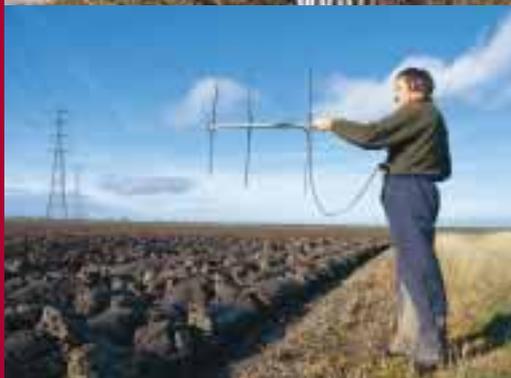


BAP fungi handbook

English Nature Research Reports



working today
for nature tomorrow

English Nature Research Reports

Number 600

BAP fungi handbook

Dr A. Martyn Ainsworth
53 Elm Road, Windsor, Berkshire. SL4 3NB

October 2004

You may reproduce as many additional copies of
this report as you like, provided such copies stipulate that
copyright remains with English Nature,
Northminster House, Peterborough PE1 1UA

ISSN 0967-876X

© Copyright English Nature 2004

Executive summary

Fungi constitute one of the largest priority areas of biodiversity for which specialist knowledge, skills and research are most needed to secure effective conservation management. By drawing together what is known about the 27 priority BAP species selected prior to the 2005 BAP review and exploring some of the biological options open to fungi, this handbook aims to provide a compendium of ecological, taxonomic and conservation information specifically with conservationists' needs in mind.

The opening section on fungus fundamentals is an illustrated account of the relative importance of mycelia, fruit bodies and spores, without which many ecosystem nutrient cycles would cease. It is not generally appreciated that mycelia have been recorded patrolling territories of hundreds of hectares, living over a thousand years or weighing as much as a blue whale. Inconspicuous fungi are therefore amongst the largest, heaviest and oldest living things on Earth.

The following sections describe the various formal and informal taxonomic and ecological groupings, emphasizing the often intimate and mutually beneficial partnerships formed between fungi and other organisms. The different foraging strategies by which fungi explore their environment are also included, together with a summary of the consequences of encounters between fungi ranging from rejection, combat, merger, takeover and restructuring to nuclear exchanges and mating.

The selection of species of conservation concern (SoCC) is briefly reviewed and each is placed in the taxonomic framework introduced previously. This is followed by a corresponding ecological treatment of the SoCC using broad habitat categories linked to suites of species wherever practicable. This reinforces and extends current convenient groupings such as waxcaps and boletes, but suggests splitting the 14 BAP tooth fungi grouped under one joint action plan (stipitate hydroids). The underlying rationale for this split is to recognise the significant differences in conserving their Scottish pine habitats and those of predominantly oak, beech and sweet chestnut which are scattered in clusters throughout the UK.

Tables are included for each ecological grouping showing the scientific and English names of the members, their conservation status and nutritional mode. These are followed by data sheets for each species with ecological and distribution data, identification aids including descriptions and scanned colour transparencies, management advice and sources of further published information and illustrations.

For some species it has been possible to provide generic management guidelines, a description of the features constituting the 'best' sites and a preliminary listing of known 'top' sites with reference to their SSSI or IFA (Important Fungus Areas) status. It is hoped that the inclusion of some site data at this rather premature stage will stimulate a greater focus on recording fungi of conservation interest and wider communication of the results. Confidently predicting rapid obsolescence of the site rankings, it is the author's aim to accelerate demand for online updated site based dossiers identifying the fungal interest of all protected sites, including those which are exclusively or predominantly managed for the protection of non-fungal life forms.

Contents

Executive summary

1.	Introduction.....	9
2.	Fungus fundamentals – back to basics.....	10
2.1	What does a fungus really look like?.....	10
2.2	Underground networks – the all-important mycelium.....	12
2.3	Close encounters - what happens when mycelia meet?.....	13
2.4	The fruit body and the four mushroom seasons.....	18
2.5	Travel agents and identity checks – the many roles of spores.....	20
3.	Fungal classification: formal and informal groupings.....	21
3.1	The fungal kingdom.....	21
3.2	Lower and higher fungi.....	21
3.3	Microfungi (micromycetes) and macrofungi (macromycetes).....	24
4.	Ecology and nutrition	26
4.1	Lichen partnerships.....	26
4.2	Mycorrhizal partnerships.....	26
4.3	Endophytic partnerships and latent invaders.....	28
4.4	Saprotrophs.....	29
4.5	Fungal successions.....	32
5.	Fungal recording and distribution	35
5.1	Mycodiversity in the UK.....	35
5.2	Distribution of fungi.....	35
6.	Fungal species of conservation concern (SoCC): taxonomic relationships.....	37
6.1	Selection of species of conservation concern (SoCC).....	37
6.2	Taxonomy of ascomycete SoCC.....	39
6.3	Taxonomy of basidiomycete SoCC	40
6.3.1	Agarics and allies	40
6.3.2	Boletes	41
6.3.3	Polypores	42
6.3.4	Russulales	43
6.3.5	Thelephorales	44
7.	Fungal species of conservation concern (SoCC): ecological groups, sites and management	47
7.1	‘Scottish pine’ stipitate hydnoids.....	49
7.1.1	‘Scottish pine’ stipitate hydnoids and relatives: group members.....	49
7.2	‘Broadleaved/conifer’ stipitate hydnoids	50
7.2.1	‘Broadleaved/conifer’ stipitate hydnoids: group members.....	50
7.2.2	‘Broadleaved/conifer’ stipitate hydnoids: species data sheets.....	50

7.2.3	‘Broadleaved/conifer’ stipitate hydroid sites: generic management guidelines	57
7.2.4	‘Broadleaved/conifer’ stipitate hydroids: ranking of sites	58
7.3	Thermophilous boletes	60
7.3.1	Thermophilous boletes: group members	60
7.3.2	Thermophilous boletes: species data sheets.....	61
7.3.3	Thermophilous bolete sites: generic management guidelines.....	65
7.3.4	Thermophilous boletes: ranking of sites.....	66
7.4	Bulky deadwood species	67
7.4.1	Bulky deadwood species: group members.....	67
7.4.2	Bulky deadwood species: species data sheets.....	67
7.4.3	Bulky deadwood species: generic management guidelines.....	72
7.4.4	Bulky deadwood species: ranking of sites	74
7.5	Litter/woody debris species.....	75
7.5.1	Litter/woody debris species: group members	75
7.5.2	Litter/woody debris species: species data sheet.....	75
7.5.3	Litter/woody debris species: generic management guidelines.....	77
7.6	Species ?parasitic on fungi or saprotrophic on wood	77
7.6.1	Species ?parasitic on fungi or saprotrophic on wood: group members.....	77
7.6.2	Species ?parasitic on fungi or saprotrophic on wood: species data sheets	77
7.6.3	Species ?parasitic on fungi or saprotrophic on wood: generic management guidelines	80
7.7	Waxcap grassland species	80
7.7.1	Waxcap grassland species: group members.....	80
7.7.2	Waxcap grassland species: species data sheets.....	80
7.7.3	Waxcap grasslands: generic management guidelines.....	84
7.7.4	Waxcap grasslands: ranking of sites.....	84
7.8	Lowland heath species	89
7.8.1	Lowland heath species: group members.....	89
7.8.2	Lowland heath species: species data sheets.....	89
7.8.3	Lowland heaths: generic management guidelines.....	91
7.9	Wetland species	91
7.9.1	Wetland species: group members.....	91
7.9.2	Wetland species: species data sheets.....	91
7.9.3	Wetland species: generic management guidelines	93
7.10	Scottish montane species.....	93
7.10.1	Scottish montane species: group members	93
8.	Acknowledgements	94
9.	Appendices.....	95
10.	Glossary of mycological terms.....	105
11.	References.....	107

1. Introduction

Fungi are natural communicators and networkers and yet they are widely regarded as inconspicuous and secretive. For much of the time, fungi toil in the ‘engine rooms’ of ecosystems driving the unseen but essential webs, shuttles and cycles of carbon compounds, water and minerals. These commodities are collected, stored, distributed, communicated and recycled amongst themselves and their neighbours, hosts, partners, associates, predators and prey. To begin to appreciate their invisible presence, we only need to admire an ancient oak and imagine what happened to all those tonnes of leaves, acorns, twigs, branches, roots and heartwood over the centuries. What became of it all, where are all those components now?

Although fungi are major players among the Earth’s biodiversity with an estimated 1.5 million species (Hawksworth 1991), fungal activity is often taken for granted. As with other largely unseen networks upon which our lives depend, such as those of transportation, energy and communication, we usually ignore them until things go wrong. In the case of fungi, this is usually when they consume something that we wish they had left alone. Fungi grow into and throughout their food supply, digesting the toughest plant and animal structures around them and absorbing the products. It is this chemistry, when applied to items we value such as timber products, food and our own bodies, which perpetuates a rather negative image of some fungi. Publicity is invariably and understandably generated around their impact as agents of rot and decay and as pathogens of crops, forest trees, horticulture and ourselves. Yet this is also the chemistry of recycling and redistribution that gives fungi an essential life-supporting role in naturally-occurring ecosystems. They are indispensable agents of nutrient transfer, natural pruning and habitat creation on all scales ranging from the sculpture of minute spaces within twigs to biodiversity-rich clearings in the forest.

This aim of this handbook is to provide a guide to the recent work on fungi of conservation interest with a focus on priority BAP species selected prior to the 2005 BAP review. It covers their classification, provides illustrated profiles and also groups them according to their ecology. This serves to highlight other potential species of conservation concern sharing similar habitats and raises the possibility of using fungi characteristic of certain habitats as indicator species. Ultimately, these may assist in assessing the fungal interest of sites for conservation purposes. In some cases sufficient information is available to provide some preliminary habitat-based management guidelines and provisional lists of sites ranked according to recent records of selected suites of species.

In order to appreciate the ‘behind the scenes’ activity that leads to the often fleeting appearance of fungal fruit bodies, the handbook also covers aspects of fungal biology, classification and ecology of most relevance to conservationists. Some of the more frequently asked questions are included in the hope that, through further observation and research, more people will be encouraged to find more answers in the near future.

