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SNAREs in Plant Endocytosis and the Post-Golgi Traffic

Masa H. Sato[1] (✉) · Ryosuke L. Ohniwa[2] · Tomohiro Uemura[3]

[1]Faculty of Human Environmental Sciences, Kyoto Prefectural University, Shimogamo-nakaragi-cho, Sakyo-ku, 606-8522 Kyoto, Japan
mhsato@kpu.ac.jp

[2]Graduate School of Biostudies, Kyoto University, Yoshidanihontsu, Sakyo-ku, 606-8501 Kyoto, Japan

[3]Molecular Membrane Biology Laboratory, RIKEN Discovery Research Institute, 2-1 Hisosawa, Wako, 351-0198 Saitama, Japan

Abstract In eukaryotic cells, the transport vesicles carry various cargo proteins from a donor compartment to a target compartment, and discharge the cargo into the target compartment by fusing with the membrane of the target compartment. SNARE molecules have a central role for initiating membrane fusion between transport vesicles and target membranes by forming a specific trans-SNARE complex in each transport step. In higher plants, the numbers of SNARE molecules are greater than those of yeast and mammals, suggesting a higher complexity of membrane traffic in higher plant cells.

In this chapter, we will focus on the functions and subcellular localizations of plant SNARE molecules and discuss the complexity and evolution of endocytosis and the post-Golgi traffic in the higher plant cells.

1 Introduction

In eukaryotic cells, endocytosis starts from the plasma membrane to take up macromolecules, particular substances, plasma membrane surface proteins as well as lipid components of the plasma membrane by forming endocytic coated vesicles. Most of the internalized cargo molecules residing in the transport vesicles are then transported via the endocytic pathway to the lysosomes or vacuoles, where the transported proteins are finally degraded, although some molecules are recycled in the endosomes back to the cell surface.

In mammalian cells, endosomes represent organelles involved in the endocytic pathway, and they are mainly classified into four classes; early endosomes, late endosomes, recycling endosomes, and lysosomes. Early endosomes and recycling endosomes are tubulo-vesicular compartments distributed throughout the peripheral and perinuclear cytoplasm. They are regarded as sites of the recycling of internalized proteins and membranes to the plasma membrane. Late endosomes are defined as vesicular structures that accumulate internalized components after their passage through early

endosomes. Late endosomes are also called multivesicular bodies (MVBs) because they often contain abundant internal membranes. Lysosomes contain hydrolytically active hydrolases and are involved in the degradative process (Mellman, 1996; Brodsky et al., 2001).

In plant cells, the occurrence of endocytosis has been in doubt for a long time because the endocytic process was regarded as unlikely to occur under high turgor pressure (Cram, 1980). However, a lot of evidence supports the occurrence of endocytosis in higher plants now (Low and Chandra, 1994; Battey et al., 1999; Holstein, 2002; Šamaj et al., 2004, 2005). For example, calculations of membrane flow during secretory vesicle fusion indicated that an endocytic pathway must exist for the retrieval of membrane material into the cell (Phillips et al., 1988). Studies using electron-dense endocytic markers applied to plant protoplasts showed that the sequential movement of these markers through the endocytic compartments was analogous to that found in animal and yeast cells (Nishizawa and Mori, 1977; Joachim and Robinson, 1984; Hillmer et al., 1986). Recently, fluorescent dyes, FM1-43 and FM4-64, were used for tracing the endocytic process in both protoplasts and intact plant cells (Ueda et al., 2001; Emans et al., 2002). These dyes initially label the plasma membrane, but are gradually internalized and then stain rapidly moving punctate organelles (Šamaj 2005, Šamaj et al., 2005). Finally, these dyes are delivered to vacuoles via ring-like organelles (Ueda et al., 2001). The endocytic process is inhibited by low temperature treatment, and inhibitors such as wortmannin, which is a phosphatidylinositol 3-kinase inhibitor, or latrunculin B, a F-actin depolymerizing drug, indicating that this process is strongly energy and actin dependent (Emans et al., 2002; Baluška et al., 2004). Furthermore, several recent studies have indicated that endocytosis plays important roles in the establishment and maintenance of the asymmetric distribution of particular membrane protein such as AtPIN1 (Geldner et al., 2001; Friml et al., 2002), and in the sequestration of receptor-like kinases (Shah et al., 2002). Thus growing evidence supports that endocytosis plays various important roles in plant physiology.

Most of the molecules involved in the endocytic process are highly conserved in plant cells (Sanderfoot and Raikhel, 1999; Sanderfoot et al., 2000; Holstein, 2002; Šamaj et al., 2004; Sanderfoot and Raikhel, 2003). In particular, SNARE molecules have a central role for initiating membrane fusion between transport vesicles and target membranes by forming specific trans-SNARE complexes throughout the fusion process.

In this chapter, we will firstly review the endocytic organelles so far identified in plant cells and then discuss the SNARE molecules that are involved in each fusion step.