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# Dynamic membranes—the indispensable platform for plant growth, signaling, and development

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Editorial

Membranes are highly dynamic structures. Though often glossed over, plant cells turnover the lipid and proteins of membranes over time scales from seconds to many hours. Even crude estimates show that the total membrane surface of a typical plant cell is recycled every 90–120 min. These hydrophobic fluid barriers consist of phospholipids, sphingolipids, glycolipids, and sterols, each with unique biochemical and biophysical properties. Membranes contain a wide range of integral membrane proteins crucial for transporting ions and biomolecules, from sugars to miRNAs, across the lipid bilayer. They serve as platforms, also for peripheral proteins, including many assemblies for membrane energization, signal detection and transduction, and enzymes for primary and secondary metabolism. Indeed, membranes are indispensable for plant growth, development, and responses to environmental stimuli. This Focus Issue on Dynamic Membranes captures up-to-date views and perspectives on developments at the forefront of membrane biology research and highlights the most important gaps in our understanding of future studies.

Being impermeable to most polar and charged molecules, membranes divide solute concentrations and support ion gradients, thereby providing cells, organelles, and subcellular compartments with their own source of electrochemical energy, each primary ion gradient functioning as a battery. To build up and maintain subsequent water and membrane potentials, a multitude of transporters, channels, carriers, and pumps are being used. While this will be the main topic of an upcoming Focus Issue on Transport and Signaling, this Focus Issue will include in the online collection two reviews

addressing the topics of membrane function in systemic, long-distance signaling by [Johns et al. \(2021\)](#) and [Klejchova et al. \(2021\)](#). While numerous chemical signaling molecules are known to perform systemic signaling, ranging from mobile hormones and peptides to metabolites and RNAs, there is much evidence for the transmission of parallel information that is mediated by ion fluxes, reactive oxygen species (ROS), and electrical signaling. [Johns et al. \(2021\)](#) introduce the communication pathways that operate over different scales and time frames for systemic signaling within the plant. They discuss recent findings that suggest an unexpected connection between  $\text{Ca}^{2+}$  and ROS in electrical signal propagation, notably following localized herbivory, and its contributions to mounting cross-tissue defense responses. [Klejchova et al. \(2021\)](#) examine the history of plant membrane biophysics, describing how an understanding of transport mechanics helps to define the mechanics of long-distance, spatiotemporal signaling, and bioenergization. They discuss the molecular identities of some of the channels and pumps, emphasizing their entanglement that gives rise to the dynamics of membrane voltage.

Membranes play key roles in vesicular trafficking and cell signaling by hosting-specific proteins but also by providing substrates for the production of various (lipid) second messengers. [Dubois and Jaillais \(2021\)](#) discuss the emerging role of anionic lipids and their specific interaction with target proteins, while [De Jong and Munnik \(2021\)](#) review the current status on lipid-binding domains (LBDs) in target proteins that facilitate signaling and membrane trafficking. Anionic phospholipids include phosphatidic acid (PA),

phosphatidylserine (PS), phosphatidylinositol (PI), and its phosphorylated derivatives, including the phosphoinositides phosphatidylinositol-4-phosphate (PI4P) and phosphatidylinositol-4,5-bisphosphate (PI[4,5]P<sub>2</sub>). While their concentration is low, they are extremely important for membrane functions, acting as biochemical and biophysical “landmarks” that contribute to membrane identity, signaling, and compartment morphodynamics. Each anionic lipid accumulates in specific proportions in different endomembranes according to a unique subcellular pattern, though evidence for the existence of anionic lipid gradients is also emerging (Dubois and Jaillais, 2021). Locally these lipids provide docking platforms for proteins that contain specific LBDs, while at the same time some of these lipid-binding proteins affect local lipid composition—e.g. phospholipases, lipid kinases, and phosphatases (De Jong and Munnik, 2021). Protein crystallography, lipid-binding analyses, subcellular localization studies, and computer modeling have greatly advanced our recent knowledge of how the precision in binding is achieved, which lipids and LBDs are involved, and how this regulates signaling and membrane trafficking in growth, development, and stress responses (Dubois and Jaillais, 2021; De Jong and Munnik, 2021).

Another source of membrane targeting is discussed by Wojcik and Kriechbaumer (2021), who provide new insights into the variety and complexity of protein targeting, and identify signals relevant for certain pathways, including those recently discovered for inner nuclear membrane, peroxisome membrane, and tonoplast (Wojcik and Kriechbaumer, 2021).

In a crowded environment, it can take a long time before molecular partners find each other. Biological membranes have solved this problem through a combination of localized fluidity and compartmentalized subdomains. The nanoscale organization of these subdomains is often based on weak-, local-, and multivalent interactions between lipids and proteins, but they can emerge as large-scale complexes. Smokvarska et al. (2021) offer the Rho of Plant (ROP) family of small G-proteins as example for organizing such complexes. ROPs are involved not only in hormone and stress signaling, but also in fundamental cell biological processes, such as polarity, vesicular trafficking, and cytoskeleton dynamics. Association with membranes is essential for ROP function and targeting, both in micrometer-sized polar domains—often referred to as microdomains—as well as in nanometer-sized clusters, or nanodomains. Smokvarska et al. (2021) review the current status on the formation and maintenance of ROP domains, and propose a model in which nanoscale organization of ROPs in membranes could determine signal specificity, amplification, and integration.