2. Fungus fundamentals – back to basics

2.1 What does a fungus really look like?

As a general rule, fungi remain hidden from view for most of their lives and only attract our attention when they break cover to produce their fruit bodies, eg mushrooms, brackets, puffballs and stinkhorns. When observing a mushroom, it is all too easy to regard the fungus as a mushroom-shaped plant with a few tiny white ‘rootlets’ attached. However, in order to gather sufficient resources to build fruit bodies, fungi produce an inconspicuous ‘feeding body’, known as a mycelium (Figure 1), from which the fruit bodies grow when triggered with the appropriate cues.

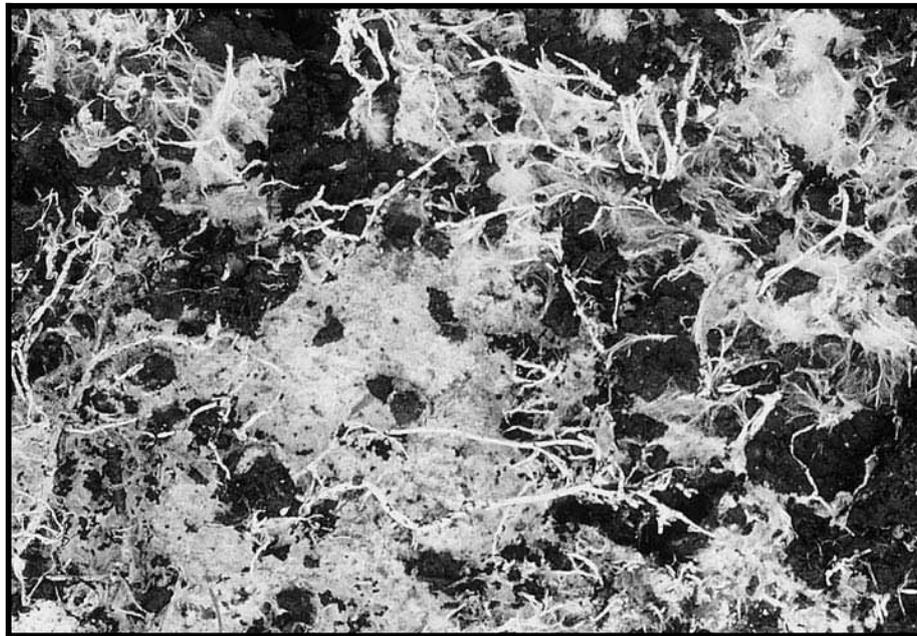


Figure 1 Naturally-occurring fungal mycelium in soil beneath rotting beech log.
Photograph © Dr Martyn Ainsworth

The underlying construction of fruit bodies and mycelia is very similar. If we tease them apart and examine their structure using a microscope, we will immediately notice a fundamental difference between the construction of fungi and that of plants and animals. Instead of consisting of recognisable cells closely packed together to form a tissue, as we might see in a sample of a leaf or a liver, fungal structures mainly consist of a densely woven system of fine filaments (Figure 2). Each filament is a microscopic tube known as a hypha (Figure 3). Although the study of individual fungal hyphae requires a microscope, they can develop and network into very large scale mycelia such that a single fungus can extend and operate over several hectares. Record-breaking fungi have been estimated to cover hundreds of hectares, living over a thousand years or weighing as much as an adult blue whale (Kirk and others 2001). Inconspicuous fungi are therefore among the largest, heaviest and oldest living things on Earth.

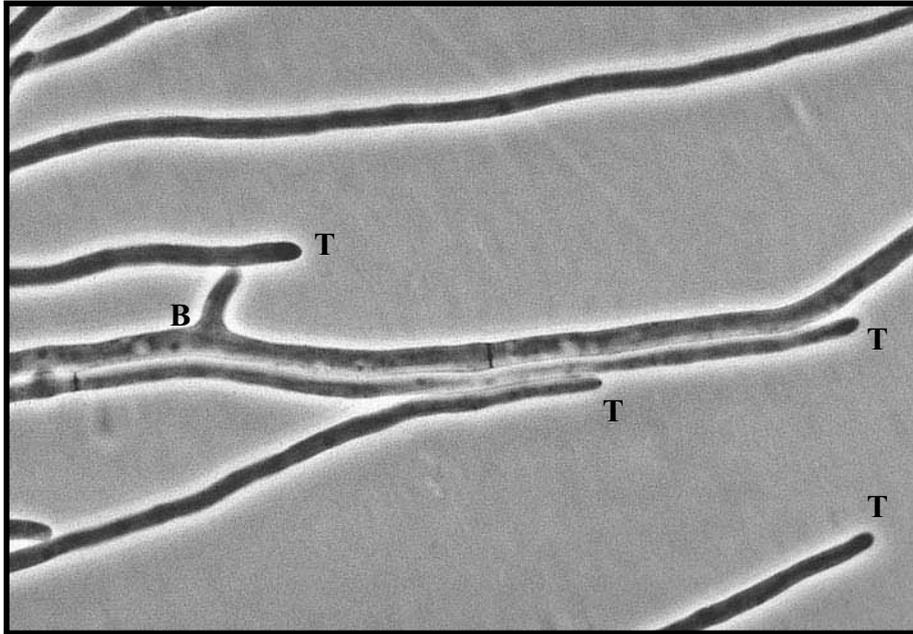


Figure 2 Microscope image showing the edge of a living fungal mycelium with individual hyphae, extending hyphal tips (T) and young branch (B). Photograph © Dr Martyn Ainsworth

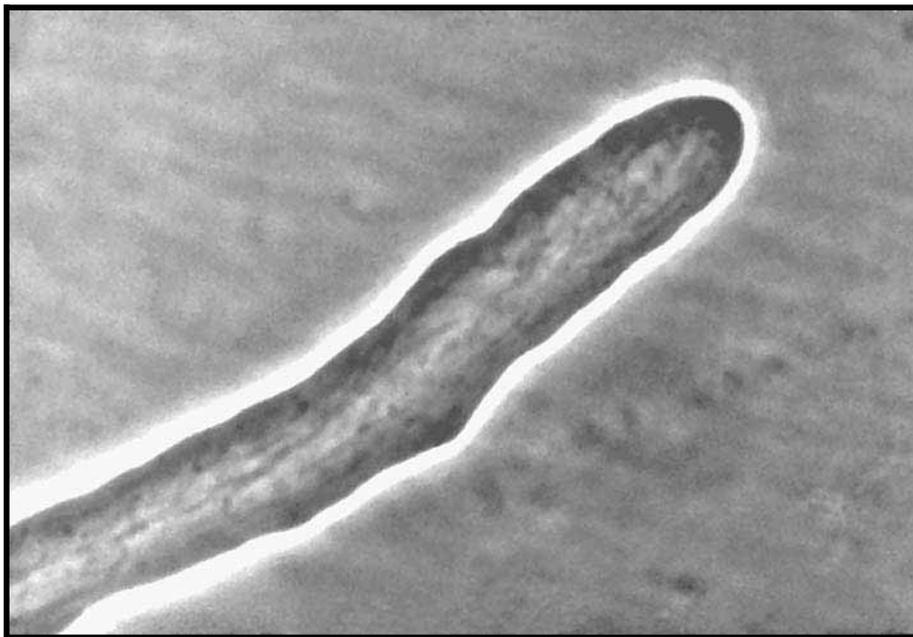


Figure 3 Microscope image showing a living hypha, about 10 µm wide, (10 thousandths of a millimetre). Photograph © Dr Martyn Ainsworth

Two basic properties of growing hyphae are that they extend and they branch. The most rigid part of a hypha is the surrounding wall which is under pressure from within. This internal pressure drives extension at the hyphal tip where the wall is softer and there is a supply of new wall materials. Branching can occur where the rigid wall is internally softened, creating weak points which then bulge outwards and become new hyphal tips. Speeding up video sequences of living hyphae reveals that hyphal elongation proceeds rather like the inflation of an endless elongated balloon.

There are also some very common soil bacteria, the actinomycetes, which resemble fungi in having mycelia, but these are much smaller and of simpler construction. Such bacteria are important sources of many life-saving antibiotics and of the earthy smell (geosmin) often noticed when rain falls on dry soil. On the other hand, there are some fungi that exist not as mycelium but as colonies of single cells commonly called yeasts. Among these are some fungi that have significant economic, medical and cultural impact on our lives including the brewers' and bakers' yeasts that give the natural dull waxy 'bloom' to the skins of grapes and plums. Other examples, such as the causal agent of candidiasis or thrush (*Candida*) and the Dutch elm disease fungus (*Ophiostoma*), can grow as yeasts or hyphae depending on the conditions.

2.2 Underground networks – the all-important mycelium

A mycelium can be regarded as a space-invading hunter-gatherer whose behaviour is constrained, like that of many commuters, within the walls of a tube network which is often located underground. Indeed the layout of a mycelium may become very similar to that of an underground railway or city road map. This is a characteristic feature of those species whose hyphae not only extend and branch, but, on meeting each other, can fuse together to open up new internal links within the mycelium. Young mycelia generally consist of hyphae which grow in a radiating form like the spokes of a wheel. Later they form branches which can become interconnected by fusions to form a networked mycelium (Figure 4). There are striking parallels with the construction of orbital motorways, circle lines and routing of internet traffic.

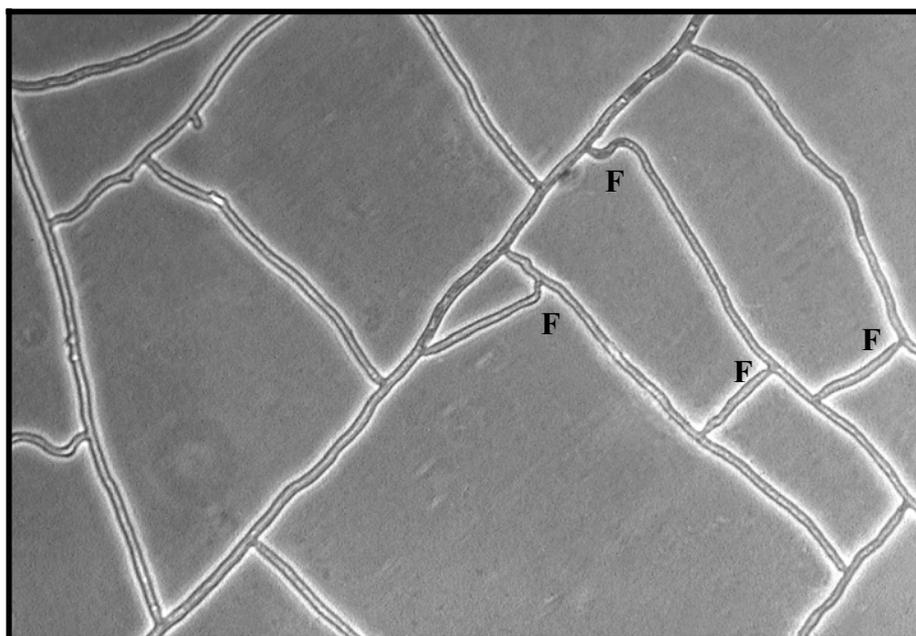


Figure 4 Microscope image showing a living mycelium and examples of fusions between hyphae (F) which have produced an efficient transport and communication network.

