CHAPTER 5

Fruit Bodies: Their Production and Development in Relation to Environment

David Moore, Alan C. Gange, Edward G. Gange and **Lynne Boddy**

Contents

Abstract

Sexual reproduction is important because it generates genetic variation, offers an escape from DNA parasites and provides a means to repair DNA damage. Many fungi exhibit particular patterns of sexual fruit body morphogenesis but the characteristics differ between species. However, it is possible to generalise that within developing fruit body tissues, fungal cells embark on a particular course of differentiation in response to the interaction of their intrinsic genetic programme with external physical signals (light, temperature, gravity, humidity), and/or chemical signals from the environment and other regions of the developing structure. Fruit body morphogenesis is affected by carbon and mineral nutrient availability, and environmental variables including temperature, water availability, CO_2, light and interactions

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with other fungi and bacteria. Changes in the seasonal pattern of fruiting in the UK can be detected from field records made in the last 50 years, and while not all species behave in the same way, mean first fruiting date is now significantly earlier and mean last fruiting date is now significantly later, which results in an extended fruiting season. Significant numbers of species that previously only fruited in autumn now also fruit in spring. Such analyses show that relatively simple field observations of fungi can detect climate change, and that fungal responses are sufficiently sensitive to react to the climate change that has already occurred by adapting their pattern of development. Unfortunately, though it is possible to deduce the decisive steps in development that are open to influence, the molecular controls that normally regulate those steps remain unknown. Extensive genomic analysis shows that sequences crucial to multicellular development in animals or plants do not occur in fungal genomes, so we are ignorant of the basic control processes of fungal multicellular developmental biology.

1. INTRODUCTION

We use the term fruit bodies to encompass all the structures that develop from fungal mycelia to produce and distribute spores or other propagules, including basidiomata—the structures that release sexual spores (meiospores) in Basidiomycota, as well as a range of structures that produce asexual spores (mitospores) and some somatic (vegetative) structures, such as stromata and sclerotia, that can survive adverse conditions. Obviously, the phrase encompasses a very wide range of organs but their common feature is that they are multicellular, and their shape and form emerge as a result of a sequence of developmental adjustments. That is, they exhibit a characteristic pattern of morphogenesis.

1.1 Fungal Morphogenesis

Within the developing tissues of a fruit body, cells embark on a particular course of differentiation in response to the interaction of their intrinsic genetic programme with external physical signals (light, temperature, gravity, humidity), and/or chemical signals from other regions of the developing structure. These chemicals may be termed organisers, inducers or morphogens, and may inhibit or stimulate entry to particular states of determination. Chemical signals may contribute to a morphogenetic field around a structure (cell or organ), which permits continued development of that structure but inhibits formation of another structure of the same type within the field. All of these phenomena contribute to the pattern formation that characterises the 'body plan' created by the particular distribution of differentiated tissues in the multicellular structure. Pattern formation depends on positional information, which prompts or allows the cell to differentiate in a way appropriate to its position in the structure and may be conveyed by concentration gradients of one or more morphogens emitted from one or more spatially distinct organisers. Pattern formation thus involves an

instructive process, which provides positional information, and a second interpretive process, in which the receiving cell or tissue responds.

Fungi are 'modular organisms' in which growth is repetitive, and a single individual mycelium will have localised regions at very different stages of development (Andrews, 1995). Consideration of developmental regulatory systems is relevant to the current discussion because *any* effect of the external environment on fruit body development must operate through an influence on the control systems that determine the distribution and growth patterns of the multicellular structure.

The constituent cells of a fungal fruit body are generally considered to be totipotent (able to follow any pathway of differentiation), because a mycelial culture can be produced in vitro from a fragment of a mature, fully differentiated structure, e.g. a fruit body stem. This feature results in a morphogenetic plasticity which surpasses that of other organisms and provides an intellectual challenge in terms of developmental biology, taxonomy and genetics (Watling and Moore, 1994). The only exceptions to totipotency are the meiocytes (the cells within which meiosis occurs), which are committed to sporulation once they have progressed through meiotic prophase (Chiu and Moore, 1988a, 1988b, 1990, 1993; Chiu, 1996). On the other hand, even meiocytes can be 'used' for non-sporulation functions: the hymenium of *Agaricus bisporus* is packed with basidia held in an arrested meiosis and serving a purely structural function (Allen *et al*., 1992).

Differentiated fungal cells require reinforcement of their differentiation 'instructions'. This reinforcement is part of the context within which they normally develop, but when removed from their normal environment most differentiated hyphae revert to vegetative hyphae. Hyphal differentiation is consequently an unbalanced process in comparison with vegetative hyphal growth. In most hyphal differentiation pathways the balance must be tipped in the direction of 'differentiation' by the *local* microenvironment, which is, presumably, mainly defined by the local population of hyphae.

Another common feature is that morphogenesis is compartmentalised into a collection of distinct developmental processes (called 'subroutines'; Figure 1; Moore, 1998a). These separate (or parallel) subroutines can be recognised at the levels of organs (e.g. cap, stem, veil), tissues (e.g. hymenophore, context, pileipellis), cells (e.g. basidium, paraphysis, cystidium) and cellular components (e.g. uniform wall growth, growth in girth, growth in length, growth in wall thickness). They are distinct genetically and physiologically and may run in parallel or in sequence. When they are played out in their correct arrangement the morphology that is normal to the organism results. If some of the subroutines are disabled (genetically or through physiological stress), the rest may still proceed. This partial execution of developmental subroutines produces an abnormal morphology. The main principles that govern fungal development as deduced from observation, experiment and computer modelling are summarised in Table 1 (from Moore, 2005).

Fungal morphogenesis must be totally different from animals, because fungal cells have walls, and from plants (whose cells also have walls) because hyphae grow only at their tips and hyphal cross-walls form only at right angles to the

