

Rab GTPases in Plant Endocytosis

Erik Nielsen^{1,2}

¹Donald Danforth Plant Science Center, St. Louis, Missouri 63132, USA
enielsen@danforthcenter.org

²Department of Biology, Washington University in St. Louis, One Brookings Dr.,
St. Louis, MO 63130, USA
enielsen@danforthcenter.org

Abstract The Rab family is part of the Ras superfamily of small GTPases. In eukaryotes Rab GTPases are present as members of gene families, and the different Rab GTPase isoforms are localized specific intracellular membranes, where they function as regulators of distinct steps in membrane traffic pathways. They perform these regulatory functions through the specific recruitment of cytosolic effector proteins onto membranes. This recruitment occurs when the Rab GTPase is in the GTP-bound, or active, form. Through these recruited effector proteins, Rab GTPases regulate many aspects of membrane trafficking including vesicle formation, actin- and tubulin-dependent vesicle movement, and membrane fusion. The recent sequencing of complete genomic sequences from animal, yeast, and plant organisms has revealed that a number of Rab GTPase families are conserved from yeast to animals and plants. The plant model system, *Arabidopsis thaliana*, contains 57 Rab GTPases, of which 40 distinct Rab GTPase members of four subfamilies RabA (26 members), RabC (three members), RabF (three members), and RabG (eight members) share significant similarity with Rab GTPases implicated in endocytic events in animals and yeast.

In this review we will highlight recent observations of the function of some of these plant Rab GTPases during endocytosis in plants, and discuss possible roles of plant endocytic Rab GTPases in relation to what is currently known in animal and yeast systems.

1

Introduction

In eukaryotic cells, endocytosis is an essential process that is necessary for the delivery of proteins, lipids, and extracellular components to various intracellular destinations. After internalization, selective sorting of cargo within endocytic compartments, budding of vesicle transport intermediates, and the efficient delivery and fusion of transport vesicles with their target membranes are all required for the efficient delivery of endocytic cargo to their correct subcellular destinations. As key regulators of membrane trafficking events, Rab GTPase family members specifically localize to these endocytic compartments and control aspects of these sorting, vesicle budding, and fusion events. Because of their specific subcellular distributions, Rab GTPases have also served as useful markers of the organelles present within the endocytic membrane trafficking pathways in plant, yeast, and animal systems. Further,

the recent genomic sequencing projects which have led to the identification of the full complements of the Rab GTPase families for *A. thaliana* (57 members; Pereira-Leal and Seabra 2001; Vernoud et al. 2003), *S. cerevisiae* (11 members; Vernoud et al. 2003), and *H. sapiens* (~ 60 members; Stenmark and Olkkonen 2001), allows for more complete comparison and analysis of the regulation of endomembrane trafficking pathways in these three eukaryotic systems.

Much progress has been made recently in our understanding of plant endocytic membrane trafficking and the roles of various plant Rab GTPases in these pathways. However, in many cases our understanding of the functioning of these plant Rab GTPases still relies primarily upon the roles defined for their evolutionarily-related counterparts in yeast and mammalian systems. As a result, while recognizing the possibility that some aspects of endomembrane trafficking in plants are likely unique to plants, we will attempt to summarize recent progress in understanding the localization and function of plant Rab GTPases during plant endocytosis and relate this to the current understanding of the roles of Rab GTPases in regulation of endocytosis in animals and yeast.

2

The First Step: Internalization at the Plasma Membrane

In animal cells, several mechanisms have been described by which molecules at the cell surface can be internalized (Fig. 1). The best characterized of these is receptor-mediated, clathrin-dependent endocytosis, in which receptor-ligand binding stimulates receptor protein recruitment into clathrin-coated pits that subsequently invaginate and are pinched off to form clathrin-coated vesicles (CCVs). In addition to this, receptor- and/or clathrin-independent processes, broadly called fluid-phase endocytosis, internalize significant amounts of membrane and solute (Gruenberg and Maxfield 1995). Internalization of cell surface components, such as GPI-anchored proteins, enveloped viruses, and certain plasma membrane proteins can also occur via caveolae, 50–60 nm invaginations in the cell surface of some mammalian cells. This process, which is linked to the propensity of the endocytic cargo to partition into lipid rafts within the plasma membrane, also can occur in cells devoid of caveolae, although the details as yet remain murky. Finally, mammalian cells internalize large particles, such as bacteria, via an actin-dependent process called phagocytosis (Maxfield and McGraw 2004).

In mammals, Rab5 localizes to the plasma membrane and early endosomes (Gorvel et al. 1991), and blockade of Rab5 function through the overexpression of dominant-negative forms of Rab5 inhibits receptor-mediated, clathrin-dependent endocytosis, but not fluid-phase endocytosis (Bucci et al. 1992). More recently, it was shown that Rab5 might also play an active role in formation and budding of clathrin-coated vesicles (McLauchlan et al. 1998).