Photograph © Dr Martyn Ainsworth

Networking is vital in order to provide an efficient communication and transport system throughout the mycelium. For example, nutrients can be drawn from storage depots across the mycelium, transported and delivered to rapidly expanding fruit bodies which may be developing in a nutrient-poor location. Another consequence of fusion is that hyphae can

grow their own bypasses to reconnect sections which have become temporarily isolated due to damage (Figure 5).

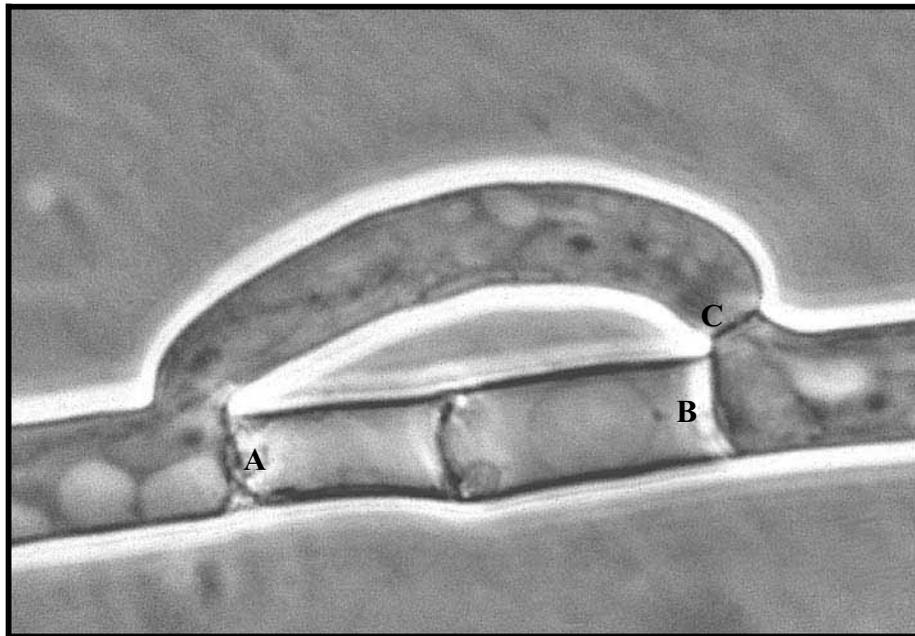


Figure 5 Microscope image showing a living hypha which has produced cross-walls (A and B) to seal off a damaged section. Later it branched from behind A and produced a bypass hypha which is in the process of fusing at C to re-establish the link and divert resources around the damage. Photograph © Dr Martyn Ainsworth

In addition to the capture and long-range distribution of nutrients, the fungal mycelium performs other important roles, some of which are covered in more detail below. These include:

- acquisition and defence of a territory using chemical weapons (antibiotics and fungicides);
- protection of the hyphal and territorial boundaries with waterproof coatings and sunscreen pigments;
- mating with others of its kind according to complex rules of compatibility;
- production of fruit bodies from which spores are dispersed.

2.3 Close encounters - what happens when mycelia meet?

A characteristic feature of the mycelia of higher fungi (Section 3) is the fusion of their component hyphae to produce networks and bypass damaged sections (Figures 4 and 5). However, in their natural habitat, hyphae belonging to different mycelia of higher fungi must also frequently encounter each other. In some cases, when the mycelia are of the same species, the result may be exactly the same as that between different hyphae of the same mycelium and a persistent hyphal bridge may form. However there are many other possibilities. The progress of the interaction is largely dependent on how closely related the hyphae are to each other or, more accurately, the degree of genetic similarity between the participating hyphae. Despite their small size and simple organisation, interacting hyphae can assess their degree of similarity before, during and after fusion, a process involving

complex overlays of signalling and compatibility systems. The capacity of two hyphae to determine if they are from the same mycelium (recognition of 'self') suggests that a fundamental similarity may exist between fungal interactions and the workings of the immune system. Indeed, the basic ability to distinguish 'self' and 'not-self' may be the evolutionary ancestor of the sophisticated human immune system which detects and destroys microbial pathogens and also rejects organ transplants. As an interesting aside, the drugs prescribed to organ transplant patients to suppress their natural rejection of the graft are based on cyclosporin, a molecule produced by a fungus originally discovered in a sample of soil.

If the interacting hyphae are genetically alike, hyphal fusion will always result in the formation of bridges and networks, regardless of whether the hyphae are from the same (Figures 4 and 5) or different mycelia. Scenarios involving physically separate mycelia which are genetically alike can arise in a number of ways. A single mycelium may become damaged and cut into separate units or it may produce asexual spores which germinate to form a clone of genetically identical mycelia. When such mycelia meet they have the capacity to fuse into a single mycelium. This can easily be shown in a Petri dish by allowing two identical mycelia to interact and merge into one (Figure 6).

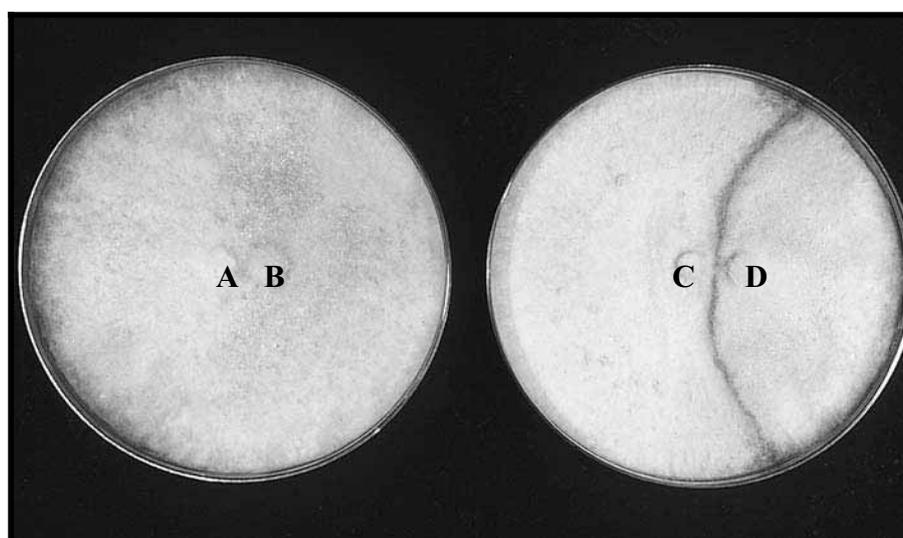


Figure 6 Merger (left) and rejection (right) between pairs of mycelia of a single species grown in Petri dishes. Genetically identical mycelia were introduced at A and B which have united to form a single individual. Genetically different mycelia were introduced at C and D which have rejected each other and produced a brown rejection zone marking the territorial boundary between the two individuals. Photograph © Dr Martyn Ainsworth

When considering fungi from a population biology and conservation standpoint it is important to remember and distinguish the concepts of genetic and physical individuals. Care is required in deciding whether genetically identical samples of fungi are likely to have been collected from a single large mycelium or many separate smaller mycelia. A system of terminology to clarify the different concepts of a fungal individual has been proposed in Brasier & Rayner (1987).

If the interacting hyphae are of the same species and are genetically different, hyphal fusions result in the interplay of incompatibility systems leading to various outcomes ranging from mating to death. In simple terms, mating occurs between different mating types. These are similar to our familiar concept of male and female, except that the different mating types are indistinguishable and, in some mushrooms at least, there may be over 20,000 different mating

types in a single species (Raper 1978). Mating involves varying degrees of movement of cell nuclei within and between partner hyphae. Ultimately it results in the shuffling of genes and the production of sexual spores which genetically differ from each other.

Encounters between mycelia that have already mated or cannot mate always result in a form of incompatibility which is often called the rejection response (Figure 6). Between mycelia of the same species, rejection occurs after the hyphae have fused and results in a remarkable process of destruction of the fused hyphae (Figure 7). Pigments are sometimes released as the interacting hyphae die in the zone of combat (Figure 6) and these can be used to map the territories of different individuals in their natural habitat. Different species can also interact by producing pigmented rejection zones although these reactions usually occur on or before contact rather than after fusion.

Territorial battles, both within and between different fungal species, leave their mark in decaying wood in the form of exquisite mosaic patterns (Figure 8). Often on display and sale as polished 'spalted beech' at craft markets, these attractive mosaics actually consist of fungal battlefields stained by dying hyphae and fungal boundaries sealed by waterproof layers. Fungal warfare reveals the territories of fungi in their natural habitat and provides us with a tool with which to analyse fungal populations. By sectioning and sampling decaying wood and culturing and identifying the isolated fungi, we can reconstruct the outline of each individual mycelium in the laboratory.

