and described by various terms as lipid bodies, oil bodies, spherosomes or
529 oleosomes (Wanner and Theimer, 1978). However, the contemporary, unifying terminology of “lipid
530 droplets” emphasizes the evolutionary conservation of this compartment across kingdoms of life
531 where there are increasing reports of functions beyond the efficient storage of carbon (Lundquist et al.,
532 2020).

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

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

554 Another recently-identified LD protein is the PLANT UBX DOMAIN-CONTAINING PROTEIN10
555 (PUX10). PUX10 localizes to LDs through a hydrophobic polypeptide sequence and recruits an AAA-
556 type ATPase CELL DIVISION CYCLE48 (CDC48) protein to the LD surface (Deruyffelaere et al.,
557 2018; Kretzschmar et al., 2018). This interaction is believed to support the selective extraction of LD
558 surface proteins, like oleosins and LDAPs, for their ubiquitin-mediated protein degradation. This LD-
559 associated degradation pathway likely operates in all cells of plants to repurpose the surface and/or
560 contents of the LD compartment during development or in response to environmental stresses.

561 *LD formation at the ER*

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

571 Existing models for LD formation suggest that newly-synthesized TAGs aggregate and form foci or
572 “lipid lens” structures between the two leaflets of the ER bilayer (Figure 6B) (Pyc et al., 2017a). An
573 oligomeric protein complex comprised of SEIPIN subunits in the ER bilayer coordinates these TAG
574 foci as they grow (Chapman et al., 2019). SEIPIN proteins direct a bulge of newly accumulating
575 neutral lipids to emerge into the cytoplasm covered with a monolayer of ER-derived
576 phospholipid. Unlike fungi and metazoans, plants have multiple genes encoding SEIPIN isoforms
577 (Cai et al., 2015). In *Arabidopsis* *SEIPIN 1* is expressed mostly in seed and seedling tissues, whereas
578 *SEIPIN 2* and *SEIPIN 3* are expressed in essentially all tissues. While loss-of-function mutants in a
579

580 single *SEIPIN* gene in *Arabidopsis* resulted in negligible phenotypes, double and especially triple
581 *seipin* mutants showed dramatic cellular disruptions in normal LD formation (Taurino et al.,
582 2018). Seeds and pollen of *sei1/sei2/sei3* mutants accumulated large aberrant-shaped LDs,
583 sometimes observable in the nucleus and ER lumen in addition to the cytoplasm. These results
584 indicate that SEIPINS play a critical and partially redundant role in the normal formation of LDs in plant
585 cells. Structural models based on homology with known structures of *Drosophila* and human SEIPIN,
586 suggests that the three *Arabidopsis* SEIPINS can form homo-oligomeric structures with different
587 numbers of subunits (Chapman et al., 2019), but future work is required to understand the functional
588 interactions of the three SEIPIN proteins in plant cells, their potential for hetero-oligomeric interactions
589 and their partners in LD biogenesis.

590 The loss-of-function of two other *Arabidopsis* genes revealed similar, large and aberrant LD
591 phenotypes in seeds, reminiscent of *seipin* mutants. These two genes encode the VESICLE-
592 ASSOCIATED MEMBRANE PROTEIN-ASSOCIATED PROTEIN 27-1 (VAP27-1) and LDIP proteins,
593 respectively, which were shown to interact with SEIPINS and with LDs (Pyc et al., 2017b; Greer et al.,
594 2020). In other work, higher order oleosin mutants also displayed aberrant formation of LDs during
595 early seed development, and this was reported to result from alteration of fusion dynamics of very
596 small LDs, not necessarily during LD formation at the ER (Miquel et al., 2014). LDAPs also occur in
597 seeds but at lower amounts than oleosins (Kretzschmar et al., 2018). And while LDAPs are
598 interactors of LDIP (Pyc et al., 2017b), their loss-of-function in *ldap* mutants did not result in dramatic
599 alterations of LD morphology in seeds (Gidda et al., 2016), although there may be some increase in
600 LD size in leaves of *ldap* knockdowns (Brocard et al., 2017). Future work will be required to piece
601 together the mechanistic associations between SEIPINS, LDIP, VAP27-1, oleosins, LDAPs and other
602 LD proteins; nevertheless, results to date support cooperative roles for these proteins in the cellular
603 process of LD formation in plant cells.

604

605 *Engineering the LD compartment*

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

615 In addition to bioenergy applications, LDs offer a stable compartment for sequestration of various
616 hydrophobic compounds. As such, several recent reports indicated that manipulation of LD machinery
617 can be exploited for the subcellular storage of secondary metabolites. For example, (Sadre et al.,
618 2019) engineered the accumulation of sesquiterpenes (patchoulol) and diterpenes (abetadiene) into
619 cytoplasmic LDs. Elsewhere, the expression of lipogenic proteins from mouse elevated LDs
620 dramatically in leaves, and supported the increased accumulation of the sesquiterpene phytoalexin,
621 capsidiol, along with TAGs (Cai et al., 2019). With the preponderance of bioactive hydrophobic
622 secondary metabolites, these studies illustrate the utility of engineering the cytoplasmic LD
623 compartment in plants as a repository for high value isoprenoids in the future.

624

625 *Future prospects for LD biology*

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

637

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643 **The dynamic nature of peroxisome structures, abundance, and subcellular**
644 **interactions**

645
646 Peroxisomes compartmentalize diverse oxidative reactions, allowing metabolic, signaling, and
647 detoxification roles while limiting the potential for damage (Kao et al., 2018; Pan et al., 2020).
648 Peroxisomes are a closed system, permeable only to small (300-400 Da) molecules (Charton et al.,
649 2019; Plett et al., 2020). Lipid substrates and ATP, NAD⁺, and CoA cofactors are imported via
650 membrane transporters (Charton et al., 2019; Plett et al., 2020), whereas enzymes are imported by
651 cytosolic receptors that recognize a peroxisomal targeting signal (PTS1/PTS2; (Reumann and
652 Chowdhary, 2018; Pan et al., 2020)). Plant peroxisomes are indispensable during early development,
653 when seedlings rely on lipid breakdown prior to photosynthetic initiation (Graham, 2008) for
654 photorespiration in leaf cells, and reactive oxygen (ROS) and nitrogen species (RNS) metabolism
655 throughout development and under changing conditions (Del Rio and Lopez-Huertas, 2016; Kao et al.,
656 2018; Corpas et al., 2020; Pan et al., 2020; Su et al., 2020).

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

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

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

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

690 These microscopic images led to an enhanced understanding of peroxisomal structures: peroxisomes
691 have an outer membrane surrounding luminal space that contains imported matrix proteins, as well
692 as a dynamic number of membrane-bound vesicles clear of matrix proteins (Figure 7) (Wright and
693 Bartel, 2020). Further, two proteins with unique peroxisomal localization (SCO3/UP9; (Albrecht et al.,
694 2010; Quan et al., 2013) accumulated within a subset of ILVs that lacked matrix proteins. This
695 apparent segregation yields at least three distinct spaces within peroxisomes, potentially housing
696 unique proteins, substrates, cofactors, and/or environments.

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

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

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

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

719 Peroxisomes and chloroplasts can form specific pairs that remain intact over time (Oikawa et al.,
720 2015). Peroxisome shape alterations expand the surface area to increase chloroplast interactions. In
721 the light, peroxisomes extend into an elliptical shape, versus a spherical shape in darkness. Tethering
722 factors connecting peroxisomes and chloroplasts may facilitate this interaction (Oikawa et al., 2015;
723 Gao et al., 2016), potentially including the PEX10 RING finger protein (Schumann et al., 2003;
724 Sparkes et al., 2003; Schumann et al., 2007). A dominant-negative PEX10 line had clustered
725 peroxisomes that did not associate with chloroplasts; this line had phenotypes similar to
726 photorespiration mutants (Schumann et al., 2007), consistent with a role for organelle association in
727 efficient metabolic transfer.

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

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

737 Another shape alteration to peroxisomes are thin organelle protrusions known as peroxules (Mathur,
738 2021). These structures are up to 15 μ m, dramatically increasing the surface area (Sinclair et al.,
739 2009; Barton et al., 2013). Formation of these organelle extensions is transient and dynamic (Mathur,
740 2021). The interactions between organelles described above may be mediated by peroxules,
741 including proposed interactions with oil bodies (Thazar-Poulot et al., 2015), chloroplasts (Schumann
742 et al., 2007), mitochondria (Jaipargas et al., 2016), and ER (Sinclair et al., 2009). Extended structures
743 are seen following H_2O_2 , UV-A, and hydroxyl radical stress, but retract when stress is minimized
744 (Sinclair et al., 2009). In addition, elongations are common during the constriction and fission steps of
745 peroxisome division (Sinclair et al., 2009; Barton et al., 2013). Cadmium induces ROS and similarly
746 leads to peroxule formation that results in division to increase peroxisome numbers (Rodriguez-
747 Serrano et al., 2016). Increased peroxule frequency in cells exposed to ROS leads to a hypothesis
748 that extensions facilitate neutralization to prevent or reduce damage (Sinclair et al., 2009; Barton et al.,
749 2013; Rodriguez-Serrano et al., 2016). Separately, peroxule-mediated contacts might assist in protein
750 localization. The SDP1 lipase (Eastmond, 2006) localizes to peroxisomal membranes and then the oil
751 body, a transition concurrent with peroxule development (Thazar-Poulot et al., 2015)

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

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

760

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765 included within this short overview.