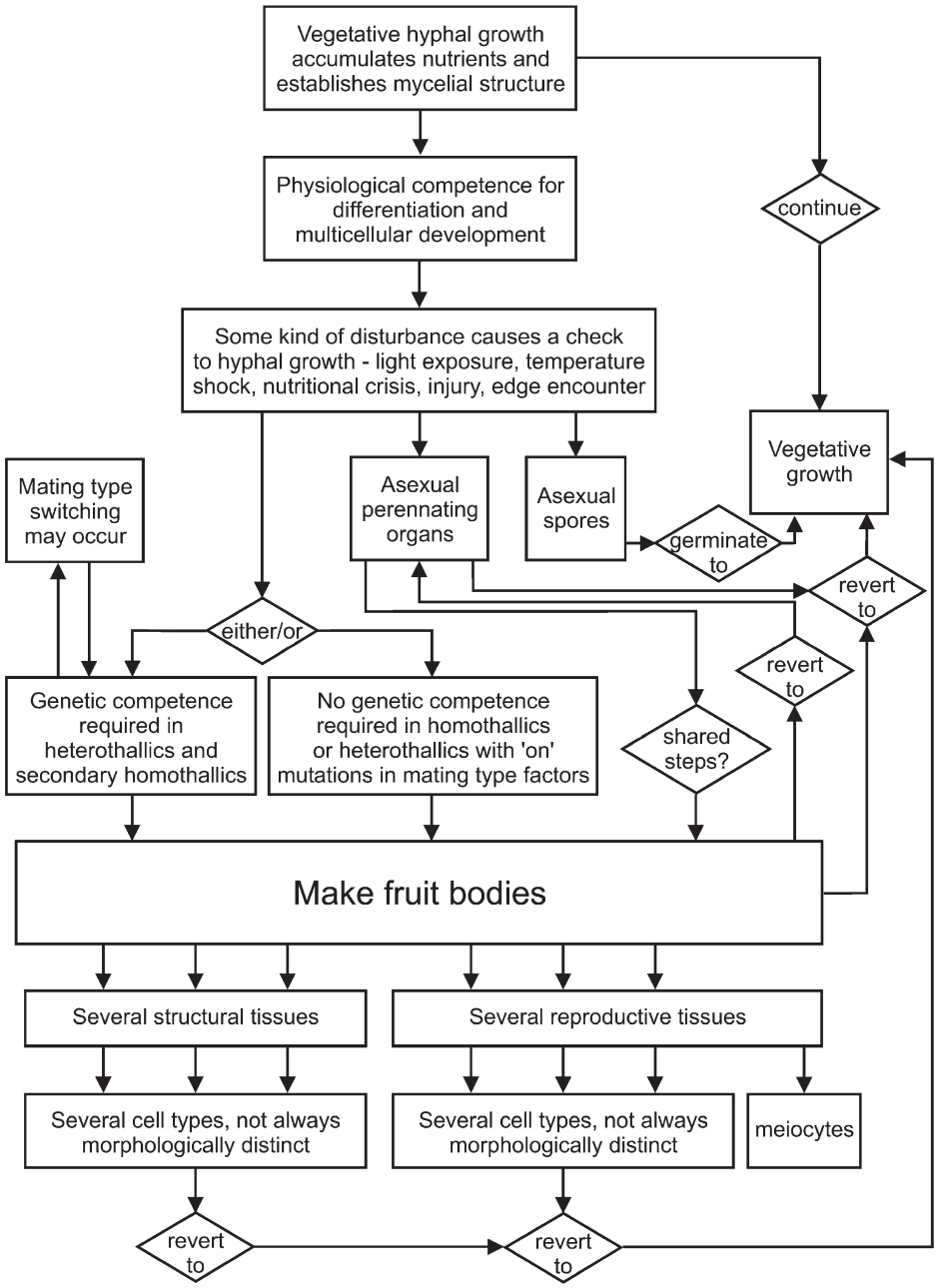

Figure 1 Flowchart showing a Simplified View of the Processes involved in Development of Fruit Bodies and other Multicellular Structures in Fungi (from Moore, 1998a).

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Table 1 The Eleven Principles that Govern Fungal Development

Principle 1	The fundamental cell biology of fungi on which development depends is that hyphae extend only at their apex, and cross-walls form only at right angles to the long axis of the hypha
Principle 2	Fungal morphogenesis depends on the placement of hyphal branches
Principle 3	The molecular biology of the management of cell-to-cell interactions in fungi is completely different from that found in animals and plants
Principle 4	Fungal morphogenetic programmes are organised into developmental subroutines, which are integrated collections of genetic information that contribute to individual isolated features of the whole programme. Execution of all the developmental subroutines at the right time and in the right place results in a normal structure
Principle 5	Because hyphae grow only at their apex, global change to tropic reactions of all the hyphal tips in a structure is sufficient to generate basic fruit body shapes
Principle 6	Over localised spatial scales coordination is achieved by an inducer hypha regulating the behaviour of a surrounding knot of hyphae and/or branches (these are called Reijnders' hyphal knots)
Principle 7	The response of tissues to tropic signals and the response of Reijnders' hyphal knots to their inducer hyphae, coupled with the absence of lateral contacts between fungal hyphae analogous to the plasmodesmata, gap junctions and cell processes that interconnect neighbouring cells in plant and animal tissues suggest that development in fungi is regulated by morphogens communicated mainly through the extracellular environment
Principle 8	Fungi can show extremes of cell differentiation in adjacent hyphal compartments even when pores in the cross-wall appear to be open (as judged by transmission electron microscopy)
Principle 9	Meiocytes appear to be the only hyphal cells that become committed to their developmental fate. Other highly differentiated cells retain totipotency — the ability to generate vegetative hyphal tips that grow out of the differentiated cell to re-establish a vegetative mycelium
Principle 10	In arriving at a morphogenetic structure and/or a state of differentiation, fungi are tolerant of considerable imprecision (= expression of fuzzy logic), which results in even the most abnormal fruit bodies (caused by errors in execution of the developmental subroutines) being still able

Table 1. (*Continued*)

	to distribute viable spores, and poorly (or wrongly) differentiated cells still serving a useful function
Principle 11	Mechanical interactions influence the form and shape of the whole fruit body as it inflates and matures, and often generate the shape with which we are most familiar

Source: From Moore (2005).

long axis of the hypha. Consequently, fungal morphogenesis depends on the placement of hyphal branches. A hypha must branch to proliferate. To form a multicellular structure, the position at which the branch emerges and its direction of growth must be controlled. A major aspect of that directional control is an autotropism—a tropism to self—in which growth direction of each hyphal branch is influenced by the position of the rest of the mycelium. Exploratory mycelia experience a negative autotropism, which causes them to grow away from the main mycelium and this maintains the outward exploration of the substratum. On the other hand, to create a multicellular structure like a fruit body, positive autotropism is essential to cause hyphae to grow together for hyphal branches to cooperate and coordinate their activities. Tropic reactions imply a signalling system, a signal sensing system and a reaction system. Mathematical models of these systems can be created very successfully (Stočkus and Moore, 1996; Meškauskas *et al*., 1998, 1999a, 1999b, 2004a, 2004b; Moore *et al*., 2006), but we know nothing yet about their biochemistry, cell biology or molecular nature. However, it is clear that what mechanisms exist must be *different* to animals and plants because gene sequences known to regulate development in animals and plants do not occur in fungal genomes (Moore *et al*., 2005; Moore and Meškauskas, 2006).

1.2 Morphogenetic Control Elements

The only major morphogenetic control elements known in fungi are the mating type factors, which regulate pheromone production and pheromone receptors involved in mating, ranging from recognition between sexually competent cells in yeast to governing growth of clamp connections, internuclear recognition and regulation of the distance between the two nuclei in Basidiomycota (Casselton, 2002). However, not all fungi possess mating type factors, and, indeed, even in species that have a well-developed mating type system apparently normal fruit bodies can be formed by haploid cultures, and fruit body formation can usually be separated from other parts of the sexual pathway by mutation (see Chapter 5 in Moore, 1998a).

