DISPERSAL OF FUNGAL SPORES

D.W.Gover

Dispersal for fungi, as with plants, is an important reproductive function, in order to maintain the species, extend the existing habitat range and also to spread genetic variability, when it occurs, throughout the population.

Spore dispersal may be achieved by the physical mechanisms of gravity, wind, water and animals. Also, many fungi have active mechanisms to effect release of their spores, which are then dispersed by these external agencies.

GENERAL FEATURES OF SPORES

a. SPORE STRUCTURE AND GERMINATION

A spore may be defined as a reproductive unit which lacks a preformed embryo and is produced by fungi, bacteria and cryptogamic i.e. non-flowering, plants. While the diversity of fungal spores makes it impossible to generalise, many fungal spores differ from that of vegetative cells in two major respects. The wall is often thick and is impregnated with melanin, lipids, etc. and there is little differentiation of the cytoplasm, the endoplasmic reticulum and mitochondria being poorly developed.

Spore germination involves a number of metabolic and ultrastructural changes. Initially, the spore swells due to absorption of water, food reserves (lipids) are converted to metabolically active compounds, and there is a rapid increase in respiration. The spore continues to swell as a direct result of its metabolic activities, and a new wall layer is usually formed inside the existing spore wall. Ultimately, one or more germ tubes emerge by rupture of the old spore wall, and the wall of the germ tube arises as a direct extension of the newly formed wall of the spore.

b. DORMANCY

Some spores fail to germinate, remaining dormant, yet viable, even when the environmental conditions are suitable. Dormancy provides a further 'dispersal' mechanism, in that while dispersal is normally thought of as a distribution in space, dormancy mechanisms allow spores to remain viable for an extended period thereby achieving a distribution in time, waiting for a suitable substrate to become available.

There are a number of types of dormancy mechanisms recognised, a common type is constitutive dormancy. This type of dormancy may be released by activating the spore with specific conditions, such as heat-shock or cold-shock. Constitutive dormancy has been ascribed to permeability barriers in the spore walls or to the presence of endogenous germination inhibitors, although there may be other reasons.

Exogenous dormancy is a more common type of dormancy; one, that is imposed by the environment where the temperature, water activity, etc. may be unsuitable for germination or where an exogenous carbon or nitrogen source may be required.

Many soil fungal spores fail to germinate in the presence of other micro-organisms and therefore have dormancy imposed upon them. This phenomenon known as soil fungistasis prevents the germination of fungal spores in soil except under special circumstances.

It has been known for a long time that there is intense biological activity on and around the surfaces of plant roots. The main chemical components exuded by plant roots are amino acids and sugars. These simple nutrients may override the inhibition caused by soil fungistasis when a root comes close to a dormant spore. The mechanism of soil fungistasis has not been determined but is probably due to the presence of volatile substances produced by soil micro -organisms, such as ethylene.

Some fungi such as *Plasmodiophora brassicae*, the Club Root fungus that causes the disease of that name in cabbages and other brassicas produces resting spores; chlamydospores, that are able to survive in the soil for more than ten years. Such spores must not germinate unless there is a suitable host nearby, and so spore germination is specifically linked with the chemicals produced by growing cabbage roots. Similarly, the resting spores of *Spongospora subterranea*, the cause of powdery scab of potato, are stimulated to germinate only by the roots of potato and a few other solanaceous host species.

Although recent work on mycorrhizal associations has given some insights into the specificity of fungi-host relationships, spore dormancy of this type is not thought to be common among the toadstools and mushrooms, but this may be partly a reflection of the present level of knowledge concerning this aspect of their biology.

SPORE DISPERSAL BY GRAVITY

Spore dispersal in space for many mushroom and toadstool species is influenced by the effects of gravity.

When mature the four basidiospores of the field mushroom, (*Agaricus campestris*) are violently discharged from the basidium to a distance of 0.1-0.3 µm. The four spores are liberated consecutively with about a minute or two between each discharge. The basidium collapses soon after the discharge of the spores. While the mechanism of discharge is not fully understood, it seems that when mature the basidiospore exudes a minute drop of fluid which grows to a definite size and then the spore and drop are discharged. It has been suggested that the surface energy of the exuded drop is mobilised for the discharge or since liberated spores are known to be electrically charged, the spore may be repelled from the basidium by electrostatic forces. Thus while these basidiospores are actively discharged horizontally from between gills, they must be able to drop freely into the air below the pileus.