766

767

768 **Plant mitochondria**

769
770 In plants, mitochondria provide a large portion of the ATP in the cytosol through oxidative
771 phosphorylation, and are the sites of some amino acids, nucleic acids, lipids, and plant hormone
772 metabolism. Plant mitochondria also control redox balances when photosynthesis is on or off or
773 fluctuating (Noguchi and Yoshida, 2008; Finkemeier and Schwarzlander, 2018), have roles in cellular
774 signaling (Huang et al., 2016; Welchen et al., 2021) et al., 2021), and in resistance to diseases (Fuchs
775 et al., 2020). In agriculture, cytoplasmic male sterility, which is caused by genes encoded in the
776 mitochondrial genome, is used for production of F1 hybrid seeds in diverse crops and vegetables. The
777 fine structure and dynamics of plant mitochondria are briefly reviewed here.

778
779 Mitochondria have two lipid bilayers that form the outer and inner membrane (Figure 8). Some parts
780 of the inner membrane are invaginated to form sacs, called cristae, that increase the area of oxidative
781 phosphorylation complexes. Five diverse eukaryotic-conserved complexes are embedded in the
782 cristae membrane. In contrast, plant-specific proteins (alternative oxidases and extra NDH and NDPH
783 dehydrogenases) for alternative respiration pathways mainly reside in the non-cristae parts of the
784 inner-membrane (Schwarzlander and Fuchs, 2017). Plant ATP synthase dimers (complex V) are in
785 the cristae membrane, where they contribute to its curvature (Zancani et al., 2020. Complexes I to V
786 have roles in oxidative phosphorylation. Some of them form super-complexes for functional efficiency
787 and to regulate oxidative phosphorylation [Braun, 2020 #2342. Protein-protein interactions and
788 metabolite channeling are observed also in the TCA cycle in the matrix [Zhang, 2017 #2382).
789 Additionally, glycolysis enzymes in the cytosol dynamically associate on the outer surface of
790 mitochondria (Giege et al., 2003; Graham et al., 2007), probably to more efficiently transport
791 metabolites.

792 The mitochondrial outer membrane has the most abundant protein in plant mitochondria, the Voltage-
793 Dependent Anion Channel (VDAC1). A single mitochondrion contains 40,000 VDACs out of a total of
794 1.4 million proteins (Fuchs et al., 2020). The outer membrane does not just encapsulate the inner
795 membrane but also sometimes extends into the cytosol and other organelles (without extending the
796 inner-membrane), and occasionally the extensions are pinched off to form small vesicle-like structures
797 (Yamashita et al., 2016); Figure 8D). In mammals, mitochondria-derived vesicles which do not contain
798 inner membranes are reported to be involved in the transport of specific proteins to peroxisomes,
799 endosomes, and multivesicular bodies (Sugiura et al., 2014), and in the biogenesis of peroxisomes
800 [Sugiura, 2017 #2376.

801
802 Each Arabidopsis leaf cell contains 300-450 mitochondria. Many plant mitochondria move along
803 microfilaments at 0.05 - 3 $\mu\text{m}/\text{sec}$ [Doniwa, 2007 #2344](Oikawa et al., 2021), which is about an order
804 of magnitude faster than mammalian and yeast mitochondria, which mainly move along microtubules.
805 Some plant mitochondria stop and wiggle, as if they were anchored to the cytoskeleton or other
806 organelles, such as plastids and peroxisomes (Jaipargas et al., 2016; Oikawa et al., 2021) et al.,
807 2016). Moving plant mitochondria can change their speed and also can change their shapes from
808 granular to linear to attach to other organelles in response to the presence of sucrose or light
809 (Jaipargas et al., 2016). A single plant cell can have mitochondria with different shapes (Jaipargas et
810 al., 2015), different DNA contents (Arimura et al., 2004b; Preuten et al., 2010), (Figure 8E) and
811 transiently fluctuating membrane potentials (Schwarzlander et al., 2012). In addition, as shown in
812 Figure 8B, differently colored groups of mitochondria in a cell achieve a unified color in two hours,
813 indicating that mitochondria undergo frequent fusion and fission, resulting in the sharing of internal
814 proteins. Mitochondria involved in such dynamic sharing of materials in a plant cell are referred to as
815 a dynamic syncytium (Lonsdale et al., 1988), and the collective mitochondria in a cell are thought to
816 exist as a discontinuous whole (Logan, 2017). Fusion of mitochondria results in the formation of
817 elongated and/or branched mitochondria in some meristematic tissues, such as shoot apical apices
818 (Segui-Simarro and Staehelin, 2006), germinating seeds (Paszkiwicz et al., 2017), and
819 dedifferentiating protoplasts (Sheahan et al., 2005; Rose and McCurdy, 2017).

820
821 Mitochondrial fission is achieved by dynamin-related proteins that are well-conserved in eukaryotes
822 (e.g. DRP3A and 3B in Arabidopsis (Arimura and Tsutsumi, 2002; Arimura et al., 2004a; Arimura et
823 al., 2004b; Fujimoto et al., 2009), Figure 8A), which polymerize to form ring-like structures outside
824 mitochondria (Ingerman et al., 2005). Plant-specific ELM1, an outer surface protein, localizes DRP3s
825 from the cytosol (Arimura et al., 2008). An outer-membrane embedded protein that is conserved in
826 eukaryotes (Fis1) functions as a molecular adapter for DRP in budding yeast (Okamoto and Shaw,
827 2005). Fis1 had been thought to carry out the similar functions but is now thought to have only a

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

836
837 Mitochondrial-specific autophagy (mitophagy) has been extensively studied in mammals and yeasts
838 (Onishi et al., 2021), in which it is involved in mitochondrial quality control. In these organisms,
839 degraded mitochondria with low membrane potential could not fuse with other “healthy” mitochondria,
840 but they are specifically recognized, captured and engulfed by autophagosome membranes (Figure
841 8C). The engulfed mitochondria are transported to the vacuole to be digested to prevent accidental
842 ROS generation and/or other negative effects. Therefore, mitophagy, fission, and fusion are thought
843 to function as a quality control system for all the mitochondria in a cell (Twig et al., 2008).
844 Mitochondrial-specific degradation in *Arabidopsis* has also been observed in several situations,
845 including during leaf senescence (Broda et al., 2018) greening of cotyledons (Ma et al., 2021), after
846 UV-irradiation (Nakamura et al., 2021) and after treating the inner membrane with ionophores (Ma et
847 al., 2021). Orthologues of factors specific to mitophagy in mammals and yeasts have not yet been
848 found in plant genomes, although FMT was recently reported to be involved in mitophagy in
849 *Arabidopsis* (Ma et al., 2021).

850
851 Super resolution microscopy is a promising new technique that can clarify the internal structures of
852 mitochondria in more detail with their diverse physiology and functions. In addition, recent trials to
853 understand molecular numbers of averaged single mitochondrion (Fuchs et al., 2020) or estimated
854 single mitochondrion (Moller, 2016) will hopefully develop to the next stage of analysis of the exact
855 individual mitochondria to answer the actual quantitative dynamics of molecules (or “factfulness”) of
856 diverse mitochondria. Until recently, transformation of mitochondrial genomes in multicellular plants
857 has been impossible, but new genome editing methods (Kazama et al., 2019; Arimura et al., 2020)
858 have opened the door to analyzing the functions of mitochondrial genes, as well as to regulate their
859 expressions to breed crops with agriculturally important characteristics.