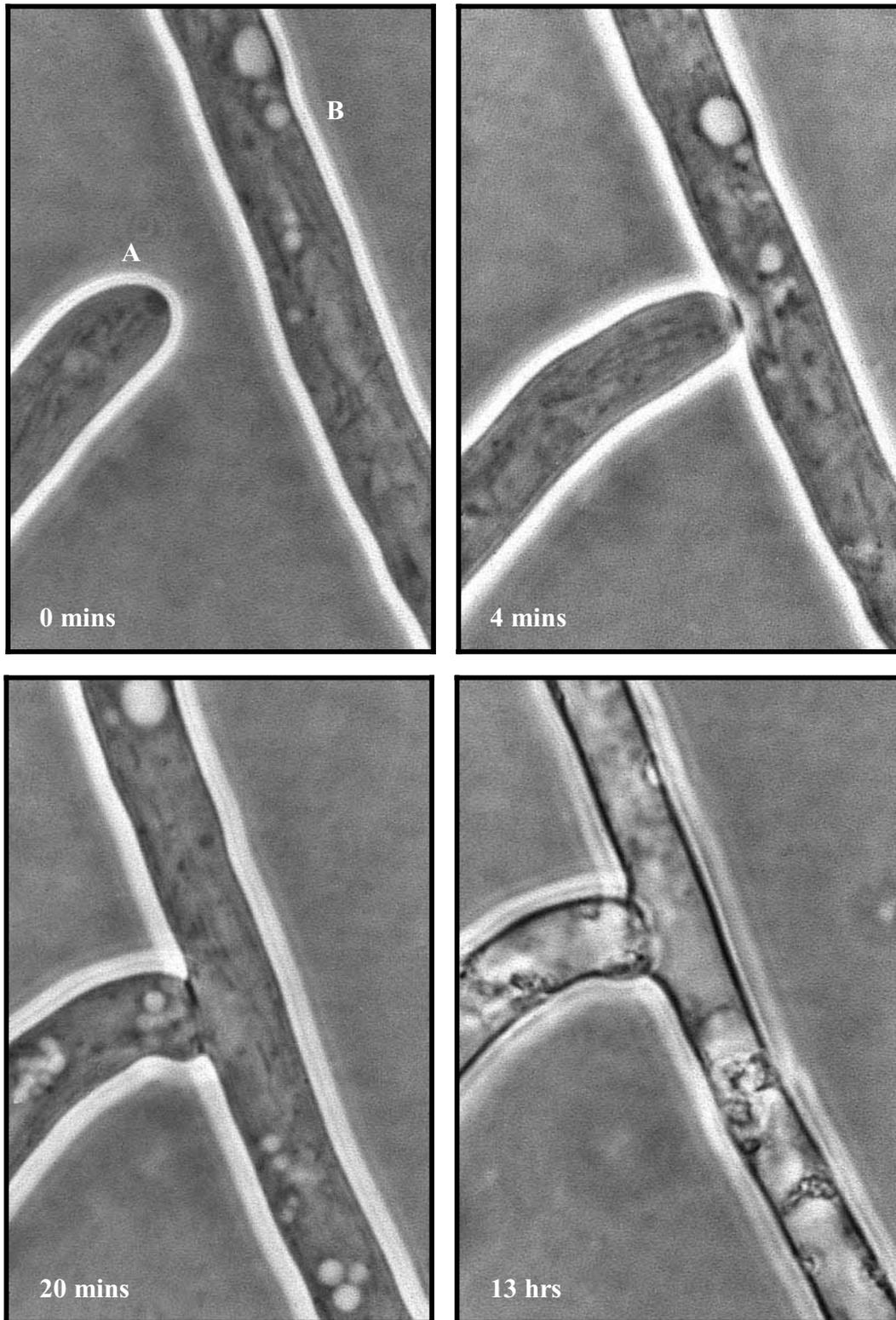


Figure 7 Sequence of microscope images showing contact and fusion between two living hyphae (A and B, each approx. 6 μm wide) from genetically different mycelia of the same species. The outcome of this encounter is rejection which results in the destruction of the contents of the fused hyphae within 13 hrs. Elapsed time is shown in the bottom left corners.

Photograph © Dr Martyn Ainsworth

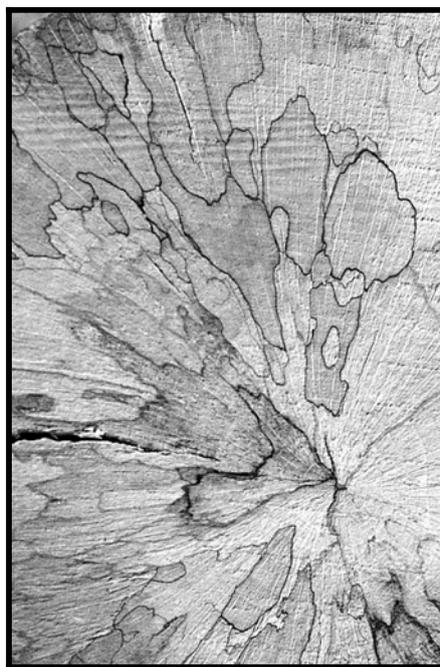
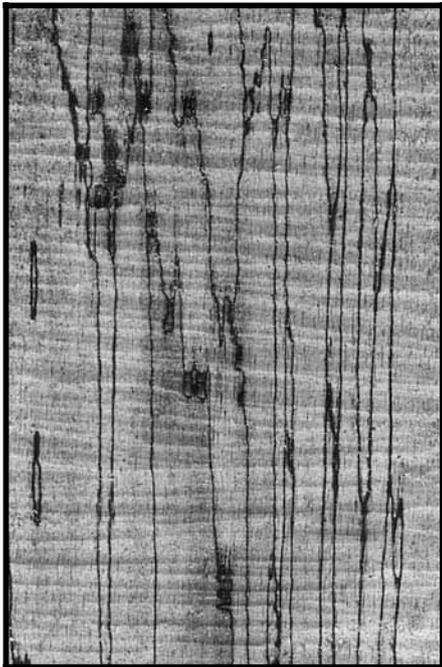


Figure 8 Dead ‘spalted’ beech trunk with outer wood cut away (top) to show dark fungal rejection zones produced between territories of different species and between individuals of the same species. The territories are often called ‘decay columns’. Their elongated form is revealed when the wood is cut along the grain (lower left) and compared to the more compact territorial mosaic seen when the wood is cut across the grain (lower right). Photographs © Dr Martyn Ainsworth

In passing, it should be noted that some fungal species can be found eking out their existence on the rejection zone battlefields and confined to the narrow strips of wood between the major combatants. Indeed it was just such a chance discovery by Rayner (1976) that opened the entire field of research on the individualistic and interconnected aspects of fungal behaviour (Rayner 1991; Rayner, Griffith & Ainsworth 1994).

Interactions between different species can also result in gain and loss of territory and the partial or complete replacement of one combatant by the other. Some species may depend on the earlier arrival of others to render the habitat suitable for their establishment, perhaps by removal of toxins or some initial digestion of the available resources.

2.4 The fruit body and the four mushroom seasons

Traditionally, we associate fungal fruiting with the autumnal appearance of wild mushrooms and toadstools. This immediately raises the question most frequently asked of the expert who leads beginners on their first guided mushroom searches or ‘fungus forays’. How can one tell the difference between a mushroom and a toadstool? The answer is that although we usually associate mushrooms with mealtimes and toadstools with toxicity, most species fall somewhere in between and there is no precise distinction between the two. To add to the confusion, there are the yellow-staining mushrooms which are poisonous to some people and there are edible toadstools. Consequently the terms are not very useful and have little scientific value. In passing, it should be noted that foray leaders may become even more evasive when challenged with innocent enquiries regarding the natural role of fruit body colour. It is difficult to explain the enormous range of fruit body shades in terms of our familiar ideas of colour as a biological attractant, warning or camouflage. Perhaps the existence of such diversity is simply telling us that colour chemistry is neither strongly advantageous nor disadvantageous to fungal fitness.

Equating fruiting with autumn also deserves comment. The notion of an autumn season certainly holds for many species, but it would be wrong to assume that this is the only time to find fungi fruiting. Those who search for edible morels and St George’s Mushroom *Calocybe gambosa* will know that some species have a spring fruiting season in April and May. These species are probably responding to the sequence of chilling followed by warmer spring temperatures. However, regardless of the time of year, there are always some fruit bodies to be found and the diversity of shapes and textures arising from woven bundles of hyphae is staggering. Figure 9 illustrates this with four very different types of fruit body produced by species on the provisional red data list of British fungi (Ing 1992). Each of the species shown was found fruiting in a different season of the year.

Some fruit bodies are in good condition for less than a day, the majority last for a few days and some woody brackets are described as “perennial”. This refers to their ability to produce a tough layered fruit body using the existing structure as a foundation upon which to build extensions during each successive fruiting period. Unfortunately, however, this carries the risk of implying that other fungi are not perennial. In general, mycelia can only persist for as long as there is an adequate food supply. Hence it is quite likely that mycelia attached to living tree roots and seen repeatedly fruiting around the same spot for decades are at least as deserving of the description “perennial”. Examples of such potentially long-lived fungi include many species whose fruit bodies seem particularly decay-prone and short-lived, such as the BAP *Boletus* species (Sections 4 and 6).

Fruit bodies provide a range of environmental services, such as food, water, shelter and a meeting place for a diversity of wildlife including mites, flies, beetles, slugs, snails, mice, squirrels, badgers, wild boar, deer and insectivorous birds. Their role in the fungal lifecycle, however, lies in the production of dust-like spores and their release into the environment for dispersal (see below). Since most spores are wind-dispersed, the fruit body is usually regarded as a means to discharge spores into turbulent air currents away from environmental surfaces.

Fruit body characteristics are also very useful in fungal identification. Some characters, such as sliminess, cobwebby scales and smells, have to be noted in the field because they can change during the journey home. An appreciation of subtle differences between fragrances is as important to the identifier of fungi as it is to the perfume and wine-making industries. Having a memorised 'palette' of basic fragrances such as anise, marzipan, meal (flour), cabbage water, coconut, crabs, cucumber, cheap soap, henhouses, iodine, mice and vinegar, not forgetting coalgas, cedarwood pencils and bed bugs, is a definite advantage!