In many species of mushroom the stipe raises the pileus some distance above the ground and is negatively geotropic, thus giving a rough vertical orientation to the gills. Additionally, each individual gill is positively geotropic.

The combined effect of stipe and gill growth movements are such to provide a vertical escape path between the gills. Since the mass of the spore is not large, it falls relatively slowly in still air. For example, in still air the spores of *Agaricus campestris* fall at the rate of just over one millimetre per second. This low rate of fall under gravity ensures that even the most delicate of air current will disturb their gradual fall and readily divert the spores into turbulent air.

In contrast to the 0.1-0.3 mm range of the discharged basidiospores, in the Ascomycetes the range of discharged asci is much greater, varying, according to species, from 2-30 µm.

The ascus is positively phototropic, so that in a cup-shaped fungus such as *Discanella terrestris*, with the light from above, the asci at the base are pointing vertically upwards while those on the side wall are curved upwards. Each mature ascus is a single cell surrounded by a cell wall stretched by the hydrostatic pressure within. The ascospores are suspended in a fluid within and when the turgid ascus bursts the wall contracts and the spores are ejected into the air.

Ascospores may be ejected either through the bursting of the ascus at the top, through a pore or slit, or cap-like operculum hinged at one end. Large numbers of ascospores are liberated simultaneously. Small clouds of ascospores are easily seen as the are puffed out quite high into the air from the hymenium of a cupfungus such as *Discanella terrestris*. Air moisture content, temperature, light and air currents are some of the many factors responsible for ascospore release.

As many ascomycetes grow relatively close to the ground, the greater distance of discharge provided to ascospores enhances their chances of reaching the turbulent layer of air in the atmosphere where they stand a good chance of wide dispersal.

While gravity is not a primary means of spore dispersal, evolutionary adaptations have been required of many fungi to overcome gravitational effects for effective spore dispersal.

SPORE DISPERSAL BY WIND

Dispersal of fungal spores by wind is by far the most common method for terrestrial fungi. Wind -borne spores finally coming to rest by sedimentation, impaction or rain-wash.

Most air-borne spores are small, often about 1-8 µm in diameter, with a rate of fall, in still air, of less than 10 mm/sec. Consequently their movement in turbulent air is determined primarily by the mass movement of the air and only to a small extent by gravity.

The thin boundary layer of air in contact with the ground is still or in laminar flow and spores in this layer will sediment rapidly. The active discharge of spores in the Ascomycetes and Basidiomycetes provides a means for the spores to avoid local settlement in this boundary layer and to reach the potentially turbulent air layer above. Some fungi such as the rusts, smuts and powdery mildews, have no active discharge of spores although their spores are often abundant in the air-spora. However, their spores are mostly borne on diseased plant surfaces well above ground level, so that the spores are usually liberated into air that is likely to be turbulent.

The movement of spores in air from their site of liberation takes place in three dimensions and has been likened to the movement of smoke from a chimney. The concentration of spores in air may be thought of as being inversely proportional to the distance from the source of production due to the effects of dilution. For many air-borne fungi the horizontal concentration of spores in air normally approaches zero at about 100 m to 200 m from the source of liberation.

The vertical concentration of spore in air for some species of fungi has been found to decrease logarithmically with height above the ground.

Despite most fungal spores being deposited within about 200m from their point of liberation, there is considerable evidence that some spores travel long distances (eg. spores of *Puccinia gramminis*, the wheat stem rust fungus, from Australia to New Zealand).

However, an important consideration in dispersal is the viability of the spores. The spores of rusts are able to remain viable for periods of many days, while basidiospores soon lose their ability to germinate. Thus basidiospores normally infect only nearby hosts while rusts can carry infection over great distances.

Spore size has a significant effect on impaction or by washout by rain. As air travels around objects such as plants, spores are carried with it; only those spores that have sufficient kinetic energy (KE= 1/2mass x velocity^2) are able to break free of the air currents and impact. At low wind speeds only the largest (heaviest) particles impact, smaller spores require progressively greater wind speed. The same argument applies to wash-out by rain, except here the rain drop travels towards the spore rather than vice versa.

The wheat stem rust fungus *P. gramminis* has spores of about 20 µm. Soil fungi, by contrast, have no need to impact, rather they sediment from the air in calm weather, and have generally smaller spores of about 4-8 µm.

It is likely, however, that rain will be of greater importance in returning spores to the ground. Each of the many raindrops which fall has the potential to carry many spores.