860
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863
864

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 CO₂ 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,

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

926

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

937

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941

942

943 **Plant Membrane Contact Sites – Questions from the membrane interface.**

944

945 *Membrane Contact sites: Does one definition fit all?*

946 Membrane Contact Sites (MCS) are evolutionarily conserved structures where the close proximity
947 between two or more membrane-bound organelles enables direct exchange of molecules and
948 facilitates coordinated inter-organelle adaptive responses (Figure 10 A-B). Recent advances in plant
949 cell imaging and the development of novel genetic and molecular tools have fueled an emerging field
950 of research devoted to the investigation of their structural organization, dynamics, and physiological
951 functions. This interest is uncovering plant-specific MCS structures and molecular mechanisms, but
952 also exposing some limitations on the commonly accepted definitions and physiological functions
953 inferred from different model organisms. As in yeast and animal cells, the plant endoplasmic reticulum
954 (ER) is an interconnected organelle that establishes MCS with multiple cellular structures including
955 the plasma membrane (PM), mitochondria, endosomes, peroxisomes, Golgi and trans-Golgi network
956 (Barton et al., 2013; Stefano et al., 2014; Wang et al., 2014; Perez-Sancho et al., 2015; Wang et al.,
957 2019b; Brandizzi, 2021). Unique to plants; however, are the functional interactions at ER-plastids
958 MCS for lipid synthesis and transport (Liu and Li, 2019), the control of intercellular communication
959 through plasmodesmata MCS-regulated intercellular bridges (Tilsner et al., 2016), and the MCS
960 activities driven by a super-continuum that encompasses the cell wall, PM, ER, and cytoskeleton
961 (Wang et al., 2014; Perez-Sancho et al., 2015; Zang et al., 2021). These plant-specific features are
962 placing MCS research in plants at the forefront of discovery, broadening the MCS definition beyond
963 yeast and animal systems.

964 In plants, MCS can be defined as environmentally and developmentally regulated microdomains with
965 an intermembrane gap as small as 3 nm in plasmodesmata, and an arbitrarily defined upper limit of
966 80-100 nm. Plant MCS are enriched with a variety of protein-protein, and/or protein-cytoskeleton
967 tethering assemblies that establish dynamic interactions with membrane phospholipids and/or the cell
968 wall. Plant MCS carry out essential cellular functions including, but not restricted to maintenance of
969 membrane lipid homeostasis, cell-to-cell communication, organelle biogenesis, autophagy,
970 endocytosis, receptor kinase signaling, and the regulation of Ca^{2+} -dependent stress responses
971 (Figure 10 C-D), reviews in (Perez-Sancho et al., 2016; Wang and Hussey, 2017; Liu and Li, 2019;
972 Petit et al., 2020; Rosado and Bayer, 2021).

973

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

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

994

995 *MCS in motion: Who controls MCS plasticity and dynamics?*

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

1000 Anionic phospholipids represent only a few percent of the total lipids but they are critical biochemical
1001 and biophysical landmarks of membrane identity (Noack and Jaillais, 2020). Within the

1002 endomembrane system, they consist of the phosphoinositides (PIPs), phosphatidic acid (PA) and
1003 phosphatidylserine (PS), and determine the electrostatic potential of each membrane being highest at
1004 the PM, intermediate in endosomes and low in the ER (Platre et al., 2018; Dubois and Jaillais, 2021).
1005 *In vitro* or *in silico* data for MCS tethers such as the synaptotagmins (SYTs), Multiple C2 domains and
1006 transmembrane region (MCTPs), and Vesicle-associated membrane protein (VAMP)-associated
1007 proteins (VAPs) families, support the notion that anionic lipids profoundly impact the structure and
1008 function of MCSs by enabling protein-lipid interactions that regulate the association of the ER with the
1009 PM, TGN and early endosomes (Perez-Sancho et al., 2015; Stefano et al., 2018; Brault et al., 2019;
1010 Ruiz-Lopez et al., 2021). Interestingly, these interactions appear to be mostly non-specific, the
1011 primary determinants being the negative charge carried by the anionic lipids and, in some cases, the
1012 presence of Ca^{2+} (Schapire et al., 2008). Accordingly, electrostatic interactions between
1013 phosphatidylinositol-4-phosphate (PI4P) and SYT1/SYT3 underpin the localization of SYT1/SYT3 to
1014 ER-PM MCS (Ruiz-Lopez et al., 2021), MCTP4 to plasmodesmata-MCS, (Brault et al., 2019), and the
1015 remodelling of SYT1 ER-PM MCS in response to rare-earth elements (Lee et al., 2020). Similarly, the
1016 accumulation of phosphatidylinositol 4,5-biphosphate (PI(4,5)P₂) at the at the PM enables interactions
1017 with SYT1 and correlates with the rearrangement and expansion of ER-PM MCS in response to ionic
1018 stress (Lee et al., 2019).

1019 MCS plasticity is also controlled by components that crosslink the actin cytoskeleton at MCS and
1020 create trapping mechanisms that influence MCS architecture and expansion. In plants, this cross-
1021 linking seems to be carried out by a plant-specific complex that includes the actin associated NET3C
1022 protein, and the microtubule associated Kinesin light chain related (KLCRs) and IQ67-Domain (IQD)
1023 proteins (Zang et al., 2021) (Figure 10E). Remarkably, in plants, the presence of cell walls underlies
1024 the formation of a plant-specific supramolecular assembly known as the MCS super-continuum. This
1025 super-continuum encompasses the cell wall, PM, ER, and cytoskeleton, and renders MCS with
1026 distinct kinetics, shapes, geometries, and functions (Rosado and Bayer, 2021; Zang et al., 2021).
1027 Recent studies propose that the MCS super-continuum serves as a nexus that limits the mobility of
1028 MCS tethering assemblies (Wang et al., 2016; Lee et al., 2019; Zang et al., 2021), and control their
1029 activities. Examples of regulation mediated by this continuum may include the activity of receptor like
1030 kinases in pollen and/or stomatal cells (Ho et al., 2016; Duckney et al., 2021), and the regulation of
1031 phospholipase C mediated stress signals at the PM (Ruiz-Lopez et al., 2021). Last, a unique type of
1032 regulation occurs at plasmodesmata MCS where the transfer of molecules is parallel to the
1033 membranes, as opposed to orthogonal to them. In those ER-PM MCS the intermembrane space may
1034 not be solely regulated by the tethers, lipids, and cytoskeleton elements in the super-continuum, but
1035 also by wall polymers (e.g. callose), which are locally synthesized around the PD structure (Petit et al.,
1036 2020).

1037
1038 *Future MCS research: What's in the plant toolkit?*

1039 MCS are microdomains with an intermembrane distance below the resolution limit of conventional
1040 fluorescence microscopy, and with a dynamic behavior that requires the use of live-cell compatible
1041 techniques (McFarlane et al., 2017). In recent years, advances in super-resolution microscopy (e.g.
1042 Total Internal Reflection Fluorescence (TIRF), and Structure illumination microscopy (SIM), (Figure
1043 10F), and electron tomography (Figure 10G) are providing for the first time detailed high-resolution
1044 visualizations and 3D reconstructions of the MCS ultrastructure in plants (Baillie et al., 2020). In
1045 parallel, the use of optical laser tweezers to manipulate plant MCS *in vivo* is facilitating the
1046 characterization of putative MCS components such as the AtCASP tether identified at ER-Golgi MCSs
1047 (Osterrieder et al., 2017) and the mitochondria-associated GTPase, Miro2 at ER-mitochondria contact
1048 sites (White et al., 2020). Plant MCS research is also adopting genetically encoded tools such as
1049 synthetic tethers that bridge apposed membranes (e.g. MAPPER-GFP, (Lee et al., 2019), or split-
1050 fluorescence systems (e.g. split super-folder (sp) GFP proteins, (Li et al., 2020) to visualize MCS
1051 contacts. These artificial systems, however, have limited application in functional studies as their
1052 expression could induce non-physiological changes in the MCS structure. Additional molecular tools
1053 with broad application such as inducible phosphoinositide depletion systems (Doumane et al., 2021),
1054 and phosphoinositide fluorescent markers (Simon et al., 2014) are being currently adopted for MCS
1055 research and represent promising avenues to elucidate the roles of anionic phospholipids in plant
1056 MCS function and dynamics.

1057 We forecast that the combination of collaborative research, technical advances, and novel molecular
1058 tools in this quickly evolving field will provide breakthroughs that will transcend plant MCS research. In
1059 this context, we apologize to those whose important contributions to plant MCS research were not
1060 included in this brief review.

1061

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1064 important contributions to the field were not featured due to length constraints.
1065
1066

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.

1127 The insertion of these new PD is likely necessary to establish or maintain symplastic connectivity as
1128 in graft unions or when cells divide and grow (Ehlers and Kollmann, 2001). Studies in Arabidopsis
1129 trichomes suggest that new secondary PD form in close proximity to existing PD, as described in the
1130 multiple twinning model (Faulkner et al., 2008). It is proposed that PD divide by fission, although a
1131 mechanism for this is unclear.

1132 PD may also be removed from existing cell walls by a still unknown process. Studies on cambial
1133 division and vascular differentiation have shown that PD numbers can increase and decrease over
1134 the lifespan of a given cell-cell interface, and this would necessarily involve the removal and insertion
1135 of PD at a given interface (Ehlers and van Bel, 2010; Fuchs et al., 2010). In other instances, PD can
1136 be drastically modified or even truncated to disrupt intercellular trafficking. For example, guard cell
1137 initials contain PD, and PD trafficking is critical for guard cell development (Guseman et al., 2010). As
1138 stomata develop, however, PD are lost from the guard-cells, rendering them symplastically isolated
1139 (Wille and Lucas, 1984). It may be that PD removal is a more common occurrence in plant cell
1140 development and differentiation than previously reported. This aspect of PD biology awaits further
1141 exploration using advanced imaging approaches.