Generally, vegetative compatibility genes define the individuals of fungal populations, while mating type factors are usually interpreted as favouring the outbreeding of a fungal population (Chiu and Moore, 1999). Consequently, mating type genes contribute to management of the genetics of the population as

well as to the sexual development of the individual. Sexual reproduction generates genetic variation, offers an escape from DNA parasites and provides a means to repair DNA damage (Bernstein *et al.*, 1985).

1.3 Importance of Sexual Reproduction

The crucial step in sexual reproduction, which provides the contrast with asexual reproduction, is the fusion of nuclei derived from different individuals. If the individuals involved in a mating have different genotypes, the fusion nucleus will be heterozygous and the products of the meiotic division can be recombinant genotypes. Thus, in one sexual cycle, new combinations of characters can be created in the next generation for selection. Consequently, the most common 'explanation' for sex is that it promotes genetic variability through out-crossing and that variability is needed for the species to evolve to deal with competitors and environmental changes. There is plenty of evidence to show that asexual lineages change little in time and that out-crossing certainly does promote variability in a population, which enables the organism to survive environmental challenges (Hurst and Peck, 1996; Burnett, 2003).

This, though, is a 'group selectionist' interpretation. It argues that variation generated in an *individual* meiosis benefits the *group* or population to which the individual belongs. Yet current theory prefers to emphasise that selection acts on individuals (Carlile, 1987; Dawkins, 1989). A feature that is advantageous in selection must be so because of benefit to the individual itself or its immediate progeny. As noted above, an alternative interpretation of the selective value of a sexual cycle suggests that repair of damaged DNA is the crucial advantage of meiosis (Bernstein *et al.*, 1985). It is argued that bringing together genomes from two different individuals enables DNA damage in one parental chromosome, caused by mutation or faulty replication, to be repaired by comparison and recombination with the normal chromosome provided by the other parent. Genetic fitness would be increased but only when out-crossing ensures heterozygosis. Even an incomplete sexual cycle might be of advantage in this case.

Gene mutations can be recessive and damaging, and different mutations are likely to occur in different mitotically generated cell lines. Just the formation of the diploid (or heterokaryon in most Basidiomycota) by out-crossing will benefit the mated individual if recessive adverse mutations are masked by non-mutant ('wild-type') alleles in the nuclei of the other parent. Out-crossing might also give rise to heterozygous advantage, where the heterozygous phenotype is better than either of its homozygous parents. This has been demonstrated frequently in plants and animals, and also in *Saccharomyces cerevisiae* (James, 1960).

Clearly, the genotype of the parental mycelium makes a crucial contribution to the genetics of the progeny population, but to produce a progeny population the parental mycelium must first produce a crop of fruit bodies and to do that it must grow into and through the substratum to capture, translocate and accumulate sufficient nutrients to support the formation of what can be massive multicellular structures.

2. PHYSIOLOGICAL FACTORS FAVOURING FRUIT BODY PRODUCTION

Fungi enjoy an adaptable and flexible metabolism. It is unlikely that there is a compound, organic or inorganic, on the planet that some fungus cannot utilise, transform, modify or otherwise metabolise (see Chapter 3 in Moore, 1998a). These versatile biochemical capabilities are used in a variety of ways during morphogenesis in fungi and over the past century there have been numerous *in vitro* studies of the nutritional physiology of fruit body production. Nutrients that are inferred to be 'favourable' for fruiting are those that allow the organism to exert its own intrinsic controls over the progress of its metabolism (Hawker, 1950).

2.1 Carbohydrates

An enormous volume of research has been done on this topic (for reviews see Moore-Landecker, 1993; Jennings, 1995; Moore, 1998a), though it is important to remember that conditions in the laboratory are far removed from the natural environment. The crucial insights came from Hawker's (1939, 1947) experiments: simple sugars tend to favour asexual spore production while oligo- and polysaccharides are especially good carbon sources for production of fruit bodies. Glucose often represses fruit body production, even in very low concentrations. The rate with which a fungus can hydrolyse a carbohydrate determines the ability of the carbohydrate to promote fruit body formation (Hawker and Chaudhuri, 1946), so what seems to matter most is the rate of supply and ease of use of substrates as determinants of their value in promoting fruit body formation. It comes as no surprise, therefore, that saprotrophic Basidiomycota on dung fruit more readily than those utilising leaf litter, and in turn than wood decomposers, though, of course, these resources also differ in mineral nutrient content. Likewise, fungi that participate early in community development within a resource fruit more readily than most later colonizers (Cooke and Rayner, 1984; Rayner and Boddy, 1988; Chapter 11), whose carbon sources are more recalcitrant.

2.2 Nitrogen Sources

Similar conclusions are reached when attention turns to the 'best' nitrogen source, which usually proves to be one amino acid or a mixture of amino acids. In most cases inorganic nitrogen and ammonium salts fail to support fruit body development although they may support production of primordia, but amino acids are required to produce the *mature* fruit bodies (reviewed in Moore, 1998a). This suggests that the formation of fruit body initials may be an activity of the vegetative mycelium and it is their further development which constitutes the fundamental 'mode switch' into the fruit body morphogenetic pathway. At least some of the deleterious effects of ammonium salts may be due to their influence on the pH of the medium, though metabolite repression caused by ammonium ions in many Ascomycota may be another cause. Fruit body formation in some fungi is favoured by provision of protein as source of nitrogen. Several

