

Ultrastructure and Function of Fungal Cells

1- The Fungal Cell Surface

The fungal cell wall is a dynamic structure that protects the cell from changes in osmotic pressure and other environmental stresses, while allowing the fungal cell to interact with its environment. The structure and biosynthesis of a fungal cell wall is unique to the fungi, and is therefore an excellent target for the development of anti-fungal drugs.

In filamentous fungi, cell-wall formation and organization is intimately bound to the process of apical growth. Thus, for example in *Neurospora crassa*, the wall is thin (approximately 50 nm) at the apex but becomes thicker (approximately 125 nm) at 250 μm behind the tip. The plasma membrane component of the fungal cell envelope is a phospholipid bilayer interspersed with globular proteins that dictates entry of nutrients and exit of metabolites and represents a selective barrier for their translocation.

Ergosterol is the major sterol found in the membranes of fungi, in contrast to the cholesterol found in the membranes of animals and phytosterols in plants. This distinction is exploited during the use of certain antifungal agents used to treat some fungal infections, and can be used as an assay tool to quantify fungal growth. The periplasm, or periplasmic space, is the region external to the plasma membrane and internal to the cell wall.

In yeast cells, it comprises secreted proteins (mannoproteins) and enzymes (such as invertase and acid phosphatase) that are unable to traverse the cell wall. In filamentous fungi, the cell membrane and wall may be intimately bound as hyphae and are often resistant to plasmolysis.

Table 1 The major polymers found in different taxonomical groups of fungi, together with the presence of perforate septa in these groups

Taxonomic grouping	Fibrillar polymers	Matrix polymers	Perforate septa present or absent
Oomycetes	$\beta(1,3)$ -, $\beta(1,6)$ -Glucan Cellulose	Glucan	Absent
Chytridomycetes	Chitin; glucan	Glucan	Absent
Zygomycetes	Chitin; chitosan	Polyglucuronic acid; glucuronomannoproteins	Absent
Basidiomycetes	Chitin; $\beta(1,3)$ -, $\beta(1,6)$ -glucans	$\alpha(1,3)$ -Glucan; xylomannoproteins	Present (mostly Dolipore)
Ascomycetes/ Deuteromycetes	Chitin; $\beta(1,3)$ -, $\beta(1,6)$ -glucans	$\alpha(1,3)$ -Glucan; galactomannoproteins	Present (mostly simple with large central pore)

Ultrastructural analysis of fungal cell walls reveals a thick, complex fibrillar network. The cell walls of filamentous fungi are mainly composed of different polysaccharides according to taxonomic group. For example, they may contain either **chitin, glucans, mannoproteins, chitosan, polyglucuronic acid or cellulose**, together with smaller quantities of proteins and glycoproteins.

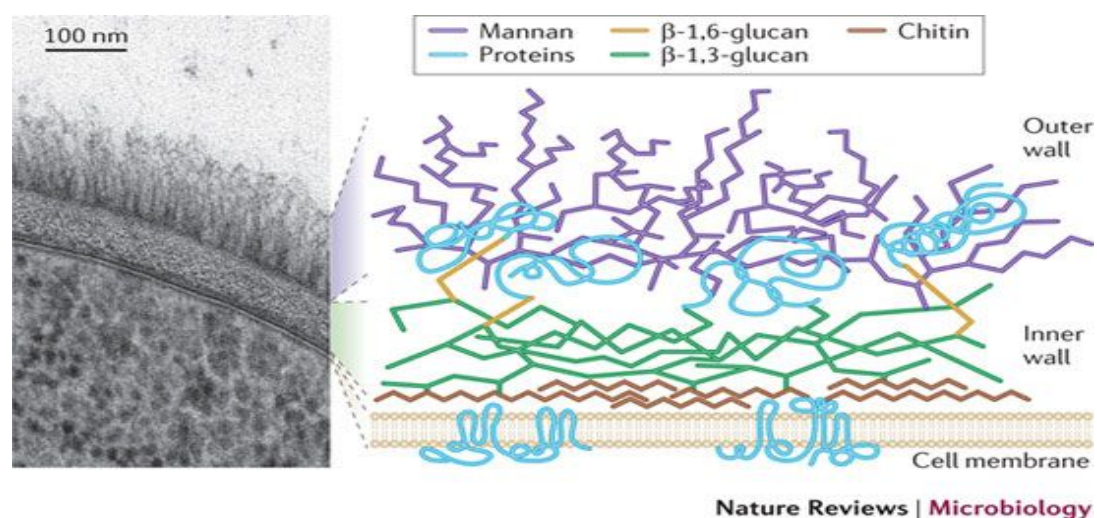
Generally, the semi-crystalline microfibrillar components are organized in a network mainly in the central cell wall region and are embedded within an amorphous matrix. Bonding occurs between certain components behind the extending hyphal tip, thereby strengthening the entire wall structure.