1142 1143 *Structure-function relationships in PD*

1144 PD are often depicted as simple linear structures traversing the cell wall but PD structure is much
1145 more diversified. PD are often branched, consisting of multiple pores that connect in the vicinity of the
1146 cell wall middle lamella (Figure 11). The formation and origins of branched PD are unclear, but they
1147 likely arise through modification of existing simple PD (Burch-Smith et al., 2011). This diversity in
1148 structure suggests diversity in function. Exemplary studies of PD in tobacco leaves undergoing the
1149 sink-source transition demonstrated that simple PD were converted to branched PD
1150 contemporaneously with decreased import of fluorescent dye (Oparka et al., 1999; Roberts et al.,
1151 2001). Another common variation of PD form is the dilation of PD pores away from the PD openings
1152 or the constriction of PD at their necks (region just below opening). This PD variation seems to
1153 correlate with PD maturation (Nicolas et al., 2017b) or with trafficking capacity (Ding et al., 1992).
1154 Mathematical modeling supports that dilation increases trafficking capacity as the cell wall thickens
1155 (Deinum et al., 2019), a correlation previously observed by TEM (Nicolas et al., 2017b). Another PD
1156 form that has a specialized role in trafficking is the 'funnel PD' in sink root tissue (Ross-Elliott et al.,
1157 2017). These PD have wide openings at the phloem sieve elements that narrows considerably as
1158 they cross the cell wall and open on the phloem-pole pericycle creating a 'funnel' shape. The
1159 specialized PD shape appears to facilitate the unloading of sucrose in the root phloem and
1160 mathematical modelling supports the need for this unusual PD form to allow phloem unloading at
1161 physiological sucrose concentrations. Specialized PD forms have also been reported at sites where
1162 sugars are loaded into the phloem in source tissues. For example, PD at the phloem parenchyma-
1163 companion cell interface in Arabidopsis leaf veins have many openings to the phloem parenchyma
1164 but only one to the companion cells (Haritatos et al., 2000). These distinct PD forms correlate with
1165 specialized functions, and raise the possibility of PD sub-functionalization between tissues and even
1166 at a given cell-interface. Despite the importance of PD to plants, many aspects of their formation,
1167 structure and function remain unknown. Undoubtedly, comprehensive understanding of PD will enable
1168 novel approaches to engineering solutions for challenges in plant growth and development.

1169

1170 **Acknowledgements:** Our apologies to colleagues whose work we could not cite due to this article's
1171 format. Thanks to Dr. Brandon Reagan for critical reading of the manuscript and helpful
1172 feedback. This work was supported by the National Science Foundation (MCB1846245).

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1174 **So much more than bricks and mortar: plant cell walls as dynamic**
1175 **extracellular “organelles”**
1176

1177 Much as the skin is the largest organ in the human body, the plant cell wall can be thought of as the
1178 largest organelle in the plant cell, even though the wall is not bound by a membrane but instead
1179 encases the plasma membrane-delimited protoplast that contains the canonical organelles. Our
1180 understanding of cell wall composition, structure, and mechanics has expanded rapidly over the past
1181 decade due to advances in high-resolution imaging (Zeng et al., 2017; Rydahl et al., 2018; Voiniciuc
1182 et al., 2018; Zhao et al., 2019), biochemical and spectroscopic analyses of wall polymers and their
1183 interactions down to single-molecule and nanoscale levels (Voxeur et al., 2019; Zhao et al., 2020; Cai
1184 et al., 2021), and new computational modeling methods that relate wall mechanics to the
1185 deformations, movements, and interactions of individual wall polymers (Zhang et al., 2021). In
1186 contrast to its previous conception as simply “dead wood” that is the fossilized product of
1187 polysaccharide secretion by plant cells, the plant cell wall is now starting to be appreciated as a
1188 dynamic structure that changes over time and encompasses specialized metabolic processes,
1189 including wall polymer polymerization, coalescence, binding/unbinding, cleavage, and re-ligation that
1190 facilitate both plant growth and the processing of plant biomass for human use (Obro et al., 2011).
1191 The intercellular transport of nutrients, secreted peptides, hormones, and other metabolites across the
1192 wall (Ramakrishna and Barberon, 2019), the discovery of extracellular vesicles that can deliver small
1193 RNAs to silence virulence genes in plant pathogens (Cai et al., 2018) and the ability of plants to sense
1194 pathogen-generated wall fragments (Vaahtera et al., 2019) and other aspects of wall integrity (Rui
1195 and Dinneny, 2020) together highlight how the apoplast, the extracellular compartment in which the
1196 cell wall exists, might also allow for previously unappreciated forms of trafficking and act as a
1197 molecular frontier in the interactions between plants and their abiotic and biotic environments.
1198

1199 *Cell wall assembly and structure*

1200 Consider the plant cell wall as a futuristic building that can grow (and sometimes shrink) and protects
1201 and shapes its occupant, in this case the protoplast, and also helps sense and transduce important
1202 environmental and mechanical information. Cellulose, the most abundant biopolymer on Earth, forms
1203 the “girders” of the cell wall as its primary load-bearing component, and coincidentally has a tensile
1204 strength similar to that of steel. Cellulose is extruded directly into the apoplast by multi-subunit
1205 Cellulose Synthase Complexes (Wilson et al., 2021), which move through the plasma membrane
1206 along trajectories that are likely driven by the force of polymerization and are guided by either cortical
1207 microtubules or existing wall patterning (Chan and Coen, 2020). The estimated 18 catalytic subunits
1208 in each Cellulose Synthase Complex (Nixon et al., 2016) produce strands of β -1,4-linked glucose that
1209 coalesce into cable-like microfibrils that are predicted to have 18-24 chains (Yang and Kubicki, 2020).
1210 Forming the “cross-beams” and “insulation” between the cellulose “girders” are matrix
1211 polysaccharides that include pectins and hemicelluloses. Pectins are acidic polysaccharides that are
1212 composed of homogalacturonan, rhamnogalacturonan-I, and rhamnogalacturonan-II domains
1213 (Anderson, 2019), whereas hemicelluloses contain mostly neutral sugars and include xyloglucans,
1214 xylans, and mannans (Scheller and Ulvskov, 2010). In growing cells, matrix polysaccharides initially
1215 interact with cellulose upon their secretion at the cell surface, following polymerization in the Golgi
1216 lumen and post-Golgi trafficking (Hoffmann et al., 2021) (Figure 12). Both pectins and hemicelluloses
1217 can associate with the surfaces of cellulose microfibrils, potentially preventing cellulose agglomeration
1218 and thus assembling a strong but deformable wall that also contains glycoproteins, enzymes,
1219 metabolites, ions, and water (Cosgrove, 2018). In the secondary walls produced by certain cell types,
1220 a polyphenolic, hydrophobic compound called lignin is also deposited (Dixon and Barros, 2019). In
1221 many cell types, the wall is deposited in layers with differing cellulose orientations, conferring
1222 multidirectional resistance to mechanical failure.
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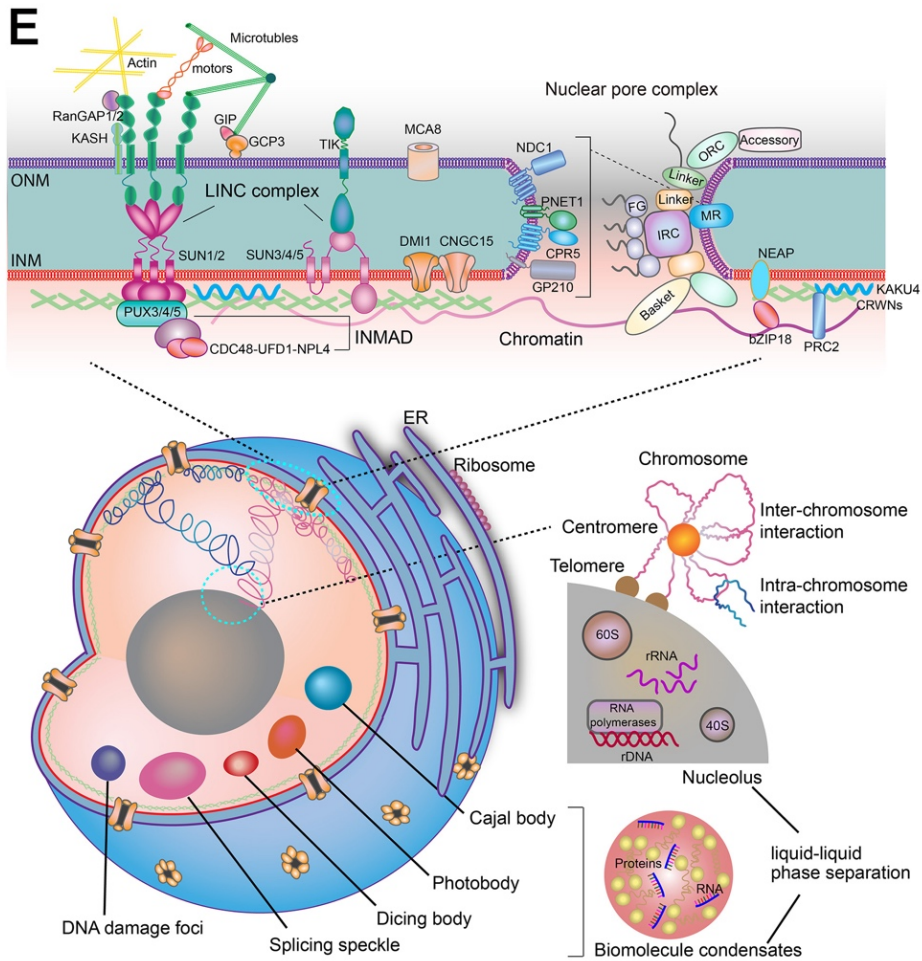
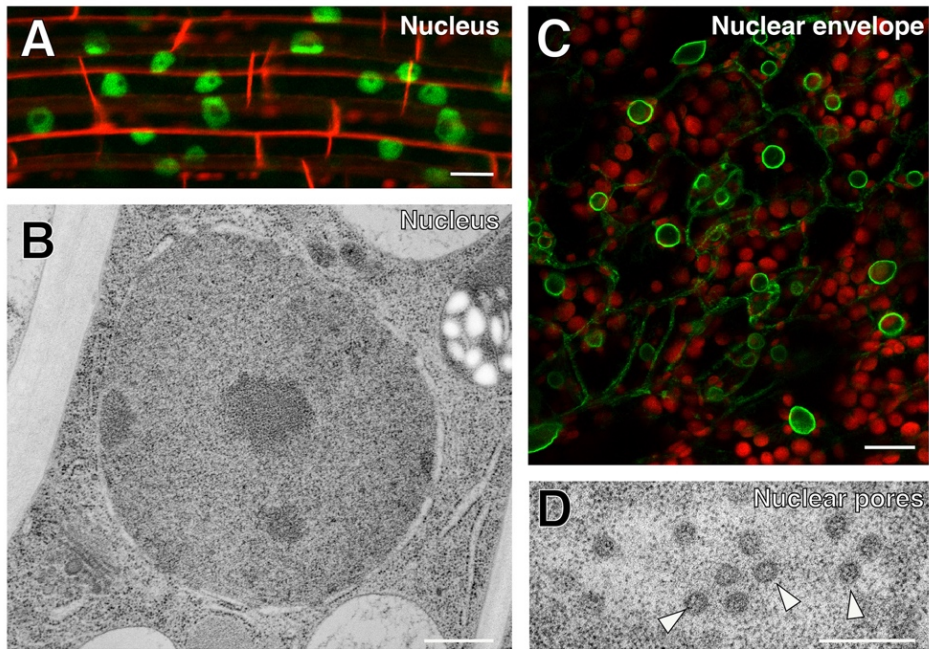
1224 *Dynamics and functions of plant cell walls*

