

# **Developmental biology of higher fungi**

Edited by D. Moore, L. A. Casselton, D. A. Wood  
and J. C. Frankland

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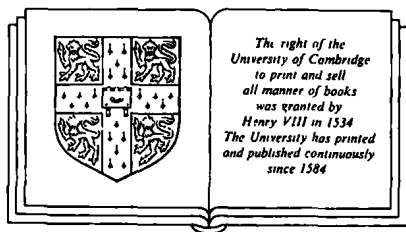
# Developmental biology of higher fungi

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*SYMPOSIUM OF  
THE BRITISH MYCOLOGICAL SOCIETY  
HELD AT THE UNIVERSITY OF MANCHESTER  
APRIL 1984*

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*EDITED BY*  
**D. MOORE, L. A. CASSELTON,  
D. A. WOOD & J. C. FRANKLAND**



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# Preface

There are probably as many definitions of developmental biology as there are developmental biologists. In the context of this book we consider that it includes not only structural form – both vegetative and reproductive – but also how that form relates to an organism's ecological niche. We feel that it would be a grave error to deal with development and differentiation as an abstraction, independent of the role that an organism may have to play in the ecological community to which it belongs. Many of the most obvious, and most intellectually challenging, morphogenetic features are a direct contribution to ecological performance, so ignorance of the ecological aspects can limit appreciation of the developmental process under consideration.

Over recent years the British Mycological Society has published a number of Symposium volumes which provide excellent background for this one. We particularly draw attention to: *Fungal Walls and Hyphal Growth* (1979; ed. J. H. Burnett & A. P. J. Trinci); *The Fungal Nucleus* (1981; ed. K. Gull & S. G. Oliver); *Decomposer Basidiomycetes* (1982; ed. J. C. Frankland, J. N. Hedger & M. J. Swift); and *Ecology and Physiology of the Fungal Mycelium* (1984; ed. D. H. Jennings & A. D. M. Rayner). In a very real sense these separate volumes contribute to a common narrative which reaches a climax with the publication of this volume on *Developmental Biology of the Higher Fungi*, uniting form, function and ecology.

The resource relations of agaric and agaricoid fungi with respect to developmental factors are discussed in the first six chapters, including aspects poorly represented in earlier volumes: namely tropical, parasitic and mycorrhizal fungi. Although only a small selection of such articles appears here, the connection between ecological habit and developmental form is clearly demonstrated.

The chapters on 'pure' developmental biology that follow relate cell structure, biochemistry and molecular biology, and extend to consideration of the ways in which such cellular processes are integrated in construction of multicellular fungal structures, including those of commercial importance. The most recent observations and interpretations are stressed throughout and we hope the content of this volume will remain of value for many years to come. Our authors have been imaginative and provocative where necessary, however, so we also hope to generate lively debate.

The idea for this Symposium topic was initiated in early 1981. It culminated in the 2nd General Meeting of the British Mycological Society held at Manchester University in April 1984, and we hope that now it will be disseminated more widely. We have many people to thank for their help with this enterprise, and too little space to name them; our thanks, though, are no less sincere for that. The British Mycological Society records its appreciation to the H. J. Heinz Co. Ltd., the Mushroom Growers Association and the British Council for donations in support of the Symposium.

Finally, we recall with sadness that just a few months before the meeting in Manchester we heard of the death of Dr G. H. Banbury, whose keen interest in basidiomycete physiology was an inspiration to many students of these organisms.

David Moore  
Lorna Casselton  
David Wood  
Juliet Frankland  
January 1985



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## Resource relations – an overview

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### Introduction

An important constituent of the developmental cycle of fungi is the way in which they interact with those living or non-living materials (resources/substrata<sup>1</sup>) which provide them with a source of organic nutrients. In this overview, which focuses on Agaricales and agaricoid Aphyllophorales (e.g. *Schizophyllum* and *Pleurotus* spp.), we hope, by consideration of these interactions, to provide a framework which will aid understanding of the diversity of habitats in which these fungi are found. An attempt will also be made to characterise the widely differing degrees of selectivity shown by these fungi for particular types of resource (resource selectivity), and to seek underlying causes. Our discussion will be based on the occurrence of interactions during four distinctive phases: *arrival at, establishment in, exploitation of, and exit from a resource.*

### Resource and habitat types

To set the background, we will first attempt to summarise what is actually known about the diversity of locations in which agarics are found and their relation to fungal modes of nutrition and type of resource. Then we will consider how the distribution patterns can be related to interactions during each of the four phases itemised above. At the outset, however, we must point out that information regarding the distribution of agarics is still overwhelmingly based on that of their fruit bodies

<sup>1</sup> In this chapter the term 'habitat' is used to describe the place where a fungus lives, 'substratum' is the medium within the habitat which physically supports the fungus during development, and 'substrate' is a specific biochemical component of the substratum. 'Resource' denotes any material which sustains fungal growth, and a 'resource unit' is a physically determinate unit of such material.