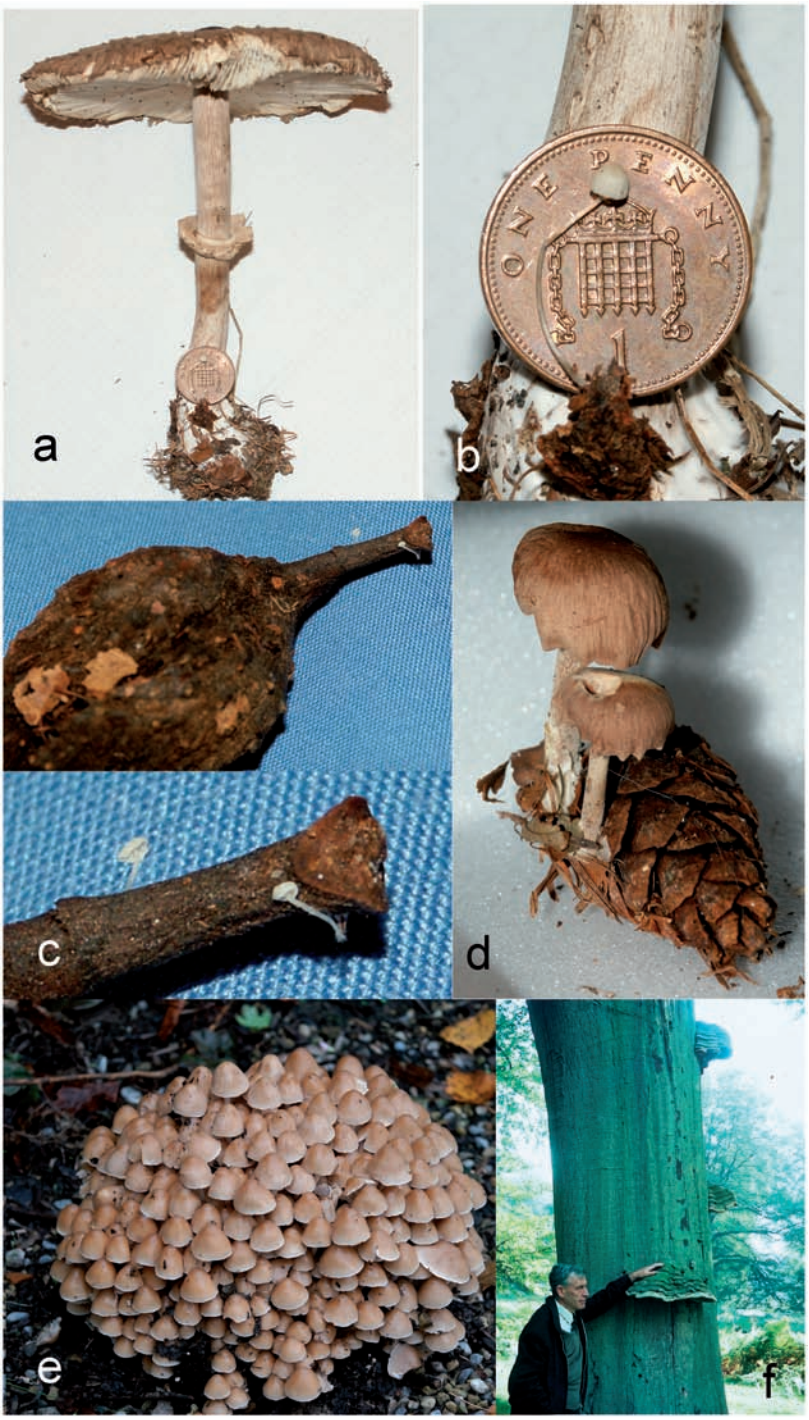
basidiomycetes (*A. bisporus*, *Coprinus cinereus* (= *Coprinopsis cinerea*) and *Volvariella volvacea*) are able to use protein as a carbon source as efficiently as they use glucose (Kalisz *et al*., 1986), so an advantage of protein is that it serves as a source of carbon, nitrogen and sulphur. In more natural conditions, *A. bisporus* and a wide range of other filamentous fungi can utilise dead bacteria as sole source of carbon, nitrogen, sulphur and phosphorus (Fermor and Wood, 1981; Grant *et al*., 1986).

Higher carbon than nitrogen concentrations are usually required for fruit body production but the optimum C:N ratio varies from ~30:1 to ~5:1 (references in Moore-Landecker, 1993). High concentrations of amino acids tend to delay and/or depress maturation of fruit bodies even in organisms in which fruit body formation is optimal on media containing lower concentrations of amino acids, an effect that may result from the production of large quantities of ammonium as a nitrogen-excretion product on such substrates. When grown on protein as sole carbon source, nitrogen needs to be excreted from the mycelium; when this happens *in vitro* the ammonium concentration of the medium *increases* drastically during mycelial growth. One-third to one-half of the supplied protein-nitrogen was metabolised to ammonia by batch cultures of three saprotrophic basidiomycetes when protein was the sole source of carbon (Kalisz *et al*., 1986).

2.3 Nutrient Capture

Hyphae absorb sufficient nutrients to support their active vegetative growth *and* to allow accumulation of reserve materials, which may subsequently be translocated to sites of need, including developing fruit bodies. Fruit body primordia may be fairly uniformly dispersed, but locations of enlarging and maturing fruit bodies may be much less evenly spread. For example, in *Coprinus lagopus*, certain favourably placed young fruit bodies may initiate a flow of nutrients in their direction, others that are deprived then fail to mature (Madelin, 1956a, 1956b, 1960). When *C. lagopus* colonies were physically divided in half early in growth, the two halves yielded similar fruit body biomass, whereas the two sides of an intact colony could differ by as much as 10:1, implying that in the latter case the 'minority' half is exporting its nutrients to the 'majority' half (Madelin, 1956b).

Mycelia must have access to sufficient substrates before fruiting is possible. Buller (1931, p. 165) discussed the requirement for a minimum amount of mycelium to support a minimum fruit body in *Coprinus sterquilinus*, arguing that one of the functions of hyphal fusions between (clonal) germlings is to ensure the rapid formation of that minimal size mycelium encompassing a corresponding minimum quantity of substrate. Obviously, the minimum quantity of substrate required varies between species depending on size of the fruit bodies produced. Fungi producing small fruit bodies are able to do so with only a small amount of resource, e.g. minute *Marasmius* and *Mycena* species restricted to leaf petioles, small portions of leaf lamina, beech cupules, etc. (Figure 2). A very large mycelial domain is required to produce the large, perennial brackets of heart-rot fungi (Rayner and Boddy, 1988). It was estimated that all of the nitrogen in 13.6 g of wood would be required to supply 1 g of *Ganoderma applanatum* basidiome, and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36.1 g wood to supply 1 g of spores, based on mean nitrogen content of fruit bodies (1.13%), spores (3.05%) and *Betula* sapwood (0.83%; Merrill and Cowling, 1966). Since fruit bodies are commonly 1 kg or more, and several grams of spores are produced each year (*Fomes fomentarius* produced 1.115 g spores in 20 days (Meyer, 1936)), a mycelium would need to draw upon the entire nitrogen content of more than 14 kg wood.

Culture studies indicate that once the minimum substrate size is reached fruit body distribution is governed by a flow of nutrients towards particular developing fruit bodies, rather than localised nutrient depletion or inhibition of development. The generality of this interpretation is based on two consistent observations. First, that many fruit body primordia are generally formed, but only a comparatively small number of them develop into mature fruit bodies; but if fruit body size is related to local nutrient supply, one would expect that all of the primordia on a colony would develop into mature but small fruit bodies, each using those quantities of materials which are available locally and adjusting its size accordingly. Second, a crop consisting of several fruit bodies will often develop as a group, so that any general inhibitory action is unlikely. The concept that nutrients flow towards a favoured centre would permit several neighbouring primordia to mature in a clump, while still withholding nutrients from unfavourably situated primordia. Clearly, different species emphasise different aspects of this physiology in their fruiting behaviour and some are characteristically solitary, e.g. *Phallus impudicus*, while others are caespitose, e.g. *Hypholoma fasciculare* and *Psathyrella multipedata* (Figure 2). Some Basidiomycota, notably Corticiaceae, form fruit bodies over the entire resource surface that they have access to, e.g. *Vuilleminia comedens* on branches in the canopy. Large, skin-like fruit bodies of some Corticiaceae may form at individual sites, subsequently coalescing on contact. Detail is, however, lacking as much less research has been done on these species than on Agarics.

