Mycology Answers

How do hyphal tip regions differ from the main body of the hypha in terms of function and activity?

For the majority of fungi the hypha is the main growth form. Hyphae are essentially fine, tubular structures, with a strong and rigid cell wall for protection. All extension and penetration into the substrate occurs at hyphal tips and the nature of this filamentous growth habit enables close contact with, and exploitation of, the surrounding environment. Colonies of growing hyphae are composed of young, ageing and aged hyphae (collectively a mycelium), perhaps with some differentiated structures. Some hyphae may fuse together (anastomose) and in interconnected regions cytoplasm and cytoplasmic components are able to move within the hyphal wall so that the cellular contents are mixed and redistributed within a cooperative system.

Apical regions are very distinctly different from more mature regions of the hypha, both in their cytoplasmic contents and in the biochemical activities that are associated with them. As a result there is a zonation of activity along fungal hyphae. It is clear that hyphal extension is driven from the apical zone and it has been shown that extension only occurs over the apical 30 μm, or less, of active hyphae. In addition, some physiological and biochemical activities can become compartmentalised within hyphae by virtue of the formation of cross walls (septa) and some processes are associated with specific organelles.

The main characteristic of the apical zone is the presence of large numbers of small vesicles, largely to the exclusion of other organelles. These vesicles are tiny membrane-bound bodies containing various biochemical components. It is notable that in the dense cytoplasm of this region there is a general lack of other organelles at the extreme tip, although large numbers of mitochondria and amounts of endoplasmic reticulum are to be found immediately behind this vesicle-rich zone. It has been recognised for some time that the vesicles are involved in cell wall synthesis, delivering wall polymers and appropriate enzymes to the apex. This region appears to act as a "supply centre" distributing very large numbers of vesicles to the extending wall to enable tip growth. It has been estimated that 38,000 vesicles per minute fuse with hyphal tips in active mycelium of *Neurospora crassa.*

The highly vesicular region at tips of hyphae was first noticed by light microscopy as a dark staining body which was named the Spitzenkörper (apical body). Following the application of electron microscopy and video microscopy it has become clear that this is a highly complex and dynamic region that appears to influence tip growth and the direction of hyphal extension. If the direction of growth of a hypha alters the Spitzenkörper becomes displaced towards the new direction of extension to supply vesicles directly to the newly expanding wall. Although the Spitzenkörper is an important functioning component of the cytoplasm it is not strictly an organelle because it is not delimited by a membrane. It is however, a complex zone with distinct structure. It is far from being simply a random collection of vesicles.

Different types of vesicles and vesicle arrangements are found in this region. Some vesicles are small (micro vesicles, 30 nm diameter), but others are larger (70-90 nm diameter). Among the larger vesicles some are electron-dense and some more electron-transparent, suggesting different contents and/or functions. The arrangement of these vesicle types varies in the apical domes of hyphae of different species of fungi. The packing of vesicles (vesicle density) varies giving rise to the formation of clusters and clouds of vesicles around a central core. When viewed under the microscope the core of the Spitzenkörper may appear light (phase-light) or dark (phase-dark) and granular. Within the fungi eight different arrangements of vesicle clusters and core morphologies have now been described in growing hyphae, although the significance of these differences is not yet well understood.

In addition to the rigid support of the cell wall surrounding the hypha there are components within the cytoplasm, and particularly at the tip region, which act as a highly dynamic structural skeleton (cytoskeleton). In addition, these components aid in generating forces and effecting movements within hyphae. Organelles move through hyphae and can traverse colonies, passing through interconnected hyphal filaments. It is clear that these movements are not simply the result of bulk flow of cytoplasm.

In some instances organelles may move in opposite directions in the same hypha. Some organelles move very quickly and the passage of different organelles may be effected by different mechanisms. The supply and direction of vesicles towards the tip region is of great importance in the growing hypha. The Spitzenkörper includes, and has associated with it, a meshwork of microtubules and microfilaments in addition to the high concentration of vesicles. Microtubules are composed of the protein tubulin and generally lie parallel to the long axis of hyphae. These, together with microfilaments, composed of the protein actin, and also a number of other associated proteins, have a primary role in vesicle transport and the regulation of vesicle supply to the extreme apex. They are likely to have a role in the positioning and migration of organelles, generating forces for movement of cellular inclusions. The cytoskeleton also has an important role at regions further removed from the tip and is probably involved in maintaining the position of organelles within the tubular hypha and also the arrangement of chromosomes at nuclear division.

Some of the major structural components of the fungal cell wall are present as cross-linked strengthening filaments (chitin, chitosan, ß-1,3-glucan), while other compounds are present as more amorphous packing materials (xylomanno-proteins) that help to build up the overall structure and protect the underlying membrane. The biosynthesis of these individual polymers is now fairly well understood. However, what is much less well known are the mechanisms by which these materials are incorporated into the wall structure. It is likely that the polymers are supplied to the apical region of the wall packaged in the vesicles that collect in the Spitzenkörper region, delivered there by activities associated with the cytoskeleton. The variable population of vesicles will carry the range of components required at the tip. It is likely that in some cases the vesicles carry materials ready, or almost ready, for direct assembly into the wall structure. In other instances enzymes may be delivered to the hyphal tip region, some of which may be in an inactive form for transport. It is likely that elements of wall component synthesis take place at, or very near, the region where incorporation will occur.

The morphological and biochemical organisation of the tip region of growing hyphae is distinctly different from that of other hyphal zones. It is the site where new wall and membrane components are incorporated into the structure and the supply and final direction of these must be under very precise control mechanisms. There must also be good communication with the main body of the hypha. This is a highly integrated system and although a great deal is known about the components present and their organisation, there is still a great deal to be determined with regard to the overall operation and control systems at the hyphal tip.

Susan Isaac
School of Biological Sciences,
Life Sciences Building,
University of Liverpool,
Crown Street, Liverpool, L69 7ZB