(basidiomata). Production of the latter is dependent on a wide range of variable exogenous and endogenous influences, so that their distribution probably rarely reflects adequately the 'real' distribution of mycelia.

Another source of bias results from the longer tradition of mycology in northern temperate regions, and we must acknowledge that our own understanding is based very much on the mycoflora of western Europe, with only a limited knowledge of the agarics of other parts of the world. The British vascular plant flora in particular is depauperate, associations occurring on the continent of Europe are not found here and *vice versa*; such geographical differences undoubtedly influence the occurrence and roles of agarics, which are distributed from the most extreme tundra regions to the tropics of all continents. In desert regions some agarics have even acquired a specialised xerophytic state, as in *Montagnites*, *Galeropsis* and *Cyttarophyllum*.

#### *Occurrence of biotrophy, necrotrophy and saprotrophy*

Three distinctive nutritional modes whereby fungi obtain organic nutrients from living or non-living substrata are now widely recognised (e.g. Lewis, 1973). In biotrophy, readily assimilable, soluble nutrients, such as simple sugars, are absorbed directly from living cells with which intimate contact is made, often via specialised haustoria, and sustained by a lack of cellular rejection responses concomitant with minimal damage to the tissues. In necrotrophy, living tissues are killed by the fungus prior to utilisation of constituent substrates, which often include polymers such as pectin, cellulose, lignin and chitin. In saprotrophy, non-living material, other than that killed by the fungus itself, is utilised.

The distinction between these nutritional modes may not always be clear, however, for two reasons. First, with respect to colonisation of living tissues, essentially saprotrophic behaviour, involving utilisation of diffusates or dead cells (which occur extensively in such tissues as wood, bark and skin), can easily be confused with necrotrophy and even biotrophy. In the latter case intimacy of contact with living cells and possession of mechanisms causing a redirection of nutrient flow towards the fungus may be important criteria enabling distinction from saprotrophy to be made. In the former case, perhaps only those examples where killing of living tissues is a *precondition* for, rather than an adjunct of, successful colonisation are worth distinguishing as 'true' or 'strict' necrotrophy. The problems of delineation are particularly acute in senescing, damaged or otherwise physiologically stressed tissues where the balance between a host and its symbiotic associates may be altered, as is frequently seen in mycorrhizal

roots when they age and become decorticated. Furthermore, in such tissues there may be release of nutrients otherwise unavailable to obligate saprotrophs. Subsequent establishment of the latter may *then* result in acceleration of tissue death, giving the appearance of necrotrophy, and indeed fungi behaving in this way are often described as 'weak parasites'. Similarly, a variety of fungi – whose number may be much greater than is currently recognised – cause 'symptomless infections', and some of these only develop extensive mycelium following senescence or injury. It may be best to regard these fungi as essentially saprotrophic but exhibiting a 'latent invasion' or, more graphically, a 'wooden horse' strategy whereby colonisation is effected – via buds, spores, sparse mycelium or mycelial knots or fragments – under conditions of stress militating against full mycelial development. Subsequent alleviation of stress, which in living tissues may be due to lack of nutrients, aeration problems or host-resistance mechanisms, then allows extensive mycelial outgrowth and a territorial advantage in resource capture (Cooke & Rayner, 1984; Rayner *et al.*, 1984).

The second problem arises from the possibility of adoption, under different circumstances, of different nutritional modes by an individual fungus. This is due partly to the mycelial body-form which, almost uniquely, provides a fungus with the potential to be in two places at once, with the different parts fulfilling different roles. Our knowledge of the extent to which this potential is actually realised is limited by the lack of adequately rigorous studies of the vegetative mycelium in natural habitats. However, that the potential exists is clear from the classic associations of *Monotropa* species with ectomycorrhizal fungi and of the orchid *Gastrodia* with *Armillaria*, whereby the fungus provides a bridge across which nutrients can flow from infected tree roots to the herbaceous plant (Hamada, 1939, 1940; Campbell, 1971; Duddridge: Chapter 6). There is also evidence that some normally saprotrophic fungi can, under appropriate circumstances, become necrotrophic or biotrophic, and *vice versa*. Thus *Marasmius androsaceus*, typically a decomposer of conifer needles, can be necrotrophic on *Calluna vulgaris*, causing heather blight (Macdonald, 1949). In some cases, exploitation of one nutritional mode may play a vital role in establishment of a fungus, and precede a second, often dominant, mode. Thus temporary saprotrophy may precede establishment of a wide range of essentially biotrophic and necrotrophic fungi, including lichen- and mycorrhiza-formers as well as parasites. By the same token, necrotrophy and possibly sometimes even biotrophy, by allowing occupation of living tissues, may facilitate saprotrophic survival or colonisation in the presence

