MYCOLOGY ANSWERS

WHAT ARE THE FACTORS THAT CONTRIBUTE TO THE ONSET OF AUTOLYSIS IN FUNGAL HYPHAE AND DOES THE PROCESS CONFER ANY ECOLOGICAL ADVANTAGE?

Autolysis is the process of self-digestion which occurs locally in very aged and senescent hyphae when active growth has ceased in that region. It may be regarded as a recycling process since it leads to the repositioning and reuse of some components of fungal cells and may contribute to the continued survival of some species under growth limiting conditions. Fungal mycelium grows as a network of filaments which extend apically, branching away from each other across and through the substrate, to form a colony. The oldest regions of an undisturbed colony are usually those furthest from the growing tips whereas the most newly formed and youngest regions are those nearest the tips. The ageing of an individual hypha is influenced by a range of internal and external factors arising as the result of position within a colony and within a particular environment. As a hypha ages, accompanying biochemical and morphological changes occur with time and gradually physiological activity declines, eventually marking the end of vegetative propagation and the onset of senescence. External factors such as nutrient status in the immediate environment, alterations in local pH and the presence of toxic metabolites also influence the course of ageing and senescence. For much of the life of a hypha there is the possibility of rejuvenation and renewed growth, with the influx of fresh nutrient supplies or after branch formation. Autolysis of organelles, cytoplasm and ultimately cell wall materials, represents a point of no return to active growth. It is interesting that autolysis often occurs in single hyphae, segments of hyphae or hyphal branches and not necessarily synchronously throughout a colony.

Much active growth takes place at tip regions of hyphae and materials which are absorbed through cell walls or synthesised in older regions are transported to tips to support rapid extension and the exploitation of the substrate. For example, cell wall synthesising enzymes, some proteins and carbohydrates are localised at growing hyphal tips. Throughout a colony the types of protein and other compounds formed in the cytoplasm vary with the location in the colony and there is zonation of biochemical activity along the length of a hypha. In older regions storage compounds are laid down and the hypha becomes increasingly vacuolate. As vacuolation progresses, organelles, such as mitochondria and some nuclei, may become sequestered into pockets of cytoplasm.

As hyphae grow and extend in length compartmentation may occur. Septa (cross-walls) are laid down across the diameter of hyphae (except in some Oomycota and Zygomycota) and may serve, at least in part, as a structural reinforcement for the lengthening hyphal tube. Septa are formed from the cell wall inwards (centripetal development) and simple septa may remain perforate for some time after formation. More complex septa (dolipore septa) also have a central pore which remains free for some time after development and allows exchange of materials with neighbouring compartments. As hyphae age, in physiological terms, septa may become blocked, effectively cutting off communication and preventing that compartment from contributing to apical extension. In addition, no new supplies of nutrient can then be translocated in from other regions of the colony. The formation and plugging of septa is irreversible and as perforate septa become blocked in a hypha, ageing occurs more rapidly unless a new branch is formed, representing rejuvenation of the compartment.

Once a compartment has effectively been cut off from other active compartments it is no longer buffered from its local environment. It may be in an area of nutrient depletion or at a point where toxic metabolites have built up in the surrounding substrate. Starvation and/or poisoning leads to rapid decrease in physiological activity and senescence. However, since many fungi can survive for long periods in conditions where nutrient supplies are very low the period prior to senescence and autolysis may be prolonged. Some species have the ability to scavenge combined carbon and other nutrients from the atmosphere, which undoubtedly aids survival in natural environments. Ultimately nutrient exhaustion leads to a switch from primary to secondary metabolism (metabolism occurring when normal vegetative growth has ceased) and hence the accumulation of secondary metabolites (compounds that have no apparent role in the functioning of the producer organism) occurs.

As nutrients become more limiting an imbalance occurs in aged hyphae and as a result protein synthesis declines, nucleic acids break down and ultimately membrane damage results, so that hyphae become increasingly leaky. The release of degradative enzymes gives rise to autolytic digestion, with extensive vacuolation, disruption of organelles and cell wall lysis. Some materials are reused e.g. nitrogen-containing compounds released in this way are important for survival, especially in nitrogen limited situations. Autolysis is not synchronous throughout a colony and may fuel other hyphal filaments. The onset of autolysis may be more distinctly identified in batch liquid cultures in the laboratory and is defined as a reduction in biomass (percentage decrease in dry weight from the maximum achieved for those cultural conditions). In liquid culture some species, for example *Aspergillus nidulans*, *Neurospora crassa* and *Penicillium oxalicum* quickly show losses of dry weight exceeding 90%. Many other species also demonstrate autolysis although the dry weight reduction may be less dramatic. Levels of cell wall degrading enzymes may be high in the culture fluids of such autolysing cultures. It has been shown in some fungi (e.g. the ascomycete *Podospora anserina*) that senescence can occur after a relatively short period of vegetative growth. In such fungi senescence depends on the expression of inherited genes carried on transposable elements which are capable of movement within the fungal genome bringing about acceleration of senescence and ageing related changes. The expression of these genes is controlled by environmental conditions.

The physiological age of any one segment of a hypha or hyphal compartment will be determined by position in a colony and the nutrient status of the surrounding substrate. Ageing is a function of time but is also influenced heavily by environmental factors and local conditions.

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