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Sterol Endocytosis and Trafficking in Plant Cells

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Abstract Structural sterols are integral components of biological membranes. They regulate membrane permeability and fluidity, and they influence the activity of membrane proteins. In *Arabidopsis*, their composition is critical for normal plant development. The endocytosis and recycling of plasma membrane sterols display similar pathways as some polarly distributed proteins, and thus sterol-dependent trafficking can be an integral part of the polarity establishment in plants. Here, we summarise recent data about sterol endocytosis and sterol trafficking within endocytic pathways in different aspects of cell development in plants.

1 Introduction

Biological membranes are dynamic supramolecular and multicomponent structures that form boundaries of the cell and of intracellular compartments. They act as barriers, and in addition they play an active role in functional processes like signal transduction and intracellular trafficking.

Lipids belong to structural components of membranes and at the same time serve as a solvent for membrane proteins. The composition of lipids and their arrangement in the lipid bilayer therefore decide the physical properties of the membrane as well as the functionality of membrane proteins. Additionally, membrane-associated functions like the recruitment and assembly of membrane-bound multicomponent complexes of cytosolic proteins depend on the structure and distribution of membrane lipids (reviewed in van Meer and Sprong, 2004).

The behaviour of the membrane as a supramolecular continuum is maintained during membrane fusion, fission and all kinds of trafficking events mediated by vesicles including endocytosis. Intracellular membrane flow through vesicular trafficking redistributes not only a plethora of different cargoes, but also regulates the exchange and renovation of the membranes of different compartments within the cell. By endocytosis, an energy-dependent process conserved in all eukaryotic cells, substances of different nature be-

come internalised through the cell surface. Thus, both intracellular transport via exo- and endocytosis and the maintenance of the identity and functional diversity of distinct organellar membranes in the cell are highly regulated.

Structural sterols are essential components of the plant plasma membrane supporting not only the structure of the membrane, but also influencing considerably the physical and physiological properties. Genetic studies of the sterol biosynthetic pathway in plants revealed, in addition, that they regulate and modulate different aspects of plant development (Clouse, 2002). Proper understanding of membrane dynamics requires a basic clarification of how different membranes are specialised and how plasma membrane-resident processes are regulated. Thus, an understanding of endocytosis and recycling of sterols as well as sterol-mediated internalisation of different cargoes is an important issue in the study of the membrane physiology of plant cells. In this chapter, we therefore address the role of sterols in dynamic membrane trafficking processes, and we summarise data about sterols and their structural and physiological functions in plant cell membranes.

2
General Concept of Endocytosis: Cooperation of Lipids and Lipid-Associated Proteins

Membrane lipids play a pivotal role in most aspects of plant life such as growth, cell differentiation and response to the environment. They are involved in signal transduction, membrane trafficking and organisation of the cytoskeleton. The composition and distribution of phospholipids and of sterols in the plasma membrane are also significant for endocytosis.

2.1
Phospholipids Promote Curvature of Membranes

Curvature of the membrane is a first step and an important physical prerequisite for vesicle formation. The structure, size and chemical modification of phospholipids can induce tension on the membrane. The resulting inward or outward curvature depends on the accumulation and combination of lipid species in certain membrane domains (Kooijman et al., 2003). It is promoted by the asymmetric distribution of lipids in the bilayer (Farge et al., 1999), as was shown for instance for aminophospholipids like phosphatidylethanolamine and phosphatidylserine within the cytoplasmic leaflet of Golgi, endosomal and plasma membranes. These lipids contribute to the vesicle budding competence of diverse membranes (Pomorski et al., 2003). For establishing asymmetry, special aminophospholipid translocators like flippases translocate phospholipids through the membrane. In yeast, transmembrane lipid translocation and subsequent proper vesicle budding re-