of non-symbiotic competitors after death of the tissues (see *Crinipellis perniciosa* in Wheeler: Chapter 4). With respect to competition, necrotrophic mycoparasitism represents one important combative (antagonistic) mechanism enabling capture of resources from other fungi ('secondary resource capture'; see Cooke & Rayner, 1984; Rayner & Webber, 1984).

Given these problems, it is clearly difficult to classify *fungi* in terms of their nutritional modes; even the superficially useful prefixes 'obligate' and 'facultative' acquire shades of meaning and cannot be defined precisely. However, it is possible to distinguish the three modes as entities in themselves and to identify those fungi which characteristically exhibit them during all or part of their life cycles. This will be the approach in the following treatment of agarics.

**Biotrophy.** Agaric species and groups in which biotrophy has been detected with reasonable certainty are listed in Table 1.1. It will be evident that whereas, in general, biotrophic fungi form both mutualistic (lichens and mycorrhizas) and parasitic associations (with animals, above-ground parts of plants, and other fungi), amongst agarics biotrophy is overwhelmingly associated with the formation of ectomycorrhizas (sheathing mycorrhizas). Thus, although mycorrhiza formation is known, or reasonably suspected, in over 1975 species belonging to nine families, very few agarics are recognised as biotrophic parasites. One example is *Crinipellis perniciosa*, the cause of witches' broom of cocoa, (Hedger: Chapter 2; Wheeler: Chapter 4). Similarly, lichen formation is unusual amongst agarics, being particularly associated with the genus *Omphalina* which has many lichenised members in many parts of the world, particularly in Arctic-alpine and boreal plant communities.

We should mention here that not all mutualistic associations between agarics and other organisms are based on biotrophy. Thus, termites and attine ants cultivate, respectively, species of *Termitomyces* and *Leucoagaricus*. Here saprotrophy underlies the relationships, the fungi being grown on comminuted plant materials.

**Necrotrophy.** Examples of necrotrophy are given in Table 1.2. Although in general commoner than biotrophic parasitism, necrotrophy is apparently unusual in agarics, occurring sporadically amongst the various taxonomic groups. However, necrotrophic mycoparasitism may ultimately prove to be more common than is presently realised, due to the fact that many agarics only become dominant at relatively late stages during decomposition processes, when opportunistic parasitism may facilitate their establishment

Table 1.1. Examples of biotrophy among agarics

Ectomycorrhizal	Parasitic on angiosperms	Lichenised forms
Russulaceae:	Tricholomataceae:	Tricholomataceae:
<i>Russula</i> , <i>Lactarius</i>	<i>Crinipellis perniciosa</i>	<i>Omphalina ericetorum</i> group
Amanitaceae:		<i>O. grisella</i>
<i>Amanita</i> , <i>Limacella</i>		<i>O. chrysophylla</i>
Gomphidiaceae:		<i>O. huásoniana</i> (= <i>luteolilacina</i> )
<i>Gomphidius</i> , <i>Chroogomphus</i> , <i>Cystogomphus</i>		<i>O. flava</i> (= <i>luteovittellina</i> )
Paxillaceae:		<i>Myxomphalia naura</i>
<i>Paxillus</i>		
Boletaceae (including Xerocomaceae & Strobilomycetaceae):		
<i>Boletus</i> , <i>Suillus</i> , <i>Xerocomus</i> , <i>Strobilomyces</i> ,		
<i>Boletellus</i> , <i>Heimiella</i> , <i>Austroboletus</i> , <i>Fistulinella</i>		
Cortinariaceae:		
<i>Cortinarius</i> , <i>Descolea</i> , <i>Stephanopus</i> , <i>Inocybe</i> ,		
<i>Hebeloma</i> , <i>Naucoria</i> <sup>a</sup> , <i>Rozites</i>		
Tricholomataceae:		
<i>Tricholoma</i> s.s., <i>Laccaria</i> , <i>Leucopaxillus</i>		
Hygrophoraceae		
<i>Hygrophorus</i> (excluding <i>Hygrocybe</i> , <i>Camarophyllus</i> )		

<sup>a</sup> An unexplained association with *Alnus* and *Salix*, not generally considered to be ectomycorrhizal.

