One interesting possibility is that heat-shock proteins may be involved in the mechanism for branch initiation. Heat-shock proteins are polypeptides which interact with other proteins. They are '**molecular chaperones**' which bind to and stabilise other proteins to prevent incorrect intermolecular associations, then aid their correct folding by releasing them in a controlled manner. It is feasible that branch initiation requires assisted conformational alterations of wall proteins or that heat-shock proteins assist in the delivery of a branch-initiating polypeptide to the appropriate position.

4.12 Septation

The hyphal growth form of filamentous fungi is an adaptation to the active **colonisation of solid substrata**. By hyphal extension and regular branching, the fungal mycelium can increase in size without disturbing the cell volume/surface area ratio so that metabolite and end-product exchange with the environment can involve translocation over very short distances. Fungal hyphae differ between species, but the hyphal filament, when separated into compartments by cross-walls, has an apical compartment which is perhaps up to ten times the length of the intercalary compartments. The septa which divide hyphae into cells may be:

- complete (imperforate),
- penetrated by cytoplasmic strands,
- perforated by a large central pore.

The pore may be open and offer little physical hindrance to the passage of cytoplasmic organelles and nuclei, or may be protected by a complex cap structure, called the **parenthesome**, derived from the endoplasmic reticulum (the **dolipore septum** of many Basidiomycota). In Ascomycota, which characteristically lack the parenthesome apparatus, the pore may be associated with cytoplasmic organelles known as **Woronin bodies**.

Over the years mycologists have been very sensitive to the question of whether fungi have cells, and how fungal cells and their interactions compare with those of plant and animal cells. Lower filamentous fungi (e.g. *Mucor*) have coenocytic hyphae; but they do not form multicellular structures. Hyphae of fungi which do exhibit complex developmental pathways form septa at regular intervals, though the septa usually have a pore. The pore is what worries people about the definition of fungal cells, because the implication carried with the word 'pore' is that all of the cytoplasm of a hypha is in continuity even though it might be subdivided by the septa into compartments.

Although movement of cytoplasm and organelles through septa has often been described and is frequently easy to demonstrate, it is also clearly the case that the movement or migration of cytoplasmic components between adjacent cells is under very effective control. There are instances in which nuclei move freely, but mitochondria do not, and others in which rapid migration of vacuoles is not accompanied by migration of any other organelle. Some biochemical experiments have even demonstrated that different sugars can be translocated in opposite directions in a hypha at the same time. There are also numerous examples available where grossly different pathways of differentiation have been followed on the two sides of what appear (to the electron microscope) to be open septal pores (see Section 12.6).

Clearly, whatever the appearance, the hypha can be separated into compartments whose interactions are carefully regulated and which can exhibit contrasting patterns of differentiation. There may still be a semantic argument for preferring 'compartment' to 'cell', but from this point on we will take the pragmatic view that if it looks like a cell and if it behaves like a cell, then we will call it a cell. But please don't forget that every fungal cell is just a segment of a tubular hypha!

Cross-walls in fungal hyphae are pretty well always formed at right angles to the long axis of the hypha and this has a major impact on understanding the development of fungal tissues. Except in cases of injury or in hyphal tips already differentiated to form sporing structures, hyphal tip cells are not subdivided by oblique cross-walls, nor by longitudinally oriented ones. Even in fission yeast cells which are forced to produce irregular septation patterns under experimental manipulation, the plane of the septum is always perpendicular to the plane including the longest axis of the cell. In general, then, a fungus converts the one-dimensional hypha into a two-dimensional plate of tissue or three-dimensional block of tissue **by controlling the formation of branches**. The septum in any branch will be formed at right angles to the long axis of the branch, but its orientation relative to the parent hypha will depend entirely on the positioning of the apex of the new branch.

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Primary septa in fungal hyphae are formed by a constriction process in which a belt of microfilaments around the hyphal periphery interacts with microvesicles and other membranous cell organelles (see Chapter 5). Except for the fact that there is no close linkage with mitosis (see above), there is a superficial similarity between fungal septation and animal cell cleavage (cytokinesis); but remember, fungi use organised microvesicles to divide blocks of cytoplasm in the free cell formation process (see Chapter 3; CLICK HERE to view now).

