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The Plant Plasma Membrane

Springer
Editors

Angus Murphy is a professor of molecular plant physiology in the Department of Horticulture at Purdue University, Indiana, USA. He received his Ph.D from the University of California, Santa Cruz. His primary research interests are the study of auxin transport mechanisms, the role of auxin transport in plant tropic and environmental responses, and structure function analyses of plant ABCB/G transporters. He currently serves on the editorial board of the Journal of Biological Chemistry, Plant and Cell Physiology, and Frontiers in Plant Science.

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The spontaneous formation of lipid-bounded compartments is one of the preconditions for the genesis of the earliest living cells. Such membranous structures retain essential components, serve as a barrier to intrusion of external contaminants, and, via differential diffusion of ions, generate transient electrochemical gradients that can energize selective exchange processes. In plant cells, the outer barrier plasma-lemma, or plasma membrane, is a highly elaborated structure that functions as the point of exchange with adjoining cells, cell walls, and the external environment. Transactions at the plasma membrane include uptake of water and essential mineral nutrients, gas exchange, movement of metabolites, transport and perception of signaling molecules, and initial responses to external biota. Central to all of these processes is the formation of a chemiosmotic gradient across the plasma membrane that results from ATP-driven proton extrusion. This gradient generates a net negative charge on the inner surface of the membrane and a delta pH of 1.5–2. Selective channels and carriers harness this electromotive force to control the rates and direction of movement of small molecules across the membrane barrier and manipulate the turgor that maintains plant form and drives plant cell expansion. Where required, ATP-dependent transporters mobilize the movement of essential molecules against the gradient.

However, it is erroneous to view the plasma membrane as just a diffusion barrier studded with transport proteins. Like other cellular membranes, the plasma membrane provides an environment in which molecular and macromolecular interactions can occur more efficiently. This is primarily a result of the enhanced efficiency of diffusional interactions taking place in two dimensions, the clustering of proteins in oligomeric complexes via protein–protein or protein–lipid interactions for more efficient retention of biosynthetic intermediates, and the anchoring of protein complexes to enhance regulatory interactions. Coupling of signal perception at the membrane surface with intracellular second messengers also necessarily involves transduction across the plasma membrane. Finally, the generation and ordering of the external cell walls involve processes mediated at the plant cell surface by the plasma membrane.
This volume is divided into three parts. Part I, consisting of five chapters, describes the basic mechanisms that regulate all plasma membrane functions. Chapter “Lipids of the Plant Plasma Membrane” by Furt et al. describes the most fundamental aspect of the plasma membrane – its lipid composition and the ordering of membrane lipids into leaflets and domains. The chapter “Plasma Membrane Protein Trafficking” by Peer describes the mechanisms by which proteins are trafficked to and from the plasma membrane. The chapter “The Plasma Membrane and the Cell Wall” by Sampathkumar et al. describes the role of the plasma membrane in cell wall production as well as the interactions between the plasma membrane surface and the cell walls during development. The chapter “Plasmodesmata and non-cell autonomous signaling in plants” by Lee et al. describes the plasmodesmal structures that provide unique regulated conduits that can partially bridge cell wall barriers to provide direct intercellular interactions. The chapter “Post-translational Modifications of Plasma Membrane Proteins and Their Implications for Plant Growth and Development” by Luschnig and Seifert details the regulatory posttranslational modifications made to many plasma membrane proteins.

Part II describes plasma membrane transport activity. Chapter “Functional Classification of Plant Plasma Membrane Transporters” by Schulz provides an overview of the structure and classification of plasma membrane transporters and uses structural characteristics to classify these proteins into groups. In the chapter “Plasma Membrane ATPases” by Palmgren et al., a similar structural analysis is combined with functional analyses derived from experimental results to describe the ATPases that export protons and calcium at the plasma membrane. Chapter “Physiological Roles for the PIP Family of Plant Aquaporins” by Vera-Estrella and Bohnert uses a similar approach to characterize the aquaporin intrinsic membrane protein channels that transport water and other small molecules in and out of the cell. In chapters “The Role of Plasma Membrane Nitrogen Transporters in Nitrogen Acquisition and Utilization” by Tsay and Hsu, “Plant Plasma Membrane and Phosphate Deprivation” by Nussaume et al., “Biology of Plant Potassium Channels” by Hedrich et al., “Mechanism and Evolution of Calcium Transport Across the Plant Plasma Membrane” by Connorton et al., “Sulfate Transport” by Hawkesford, “Metal Transport” by Atkinson, and “Organic Carbon and Nitrogen Transporters” by Tegeder et al., the regulated transport of nitrogen, phosphorus, potassium, calcium, sulfur, metals, and cellular metabolites across the plasma membrane are described. Chapter “ABC Transporters and Their Function at the Plasma Membrane” by Knöller and Murphy returns to a more structural approach to describe what is currently know about the plasma membrane ATP-binding cassette transporters of the ABCB and ABCG subfamilies. The transporter part of the book is rounded out by a description of hormone transport in chapter “Hormone Transport” by Kerr et al.