In vitro experiments consistently indicate a general correlation between nutrient exhaustion of the medium and the onset of multicellular morphogenesis; however, reproduction is not an alternative to vegetative hyphal growth but an aspect of the differentiation of vegetative hyphae. Continued growth of the vegetative mycelium is necessary to provide sustenance to its developing fruit bodies. Correlation of fruiting with nutrient exhaustion of the medium does *not* mean that development is prompted by a mycelium that is starving, because the mycelium has accumulated nutrient reserves. Further, the timing of fruiting and the amount of biomass that a fungus commits to fruiting varies with life history

Figure 2 Some Fruit Bodies of Saprotrophic Basidiomycota, illustrating a Range of Sizes and Resources: (a) the Solitary *Macrolepiota rhacodes* with a Coin Size Marker (20 mm Diameter); (b) a Fruit Body of *Marasmius setosus* with the Same Coin Size Marker; (c) even Smaller *Marasmius* Specimen on the Petiole of a Beech Cupule; (d) *Collybia peronata* on a Pine Cone; (e) the Decidedly Caespitose *Psathyrella multipedata*; (f) Terence Ingold Posing with *Fomes fomentarius* on a Beech Tree in Knole Park, Sevenoaks, Kent, 1969 (see Ingold, 2002). Photographs (a)–(e) by David Moore of Specimens Collected by Members of the Mid-Yorkshire Fungus Group at Harlow Carr Gardens.

strategy (Cooke and Rayner, 1984; Rayner and Boddy, 1988; Chapter 11). Rapid and extensive commitment of mycelial biomass is an R-selected (ruderal) characteristic, typical of fungi that rapidly dominate following disturbance. Such fungi are usually not combative and are often rapidly replaced by later arriving, more combative species. They, therefore, must commit to reproduction before they are killed and replaced. By contrast, slower and intermittent commitment to reproduction is characteristic of fungi in stressful environments and/or that are combative, dominating middle stages of community development. Laboratory studies have largely employed species, e.g. *Coprinopsis* spp., *Pleurotus* spp. and *Schizophyllum commune*, that fruit readily in culture, which is a ruderal characteristic; thus, we must be cautious in extrapolating to fungi with other life history strategies.

As we have discussed above, only preconditioned mycelium is capable of undergoing morphogenesis. The preconditioned mycelium must be beyond a particular minimum size, perhaps be of a particular minimum age, and the underlying nature of both these preconditions is that the mycelium has been able to accumulate sufficient supplies of reserve materials to support development of the minimum reproductive structure. For some fungi, exhaustion of a particular metabolite from the medium or substrate may be a signal that prompts morphogenesis in a mycelium that is *not* starving, but is healthy and well provisioned. Exhaustion of one or more constituents of the medium changes the balance of nutrient flow. If the medium is no longer fully supportive, the requirements of active hyphal growth can no longer be met by import from outside the hyphae and the balance must shift from 'reserve material accumulation' to 'reserve material mobilisation'. That change from balanced growth to growth under limitation in external nutrient supply is what signals the onset of morphogenesis. Cellular differentiation leading to fruit body morphogenesis is an expression of unbalanced growth which is precipitated by one or more changes in the balance of metabolism, and itself causes further cycles in which cellular components are re-allocated. Even though nutritional dependence on the external substrate may still be demonstrated, the emphasis shifts towards intramycelial regulation.

While this metabolic change is proceeding there is a change in the behaviour of hyphal branches. For some branches, negative autotropism becomes positive autotropism, so that neighbouring hyphae, often those of the surface or more aerial parts of the mycelium, can interact. They form centres of rapid but self-restricting growth and branching which become the hyphal aggregates or mycelial tufts, perhaps 100–200 μm in diameter, that are the 'initials' of the reproductive structure the organism can produce. Frequently, and especially in culture, these aggregates are formed in great number over the whole surface of the colony. As supplies of nutrients in the medium approach exhaustion repression of the morphogenesis of these hyphal aggregates is lifted and they proceed to develop further. As mentioned above, only a small number of the first-formed hyphal aggregates usually undergo further development and these become the focus for translocation of nutrients, mobilised from the stores in other parts of the colony and transported through the hyphal network to the developing reproductive structures.

Illumination may be required, either to promote further morphogenesis or to direct development into one of a small number of morphogenetic pathways (see below). Particular temperatures may also be required for particular pathways of development. Development usually proceeds in a series of steps that may be coordinated by environmental cues (illumination, temperature, atmosphere) and often involve sweeping re-allocation of cellular components. Within the young fruit body, therefore, new accumulations of 'stored' nutrients arise, and there may be a number of these accumulation–mobilisation–translocation–accumulation cycles during the development of the reproductive structure.

2.4 Non-Nutritional Environmental Variables

As well as carbon and nitrogen nutrition, discussed above, many more environmental variables affect fruit body initiation and development (reviewed by Jennings, 1995; Moore, 1998a; Scrase and Elliott, 1998; Kües and Liu, 2000). Such is the bulk of the literature that we can do little more here than list the major observations.

As the above discussions of metabolism imply, fruit body development requires oxidative metabolism (glycolysis and TCA cycle activity are often amplified) and good aeration is, not surprisingly, associated with successful fruiting. This means not only oxygen but also various volatile metabolites including carbon dioxide. Elevated carbon dioxide concentrations can suppress basidiome initiation in *S. commune* (Raudaskoski and Salonen, 1984). In *Agaricus*, increased elongation of the stem occurs with elevated CO_2, accumulated naturally from respiration, whereas cap and gills expand and spores mature more rapidly when CO_2 is removed (Turner, 1977). It has been argued that the morphogenetic effect on maturation of the fruit body may have ecological advantage: CO_2-enhanced elongation of the stem would raise the gills away from the surface of the substratum where the concentration of CO_2 might be expected to be higher than in the wider atmosphere because of the respiratory activity of microorganisms in the casing soil (Turner, 1977).

High CO_2 levels promote formation of long hyphal compartments in *S. commune*. It has been argued (Raudaskoski and Salonen, 1984) that a wood decomposer like *S. commune* is likely to experience elevated CO_2 within the wood as respiratory CO_2 accumulates. Mycelium that reaches the surface of the wood, however, will be exposed to CO_2 reduced to the atmospheric normal. Such mycelium will be able to form the shortened cells and more compact branching habit, and be predisposed to fruit body formation.

Light has diverse effects on formation of reproductive structures in different basidiomycetes, increasing or decreasing their number, affecting their development or determining whether or not they are produced (Carlile, 1970; Elliott, 1994). In general, the most effective parts of the spectrum are the near-ultraviolet and blue wavelengths, typical of the shaded and litter-covered forest floor. There are indications that the photoreceptor involved in fruit body morphogenesis may be membrane bound. In some fungi levels of intermediary metabolites and coenzymes, and activities of several enzymes respond very rapidly to changes in

illumination. The vegetative mycelia of many Ascomycota require exposure to light before they will produce fruit bodies and/or asexual spores, and show specificity not only for particular wavelengths but also for a particular dosage of light radiation. In some Basidiomycota, sequential light exposures are responsible for initiating and programming fruit body morphogenesis, and periods of darkness between illumination events are important. Again, blue (400–520 nm) to near-ultraviolet (320–400 nm) light is the most effective and the work suggests that at least two photosensitive systems operate in fungi, one stimulated by near-ultraviolet and the other by blue light. Because their absorption spectra parallel the action spectra of the blue light photoresponses, carotenes and flavins appear to be the best candidates for photoreceptors.