4.13 Ecological advantage of mycelial growth in colonising solid substrates

The apical growth characteristic of the fungal hypha is the prime attribute of fungi and is, of course, an extreme cellular polarity. Because true extension growth is absolutely limited to the hyphal tip, the whole morphology of the hypha depends on events taking place at its apex. It follows from this that the pattern of hyphae in a mycelium, which is largely a consequence of the distribution of hyphal branches, depends on the pattern of formation of the hyphal tips which initiate those branches.

The dominance of filamentous fungi within the ecosystem is attributed to their lifestyle. By growing in a filamentous fashion, fungi can colonise substrates rapidly and grow away from nutrient poor areas. Branching of the filament enables substrates to be efficiently captured for absorption from the environment. Maintaining a high extension rate even under poor nutrient conditions allows fungi to maximise their chances of finding new food sources. The success of this growth habit for exploiting the natural environment can be judged on a number of factors: the extraordinary diversity of fungal species (second only to the insects, but then every insect harbours a few parasitic fungi!), their distribution in virtually every habitat on the planet and the parallel evolution of a similar growth habit by other important soil microorganisms, the prokaryotic streptomycetes and the more fungus-like members of Kingdom Straminipila, like the Oomycota. Clearly the ability of a microbe to colonise new substrates rapidly by concentrating extension at the apex of a filament makes it ideally suited for life as a heterotroph in a heterogeneous environment.

Polarised growth of fungal hyphae is achieved by restricting extension to the hyphal apex. The cell wall at the hyphal tip has **viscoelastic properties**. This means it has some of the characteristics of both a liquid (being able to flow like a viscous fluid) and a solid (resisting and recovering from stretching, compression or distortion). These properties allow the wall at the hyphal apex to yield to the internal turgor pressure within the hypha by extending forward. Further behind the tip the wall is rigidified and resistant to the turgor forces. **Turgor** (the force within the cell that pushes the plasma membrane against the cell wall) powers the propulsion of hyphae through solid materials and therefore acts as the driving force for **hyphal extension** (Money, 2008).

Hyphal growth at the apex requires synthesis and insertion of new wall material and new membranes in a way that does not weaken the tip. This highly organised process is supported by the flow of vesicles generated within the cytoplasm behind the tip and is co-ordinated with the growth and replication of all the other cytoplasmic organelles and their migration towards the extending apex. It seems now to be generally accepted that the materials necessary for hyphal extension growth are produced at a constant rate (equal to the specific growth rate) throughout the mycelium and are transported towards the tip of the growing hyphae. Among the materials taking part in this polarised transport are numerous cytoplasmic vesicles, which are thought to contain wall precursors and the enzymes needed for their insertion into the existing wall to extend it. A considerable cytoplasmic architecture is involved in the **apical growth of the hypha** (Bartnicki-Garcia *et al*., 1989; Wessels, 1993). We will describe and discuss this in detail in Chapters 5 & 6.

4.14 Chapter 4 References and further reading

Bartnicki-Garcia, S. (1968). Cell wall chemistry, morphogenesis and taxonomy of fungi. *Annual Reviews of Microbiology*, **22**: 87-108. CLICK HERE to download the complete text. **WARNING**: You have to **be CAREFUL** with this paper - it is a **classic** but it predates the formal separation of the major eukaryotic Kingdoms (which was published in 1969) so Bartnicki-Garcia discusses slime moulds (Acrasiales) and two other groups (Oomycota and Hyphochytriomycota) as "lower fungi" whereas they are NOW considered NOT to be fungi at all and are placed in different taxonomic Kingdoms.

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Chang, F. (2001). Establishment of a cellular axis in fission yeast. *Trends in Genetics*, **17**: 273-278. DOI: https://doi.org/10.1016/S0168-9525(01)02279-X.