Part III of the book describes signaling interactions at the plasma membrane, with chapters describing hormone signaling (chapter “Plant Hormone Perception at the Plasma Membrane” by Pandey), light sensing (chapter “Light Sensing at the Plasma Membrane” by Christie et al.), lipid signaling (chapter “The Hall of Fame:
Lipid Signaling in the Plasma Membrane” by Im et al.), abiotic stress responses (chapter “Plasma Membrane and Abiotic Stress” by Barkla and Pantoja), and biotic interactions (chapter “The Role of the Plant Plasma Membrane in Microbial Sensing and Innate Immunity” by Nürnberg and Küfner).

Although these topics have been the subject of many current and past reviews, they are given a unique treatment in this volume, as we have made an effort to concentrate on events and mechanisms that occur at the plasma membrane rather than discuss mechanisms that occur throughout plant cells. It is hoped that this effort will provide the reader with a strong sense of the unique role that the plasma membrane plays in plant physiology and development. Further, the authors of the individual chapters have made an effort to identify areas where there are substantial gaps in our understanding of mechanisms sited on this critical cellular structure. Finally, we hope to convince the reader that a more complete knowledge of plasma membrane structure and function is essential to current efforts to increase the sustainability of agricultural production of food, fiber, and fuel crops.

Lafayette, USA

A. Murphy

1 May 2010
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Lipids of the Plant Plasma Membrane

Fabienne Furt, Françoise Simon-Plas, and Sébastien Mongrand

Abstract The plasma membrane (PM) is arguably the most diverse membrane of the plant cell. Furthermore, the protein and lipid composition of the PM varies with cell type, developmental stage, and environment. Physical properties of lipids and associate proteins allow the formation of a barrier that is selectively permeable to macromolecules and solutes. As the plasma membrane delineates the interface between the cell and the environment, it is the primary part of signal recognition and transduction into intracellular responses for nutritional uptake/distribution, environmental responses, and developmental signaling. Many essential PM functions are carried out by proteinaceous components. However, PM lipids play a crucial role in determining cell structures regulating membrane fluidity and transducing signals. The composition and physical state of the lipid bilayer influence lipid–protein and protein–protein associations, membrane-bound enzyme activities, and transport capacity of membranes. Analyses of membrane function require highly selective and efficient purification methods. In this chapter, we first briefly review the methods to isolate PM from plant tissue and describe the lipid content of purified membranes. We further examine the involvement of different lipid species on signaling events that allow the plant cell to cope with environmental fluctuations. Finally, we discuss how regulated segregation of lipids inside the PM is of crucial importance to understand signaling mechanisms.
1 Biochemical Analysis of Plant Plasma Membrane

1.1 Isolation of Highly Purified Plasma Membrane Fractions from Plant Tissues

Isolating highly purified fractions of organelles or membranes from other cellular compartments is a key requirement for in-depth identification and characterization of membrane proteins and lipids. PM fractions were first purified from microsomal membranes (a mix of various cellular membranes) by their high density on flotation gradient after high-speed ultracentrifugation. This approach has been shown to inefficiently fractionate the PM from other membranes, particularly the tonoplast. Higher efficiency partial separations of PM vesicles by free flow electrophoresis have also been reported (for review Canut et al. 1999).