Table 1.2. Examples of necrotrophy in agarics

Fungi	Hosts
Fungicolous	
<i>Armillaria</i> spp.	<i>Entoloma abortivum</i>
<i>Claudopus parasiticus</i>	<i>Polyporus squarrosus</i>
<i>Collybia cirrhata/tuberosa</i> group	Tricholomataceae
<i>Nyctalis</i> spp.	Russulaceae
<i>Omphalina cupulatoidea</i>	<i>Peltigera</i>
<i>Psathyrella epimyces</i>	<i>Coprinus comatus</i>
<i>Volvariella surrecta</i>	<i>Clitocybe nebularis</i> and allies
On animals	
<i>Hohenbuehelia</i> spp.	Nematoda
<i>Coprinus cinereus</i>	Human beings (but see text)
<i>Schizophyllum commune</i>	
On plants	
<i>Agrocybe parasitica</i>	<i>Beilschmiedia tava</i> and introduced dicotyledonous trees
<i>Armillaria</i> spp.	Gymnospermous and angiospermous trees and shrubs
<i>Flammulina velutipes</i> <sup>a</sup>	Deciduous trees
<i>Marasmius androsaceus</i>	<i>Calluna</i>
<i>Mycena citricolor</i>	<i>Coffea</i>
<i>Oudemansiella mucida</i> , <i>O. radicata</i> <sup>a</sup>	<i>Fagus sylvatica</i>
<i>Pholiota</i> spp. <sup>a</sup>	Deciduous trees
<i>Pleurotus</i> spp. <sup>a</sup>	Shore forest, Madagascar
<i>Russula annulata</i>	Amazonian rain forest
<i>Xerocomus radicitola</i>	

<sup>a</sup> These wood-inhabitants may not be strict necrotrophs; see text.



and replacement of other fungi. At present, however, much of our knowledge of mycoparasitism amongst agarics is based on those which produce fruit bodies on those of other fungi, notably other agarics, e.g. species of *Nyctalis* on Russulaceae; *Armillaria* inducing gasteroid fruit bodies in *Entoloma abortivum* (Watling, 1974a), and *Psathyrella epimyces* on *Coprinus comatus* (McDougall, 1919).

Very few agarics have been reported to be necrotrophic on animals. True necrotrophy occurs in *Hohenbuehelia*, where the anamorphic state, *Nematocionus*, is nematophagous. *Schizophyllum commune* has been associated with infections of the mouth (Watling & Sweeney, 1971), although more familiar are the records of colonisation of skin and other keratinised tissues, the resulting pathogenesis is not considered to be true necrotrophy. *Coprinus cinereus*, as *C. delicatulus* (see Kemp, 1975), has been isolated as an opportunistic but fatal pathogen of human heart (De Vries, Kemp & Speller, 1971), but little is known of the exact nature of the association.

Amongst agarics recorded as necrotrophic on plants, it is probable that many should be regarded as only secondarily or not strictly necrotrophic since they predominantly exhibit other nutritional modes, or pathogenesis is incidental to, rather than a prerequisite for, colonisation. Examples include various *Armillaria* and *Pholiota* species, *Agrocybe parasitica* in New Zealand, *Russula annulata* in Madagascar and *Marasmius androsaceus* (see above). Species of *Armillaria*, in particular, exhibit a wide spectrum of behaviour ranging from virtually pure saprotrophy, as in *A. bulbosa*, to strongly pathogenic species exhibiting a high degree of necrotrophy, as in *A. mellea sensu stricto*, *A. ostoyae* and *A. hiemii* (see also Rishbeth: Chapter 3). Clear examples of necrotrophy are provided by *Mycena citricolor* which causes a sometimes severe leaf spot on *Coffea* (Buller, 1934, as *Omphalia flavida*), and *Tephrocybe palustris*, which causes distinctive white patches in *Sphagnum* beds, probably utilising proteinaceous material from the moss cells (Redhead, 1981).

**Saprotrophy.** The occurrence of saprotrophy amongst agarics of western Europe, together with an indication of the range of resource and habitat types, is given in Table 1.3. The widespread occurrence of agarics exhibiting saprotrophy and the diversity of their resource relations will be immediately apparent. However, the exact nature of these relations often remains obscure in the absence of rigorous studies. For example, in the case of those fungi listed as 'terricolous', largely because they are not obviously mycorrhizal or attached to visible particulate debris, it would