There is evidence to suggest that the cell wall is a dynamic structure where considerable quantitative and qualitative differences occur not only between different fungal species, but also between different morphological forms of the same species and even in response to environmental stress. For example, a class of hydrophobic proteins called hydrophobins are localized within the aerial growth or appresoria (terminal swellings involved in infection) of certain fungi, whereas pigmented melanins are often found within some fungal cell walls to insulate against biotic and abiotic stresses.

The hyphae of higher fungi extend via tip growth followed by cross-wall formation or septation, whereas the lower fungi remain aseptate (except when segregating spores or in damaged colony regions).

Septa may offer some structural support to hyphae. Significantly, septa serve to compartmentalize hyphae but are typically perforated, thereby permitting passage and communication of cytoplasm or even protoplasm between compartments. However, septal pores can become blocked by **Woronin bodies** or other materials. This aids morphological and biochemical differentiation and serves to seal off stressed or damaged hyphae from undamaged colony regions. Again, different pore types are representative of different taxonomic groups and species (Table 1).

In yeasts, the cell-wall structure comprises **polysaccharides** (predominantly β -glucans for rigidity), **proteins** (mainly mannoproteins on the outermost layer for determining porosity), together with some **lipid, chitin** (e.g. in bud scar tissue) and **inorganic phosphate material**. Hyphal cell walls generally contain fewer **mannans** than yeast cell forms, and such changes in composition are even observed during the transition from unicellular to mycelial growth of dimorphic fungi.

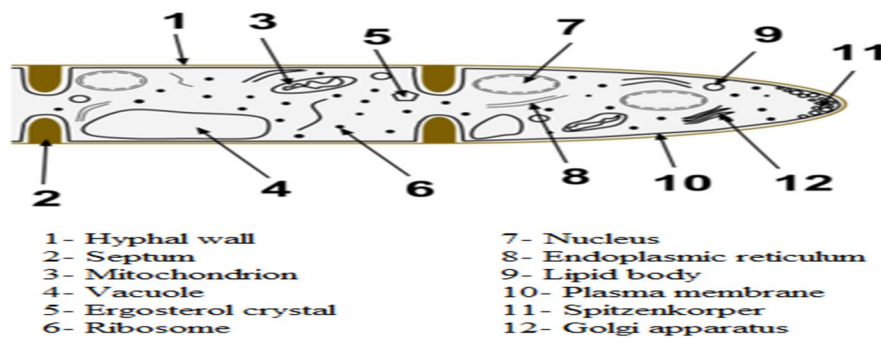


Chitin is also found in yeast cell walls and is a major constituent of bud scars. These are remnants of previous budding events found on the surface of mother cells following birth of daughter cells (buds). The chitin-rich bud scars of yeast cells can be stained with fluorescent dyes

(e.g. calcoflour white), and this can provide useful information regarding cellular age, since the number of scars represents the number of completed cell division cycles.