Another group of proteins emerging as markers for plasma membrane nanodomains is REMORINs. These plant-specific proteins are relatively new arrivals on the scene. Gouguet et al. (2021) highlight their involvement in various processes, including plant–pathogen and plant–symbiont interactions, abiotic stress responses, hormone signaling, and cell-to-cell communication.

Beyond the differential distributions of proteins and lipids in subdomains, lipid asymmetry between the two leaflets of a bilayer itself provides another source of chemical heterogeneity for the dynamics of membranes. For example, in vesicular trafficking, both budding and fusion events require an asymmetric phospholipid distribution. One mechanism generating asymmetry between lipid bilayers involves the action of lipid flippases, which are biological pumps that use ATP as an energy source to flip lipids from one leaflet to the other. López-Marqués et al. (2021) review the exciting advances of the P4 and P5 ATPases in this field.

Biological membranes are highly dynamic and deformable, allowing them to form curved, tubular, and flat conformations, each with different biophysical properties. At membrane contact sites (MCSs), the membranes of adjacent organelles come together into a unique three-dimensional (3D) configuration, which forms functionally distinct microdomains and facilitates spatially regulated functions, including interorganellar communication. Rosado and Bayer (2021) review the shaping and function of MSCs, which act as rapid and local responses to cellular perturbations, and summarize the current understanding of how structural changes confer functional specificity to cellular territories.

Live-cell imaging of targeted fluorescent proteins has revealed many new dimensions of membrane dynamics. These techniques draw on lipid biosensors, tagged membrane proteins, and signal transducers. These approaches have uncovered rapidly induced organelle responses among others. Several organelles, including plastids, mitochondria, and peroxisomes, extend and retract thin tubules—so-called stromules, matrixules, and peroxules—that enable transfer of material between organelles. Mathur (2021) reviews these thin tubular forms under the common head of “organelle extensions.” These extensions change shape continuously, and in their elongated form considerably increase organelle outreach into the surrounding cytoplasm. These pleomorphic effects reflect their interaction with the dynamics of the endoplasmic reticulum (ER) and cytoskeletal elements. Using foundational images, time-lapse movies, and mutants with increased organelle extensions, Mathur (2021) argues their common role in maintaining plant cell homeostasis.

Sandor et al. (2021) provide additional information on the plasticity of the ER, emphasizing its capacity to rapidly change in structure to accommodate different functions based on intra- and extracellular cues. They focus on an ER structure observed in all eukaryotes, known as organized smooth endoplasmic reticulum (OSER), which consists of symmetrically stacked ER membrane arrays. In plants, this field is relatively new, with structures first described in certain specialized tissues, e.g., phloem sieve elements, and more recently in transgenic plants overexpressing ER membrane-resident proteins. In the Update of Sandor et al. (2021), the current status on plant OSER is highlighted, and mechanisms of formation and potential applications uncovered.

Finally, protein trafficking and organelle biogenesis, too, are highly dynamic events and play important roles in regulating plant growth and development, as well as responses to the environment. Visualization of membrane structure and dynamics require high spatial and temporal resolution, a challenge that has been overcome through a gamut of novel imaging approaches (Sezgin, 2017). Earlier, this was performed with two-dimensional (2D) and 3D confocal laser scanning microscopy (CLSM) live-cell imaging analysis, together with 2D transmission-electron microscope (TEM). These techniques are limited, however, to a 200-nm resolution for CLSM and inevitably engage a trade-off between temporal and spatial information. Recent advances by super-resolution microscopy have substantially improved the spatial resolution of plant membrane dynamics. In Liu et al. (2021), the recent advances in membrane imaging of the plant endomembrane system are discussed. These include 2D and 3D CLSM and TEM, and provide future perspectives of new techniques, including whole-cell electron tomography (ET) and new exciting technologies for sample preparation and visualization under cryogenic conditions such as cryo-focused ion beam (cryo-FIB) milling, cryo-lift-out, cryo-correlative light and electron microscopy (CLEM), and cryo-ET. These new techniques provide an unprecedented opportunity to analyze cellular structures and molecules in their native state in various organisms (Liu et al., 2021).

In closing, we must marvel at the progress that is summarized in these reviews and the breadth of knowledge that they encapsulate. It is profoundly humbling and at the same time deeply satisfying to realize that our understanding of membranes, their composition, function, and integration in the biology of plants is very much rooted in the 20th century. As Klejchova et al. (2021) point out, the concept of membranes as cellular barriers is but a century old, a recognition of their roles in bioenergetics is only just passing its 50th birthday, and our abilities to visualize their molecular

dynamics is still in its infancy. The next 20 years are certain to be exciting!

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