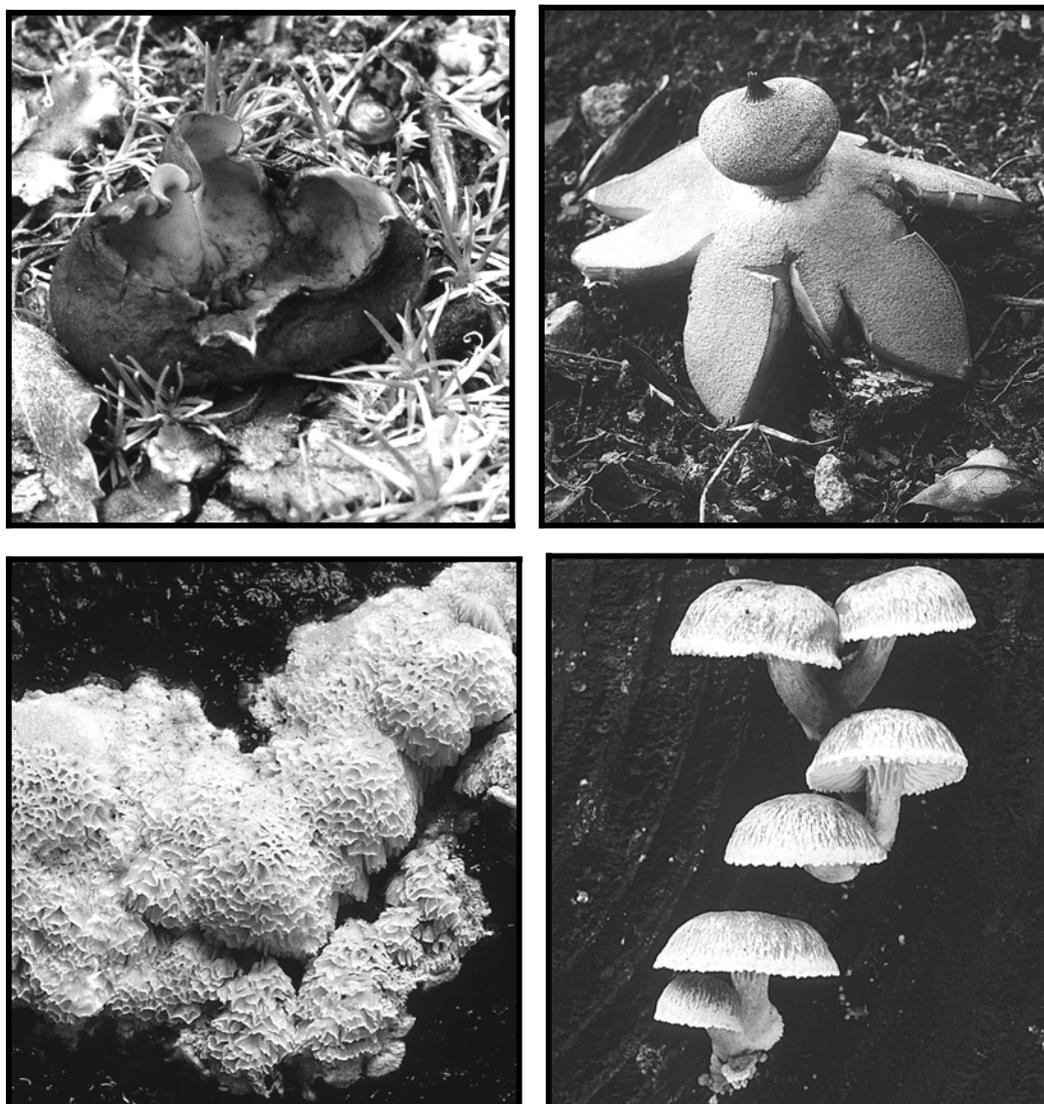


Figure 9 Four species selected from the provisional red data list of British fungi (Ing 1992) showing a wide range of fruiting structures. Each was found fruiting in a different season of the year as follows: spring (upper left) golden cup *Caloscypha fulgens*, summer (upper right) Berkeley's earthstar *Geastrum berkeleyi*, autumn (lower left) frothy porecrust *Oxyporus latemarginatus* and winter (lower right) sticky sawgill *Neolentinus adhaerens*. Photographs © Dr Martyn Ainsworth

2.5 Travel agents and identity checks – the many roles of spores

Spores are produced in a vast array of fruit body structures and some may also be produced directly by the mycelium. They range from bulky thick-walled forms that may not be dispersed very far but play a major role in surviving adverse conditions (like a plant tuber or corn) to aerodynamic long-haul specialists that can blow across continents.

Spore dispersal may be accomplished by various means of transport and some examples are given below:

- By air: birds, insects and wind.
- On or in water: dew, rain, streams, foam and the sea.
- On land: vertebrates, slugs, mites and other invertebrates.

Some fungi depend entirely on animals for spore dispersal and truffles are the most well-known example. They produce their spores underground and dispersal would not occur without the efforts of insects, squirrels, wild boar, badgers and other animals attracted to the pungent sulphurous chemical cocktail, containing various mating pheromone mimics, that percolates through the surrounding soil. A less well-known example is provided by a microscopic fungus (*Basidiobolus ranarum*) which grows and produces its spores on frog dung and propels them on to surrounding vegetation. Only those spores that are attached to beetles or other invertebrates caught and eaten by frogs are likely to be incorporated into fresh frog dung to germinate and complete the cycle (Webster 1980). Some dung-loving fungi have spores with outer coats that require removal by gut enzymes of snails or much larger herbivores before germination can occur.

Most terrestrial fungi with large fruit bodies efficiently disperse spores directly into the air. Buller (1909, 1922) calculated that the detached cap of a field mushroom discharged spores at an average rate of 40 million per hour over two days and he estimated that an average-sized giant puffball could produce a total of 7 million million spores.

Spores have traditionally been invaluable, particularly in terms of their size, shape, ornamentation and means of production, in the classification of fungi. Even today, some of the most important initial questions asked by someone trying to identify a fungus are “what colour are the spores, what do they look like under the microscope and what ranges do their lengths and widths fall into”. Most mushroom spores are under 15 μm (microns, micrometres) in length, that is 15 thousandths of a millimetre. Hence a microscope is an invaluable tool in the examination of spores and the structures producing them to check identifications based on more visible characteristics. Some characters such as fruit body size may vary alarmingly within a species and are quite unreliable as guides to species identification. One champion bracket of elm polypore *Rigidoporus ulmarius* even secured a place in the record books. In 1995 it had a circumference of 4.8 m when measured, appropriately enough, in the grounds of the Mycology Building at Kew Gardens (Kirk and others 2001).

3. Fungal classification: formal and informal groupings

3.1 The fungal kingdom

Fungi were once classified as lower plants, then accorded a kingdom of their own and are currently dispersed among at least three kingdoms. This more accurately reflects the view that the organisms generally recognisable as fungi have evolved *not* from a single common ancestor, but from a diversity of ancestral lineages. Although they have become increasingly similar in terms of structure and function over time, analysis of their DNA reveals the gradual convergence of different evolutionary strands.

The *Dictionary of the Fungi* 9th edition (Kirk and others 2001) accepts the placement of fungi in the following kingdoms:

Chromista: includes organisms interpreted as having evolutionarily lost their light-harvesting chloroplasts such as those in the genus causing potato blight and sudden oak death (*Phytophthora*).

Protozoa: includes slime moulds. Myxomycete slime moulds are beyond the scope of this handbook, but important aspects of their conservation have been summarised in a recent research report (Ing 2002) reproduced in part in Appendix IV.

Fungi: the ‘true’ fungi or Eumycota housing the majority of species.

Fungi within this handbook are classified within the Eumycota and are characterised by hyphae bounded by walls containing chitin. This is a structural material and familiar to us in the form of the external coats or shells of insects and crabs. Higher and lower plant cell walls are fundamentally different and gain their strength from cellulose but not chitin. This, together with their lack of chlorophyll and inability to obtain carbon compounds directly by photosynthesis, clearly demarcates fungi from plants with which they have been historically allied. Interestingly, plants lacking chlorophyll such as the bird’s nest orchid *Neottia* and yellow bird’s-nest *Monotropa* tap into fungal hyphae for nutrients. These plants exploit the underground fungal distribution network which, depending on species, captures nutrients from living tree roots or dead components of the litter layer. Their flowering spikes act as a drain on the resources of the mycelium rather like substitute fruit bodies.

3.2 Lower and higher fungi

Lower fungi are fungi with a relatively simple organisation. This informal group comprises the fungi now classified in the Chromista and Protozoa together with two groups, the chytridiomycetes and zygomycetes (see below), of the Eumycota or true fungi. Although some have undoubted significance as disease-causing agents of plants and animals, they are not usually detectable unless isolated and cultured in a laboratory and remain poorly studied and of low conservation priority.

Chytridiomycetes: microscopic forms associated with plants and animals mainly in soils and aquatic systems, although some are specialised inhabitants of herbivore guts. Unusually for fungi, they possess self-propelled free-swimming spores restricting part of their life-cycle to water or watery films.

Zygomycetes: usually microscopic but sometimes visible as tiny pea truffles in soil or rapidly growing pinmoulds such as *Mucor* on bread and *Rhizopus* on strawberries. Others are parasites of invertebrates and some are confined to the guts of insect larvae. One group forms structures inside the root cells of plants whereby the fungus absorbs plant nutrients and the root absorbs fungal nutrients obtained from the surrounding soil. This relationship, described as endomycorrhizal symbiosis, is of interest today because it is important to many crop plants and has a proposed role in regulating plant diversity in grassland and other ecosystems. However it also has great historical significance in that the earliest known (Devonian) vascular plants had similar associations 400 million years ago (Webster 1980).

Higher fungi are the groups of true fungi with a relatively complex organisation. Two of these groups, the ascomycetes and basidiomycetes (see below), include the species currently of conservation concern and so form the focus of this handbook. The fundamental distinguishing feature is the microscopic structure of the two types of specialised hyphal tips that produce the sexual spores. Hyphal tips producing ascospores in ascomycetes are known as asci and those producing basidiospores in basidiomycetes are known as basidia.

Ascomycetes: range in size from the microscopic single cells of brewers' yeast through moulds seen on damp fabrics, leather, paper and food to species producing large fruit bodies including morels, truffles, elfcups, earthtongues, cramp balls, tarcrusts and woodwarts. Sexual spores are produced in an ascus which usually consists of a sausage-shaped hyphal tip in which a row of eight ascospores develops (Figure 10). For most asci, the internal pressure increases as the spores ripen within. This is eventually released by various patterns of wall rupture at or near the tip. The row of ascospores is then squirted into the surrounding air by jet propulsion and asci have been referred to in the literature as spore guns and ascomycetes as spore shooters.