1225 What happens to the strong but flexible wall as a plant cell grows? Atomic force microscopy (Zhang et
1226 al., 2017) and coarse-grained modeling (Zhang et al., 2021) indicate that cellulose microfibrils bend,
1227 bundle, unbundle, and slide during experimentally imposed or computationally simulated wall
1228 deformation, respectively; one remaining question is exactly how these processes occur in the
1229 growing cells of living plants, where wall deposition is typically ongoing, matrix polysaccharides also
1230 undergo reorganization (Anderson et al., 2012), and wall-modifying enzymes can modulate cell
1231 growth (Xiao et al., 2014). Also unclear is the extent to which extracellular ATP and other energetic
1232 compounds might be used in wall metabolism, in addition to their functions as signaling molecules
1233 (Pietrowska-Borek et al., 2020). Cell walls are highly diverse across plant tissues and taxa (Hoffmann

1234 et al., 2021) and allow cells to adopt myriad shapes and perform specialized functions that include
1235 nutrient and water absorption (e.g., root epidermal cells), transport (e.g., xylem and phloem), and
1236 secretion (e.g., aerial epidermal and nectary cells). Autodegradation of the plant cell wall allows for
1237 developmental processes that include organ abscission and pollen dehiscence, and might allow for
1238 recycling of some wall components to produce new wall polymers (Barnes and Anderson, 2018).
1239 Overall, the plant cell wall is a fascinating biological environment, one for which we are only beginning
1240 to be able to understand well enough to be able to engineer ourselves.