The air spora is heavily influenced by the seasonal weather. A dry air-spora and a wet air-spora have been recognised. In dry weather the air-spora is rich in spores of moulds, rusts, downy and powdery mildews. Heavy rain soon scrubs spores out of the air, thereafter a short-lived wet air-spora develops dominated by ascospores discharged from Ascomycetes in which spore discharge depends on wetting.

SPORE DISPERSAL BY WATER

Some fungi produce spores (zoospores or motile gametes) during their life cycle which are propelled by one or two whip-like tails (flagella). The presence of zoospores makes it possible for these fungi to live in aquatic environments (both salt and freshwater). They are also common in damp soil where the zoospores swim in the water surrounding the particles. Some of these fungi species are important parasites of plants and animals. The zoospores of plant pathogenic fungi like *Pythium* sp.and *Phytophthora* sp. have been reported to move in response to gravity,chemicals and electric currents. It has been demonstrated that the zoospores of *Phytophthora infestans* are chemically attracted towards the root region just behindthe tip of avocado roots, apparently in response to the low molecular weight compounds released from this region.

Some motile zoospores colonise organic material in aquatic habitats while others are parasites on algae. A group of aquatic fungi that are common in freshwater habitats produce characteristic tetraradiate (stellate or star-shaped) spores. These spores are easily found in the foam that accumulates behind small obstacles in a fast-flowing stream. While not all aquatic fungi produce tetraradiate spores (some produce elongated or round spores), some marine fungi produce essentially similar types, the marine Gasteromycete *Nia vibrissa* produces basidiospores with about five filamentous appendages and some aquatic bacteria form multiply branched vegetative cells.

Despite their similar appearances in many cases, these spores are formed in a wide variety of ways, suggesting that taxonomically different fungi have independently evolved multiply branched or appendaged spores in response to the aquatic environment. The tetraradiate spore (or conidium) is so widespread among aquatic fungi that there is some speculation that this form has some dispersal significance. A number of possibilities have been suggested. The tetraradiate spore would probably sink more slowly than a spore without arms and this might increase the effective dispersal, again this form of spore may enhance the possibility of the spore becoming anchored more readily to the substrate. What is known is that tetraradiate spores are more efficiently impacted onto substrates than spores without appendages.

Some fungi in which the spores occur in a slime are liberated by rain-splash. it is notable that many splash-dispersed spores are needle-shaped or banana-shaped, but it is unclear if this form is an adaptation for dispersal in a splash drop. Rainsplash may be most significant for local dispersal, and may enable some long - distance dispersal in the rebounded small spore-bearing drops after fragmentation, when the drops may be small enough to be carried in the wind.

Specialised splash dispersal is seen in the genera *Crucibulum, Cyathus, Nidularia, Mycocalia* and *Nidula* (bird's nest fungi) where dispersal is a two -stage process. Initially, raindrops fall into the nest or splash-cup, break into several small drops which splash out in all directions. Then as these drops bounce from the bottom of the cup some of the periodoles (a glebal chamber containing basidiospores in a gelatinous matrix) contained in the cup are forcibly ejected. The periodoles of *Crucibulum* and *Cyathus* have a small cord (funiculus) attached to the inner surface of the cup, which when wet is very sticky at the base allowing it to wrap around and adhere easily to solid objects after the periodole with trailing funiculus is discharged from the cup. The periodoles of *Mycocalia, Nidularia* and *Nidula* lack funiculi, but are instead sticky themselves.

All bird's nest fungi are saprobic and mostly found on plant remains, while some species of *Cyathus* fruit on horse and cow dung. This has lead to the conjecture that grazing animals accidentally eat periodoles adhering to vegetation, the fungus passing through the animal gut unharmed and so providing a mechanism to increase the chances of successful spore dispersal.

SPORE DISPERSAL BY ANIMAL

There are many examples, usually scattered over a number of taxonomic groups, of fungi that are dispersed by insects, small animals and humankind.

A common adaptation is the production of a sticky, sugar-rich spore droplet to attract the insect vector. *Ceratocystus ulmi* (Ascomycotina) the fungus that causes Dutch elm disease, is vectored by beetles of the genus *Scolytus*. The spores are dispersed when the sticky sporing structures of *C. ulmi* bearing very small spores in a droplet of mucilage project into the brood galleries (carved by the hatched grubs), and contaminate the new generation of emerging beetles.