Basidiomycetes: range in size from yeasts and microscopic rusts and smuts to species producing familiar fruit bodies including mushrooms, milkcaps, inkcaps, waxcaps, brackets, boletes, chanterelles, puffballs, earthballs, earthstars and stinkhorns. Sexual spores are produced at the end of a basidium and, in many species, each basidiospore is formed on the tip of a prong-shaped structure (sterigma) which occurs in a group of four, more rarely two (Figure 11). Basidiospores are propelled sideways from mushroom gills into the intervening spaces and then fall from the fruit body under the influence of gravity to be dispersed in air currents. In a bracket fungus they are discharged from the lining of each tube into the central space from where they fall under gravity from the fruit body. Hence basidiomycetes are sometimes called spore droppers, but for many years there were several theories to account for the discharge mechanism. Even now the mechanism remains something of an enigma (Kirk and others 2001). The favoured explanation involves movements of liquid droplets which initially form on the outer surface of the mature basidiospore. The resultant shifts in the centre of gravity of the spore rock it from its supporting sterigma and are sufficient to propel it away from the basidium and launch it on a flight path which will take it from the fruit body and into the air under the influence of gravity.



Figure 10 Sexual spore production in an **ascomycete**. Microscope image of an ascus containing eight ascospores prior to discharge from the tip (T). In this ascomycete the ascospores are approx. 25 μm long, brown, arranged in a single row and each spore comprises a brick-like pattern of cells. Photograph © Dr Martyn Ainsworth

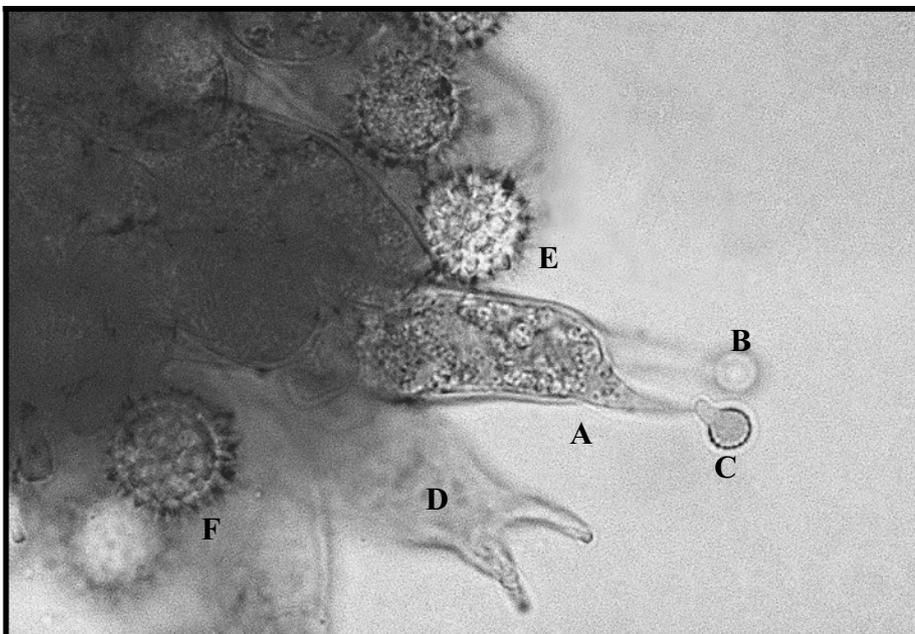


Figure 11 Sexual spore production in a **basidiomycete**. Microscope image of a two-spored basidium (A) projecting from the gill of a mushroom. It supports two immature basidiospores (B & C) on prongs (known as sterigmata; most species have four). A basidium (D) without spores is nearby. The mature spiny spherical spores (E & F) are approx. 15 μm diam. Photograph © Dr Martyn Ainsworth

The number and quality of general and specialist field guides to northern European ascomycetes and basidiomycetes have greatly improved in recent years. Although most originate from overseas authors, they are invaluable as identification aids in the UK and Eire and have prompted several successful searches for species previously unknown beyond mainland Europe. Four of the most comprehensive and popular general colour guides in current use are listed below in order of publication:

1. 1981. Mushrooms and other fungi of Great Britain and Europe by Roger Phillips. Pan Books. Over 900 species. Photographs with descriptions of field and microscopic characters.
2. 1984-ongoing. Fungi of Switzerland (5 volumes completed) by Josef Breitenbach and Fred Kränzlin. Verlag Mykologia. Over 2200 species. Photographs and drawings of microscopic characters with descriptions of field and microscopic characters.
3. 1987. The mushrooms and toadstools of Britain and North-western Europe by Marcel Bon. Hodder and Stoughton. Over 1500 species. Paintings and spore drawings with descriptions of field and some microscopic characters.
4. 1995. Collins field guide to mushrooms and toadstools of Britain and Europe by Régis Courtecuisse and Bernard Duhem. Collins. Over 1750 species. Paintings with descriptions of field characters.

3.3 Microfungi (micromycetes) and macrofungi (macromycetes)

These are informal and rather imprecisely defined terms which cut across the categories of lower and higher fungi and are defined on the size of fruit body produced. Macrofungi produce fruiting structures which are large enough for the naturalist to see and are almost all ascomycetes and basidiomycetes. In autumn, macrofungal fruiting diversity is such that annual fungus forays routinely generate records of between one and two hundred macrofungal species per site per day. Microfungi are those fungi which remain inconspicuous throughout their lives and have microscopic spore-producing structures. The terms are not used in formal classification and the boundaries are drawn in different places by different authors.

Perhaps one of the most familiar and important genera of microfungi is *Penicillium*, a genus of higher fungi containing species informally known as greenmoulds which produce a remarkably diverse range of natural products including the following examples:

- Toxins: patulin poisoning of raw apple juice, ochratoxin poisoning of coffee.
- Flavourings: blue and other mould-ripened cheeses.
- Antibiotics: penicillin (the first antibacterial), griseofulvin (antifungal).

Lesser known microfungal genera (sometimes loosely termed ‘moulds’) are of major industrial and healthcare importance as producer organisms for mycoproteins, industrial enzymes, antibiotics, cholesterol-lowering and immunosuppressive agents. Microfungi represent a rich, largely untapped and potentially life-saving reservoir of natural products, the vast majority of which have some biological activity. They may also play key roles in ecosystem function but few have been studied from an ecological perspective. While it is

currently impractical to evaluate the natural distribution and ecology of all these species, nevertheless it is anticipated that by conserving habitat diversity at all scales, their populations will not become endangered.

Many microfungi produce dark spots or other symptoms of damage on plants, sometimes causing economic losses to crops as in the case of rust and smut species. There is a conservationist's dilemma relating to the management of rare fungal pathogens associated with rare and endangered plants. Efforts to conserve rare plant species may not always include efforts to conserve the organisms which are dependent on them, such as their rare and endangered fungal associates including those that are pathogenic. Indeed, destructive pathogens may be seen as a threat to plant conservation efforts and management action may be taken which further diminishes the pathogen population, thereby increasing its threatened status. This dilemma has been highlighted by Helfer (1993).

4. Ecology and nutrition

4.1 Lichen partnerships

Although some fungi closely mimic green plants in their colours and capacity to attract insects, the nearest approximation to a photosynthetic fungus is the partnership in which some fungi exploit the ‘solar panels’ of algae or cyanobacteria to provide them with carbon-based nutrients. This partnership, or symbiosis, is at the heart of all lichens. Consequently they are sometimes called dual organisms, but closer investigation can often reveal the presence of several other species of fungal cohabitant. Some of these are associated with visibly damaged areas of the main lichen-forming fungus, but the ecological role of many of the lichen-associated species remains poorly studied.

Almost one fifth of all described species of true fungi are involved in lichen symbiosis, making it currently one of the major fungal modes of nutrition (Kirk and others 2001). The requirement for sunlight dictates that, unusually for a fungus, the whole organism is relatively conspicuous and not hidden within its nutrient supply. Hence, in contrast to fungi generally, lichen diversity is thought to be already relatively well catalogued.

Ecologically, the light-demanding nature of lichens is of major importance. This sets them apart from the non-lichenised fungi, indeed lichen ecology more closely resembles that of mosses and liverworts. This is reflected in the frequent consideration of lichens with “lower plants” for conservation purposes and the relatively high conservation profile enjoyed by this group of fungal symbionts.

Although the scientific naming of lichens is based on the fungal partner and many of these have close relatives which do not form lichens, separate learned societies (British Lichen Society and British Mycological Society) have been established concerned with the study of lichenised and non-lichenised fungi. Lichens will not be discussed further in this handbook, nevertheless there is a growing awareness that a more thorough integration of lichenised and non-lichenised fungi is the logical way forward (Hawksworth 1991).

4.2 Mycorrhizal partnerships

Mycorrhizal partnerships are associations between living plant roots and fungal hyphae to form dual organisms. Such associations are found in the majority, perhaps 85%, of plant species (Kirk and others 2001). There are two main types, endomycorrhizal and ectomycorrhizal, distinguished on the basis of the degree of penetration of plant cells by the fungus.

Endomycorrhizal partnerships, in which fungal hyphae breach the cell walls of the host plant and are in intimate contact with their cell membranes are mentioned above in relation to the zygomycetes (Section 3). Variations on this theme abound and involve a range of different fungi and several different plant groups including orchids, heathers *Erica* and relatives and strawberry trees *Arbutus* and relatives. More recently, further subdivisions of the basic types have been made based on, for example, the overall direction of sugar transport between partners. This can be from plant to fungus as occurs with wintergreens *Pyrola* or from fungus to plant as occurs with yellow bird’s-nest *Monotropa* (Duddridge 1985; Lewis 1987).

Ectomycorrhizal partnerships are of most relevance to fungal species of conservation concern and predominate in temperate and boreal woodlands. They are distinguished by the fungus forming a sheath around the finest roots and penetrating between, but not entering, their outer cells (Figure 12). There is also a considerable mycelial extension from the roots into the surrounding soil. Such partnerships ensure that some of the most conspicuous basidiomycetes (and some ascomycetes) in our woodlands gain access to carbon compounds originally produced in the tree canopy.