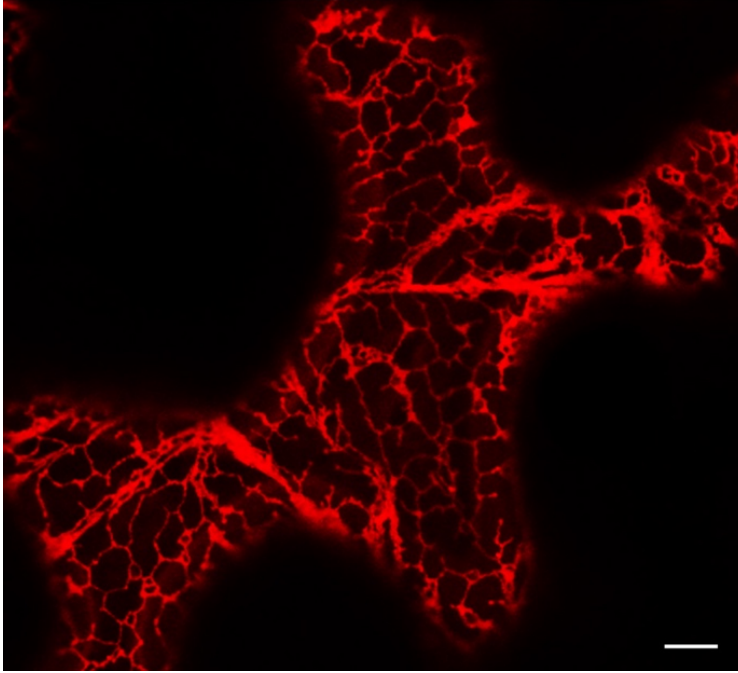
1241
1242 **Acknowledgements:** Thanks to members of the Anderson Lab and the Center for Lignocellulose
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1251 **Figure 1. The nucleus and its constituents (A-B)** Fluorescence **(A)** and electron **(B)** micrographs of
1252 nuclei in Arabidopsis root cells. Nuclei and the plasma membrane were labeled in **(A)** with NPR1-GFP
1253 and FM4-64, respectively. **(C)** Nuclear envelope of Arabidopsis leaf epidermal cells expressing GFP
1254 tagged KAH5 protein WIP1. Chlorophyll autofluorescence was overlaid. **(D)** Nuclear pore complexes
1255 in an Arabidopsis root cell. The electron micrograph shows a tangential section through the nuclear
1256 envelope. Scale bars in B and D: 500 nm. **(E)** The nucleus is defined by the double-layered nuclear
1257 envelope composed of the ONM and the INM, which join at the nuclear pore membrane. The NE
1258 hosts a specific population of proteins. SUN and KASH proteins comprise the LINC complex and
1259 function in various aspects of plant cell biology and physiology. CPR5, PNET1, GP210, and NDC1
1260 are structural components of the plant NPC membrane ring (MR). CNGC15, DMI1, and MCA8
1261 regulate nuclear calcium transport and signaling and affect symbiotic interaction with arbuscular
1262 mycorrhiza. GCP3 and GIP proteins are part of the microtubule nucleation complex and regulate
1263 nuclear stiffness. CRWN and KAKU4 proteins assemble the plant nuclear skeleton and also function
1264 as a platform to interact with INM proteins and regulate chromatin organization through binding
1265 chromatin-associating proteins (such as the PRC2 complex). NEAP proteins bind transcription factor
1266 bZIP18 and may also influence chromatin organization. The CDC48-UFD1-NPL4 trimeric complex
1267 and PUX3/4/5 proteins mediate plant INM-associated protein degradation (INMAD). The nuclear
1268 interior is organized heterogeneously. Typically, heterochromatic regions and chromocenters are
1269 associated with near the nuclear periphery and the nucleolus. Other multivalent biomolecules (e.g.,
1270 proteins and RNAs) aggregate to form various types of membrane-less condensates through the
1271 liquid-liquid phase separation mechanism.
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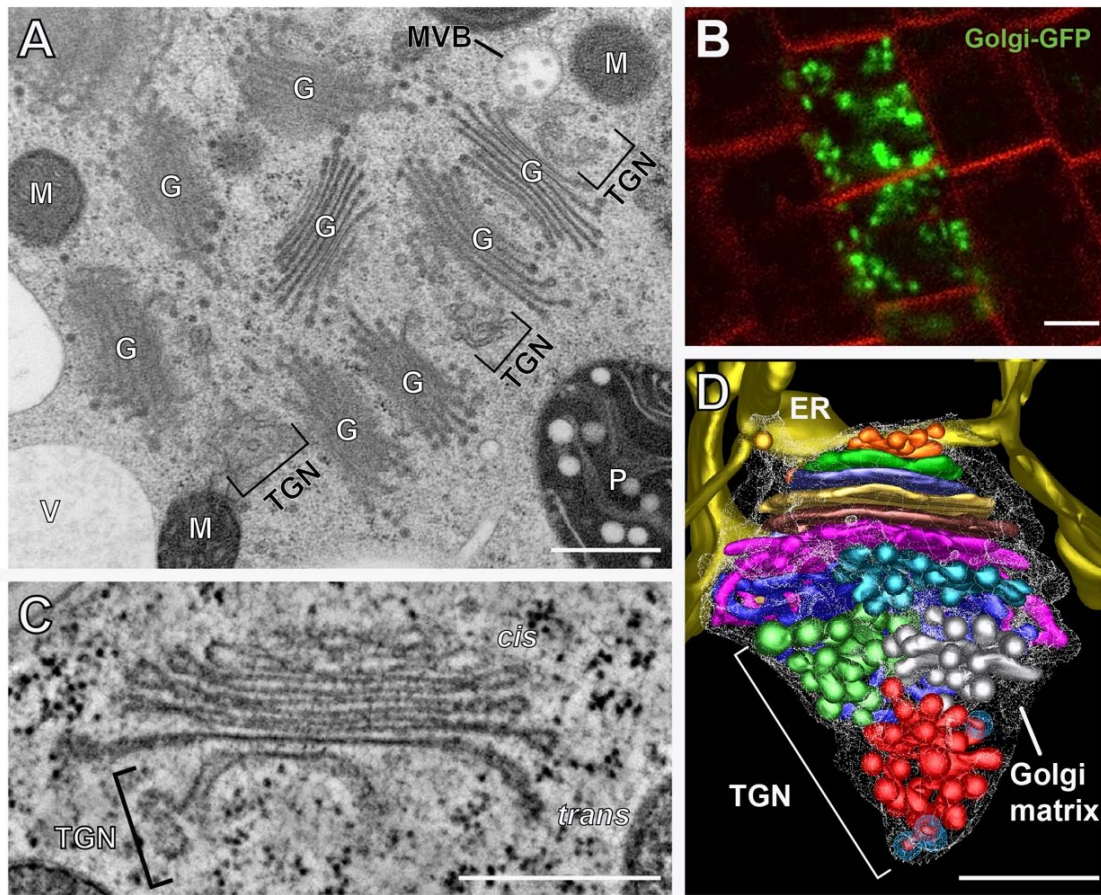
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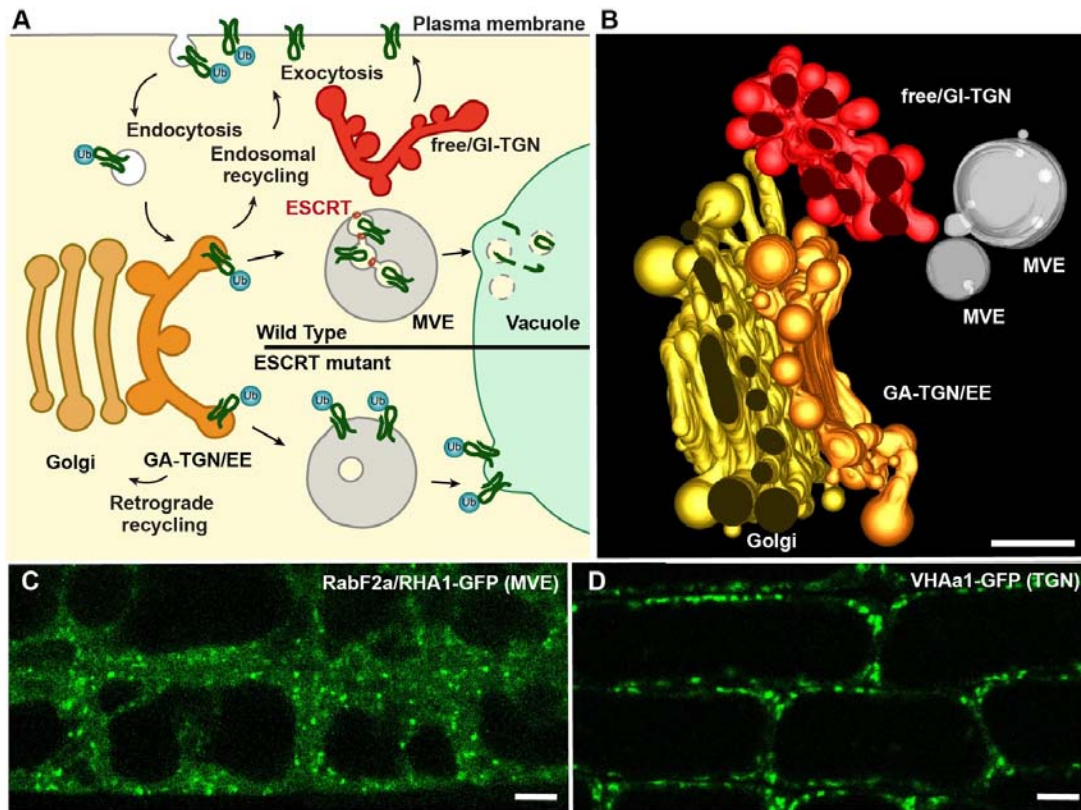
Figure 2. The plant ER forms a distinctive network of membranes at the cell cortex. Confocal microscopy image of a tobacco leaf epidermal cell transiently expressing the fluorescent luminal marker, ER-mCherry (Nelson et al., 2007), which labels the lumen of the bulk ER network. Scale bar = 40 μm .

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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.

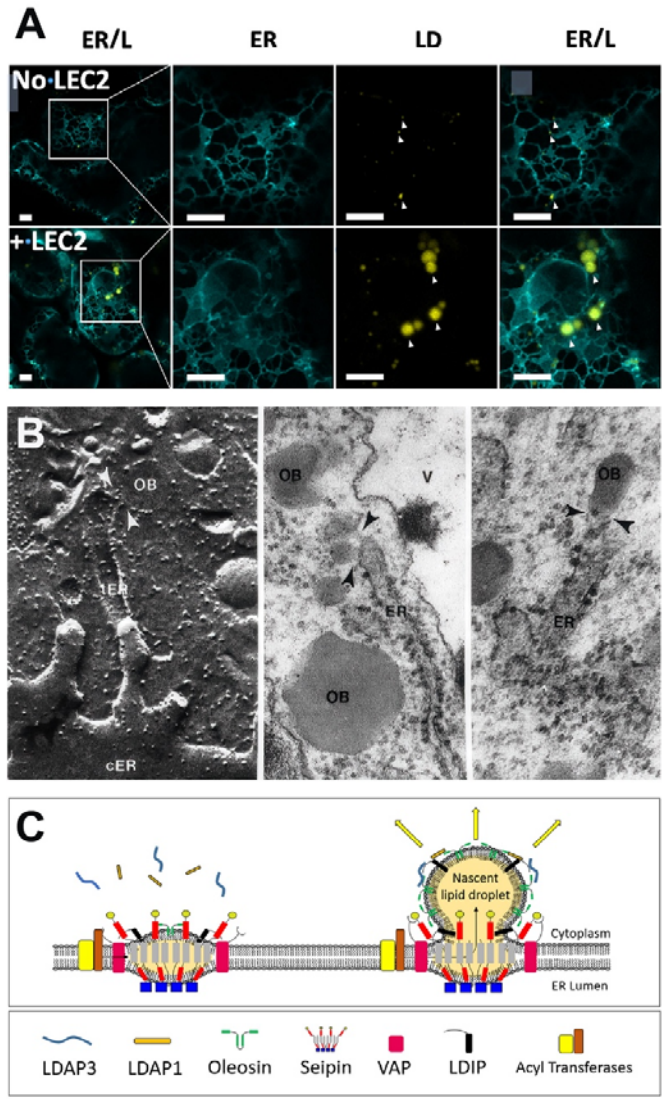


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Figure 4. Plant endosomes. (A) Diagram of plant endosomes and main associated pathways, highlighting the effects on MVE mis-sorting in ESCRT mutants. (B) Tomographic reconstructions of a Golgi, Golgi-associated TGN (GA-TGN), and free/Golgi independent (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).

