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Tip Growth and Endocytosis in Fungi

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Abstract Recent advances in molecular cell biology have provided new insights into different cellular processes that all turn out to contribute to polarized cell growth in a variety of model systems used to analyse growth, differentiation and development. Polarized cell growth, although a general feature of the living cell, can be found in a pronounced fashion during pollen tube outgrowth and root hair development in plants, during neurite outgrowth, and during filamentous hyphal growth. Filamentous fungi represent excellent model systems to analyse polarized cell growth owing to their genetic tractability and the ease of generating and keeping mutant strains. Contributing to this is the fact that already a number of fungal genomes have been sequenced, which allows the rapid analysis and comparison of gene function. This has led to the finding that polarized cell growth can be influenced by perturbations in different cellular pathways. Control of polarity establishment and the maintenance of polarized cell growth are exerted by a number of conserved GTP-binding proteins of the Ras/Rho subfamily and their specific regulators that organize the actin cytoskeleton. Hyphal tip growth requires coordination of vesicle transport using actin and microtubule cytoskeletons. Recent evidence has shown that hyphal growth not only depends on polarized secretion but also requires endocytosis, suggesting that the recycling of the membrane and sorting of vesicles is required for fast elongation of hyphal tubes. Key players on the molecular level that direct tip growth and endocytosis in the fungal hyphae based on differential regulation of the actin cytoskeleton are discussed.

1 Introduction

Endocytosis describes the general process of plasma membrane invagination and the generation of intracellular vesicles or endosomes. This process can be used for a variety of tasks such as the engulfment of extracellular particles or molecules and solutes known as phagocytosis and pinocytosis or the internalization of the plasma membrane with membrane-associated proteins (Engqvist-Goldstein and Drubin, 2003). Once internalized these compounds and membranes need to be delivered to specific cellular compartments, such as vacuoles for protein degradation, storage vesicles or recycling endosomes for reinsertion into the plasma membrane. Delivery needs to be a highly

ordered process and regulation of vesicle flow is complicated by the secretory vesicles derived from the trans-Golgi network. *Neurospora crassa*, a fast-growing filamentous ascomycete, shows a tip extension rate of more than 30 μm/min sustained by more than 30 000 vesicles/min fused with the hyphal tip (Collinge and Trinci, 1974). Vesicle delivery, therefore, is a highly dynamic process. This vesicle flow requires intracellular tracks for targeted delivery composed of either the actin cytoskeleton or microtubules. Regulation of the assembly and organization of the actin cytoskeleton may provide crucial signals for the targeted transport of vesicles. Studies in other cell systems with highly polarized growth potential have shown that both exocytosis and endocytosis are required for cell expansion (reviewed by Mellman, 1996).

Even recently the mere existence of endocytosis in filamentous fungal systems was questioned (Cole et al., 1998; Torralba and Heath, 2002). Evidence, particularly based on the exploration of fungal genome sequences as well as on the analysis of mutant strains and time lapse microscopy monitoring the uptake of the membrane-selective lipophilic dye FM4-64, has shown that endocytosis occurs in filamentous fungi and is important for polarized growth (Yamashita and May, 1998; Fisher-Parton et al., 2000; Atkinson et al., 2002; Read and Kalkman, 2003; Walther and Wendland, 2004a, b).

This chapter summarizes genomic, genetic and microscopic evidence for endocytosis in filamentous fungi and merges these data from filamentous fungi and yeasts with our current knowledge on the regulation of cell polarity establishment and the maintenance of polarized hyphal growth via the actin cytoskeleton.

2
Endocytosis in Fungi

Endocytosis has been established as an essential process in a variety of eukaryotic cell systems and fulfils functions such as membrane retrieval and degradation, and internalization of membrane receptors and other signalling molecules (Ayscough, 2004). Endocytosis can generally either be clathrin-/lipid-raft-dependent or clathrin-/lipid-raft-independent. In mammalian systems and in the yeast *Saccharomyces cerevisiae* a large number of genes have been identified encoding proteins that are involved in these processes. The presence of homologues of these genes in filamentous fungi may therefore be considered bona fide evidence for the functional conservation of this process. A variety of fungal genome sequences are available and can be searched for homologues using, for example, the Fungal Blast tool (http://seq.yeastgenome.org/cgi-bin/nph-blast-fungal.pl). By searching the genome sequences of the filamentous ascomycetes *Ashbya gossypii* and *N. crassa* homologues of proteins involved in clathrin-mediated endocyto-