One of the most familiar fruit bodies, the red and white spotted fly agaric *Amanita muscaria*, is ectomycorrhizal and so too are the lethal death cap *Amanita phalloides* and luxurious truffles *Tuber* spp. Indeed, many edible species commercially harvested directly from the wild such as cep *Boletus edulis*, chanterelles *Cantharellus* spp., horn of plenty *Craterellus cornucopioides* and wood hedgehog *Hydnum repandum* are ectomycorrhizal fungi and dependent on tree sugars. However, the flow of resources is not merely from tree to fungus. The nutrient bridge also allows the tree to gain access to mineral salts within the fungal mycelium, particularly those of phosphorus (P) and nitrogen (N) which are not always readily available in temperate habitats. Mycelia have a much greater surface area than tree roots and are more effective at P and N acquisition and hence the tree effectively gains a superior root system. Indeed, a series of laboratory studies involving live ectomycorrhizal coniferous roots led to the observation that the function of the roots appeared to have been taken over by the fungus (Read 1984).



Figure 12 The swollen pale coral-like tips of these tree roots in soil are sheathed with hyphae of ectomycorrhizal fungi and form the nutrient bridges between tree and fungus.
Photograph © Dr Martyn Ainsworth

It is easy to envisage how the growth of both fungus and tree could benefit from the initiation of the mycorrhizal symbiosis. Since both partners benefit, unlike the case of parasitism, the relationship is sometimes described as mutualistic. Furthermore, Read (1984) not only commented on the ability of ectomycorrhizal fungal mycelium to connect different trees of the same species, leading to suggestions that saplings could be ‘nursed’ with parental sugar and fungal mineral solutions whilst still in some shade, but also suggested that different tree species could also become connected. The full implications of such complex underground nutrient transportation networks (the ‘wood-wide web’) are currently being studied using labelled molecules of carbon, nitrogen and phosphorus. Undoubtedly there are other benefits

for the tree such as improved access to water when the roots are drought-stressed, exclusion of pathogens from the root zone and greater tolerance of heavy metals and other environmental toxins. Indeed, it would be worth considering whether some microhabitats thought to be stressful for tree roots, such as bare patches of well-drained, periodically sun-baked mineral soil, can only be effectively exploited by roots when in partnership with certain ectomycorrhizal fungi. This idea could be relevant to the study of some fungi of conservation concern, for example the stipitate hydroids (Section 6), some of which have been observed fruiting on the same small windswept mossy banks for at least 40 years (E.E. Green pers. comm.).

In forest ecosystems, ectomycorrhizas also provide the ‘missing link’ whereby scarce minerals, previously acquired by trees and subsequently salvaged by decay-causing fungi during the decomposition of their dead wood and leaves, re-enter their root systems in a recycling loop. In some circumstances this may occur as a very closed-circuit process within the tree itself. For example, aerial roots can grow within a hollow tree’s decomposing heartwood and become ectomycorrhizal. This can be envisaged as a strategy whereby mineral recycling occurs entirely within the tree and largely in the absence of competition from foraging mycorrhizal fungi which could pass on the salvaged nutrients to the roots of neighbouring trees. The mechanisms by which ectomycorrhizal fungi obtain such nutrients from decomposer fungi or directly from dead materials are currently under investigation. There is also a recent realisation that ectomycorrhizal fungi may also contact bare rock on the woodland floor and chemically ‘quarry’ or ‘mine’ them for minerals directly, a process formerly exclusively associated with ‘weathering’ of rocks by lichens (Landeweert and others 2002). Is it possible that site-faithful stipitate hydroids (see above) are involved in covert mineral-mining operations?

4.3 Endophytic partnerships and latent invaders

The usual definition of an endophytic fungus is that it occurs inside a plant without causing any visible symptoms. In practice, apparently healthy plant parts are taken to a laboratory and dipped into sterilising agents such as alcohol and bleach to sterilise their outer surfaces. When these are dry, small fragments are cut from within and transferred to fungal growth medium for incubation. Assuming a successful surface-sterilisation, the fungi growing from such fragments must originally have been present inside the living plant and so are described as endophytic. Whereas mycorrhizal fungi are restricted to associations with plant roots, endophytic fungi can be grown from tissues within a wide range of botanical structures including roots, stems, trunks, buds, leaves, fruits and seeds.

Growing endophytes from plant tissues yields such a vast diversity of fungi from so few materials in such a short time that it is routinely employed in natural product drug discovery to provide a diversity of natural extracts whose chemical constituents can then be tested for therapeutic potential (eg Schulz and others 2002). Dozens of different endophytes can be obtained from a few twigs and leaves but, for the majority, their biological role within the plant remains unclear. However, two possibilities are clear: firstly, their presence inside plants puts them at a competitive advantage if, under certain conditions, they can obtain nutrients from the plant (latent invasion) and, secondly, the combination of plant and fungal chemistry can benefit both partners. Examples of mutual benefit include grasses and their endophytes in which the partnership can confer increased toxicity to herbivores and so reduce grazing pressure (eg Clay 1988).

Latent invasion or latency is a type of ecological strategy whereby the endophytic fungus may be relatively inactive (as if inside a Trojan horse) until triggered to become pathogenic and kill plant tissues or triggered to become saprotrophic (see below) and obtain nutrients from surrounding dead plant tissue. Sometimes the distinction is by no means clear-cut, for example if a plant is becoming stressed by drought and an endophytic fungus enters a more active phase, exactly what are the causes and what are the effects? Do both organisms interact by feedback to accelerate the process? Examples such as this are difficult to analyse and our attempts may be hampered by our uncritical use of disease terminology and concepts of attack and defence. Standing trees are usually a complex mosaic of living and dead tissues and the stock of both is subjected to periodic gains and losses. Yet when an entire birch tree seems to be dying and several large birch polypore *Piptoporus betulinus* brackets are emerging from the trunk, it is not easy to provide clear-cut experimental evidence to answer the simple question “is the fungus killing the tree or is it merely availing itself of resources provided by a tree weakened by shortages of light and/or water?”

The presence of several latent fungi has been revealed by applying different drying regimes to cut lengths of apparently healthy branches while preventing colonisation from airborne spores. The results are striking and, as is often the case in studies of fungi in nature, water is of fundamental importance. Too slow and too rapid (seasoning) drying regimes keep the latent invaders in check. Under appropriate drying conditions, fungi which entered the tree, perhaps decades earlier, begin to develop mycelia, expand their territories and fight their neighbours. Under these conditions, any decay fungi arriving from the air as spores are at an immediate territorial disadvantage, at least initially. The fascinating role of endophytes in early stage decay communities of branches and twigs has been well researched for several broadleaved tree species in Britain (eg Boddy & Griffith 1989).

4.4 Saprotrophs

Saprotrophic fungi obtain carbon compounds from the dead tissues of (mostly) plants and animals. As is evident from the foregoing, some saprotrophs may become active following a period of latency or may be new arrivals at a resource either as freshly landing spores or foraging mycelium gaining access from the woodland litter. Occasionally, but more frequently in humid tropical forests, mycelium may emerge into the air and cross the gap between canopy twigs thus binding them together into a permanently ‘welded’ bridge (Ainsworth & Rayner 1990).

The mycelium of a saprotroph may be constrained within certain discrete elements of a habitat such as dead leaves, cupules, catkins, cones etc. In other words, mycelial spread is limited in extent by the physical boundaries of the favoured resource. Such fungi have been described as component-restricted (Cooke & Rayner 1984) or unit-restricted (Rayner & Boddy 1988; Rayner, Watling & Frankland 1985). In some species there may be some mycelial bridging between suitable components in close contact in or on the soil, but the spread of these fungi is expected to depend very heavily on spore dispersal and therefore on fruit body production.

Many fungi producing conspicuous fruit bodies on standing tree trunks are component-restricted species dependent on spore dispersal, such as the priority BAP species oak polypore *Piptoporus quercinus* (Figure 13) and bearded tooth *Hericiium erinaceum*. Hence the apparent restriction of their fruit bodies to woodlands with long continuity is an important observation that requires ecological investigation. Similarly, the possibility of periodic

surges in fruiting activity over time requires further study. For example, at least 80 oaks are known to have borne the conspicuous yellow fruit bodies of oak polypore *P. quercinus* in Windsor Forest in the last five years (Ainsworth, Green & Lucas unpubl.). This is in stark contrast to the single British record and no material deposited in the Herbarium at RBG Kew during the entire first half of the 20th century (Roberts 2002). Clearly we need more recording and survey to assess if such fluctuations are reflecting environmental fluctuations or are part of the species' normal behaviour. We also need to be aware of the effects of fluctuating recording activity.

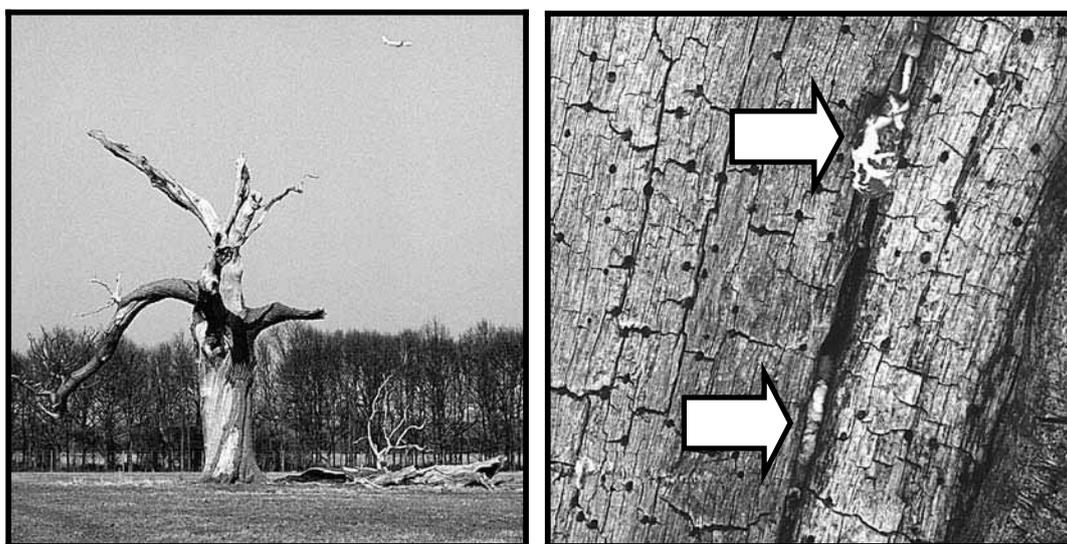


Figure 13 Heartwood hulk of a sun-exposed oak, home to the oak polypore *Piptoporus quercinus*. Close-up (right) shows the fungus emerging from seasoned heartwood (arrowed) and although these cushions were too dry to develop into fruit bodies they produced abundant thick-walled asexual chlamydospores. Photograph © Dr Martyn Ainsworth

