MYCOLOGY ANSWERS

What Factors determine the Duration of the Dormancy of Fungus Spores prior to Germination?

Fungi produce a huge variety of spores which are dispersed, in both space and time, by many different mechanisms. The formation of spores represents an interruption, of variable duration, in vegetative development and a period of low physiological activity. It is quite certain that there is no universal mechanism controlling the resumption of active metabolism or the subsequent outgrowth at germination. Most spores do contain the cellular and biochemical components required for germination although these may not all be in an active condition at the time of release. In the dormant state the cytoplasmic contents of spores is often denser than that of the mycelium from which they are derived and although organelles may be present these are often poorly developed and have limited function at that time. In general, spores have thick resistant walls which may contain varying amounts of pigment (melanin, sporopollenin), which act as added protection for the contents (particularly from the effects of irradiation). In addition dormant spores exhibit very limited respiration levels and very low protein synthesis. A new cycle of normal development is only resumed when polarity is re-established and outgrowth occurs.

Many spores are not liberated immediately after formation, but once released some types of spores will germinate quickly while others will remain dormant for a period of time, which may be quite considerable. Much of the diversity of form probably relates to the mechanism of dispersal from the parent mycelium. Some spores are regarded as agents of dispersal (xenospores), aiding dissemination to fresh substrates. These are usually relatively light, small in size (e.g. conidia, sporangiospores, basidiospores), are produced in very large numbers and carry limited stores of nutrients. Such spores may be easily released from the parent mycelium and germinate very rapidly after formation, although this ability may be lost. In addition, the long-term survival of such spores may be limited. Thicker walled, relatively large, more resistant spores are regarded as survival structures (memnospores). These (e.g. oospores, zygospores, chlamydospores) are generally longer-lived and often have the ability to survive adverse environmental conditions. In some cases these require a period of maturation and exposure to particular stimuli prior to germination and outgrowth. The grouping of spores into these functional types is a useful concept but there are many examples of spores with combinations of attributes and the divisions are not mutually exclusive. Many species of fungi produce not only large numbers of spores but also a range of different functional types of spores from one mycelium (i.e. both xenospores and memnospores) and some produce several kinds of each type of spore (pleomorphism).

Those spores that have the capacity for immediate and rapid germination are often subject to relatively short-term dormancy and can resume development providing that favourable environmental conditions are present (exogenous dormancy). Longer term survival allows spores to overwinter, surviving unfavourable environmental conditions (constitutive dormancy). Depending on the conditions under which spores are sustained they may undergo considerable periods of dormancy. Germination of conidia may occur within hours of release but some spores will retain germinability after many years (*Penicillium* spp. $<$ 10 years; *Schizophyllum commune* basidiospores 50 years).

In general terms spores have a low water content relative to that of vegetative mycelium and the exclusion of water is one of the factors that may prolong dormancy. Thickened, resistant walls help to maintain low permeability. Dehydration may also enable some spores to withstand low temperatures and/or temperature fluctuations which would damage growing mycelium. In addition, some species have specific requirements for nutrients. The thick walls of spores of coprophilous fungi (species that grow on herbivore dung) are partly digested as the spores pass through the animal gut and only after such digestion will germination occur (e.g. *Podospora* spp. *Sordaria* spp., *Coprinus* spp.). This ensures that germination occurs on voided dung where there are high levels of nutrients and ideal conditions for growth. Spores of coprophilous species also require heating to 37°C prior to germination, a temperature which corresponds to that in the herbivore gut.

Fungal storage compounds such as lipids occur in relatively high levels in spores, as well as trehalose, polyols and glycogen and are therefore available to support outgrowth at germination. Dormancy may be maintained by the physical separation of enzymes and substrate required for the metabolism of these storage materials or by the presence of enzymes in inactive forms. In *Neurospora tetrasperma* trehalase, which cleaves trehalose to glucose, is stored in spore walls and is physically separated from the stored substrate until dormancy is broken. Most spores require the presence of oxygen for outgrowth and some species are sensitive to pH levels, non-conducive conditions maintaining dormancy.

Dormancy may also be maintained by the presence of biochemical inhibitors. There is some evidence that inhibitors are present in parent mycelium, preventing germination prior to dispersal. Inhibitors may also be present on the on the outside of the spore or within the surrounding mucilage in which the spores are formed (e.g. *Septoria apiicola*). This type of mechanism will tend to prevent spores from germinating in close proximity to other potentially competing spores (autoinhibition). Spores may not germinate until the mucilage has been washed away or the spores dispersed well away from one another. In uredospores of *Uromyces phaseoli* the inhibitors which contribute to dormancy are cinnamic acid derivatives and are active at very low concentrations (levels of 10^{-11} M). In some natural mineral soils fungal spores remain dormant (mycostasis or fungistasis) when other environmental factors would normally be conducive to the breakage. This has been attributed to the activities of other soil microorganisms, possibly as the result of production of inhibitory compounds in the soil or by the depletion of nutrient supplies.

It is therefore most likely that a combination of factors contribute to the maintenance of dormancy for most fungal species and types of spore. It is clear that spore production is an area of great metabolic input, much of which is wasted, since many spores never germinate to form functioning mycelium.

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