Production of fruit bodies *in vitro* typically occurs over a more restricted range of temperature than that which will support mycelial growth. Optimum temperatures for fruit body production are generally lower than those most favourable for mycelial growth. In Basidiomycota most information relates to species adopted as laboratory models or for commercial cultivation. Cultivated species frequently need a temperature downshift (by 5–10°C) and lower CO_2 concentrations for fruiting, e.g. *A. bisporus*, *C. cinereus*, *Flammulina velutipes*, *Kuehneromyces mutabilis*, *Lentinula edodes*, *Pholiota nameko*, *Pleurotus ostreatus*, *Stropharia rugosa-annulata* and *V. volvacea* (Chang and Hayes, 1978; Stamets, 1993). This list includes compost-grown fungi as well as some wood-chip/straw and log-grown wood decomposers, and is not unrepresentative of the wider community of saprotrophic fungi, so it may be that most Basidiomycota require a temperature downshift. A prolonged downshift is not always required; thus, fruit body initiation in *F. velutipes*, which fruits in nature during late autumn to spring, occurs at a continuous regime of 20°C or following 12 h at 15°C (Kinugawa and Furukawa, 1965). Interestingly, the optimum temperature for both mycelial growth and production of fruit body initials by *A. bisporus* is 24°C (Flegg, 1972, 1978a, 1978b). However, temperature downshift is required for further development of initials beyond a cap diameter of ~2 mm.The fruit bodies develop normally when the temperature is lowered to 16°C. So, as with the reaction to nitrogen sources mentioned above, the implication is that formation of fruit body initials/primordia is an aspect of mycelial growth, but their proper development requires a further morphogenetic switch. It is tempting to conclude that these *in vitro* responses reflect the organism's natural response to seasonal changes.

Relative humidity (RH) affects fruit body initiation. Relatively high humidity is usually conducive to initiation of fruiting (Stamets, 1993), though it prevents initiation in *Polyporus ciliatus* (Plunkett, 1956). The water content of the resource may be even more critical. There is a balance between too high a water content that reduces aeration and too low a water potential that provides insufficient water for development (Scrase and Elliott, 1998; Ohga, 1999a; Kashangura *et al.*, 2006). There is variability between strains; *Pleurotus sajor-caju* was able to produce primordia at −2.5 MPa but none at −3.5 MPa even though they were able to grow under these xeric conditions (Kashangura *et al.*, 2006). pH can affect fruit body development, being optimal for several species at 6–7 (Kües and Liu, 2000), but pH 4 for *L. edodes* (Ohga, 1999b).

Physical constraints influence fruit body formation *in vitro*. Sexual reproduction is often initiated when the growing mycelium reaches an obstacle such as the edge of the dish or barriers placed onto the surface of the medium (the 'edge effect' or 'check to growth'). Reproductive structures often arise when mycelial growth had been arrested, by either physical or chemical means (Moore, 1998a). A physical barrier is not absolutely necessary for the 'edge effect', rather the important determining factor is the disturbance in metabolism which results from either encountering the edge of the dish or a major change in nutritional value of the substrate. Thus, different sorts of barrier and different sorts of medium transition are able to disturb the progress of metabolism sufficiently to initiate fruit body formation. The same applies to physical injury to the mycelium, which can stimulate fruit body formation (Leslie and Leonard, 1979a). Fruiting response to mechanical injury in *S. commune* is determined by at least four genes (Leslie and Leonard, 1979a, 1979b), showing that a number of different parallel routes lead to fruit body formation.

Inter- and intraspecific interactions can stimulate reproductive development. In interactions with other fungi this is at least partly a result of damage to vegetative hyphae (Rayner and Boddy, 1988). Many *A. bisporus* strains fruit only when associated with bacteria, e.g. pseudomonads, apparently not due to production of stimulatory compounds but to removal of inhibitory compounds (De Groot *et al*., 1998). When competing with *C. cinereus* in agar culture, *C. congregatus* fruited from a much smaller resource volume than when growing alone (Schmit, 1999). In contrast, interactions can result in a fungus being confined to territory, e.g. a decay column in wood, that is too small to support fruit body production by that species. Fruit bodies are assembled from contributions of a number of cooperating hyphal systems, usually of the same individual. Hyphal interactions are controlled by the somatic and mating incompatibility systems (Chiu and Moore, 1999) that maintain mycelial individuality. Fruit bodies of somatically compatible Basidiomycota can fuse when the fruit bodies develop in extremely close proximity, as is commonly seen when resupinate fruit bodies meet on wood, and also with stipitate basidiomata, e.g. a fused cap with three stems of *Boletus (Xerocomus) chrysenteron* in Kibby (2006). However, hyphal cooperation is so fundamental that it can even lead to the formation of chimeric fruit bodies. Mixed cultures of two genetically different heterokaryons can produce basidiomata comprising both dikaryons, as seen with *P. nameko* (Babasaki *et al*., 2003). Even more extreme is the case of fruit bodies of *Coprinus* consisting of two different species, *C. miser* and *C. pellucidus* (Kemp, 1977). The hymenium comprised a mixed population of basidia bearing the distinctive spores of the two species but the chimera extended throughout the fruit body as both species could be recovered by outgrowth from stem segments. All of these features can be interpreted as aspects of the tolerance of imprecision in fungal morphogenesis which has been discussed elsewhere (Moore, 1998a, 1998b, 2005; Moore *et al*., 1998).

Once fruit bodies have been produced environment, particularly temperature and RH, can affect spore production. For example, in the field spore production by *Hericium erinaceus* is highest at about midday reflecting diurnal temperature and

RH (McCracken, 1970). In the laboratory, at 85–95% RH, spore production increased from a minimum at 0°C to a maximum at 24–27°C, and ceased at 31–33°C. At 20°C, sporulation was greater at 30% RH than at 90% RH (McCracken, 1970).

2.5 Fruiting in the Natural Environment

It is well known that the majority of Basidiomycota fruit in autumn, following mycelial growth and decomposer activity in spring and summer. Temperature and rainfall are considered to be the two main factors affecting productivity (Salerni *et al.*, 2002). In a 21-year fruit body survey of a forest plot in Switzerland, there was considerable variation between years in species richness and productivity, only litter decomposing saprotrophs, *Collybia butyracea* var. *asema* and *C. dryophila*, appearing in all years (Straatsma *et al.*, 2001). *Appearance* of fruit bodies was correlated with July and August temperatures, an increase of 1°C resulting in a delay of fruiting by saprotrophs of ~7 days. In contrast, fruit body *productivity* was correlated with precipitation from June to October (Straatsma *et al.*, 2001), and similar relationships have also been found in Britain and Sweden (Wilkins and Harris, 1946; Wasterlund and Ingelog, 1981).