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Figure 5. The plant vacuole (A)

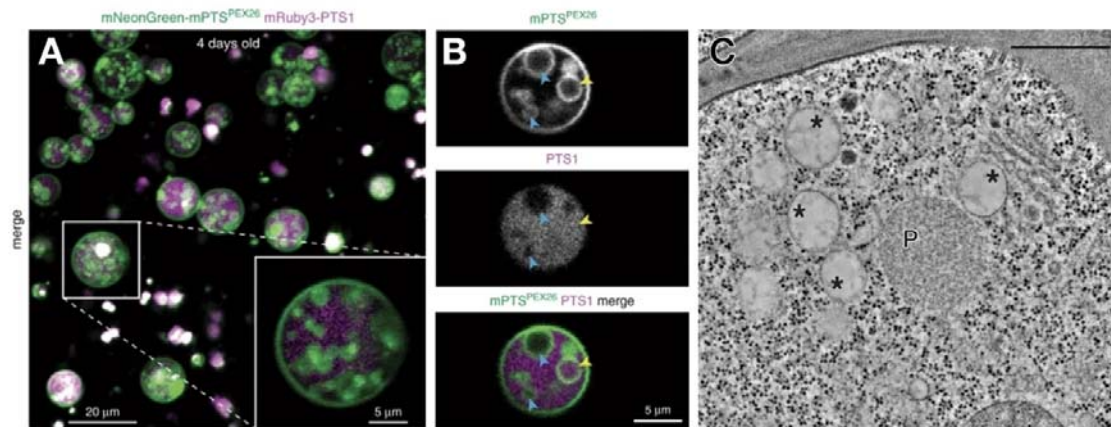


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Figure 6. Spatial association of LD with ER and a model of LD biogenesis (A) Enhanced-resolution fluorescence imaging of the relationship of ER to LDs in leaf mesophyll cells of *N. benthamiana* infiltrated with ER marker and stained with LD-specific 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.

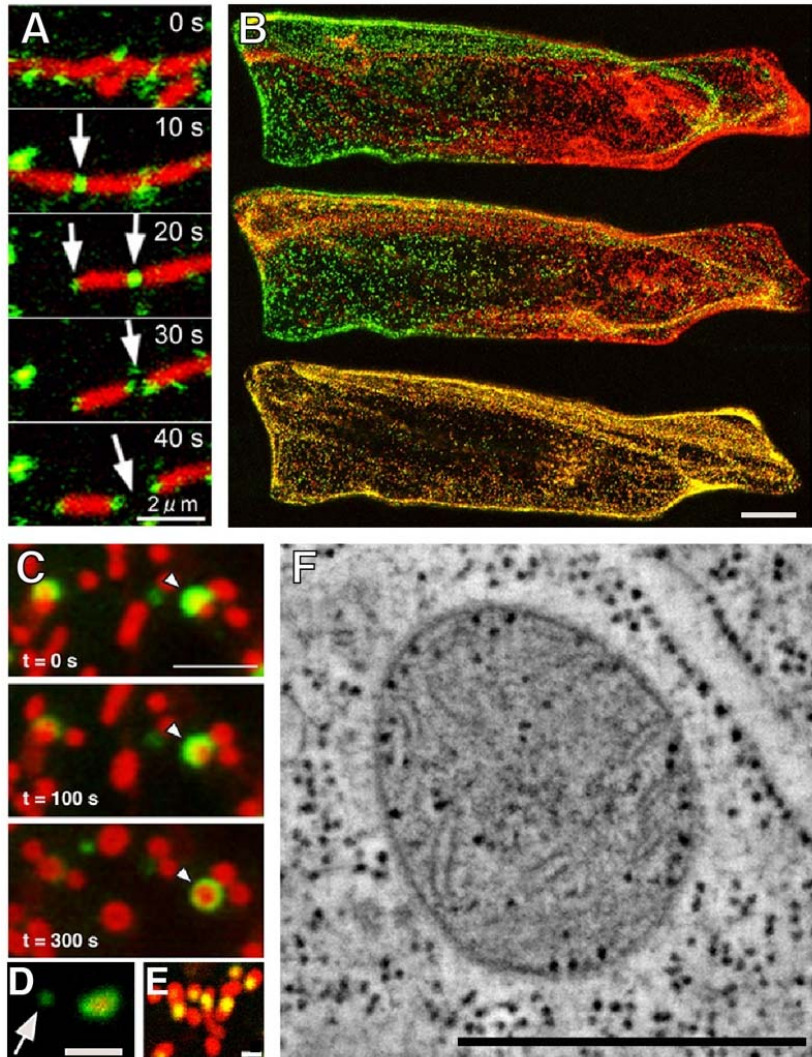
(B) TEM micrographs showing LDs emerging from the ER. Left to right- freeze-fracture; cryofixation; chemical fixation. Arrows mark ER-LD junctions. For scale, ribosomes on the ER membrane are approximately 20 nm in diameter. Electron micrographs are courtesy of Dr. Eliot Herman, University of Arizona.

(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).



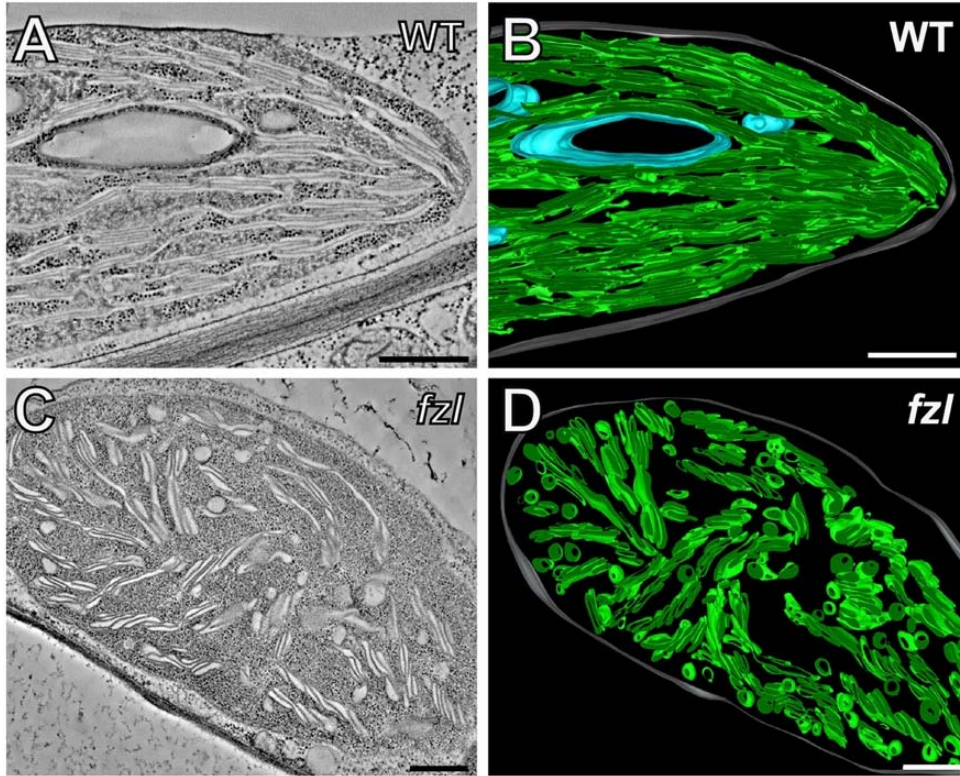
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Figure 7. Microscopic images of peroxisomal structures in Arabidopsis cells. (A) Microscopic image of 4-day-old Arabidopsis cotyledons expressing mNeonGreen with a membrane peroxisomal targeting signal (mNeonGreen-mPTS^{PEX26}; green) and mRuby with 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.



