Mycology Answers

How and why do many fungal hyphae form septa?

Fungal hyphae are essentially tubular in shape, surrounded by a very rigid cell wall that gives good protection from the external environment. Hyphae grow out across the substrate, foraging for fresh nutrients, by extension at the tip region only. This extension occurs as new materials are added to the cell wall at the extreme apex and is driven by turgor pressure. It has been shown, using the electron microscope, that fungal cell walls have a layered structure although all the components are well integrated and strongly cross-linked together. In most fungi the inner layers of the wall are composed of fibrils of chitin and glucan. It is these fibrils that provide much of the great mechanical strength of the wall and this together with the fine dimensions of hyphae enables the penetrating growth habit of the fungi. The outermost cell wall layers are composed of other polymers such as galactomannans and xylomannans in the form of more amorphous, packing materials. The cross walls (septa) that many hyphae form at intervals along the length of their hyphae have a high content of chitin and are very rigid structures. Septa are formed by localised extension of the cell wall towards the centre of the hypha (centripetal). There may be accompanying changes in the structure of the outer cell wall at the point where a septum develops and it is likely that the presence of septa may provide structural support and add to the general stability of the hypha.

Septa potentially form barriers across hyphae cutting off the cytoplasm and its contents from the rest of the hypha. Compartmentalisation may represent an important mechanism for protection of the cytoplasm from mechanical damage. However, in many cases the central region will remain open for most of the life of the hypha. Most septa are incomplete, allowing free communication between the cytoplasm in adjacent hyphal compartments. The presence of central pores (sometimes several pores as in a multiperforate septum) ensures that the cytoplasm remains interconnected. Hyphae therefore have the potential to be compartmentalised but during most of the active growth period the cytoplasm is continuous with a very high degree of communication between compartments. Most hyphae may therefore be regarded as acellular and contain many nuclei in the cytoplasm (coenocytic).

Amongst the fungi there are various strategies for septation with varying degrees of complexity of form. Hyphae of the Zygomycota are mostly aseptate throughout growth and development and the mycelium is regarded as relatively simple. The formation of full, closed, septa (adventitious septa) occurs only to isolate a specific region (e.g. at sporulation or aged areas). Amongst the higher fungi, members of the Ascomycota and many Deuteromycota have hyphae with simple septa which have large central pores (primary septa). These perforations allow cytoplasmic communication and large organelles, including nuclei, can pass through. The Basidiomycota form septa (dolipore septa) with much more complex structure. The pore aperture has an enlarged central ring of material containing high levels of glucan. Associated membrane caps (parenthesomes) form over that pore region and prevent the passage of large particles through the pore. A narrow channel of communication is therefore maintained between compartments but no movement of large organelles can occur. Dolipore parenthesome septa act as sieves in the cytoplasm.

In budding ascomycetous yeasts where full separation occurs, a septum divides the mother and daughter cells. After nuclear division a disc of chitin is formed between the two cells which is then thickened on both sides by the deposition of further material. Eventually the cells separate by the dissolution of the septum between the chitin disc and the daughter cell, leaving the chitin component as a bud scar on the mother cell surface. In this instance the septum becomes part of the outer cell wall and provides protection to both cells.

As filamentous hyphae age septal pores naturally become plugged and as a result the compartment is then cut off from further communication with apical regions of the hypha and can make no further contribution to apical growth. Simple septa may become plugged by electron-dense material which is sometimes deposited in layers. In other instances small crystalline bodies move into the pore aperture and become lodged as very effective plugs. In Ascomycota small, dense, rounded bodies (Woronin bodies) of protein-containing material are formed near septa and can move into place to occlude the pore. In some cases this plugging may be completed in seconds although the mechanism by which it occurs is not yet clear. This provides a system for emergency plugging of septa which may well provide a protection mechanism against damage and osmotic stress. Once a pore has become plugged it never regains a communication system with the rest of the hypha and does not become unplugged.

Septal plugging is considered to have a major role in the progress of differentiation in hyphae. This allows switches in metabolism to take place leading to development beyond the vegetative phase. The laying down of storage compounds and the operation of different biochemical pathways operates because specific areas of mycelium are able to operate independently. Once a septum is complete there is potential for different patterns of development to occur in the neighbouring compartments. A first step in differentiation is the formation of a branch or branches. The frequency and numbers of branches will vary with the capacity of the hypha for continued growth. If the supply of nutrients is sufficient branches may be formed, especially by hyphal compartments no longer contributing to tip extension. In some instances branches may fuse together (anastomosis) within a colony. This re-establishes cytoplasmic communication, also allowing redistribution of organelles and nutrient materials. Differentiated structures are normally delimited by the presence of septa. Different physiological processes can then operate specifically in the region that has been isolated. Some differentiated structures are highly complex, requiring the aggregation of hyphae and cooperation between neighbouring filaments. As a result, individual compartments may well be required to operate by distinct physiological mechanisms.

The largest differentiated structures produced by fungi are the toadstools and mushrooms formed by the Basidiomycota. Such fruiting bodies are highly complex and physiologically integrated. Some such structures are highly thickened and resistant and may remain functional for several years often producing extremely large numbers of spores. The formation of other reproductive structures such as conidia, sexual spores (e.g. zygospores, ascospores, basidiospores) and sclerotia are also the result of differentiation. Many sexual spores are formed within complex, multi-hyphal structures which act as protection mechanisms or may aid eventual spore dispersal. In addition, other feeding structures such as haustoria (formed for penetration into host cells), translocating organs such as cords and rhizomorphs are the result of differentiation.

It can be seen therefore that fungal hyphae form a range of septal structures which provide the mycelium not only with mechanical stability and protection but also a degree of flexibility for continued development.

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