In a 3-year study of Mediterranean oak forests, there was no evidence for influence of temperature on fruit body species diversity or productivity by most saprotrophs, though there was strong positive correlation between species diversity of wood decay fungi and maximum temperature, and with spring and summer rainfall (Salerni *et al.*, 2002). Temperature and rainfall in the 5 days prior to surveying seemed to have little effect on fruiting, but did so between 10 and 30 days prior to survey.

Climate change has resulted in phenological changes in plants, insects and birds (Parmesan and Yohe, 2003), and this has recently been shown to be the case for fungi (Gange *et al.*, 2007). Analysis of a data set of fruiting records of 200 species of decomposer Basidiomycota in Wiltshire, UK, each of which had been recorded over more than 20 years during 1950–2005, revealed that mean first fruiting date averaged across all species is now significantly earlier, while mean last fruiting date is now significantly later (Figure 3; A.C. Gange, E.G. Gange, T.H. Sparks and L. Boddy, unpublished data). Thus, the fruiting season has been extended since the 1970s. Not all species fruit earlier (47% show an advancement), or produce fruit bodies later into the year (55% continue fruiting later) but of those saprotrophic Basidiomycota that showed significantly earlier fruiting dates ($n = 94$), the average advancement was 7.9 days per decade, while for those with significantly later last fruiting dates ($n = 110$) the delay was 7.2 days per decade. The response differs depending on habitat type: 13% of grassland species fruiting earlier, 48% having later last fruiting; 53% of wood decay fungi fruited earlier, with 20% having later last fruiting. There was a significant relationship between mean fruiting date of those species that normally fruit early in the season (September) and late summer temperature and rainfall (Figure 4). Local July and August mean temperatures have significantly increased (July, $P < 0.05$; August, $P < 0.01$), while rainfall has decreased, though less markedly, over the 56 years of the survey.

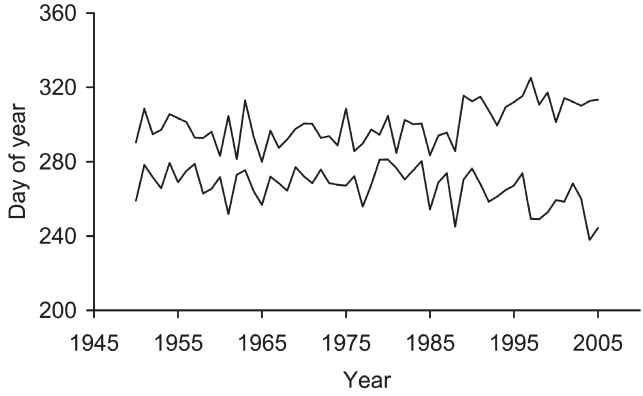

Figure 3 Mean First Fruiting Date (Lower Line) and Mean Last Fruiting Date (Upper Line) for 200 Saprotrophic Basidiomycota over 56 Years. Splitting the Data into Two Equal (28 Year) Periods Reveals no Trend in the First Half ($P = 0.97$) but a Highly Significant Trend ($P < 0.001$) in the Second Half (A.C. Gange, E.G. Gange, T.H. Sparks and L. Boddy, Unpublished Data).

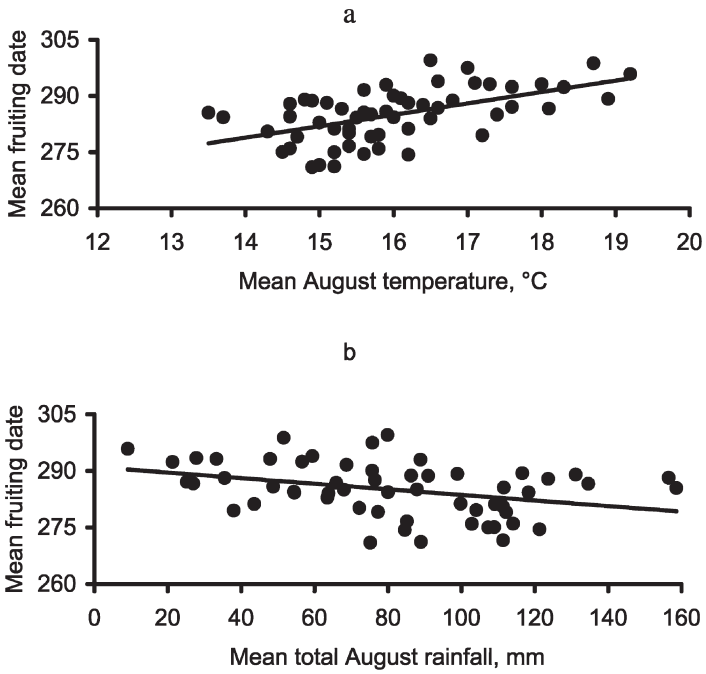

Figure 4 Relationship between Mean Fruiting Date of Saprotrophic Basidiomycota Species that Normally Fruit Early in the Season (September) and (a) August Temperature ($R^2 = 0.299$, $F(1,54) = 23.056$, $P = 0.007$) and (b) August Rainfall ($R^2 = 0.126$, $F(1,54) = 7.790$, $P = 0.000$) (A.C. Gange, E.G. Gange, T.H. Sparks and L. Boddy, Unpublished Data).

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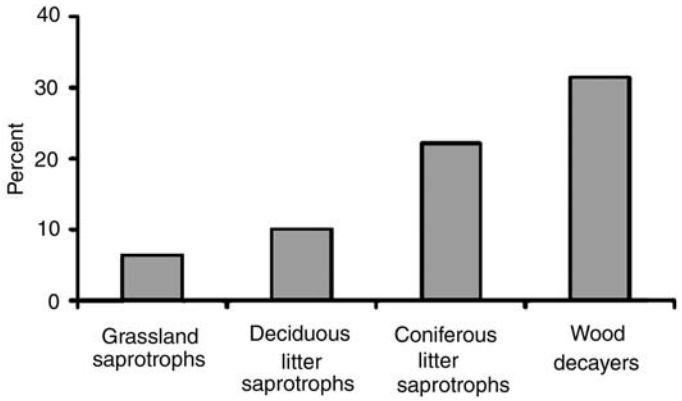

Figure 5 The Proportion of Saprotrophic Basidiomycota in Different Habitat Groups that, Before 1975, were not Recorded as Fruiting in Spring, but after This Time did so in at least 1 Year (A.C. Gange, E.G. Gange, T.H. Sparks and L. Boddy, Unpublished Data).

As well as changes to autumn fruiting patterns, significant numbers of species that previously only fruited in autumn now also fruit in spring (Figure 5). Since mycelia must be active in uptake of water, nutrients and energy sources before fruit bodies can be produced this suggests that these fungi may now be more active in winter and spring than they were in the past.