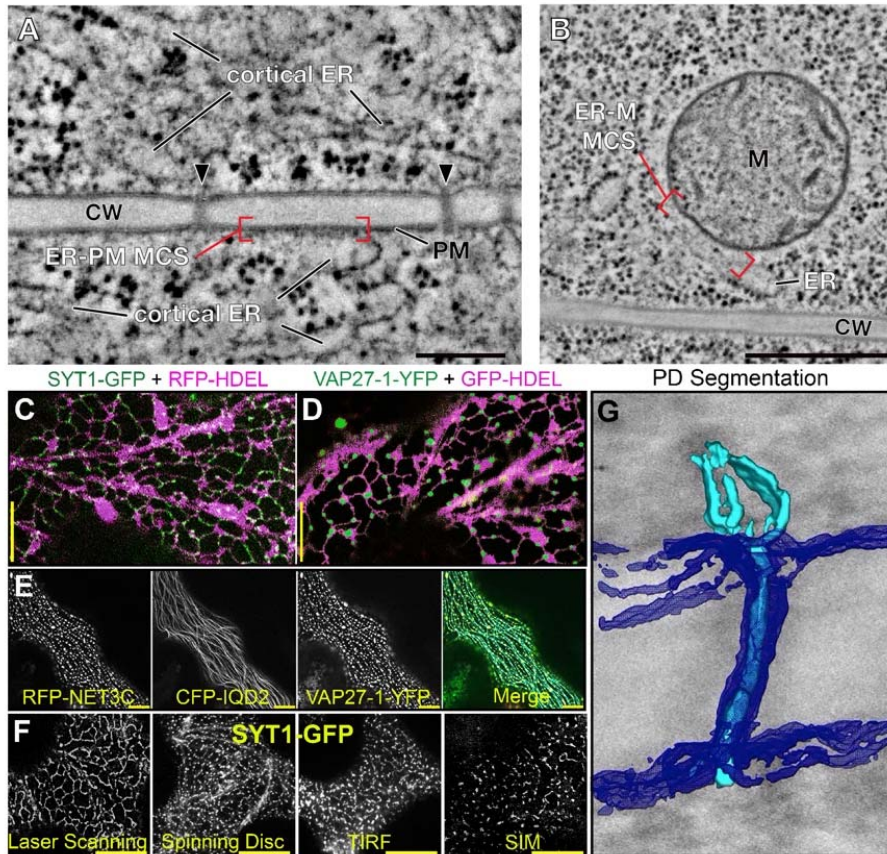
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Figure 8. Microscopy imaging of plant mitochondria dynamics. (A) Five consecutive frames showing mitochondria fission in a tobacco BY-2 cell. The mitochondria are stained red and dynamin-related protein 3A is labeled with GFP (Arimura 2018). (B) Fusion 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, 2 μ m; B, 40 μ m; E, 1 μ m; F, 500nm



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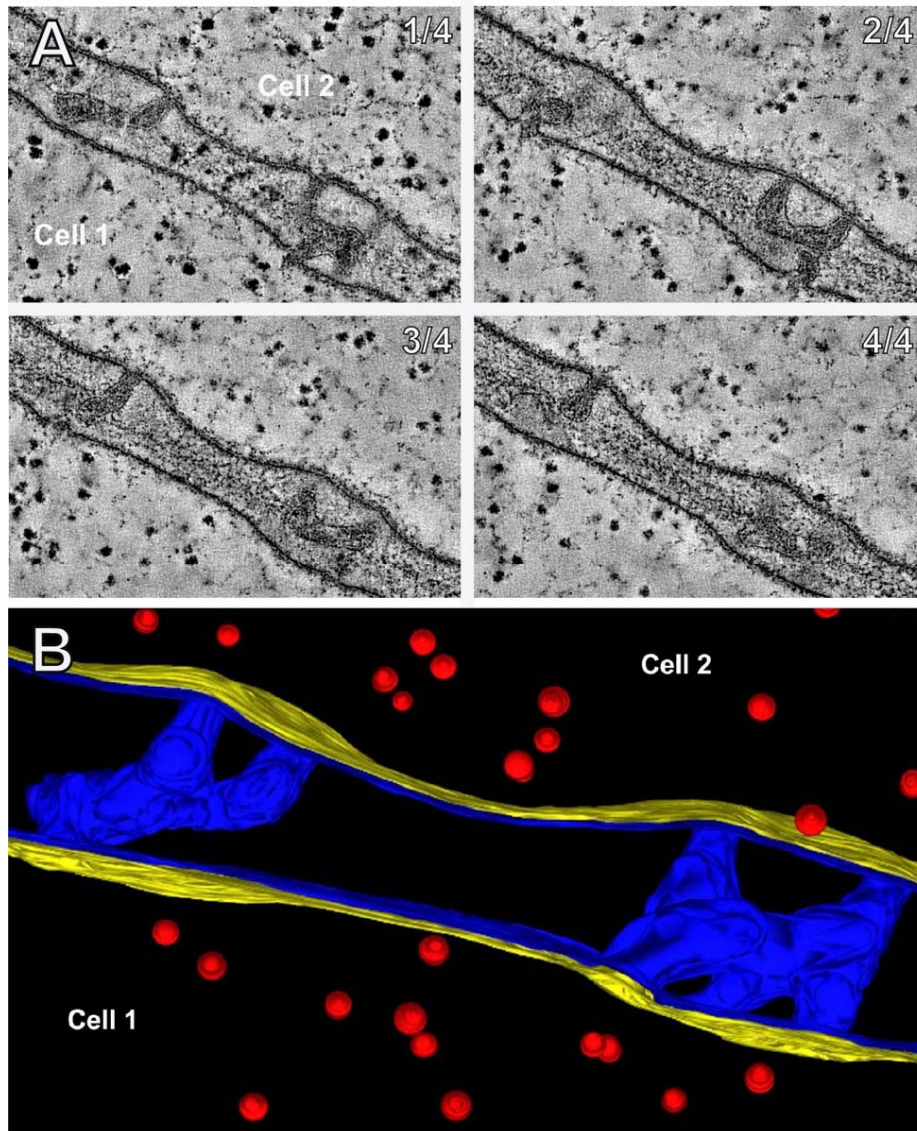
Figure 9. Chloroplast morphogenesis is a highly regulated process. (A) ET slice image of a normal-sized wild-type (WT) chloroplast with typical thylakoid differentiation into stacked (grana) and unstacked domains. (B) 3D model based on the chloroplast in A. (C) ET slice image of an oversized chloroplast (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.



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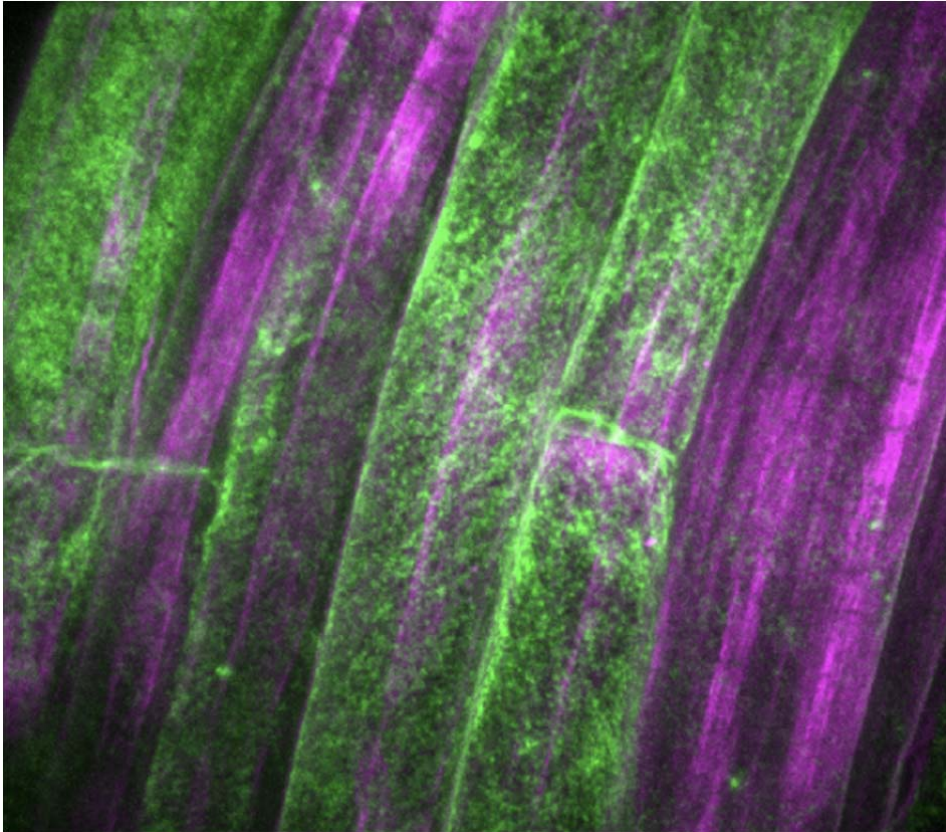
Figure 10. Examples of Membrane Contact Sites in Plants. **(A-B)** ET slice images showing different MCS present in plant cells. an ER-PM contact site (A) and an ER-mitochondrion contact site (B) are shown. Arrowheads mark plasmodesmata. CW: cell wall, M: mitochondrion. Scale bars: 500 nm. **(C-D)** 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.

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1394 **Figure 11.** Structure of branched PD in Arabidopsis tissue revealed by ET. **(A)**
1395 Representative four individual frames from a tomogram (1/4 - 4/4). While the PM is readily
1396 visible in these images the desmotubule is difficult to discern. Central cavities are found in
1397 the vicinity of the middle lamella. **(B)** 3D models of PD generated by tracing the inner (yellow)
1398 and outer (blue) leaflets of the PM in the tomogram in A. The PD on the left consists of two
1399 pores in Cell 2 and one in Cell 1. The PD on the left has two openings to Cell 2 but three to
1400 Cell 1. Ribosomes (red) are shown for scale.

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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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