In the early 1980s, Larsson developed an effective tool for preparative isolation of PM fractions by partitioning microsomal fractions in aqueous polymer two-phase systems using aqueous solutions of polyethylene glycol (PEG) and dextran (Widell et al. 1982). The method is rapid and uses only standard laboratory equipment. The separation is continued on after stirring, the system spontaneously forms two phases, and microsomal membranes separate according to differences in surface properties rather than in size and density. As PM vesicles are more negatively charged than most other cellular membranes, they are recovered into the upper phase. Up to 98% purity can be reached with this method. This technique therefore represents an attractive alternative to conventional fractionation protocols and has been shown to be effective for multiple plant tissues (root, leaves, etc.). The respective proportions of the two polymers, pH, and the ionic strength of the aqueous phase are the crucial parameters to ensure PM purity (Larsson et al. 1987).

The outer (apoplastic) side of the PM bilayer is negatively charged. Consequently, PM vesicles purified by two-phase partition are mostly sealed in a right-side-out topology. Morphological studies of highly purified PM fractions pelleted by centrifugation, fixed by chemical or high-pressure freeze substitution, and embedded in resin showed that these fractions contained mostly membrane vesicles ranging from 50 to 500 nm in diameter, should the majority of which exhibited a diameter between 200 and 300 nm. Higher magnifications showed that the membrane leaflets were highly contrasted and 8 nm thick, which corresponds to in situ observations of PM in intact tissues (Fig. 1).

1.2 Lipid Content of Plant Plasma Membrane

The lipid-to-protein mass ratio in the plant PM is ca. 1. However, considering that the average lipid molecular mass is far below than the average molecular mass of protein, the lipid-to-protein molar ratios in the PM range from 50:1 to 100:1. Analyses of highly purified PM lipid extracts are performed by thin layer
chromatography (TLC), gas chromatography (GC), high-pressure liquid chromatography (HPLC), and GC/HPLC coupled to mass spectrometer. More recently, mass spectrometry approaches have been adapted to “lipidomic” analysis. For instance, tandem mass spectrometry (MS/MS) or MS\(^3\) strategies that can simultaneously identify multiple lipid species are required because they provide structural information regarding polar head groups, length, unsaturation of fatty acid chains, and presence of glycosyl units in lipid molecules. However, as there are often close to 1,000 lipid species in a single cell (Van Meer 2005), even MS/MS methods are not sufficient to fully resolve the complexity of lipid mixtures. Therefore, although the results of lipid analyses from several plant species have been available for many years, a complete characterization of the plasma membrane is still lacking.

Three main classes of lipids exist in the PM: glycerolipids (mainly phospholipids), sterols, and sphingolipids (Fig. 2). Except for complex sphingolipids, which are synthesized in the trans-Golgi network, most lipids are assembled in the endoplasmic reticulum and are transported through the secretory pathway to the PM (Van Meer and Sprong 2004). Briefly, fatty acids are synthesized in plastids and mainly exported to the ER S-acylated to coenzyme A to enter the Kennedy pathway for phospholipids (see for review Bessoule and Moreau 2004) and sphingolipids pathway (see for review Pata et al. 2010).
A great diversity is observed in PM lipid composition across plant species (e.g., Uemura and Steponkus 1994; Uemura et al. 1995) and within the different organs of a given plant species (e.g., Sandstrom and Cleland 1989). However, compared with other cellular membranes, the PM is always strongly enriched in sterols and sphingolipids with a sterol-to-phospholipid ratio ranging from 0.6 to 1.5 (Table 1). PM lipids are generally classified by abundance as well as by structure: the most abundant are often referred to as “structural lipids” and less abundant as “signaling lipids.” These two categories are somewhat artificial as several lipids referred to as examples of abundant lipids may exhibit signal-transducing function. This chapter focuses on the biosynthesis of signaling lipids rather than on the synthesis of structural lipids (see for review Bessoule and Moreau 2004; Pata et al. 2010), and clustering of lipid and protein in PM microdomains.

1.2.1 Glycerolipids

Glycerolipids are tripartite molecules made up of a head group nucleated by a glycerol moiety to which two fatty acyl chains are esterified at positions sn1 and sn2 as shown in Fig. 2. The third position consists of a hydroxyl group to form diacylglycerol (DAG) and is further modified to form the different classes, namely, glycolipids and phospholipids (Fig. 3). With the notable exception of PM-localized digalactosyl diacylglycerol (DGDG), glyco-glycerolipids are mostly present in plastids. DGDG replaces phospholipids in the PM bilayer during plant phosphate deprivation to preserve the integrity of the membrane and remobilize the phosphate pool (e.g., Andersson et al. 2005; Tjellstrom et al. 2008).