The wasp, *Sirex noctilis* utilises a fungus as a means of providing a suitable food source for larvae. The wasp injects spores of *Amylostereum* sp. (Basidiomycotina) fungus when laying its eggs in a tree trunk of *Pinus radiata* (and a few other *Pinus* spp.). The wasp carries spores of the fungus in special pouches located at the base of its ovipositor. It usually produces two or three tunnels from a single entrance in the bark, the last formed of the tunnels contains only fungal spores. The fungus colonises the wood, forming a brown rot (ie. the cellulose is degraded by the fungus), reaching the egg tunnels in time for the young larvae to feed on the partly decomposed wood. Emerging adult wasps carry with them fres h spores for dispersal.

Not all insect-fungi relationships are so specific, most are casual, although there is usually some type of attractant. The slimy, foetid smelling spore mass of *Phallus impudicus*, *Aseroe rubra, Clathrus cibarius* and *Phallus rubicundus*, (Gasteromycetes) attracts flies and other insects which readily and rapidly devour it and as the spores pass unharmed through their alimentary tract, are effectively dispersed.

Perhaps the insects and small animals most often observed with fungi are those flies, gnats, slugs and snails that quickly find and consume those mushroom specimens sought after by field mycologists. The association of these insects and animals appears to be so ubiquitous; it is likely that they form a major role in the

spore dispersal of these fungi.
Some hypogeous (underground) fungi rely on mammals for dispersal; like the truffle (Tuber spp., Ascomycetes), the sporocarp of *Endogone* spp. (Zygomycetes) and the false truffles *Melanogaster, Leucogaster, Hymenogaster* and *Rhizopogon* (Gasteromycetes). The ripe underground sporophores exude a smell which attracts small mammals. These dig up and eat the sporophores. Studies, in America, have shown that the spores of hypogeous fungi are dispersed in the faecal pellets of some small mammals.
Some fungi are useful to humanity and consequently have been intentionally widely dispersed. These fungi, from a wide range of taxonomic families, are used as food (edible mushrooms or mycoprotein), or in the processing of foods, condiments and beverages, mould-ripened cheeses and in the production of chemicals, drugs and antibiotics. Conversely, modern rapid transportation methods have provided international mass transit of people and goods, often contaminated with spores, allowing fungal pathogens to disperse across otherwise effective natural and geographic barriers and overcoming the relatively short viability lifetime shown by some fungal spores.
Fortunately only a relatively small number of fungi infect humans and other animals, yet it is a fact that fungi have been responsible for most plant disease epidemics and are the main cause of disease in plants. The die-back of large areas of the Australian native flora, caused by the fungus *Phytophthora cinnamomi*, a relatively recent fungal introduction, which has since been dispersed by human agency to many parts of the continent. Sadly, the fungus has had a marked effect on the floristic composition and production of native forests, which in turn has also effected populations of birds, mammals and insects, that rely on wildflowers for seed, pollen, nectar and insect larvae for food.
July 1999
BIBLIOGRAPHY
Alexopoulos, C . J. & Mims, C. W. (1979), *Introductory Mycology*. John Wiley & Sons, New York.
Davison, E. M. & Shearer, B. L. (1989), Phytophthora spp. in indigenous forests in Australia. *New Zealand Journal of Forestry Science* **19**, 277-289.
Deacon, J. W. (1989?), *Introduction to Modern Mycology*. In Basic Microbiology. Volume 7. Editor J.F. Wilkinson, Blackwell Scientific Publications, Oxford.
Dickinson, C. & Lucas, J. (1979), *The Encyclopedia of Mushrooms*, Orbis Publishing limited, London.
Ingold, C. T. (1984), *The Biology of Fungi*, Fifth Edition, Hutchinson& Co. (Publishers) Ltd., London.
Marks, G. C. & Smith, I. W. (1991, *The cinnamon fungus in Victorian forests; history, distribution,management and control.* Victorian Department of Conservation and Environment. Lands and Forests Bulletin No. 11.
McMaugh, J. (1995), *What Garden Pest or Disease Is That?,* Companion Edition, Lansdowne Publishing Pty Ltd, Sydney.
Moss, S. T. (1986), *The Biology of Marine Fungi*. Cambridge University Press, Sydney.
Roelfs, A. P. & Bushnell, W. R. (1985), Editors. *The cereal rusts. Volume 2, Diseases, Distribution, Epidemiology, and control*. Academic Press, New York.