Outside the cell wall in fungi, several extramural layers may exist, including fimbriae and capsules. Fungal fimbriae are long, protein-containing protrusions appearing from the cell wall of certain basidiomycetous and ascomycetous fungi that are involved in cell cell conjugation. Capsules are extracellular polysaccharide-containing structures found in basidiomycetous fungi that are involved in stress protection. In *Cryptococcus neoformans* (the pathogenic yeast state of *Filobasidiella neoformans*) the capsule may determine virulence properties and evasion from macrophages. One extrahyphal substance, the polymer pullulan, is produced commercially from *A. pullulans*.

2- Organelle Function



Transmission electron microscopy of ultrathin sections of fungal cells reveals intracellular fine structure (Figures 1). Subcellular compartments (organelles) are bathed in an aqueous cytoplasm containing soluble proteins and other macromolecules, together with low-molecular weight metabolites. However, the hyphae of central (and therefore older) colony regions of filamentous fungi may become devoid of protoplasm and organelles, as protoplasmic components are driven forward or are recycled, to support the growth of actively growing hyphal tips. Cytoplasmic components additionally comprise microbodies, ribosomes, proteasomes, lipid particles and a cytoskeletal network.

The latter confers structural stability to the fungal cytoplasm and consists of microtubules and microfilaments. The following membrane-bound organelles may be found in a typical fungal cell: nucleus: endoplasmic reticulum (ER), mitochondria, Golgi apparatus, secretory vesicles and vacuoles. Several of these organelles form extended membranous systems. For example, the ER is contiguous with the nuclear membrane and secretion of fungal proteins involves inter membrane trafficking in which the ER, Golgi apparatus, plasma membrane and vesicles all participate. The physiological function of the various fungal cell organelles is summarized in Table 3.

The nucleus is the structure that defines the eukaryotic nature of fungal cells. It is bound by a double membrane and encases the chromosomes in a nucleoplasm. Most yeast and fungi are haploid, although some (e.g. *S. cerevisiae*) may alternate between haploidy and diploidy.

Yeasts usually contain a **single** nucleus per cell. However, the hyphal compartments of filamentous fungi may contain one or more nuclei. **Monokaryotic** basidiomycetes possess **one** nucleus per compartment, whereas **dikaryons** or heterokaryons possess **two or more** genetically distinct haploid nuclei. The maintenance of multiple nuclei within individual hyphal compartments allows fungi to take advantage of both haploid and diploid lifestyles.

Table 1.3 Functional components of an idealized fungal cell.

Organelle cellular structure	or	Function
Cell envelope		Comprising: the plasma membrane, which acts as a selectively permeable barrier for transport of hydrophilic molecules in and out of fungal cells; the periplasm, containing proteins and enzymes unable to permeate the cell wall; the cell wall, which provides protection, shape and is involved in cell–cell interactions, signal reception and specialized enzyme activities; fimbriae involved in sexual conjugation; capsules to protect cells from dehydration and immunecell attack.
Nucleus		Relatively small. Containing chromosomes (DNA–protein complexes) that pass genetic information to daughter cells at cell division and the nucleolus, which is the site of ribosomal RNA transcription and processing.
Mitochondria		Site of respiratory metabolism under aerobic conditions and, under anaerobic conditions, for fatty acid, sterol and amino acid metabolism.
Endoplasmic reticulum		Ribosomes on the rough ER are the sites of protein biosynthesis.
Proteasome		Multi-subunit protease complexes involved in regulating protein turnover.
Golgi apparatus and vesicles		Secretory system for import (endocytosis) and export (exocytosis) of proteins.
Vacuole		Intracellular reservoir (amino acids, polyphosphate, metal ions); proteolysis; protein trafficking; control of cellular pH. In filamentous fungi, tubular vacuoles transport materials bidirectionally along hyphae.
Peroxisome		Oxidative utilization of specific carbon and nitrogen sources (contain catalase, oxidases). Glyoxysomes contain enzymes of the glyoxylate cycle.