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# Dynamin-Related Proteins in Plant Endocytosis

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**Abstract** Over the past decade, it has become evident that multiple endocytic pathways operate in eukaryotic cells, and several of these are dependent on dynamins and dynamin-related proteins (DRPs). Many members of the DRP superfamily possess the ability to self-assemble into long spiral polymers that wrap around lipid bilayers and thus facilitate tubulation and vesicle pinching from the plasma membrane and other membrane compartments, a process that is fundamental for endocytosis. Here, we discuss the roles of dynamins and DRPs in plants. DRPs have been shown to be present at different subcellular locations in plant cells including the cell plate, plasma membrane, Golgi apparatus, vesicles, mitochondria, chloroplasts, and peroxisomes. *Arabidopsis* contains 16 DRP members that are grouped into six functional subfamilies (DRP1–6) on the basis of their phylogeny and the presence of functional motifs. Members of the DRP1 subfamily are closest to soybean phragmoplastin and mediate membrane tubulation at the cell plate. The DRP2 subfamily members represent the bona fide plant dynamins characterized by the presence of a pleckstrin homology (PH) domain in the middle of the molecule and a proline-rich (PR) motif near the C-terminus; they are involved in membrane recycling at the cell plate and the trans-Golgi region. The DRP3 subfamily does not contain PH or PR motifs; their function has been implicated in the division of mitochondria and peroxisomes, whereas the DRP5 subfamily in *Arabidopsis* is likely to play a role in plastid division. A DRP5 ortholog from the red alga *Cyanidioschyzon* has recently been shown to be a component of the chloroplast outer division-ring on the cytoplasmic face of the plastid double membrane. Finally, the DRP4 subfamily contains orthologs of the animal antiviral Mx proteins, but their function has not yet been established, and the role of DRP6 is entirely unknown so far. It is obvious that plant cells employ unique DRP subfamilies to carry out the mechanochemical work required for membrane deformation and segregation in various membranous compartments. However, to understand the function of DRPs in further detail, much is yet to be learned about the proteins that apparently interact with them to regulate their activity and specify their functions.

## 1 Introduction

A highly dynamic state of exocytosis and endocytosis allows a eukaryotic cell to communicate with its environment, build and maintain membrane structures, and deliver cargo to different subcellular and extracellular compartments. Over the past decade, it has become evident that multiple endocytic pathways operate in animal cells, of which some are dynamin-dependent while others are dynamin-independent. Observations of fruit fly mutant *shibire* that affects endocytosis have clearly demonstrated the role of dynamin in clathrin-coated endocytosis. Plants contain a superfamily of dynamin-related proteins (DRPs, Hong et al., 2003a). Some DRP members appear to act as a "pinchase or popase" that mediates the pinching off of endocytic vesicles from the plasma membrane. Such structures are usually generated during receptor-mediated endocytosis and for membrane recycling. Other members such as DRP1 (phragmoplastin) have been proposed to function as a tubulase that wraps around homotypically fused vesicles and helps transform these round structures into tubular membrane extensions. This creates dumbbell-shaped structures which act as building blocks for the formation of cell plate during cytokinesis in plant cells (Verma, 2001). Thus, plant cells employ unique DRP subfamilies to carry out membrane vesiculation and vesicle tubulation, two basic processes required for the endocytic and exocytic pathways, respectively (Verma and Hong, 2005). Other accessory proteins must interact with DRPs since none of the DRPs is an integral membrane protein and they function at different subcellular locations.

## 2 Dynamin-Related Proteins in Plants

Plant DRPs constitute a superfamily of large GTPases with molecular masses of 60–110 kD (Hong et al., 2003a). They all contain the dynamin signature (L-P-[PK]-G-[STN]-[GN]-[LIVM]-V-T-R) and many of them possess the ability to self-assemble into long spiral polymers that wrap around lipid bilayers and thus facilitate membrane tubulation and vesicle pinching (Verma and Hong, 2005). The first characterized plant DRPs were *Arabidopsis* ADL1 (Dombrowski and Raikhel, 1995) and soybean phragmoplastin (Gu and Verma, 1996). These proteins have since been shown to be present in many plants at different subcellular locations including the cell plate, plasma membrane, Golgi apparatus, vesicles, mitochondria, chloroplasts, and peroxisomes. They have also been implicated in diverse subcellular processes such as cell plate formation, endocytosis, exocytosis, protein sorting to the vacuole and plasma membrane, and organelle division.