Other aspects of the environment can also influence fruiting by affecting microclimate (e.g. ground vegetation and logging waste), providing additional resources or inhibitory compounds. For example, in managed forests: there was lower fruit body biomass where *Pteridium aquilinum* was abundant; in dry years *Mycena species* were more abundant in areas with logging waste, but in wet years they were equally or more abundant in areas without logging waste; fruit body biomass was negatively correlated with grass cover in dry autumns, but positively correlated in wet autumns (Wasterlund and Ingelog, 1981).

3. FRUIT BODY SURVIVAL

As well as the physical size of a fruit body, a significant feature in the ecology of the organism is the length of time that the fruit body remains sufficiently intact to distribute spores. This varies from a few days or weeks for fleshy fungi to several years for perennial brackets, longevity of the latter being associated with structural physical characteristics and production of chemicals that inhibit invertebrate feeding or are toxic to them (Kahlos *et al.*, 1994; Stadler and Sterner, 1998). AU :1
There appears only to be one detailed study of the lifespan of an agaric, an analysis of the fruit bodies of *A. bisporus* grown in an experimental mushroom farm over 36 days (Umar and Van Griensven, 1997). The fruit bodies remained healthy for 18 days before localised cytological indications of senescence became evident (nuclear and cytoplasmic lysis, permeable cytoplasmic membranes and structural changes to the cell wall). Cells of the fruit body collapsed irregularly

and the remnants of the lysed cells aggregated around and between the remaining living hyphal cells. Most of the stem hyphae became empty cylinders. After 36 days, electron microscopy showed that most of the cells throughout the fruit body were severely degenerated and malformed, yet a number of basidia and subhymenial cells remained intact and alive even at 36 days. Interestingly, when mushrooms were cultivated using conventional commercial farming procedures, ~50% of the fruit bodies were infected by *Trichoderma harzianum* and/or *Pseudomonas tolaasi* by 18 days. All such fruit bodies died at 24 days due to generalised severe bacterial and fungal infections leading to tissue necrosis and decay of the caps and stems.

Observations of a wild troop of *Clitocybe nebularis* in a garden in Stockport, Cheshire, began on 21 October 2006, at which time the fruit bodies were young, but close to maturity (5 cm diameter), and continued for 29 days (Figure 6). By 19

Figure 6 Life and Death of *Clitocybe nebularis* Fruit Bodies in a Suburban Garden in Stockport, Autumn 2006. Observations began on 21 October and Continued for 29 days to 19 November. Troops of Fruit Bodies of *Coprinus micaceus* Emerged, Matured and Decayed ~26 October and November 1 (the Latter are Illustrated). Some Disturbance and Grazing (Squirrels?) was Evident on 10 November, and Collapsed Fruit Bodies by 18 November.

November most of the fruit bodies were beginning to collapse. These basidiomata of *C. nebularis* were still actively releasing spores on 7/8 and 12/13 November, clearly indicating that agarics with large fruit bodies can distribute spores for 3–4 weeks, though viability was not tested. During the observation of *C. nebularis*, two troops of fruit bodies of *Coprinus micaceus* emerged, matured and decayed (~26 October and 1 November), illustrating the alternative (R-selected) strategy of rapid production of short-lived fruit bodies.

The longevity of fruit bodies is obviously important for dispersal, but so also is the period over which spores are actively produced and released, and the viability/germinability of spores produced at different times. While some species retain high germinability of spores produced over several weeks, e.g. *Poria tenuis* and *Trametes hispida*, with others there is a decline, e.g. germinability of *Poria placenta* and *Gloeophyllum trabeum* declined from >94 to 19 and 44%, respectively, 5 weeks after fruiting was initiated in culture (Schmidt and French, 1983).

4. PRINCIPLES OF FUNGAL DEVELOPMENTAL BIOLOGY

Numerous observations show that all aspects of the environment can influence the production and development of fungal fruit bodies. To understand *how* this occurs we need to formalise fruit body development sufficiently to allow recognition of the decisive steps that are open to influence, and we must also identify the molecular controls that normally regulate those steps.

4.1 Underlying Principles

Three generalisations can be extracted from the past century of observations on fruiting physiology. First, the organism internalises nutrients rapidly to gain regulatory control over nutrient access and distribution. By so doing the vegetative mycelium becomes *competent* to produce multicellular structures like fruit bodies. Second, factors that promote fruiting, whether physical or chemical, seem to work by disturbing the normal progress of cellular metabolism. It is the disturbance itself that is the effective factor, overcoming some block to progress and *inducing* the next stage to proceed. Consequently, parallel pathways cover some stages of fruit body development and for these stages different factors seem to be interchangeable (e.g. a particular nutritional state may replace a particular illumination requirement). Third, even relatively simple developmental pathways can be subdivided into stages (at least, initiation, development and maturation) and there seems to be a need for successive signals (successive metabolic disturbances) to maintain progress of the developmental process. Each stage involves *change* in hyphal behaviour and physiology, taking the tissue to a higher order of differentiation.

4.2 Modelling Hyphal Growth and Fruit Body Formation

Hyphal growth is well suited to mathematical modelling, and the recent neighbour-sensing model brings together the basic essentials of hyphal growth kinetics

into a vector-based mathematical model that 'grows' a life-like virtual mycelium (or 'cyberfungus') on the user's computer monitor (Meškauskas *et al*., 2004a, 2004b; Moore *et al*., 2006). The program has been used in a series of experiments (Meškauskas *et al*., 2004a, 2004b) to show that complex fungal fruit body shapes can be simulated by applying the same regulatory functions to all of the growth points active in a structure at any specific time. No global control of fruit body geometry is necessary; rather, the shape of the fruit body emerges as the entire population of hyphal tips respond together, in the same way, to the same signals. These computer simulations thus demonstrate that because of the kinetics of hyphal tip growth, very little regulation of cell-to-cell interaction is required to generate fungal fruit body structures. The program includes parameters that can be used to mimic the effects of cell-to-cell signalling and environmental variables. These give the experimenter the opportunity to study the effects of such variables on fungal growth *in silico*.

4.3 Data Mining Fungal Genomes

The notion that control mechanisms of fungal multicellular developmental biology are probably very different from those known in animals and plants that emerges from the work described so far is supported by sequence searches of genomic databases. The unique cell biology of filamentous fungi has clearly caused control of their multicellular development to evolve in a radically different fashion from that in animals and plants. There are no *Wnt*, *Hedgehog*, *Notch*, *TGF*, *p53*, *SINA* or *NAM* sequences in fungi (Moore *et al*., 2005; Moore and Meškauskas, 2006), but there are presumably analogous or homologous processes in fungal multicellular structures that need to be regulated.

Unfortunately, the demonstration that developmental control sequences of animals and plants lack fungal homologues leaves us knowing nothing about the molecules that *do* govern multicellular development in fungi. Yet these *are* the molecules and mechanisms that generate fungal fruit bodies. The molecular control elements of development *are* the things with which the environment interacts to cause its effects. While we remain ignorant of the basic control processes of fungal developmental biology we will also remain ignorant of the way environment impacts on fungal biology.

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