At the other end of the scale are litter-inhabiting saprotrophs that seem to have no preferences for particular litter components or units. Their mycelia characteristically form dense wefts which bind leaves, twigs, cupules, stems and bark together as the fungus seems to engulf, bleach and decompose every dead plant part in its path. Initially forming rounded patches within the litter of woodlands or grasslands, with time the mycelium of these fungi begins to die at the centre of the patch but continues to extend at its margin. The result is an outwardly progressing ring-shaped mycelium like the outermost ripple from a stone thrown into a pond. The shape of these mycelia in woodlands can be directly inspected by removing the upper litter and is clearly revealed when rings of fruit bodies are produced. Such curiosities have attracted much attention, particularly in lawns and undisturbed grasslands where the alternating outer zones of suppressed and enriched grass reveal the underground mycelial presence for much of the year. In this habitat, they are often called fairy rings (Figure 14) and are presumably capable of infinite expansion if supplied with infinite resources and undisturbed by neighbourly conflict. Short downland turf or permanent pastures are good places to see them and aerial photography is particularly valuable (eg those around Stonehenge are illustrated in Ramsbottom 1953). Averaging the increase in diameter per year for a fairy ring enables estimates to be made of the age of these often elderly fungi; over 700 years has been estimated for one international ring straddling the French/Swiss border near Belfort (Ramsbottom 1953).



Figure 14 Fairy rings of luxuriant grass indicating the presence of mycelia beneath a disused military parade ground. Peaceful hyphal extension will give way to combat when the rings meet. Photograph © Dr Martyn Ainsworth

A foraging strategy interposed between the two extremes described above is adopted by species whose mycelia emerge from colonised woody items (food bases) to forage in the litter in search of newly fallen debris or stumps to colonise. This is achieved by production of white rope-like bundles of hyphae (mycelial cords) which are readily visible in woodland litter if superficial leaves are removed, especially in late autumn and winter (Figure 15).

Such fungi are clearly *not* constrained within the physical boundaries of their food bases, but neither do they form a general litter-decomposing fairy ring. They can decompose leaf litter but prefer to forage until reaching bulkier elements such as fallen twigs and branches. Laboratory experiments have shown that such fungi initially extend exploratory cords in all directions from a colonised food base, eg a wood block, but only those making contact with fresh woody material are thickened and persistent while those failing to reach any resource die and are soon recycled (Dowson, Rayner & Boddy 1986). Eventually a network of twigs, cupules and branches is connected by a system of cords within the litter layer and fruit bodies may be produced for short periods from various points on the foraging network. Viewed from this perspective, is it possible to maintain any lingering preconceptions that a fungus is merely a mushroom with ‘rootlets’ at its base?



Figure 15 White mycelial cords of a saprotroph snaking beneath the woodland litter in search of stumps and woody debris. Photograph © Dr Martyn Ainsworth

The foraging cords of some species of the honey fungus genus *Armillaria* show further sophistication because they are sealed inside a UV-protective and waterproof crust (involving the human skin pigment melanin) perforated with recently discovered air pores to allow them to ‘breathe’ (Pareek, Ashford & Allaway 2002). These relatively complex structures are called rhizomorphs or ‘bootlaces’ and are of major concern to gardeners and foresters wrestling with the foraging activities of the more pathogenic species of honey fungus which cause economically important losses of trees and shrubs. Pathogens such as these generally seem to be more of a problem in commercial forests or gardens which lack the full complement of woodland saprotrophs and ectomycorrhizal species. In more natural ecosystems, fungal diversity within stumps can prevent *Armillaria* gaining access to ‘refuel’ and re-emerge as a fresh round of foraging ‘bootlaces’. On the other hand, the natural role of *Armillaria* in woodland also includes the provision of deadwood, gaps, glades and structural diversity - all of which are viewed as positive attributes in managing for biodiversity. It should also be noted that the marsh honey fungus *A. ectypa* (a BAP species) seems to be specialised for life amongst wetland vegetation and, although it also forages with rhizomorphs (Ainsworth unpubl.), much of its watery lifestyle in relation to that of its woodland relatives remains to be investigated.

4.5 Fungal successions

The changing structures of fungal communities have been popular topics for scientific study ranging from work on saprotrophs in freshly fallen wood and animal droppings to ectomycorrhizals on living tree roots. Such studies often document the changing diversity of fruiting species over time. This could be described as a *fruiting* succession, but to call it a *fungal* succession would be to fall into the trap of neglecting the mycelium. For many species, we simply do not know when the fungus arrived and began to establish as mycelium. It seems quite plausible that some of the earliest fungi to arrive are some of the last to fruit.

Clearly a fungus fruiting early in this sequence must have arrived very early (perhaps by following an initial latent strategy) and this has led to the concepts of primary resource capture and pioneer communities. Parallels have been drawn with plants showing weedy or

ruderal strategies in which there is rapid growth, rapid commitment of resources to reproduction and rapid exit from the resource. Conservation of such fungi would probably require a similar approach to that of conserving arable weeds in using disturbance to keep re-setting the clock of succession. In woodlands and grasslands however, ruderal fungi in general seem not to be the most endangered species. Our current understanding is inadequate, but it would seem that it is the fungal inhabitants of rarely occurring microhabitats or habitats that develop very slowly that require priority attention.

There is considerable doubt about the life history of fungi which fruit, or at least persist, after the pioneer species. Did they establish after primary resource capture took place and gain territory by combat and replacement of the pioneers? Did they coexist with the pioneers? It is tempting to refer to the early fruiters as early-stage species which are then followed by late-stage species. This has often been applied to the distinctive suites of mycorrhizal species seen fruiting in young and old stands of trees (examples in Dighton & Mason 1985). Once again this calls into question our reliance on fruiting as evidence for fungal presence and, furthermore, may be partially a result of studying stands of uniform age.

Interestingly, historical investigations of early/late stage concepts and their application to ectomycorrhizal fungi revealed that regenerating saplings growing near parental birch trees became ectomycorrhizal with so-called late-stage species directly. By contrast, if they were planted in soil removed from beneath the parental tree, they soon supported mycorrhizas of early-stage species presumably originating from spores. Fleming (1983) also noted that the so-called late-stage species shared a propensity to form mycelial cords, hence it was suggested that when soil was left *in situ* their mycelia had contacted the sapling roots and set up bridges with the parental trees (Dighton & Mason 1985). Therefore, for ectomycorrhizal species at least, any simple early/late stage concept has to take into account the possibility of establishment involving the spread of nearby established mycelia (short-range dispersal) and arrival of airborne spores (long-range dispersal). Only by repeated sampling of the below-ground resource and detection and identification of non-fruiting mycelia can we gain a true picture of mycelial, and hence fungal, succession.

For many saprotrophs, for example in wood or dung, detection and limited identification has been possible for some time by sampling, culturing and identification of mycelia. For some ectomycorrhizal species, and stipitate hydroids (Section 6) in particular, this has been more problematical due to the low success in obtaining cultures, sufficiently rapid growth or reliable storage techniques. Some progress has been achieved in the detection of fungal species on mycorrhizal root tips based on the microscopic characteristics of the mycorrhizal roots themselves. More recently however, the detection of non-fruiting species in natural habitats has become an increasingly routine process due to the falling costs of identifying fungi based on comparisons of DNA sequences with databases of reference sequences. DNA fingerprinting methods can now be used to distinguish between genetically different mycelia within a single species and so map the below-ground extent of different individuals. This is proving to be a very interesting and thought-provoking line of research, especially when population and community assessments based on above- (fruit body) and below-ground (mycelium) survey methods provide very different results. Similar studies will undoubtedly assist in assessing the conservation priorities of, for example, BAP boletes and stipitate hydroids.

Population dynamics within woody resources (habitats of BAP saprotrophs such as *P. quercinus* and *Hericiium* spp.) have been under investigation for a relatively long period due

to the relative ease with which their inhabitants can be cultured and manipulated in the laboratory, eg summarised in Cooke & Rayner (1984) and Rayner & Boddy (1988). This has led to a much deeper understanding of the roles of latent invaders and their interactions (eg Hendry, Lonsdale & Boddy 1998), primary resource capture by species arriving as spores, interactions between these species and with those which can replace them (secondary resource capture) and impact of foraging by cord- and rhizomorph-formers. It is clear that different diameter-classes of deadwood elements support different fungal communities. Whilst twigs and branches have been the focus for much of the existing work, larger diameter trunks and branches, and in particular their mid and later stages of decomposition, have received less attention. The BAP saprotrophs *P. quercinus* and *H. erinaceum* are usually seen fruiting on large diameter wood and this has begun to stimulate the ecological research on their establishment, interactions, breeding system, fruiting and spore dispersal which is essential to inform conservation decision-making.

5. Fungal recording and distribution

5.1 Mycodiversity in the UK

It is difficult to estimate the number of fungal species living in the UK since there are no updated comprehensive checklists and insufficient numbers of trained recorders who have been visiting sites for sufficient periods of time. These constraints are exacerbated by the declining numbers of professional taxonomists who have easy access to our national collections of dried specimens and associated primary literature. Paradoxically, the demand for taxonomic advice from an increasing number of field mycologists seems to be greater than ever. Future conservation-related fungal survey and monitoring work will undoubtedly fuel further demand for authoritative determinations and taxonomic study of specimens.

The working range adopted for the number of UK fungi (including lichens) during the Important Fungus Areas project was between 12,000 and 20,000 species (Evans, Marren & Harper 2001). The project report also noted that approximately 20 macrofungi are added to the national list annually. Recorders studying fruiting at even the most frequently-worked sites are still being rewarded by an ever-increasing species total for the site. Topping the list for small-site species diversity is Esher Common, Surrey, with 3,100 species and the area around Slapton Ley, Devon, with 2,500 species (Evans, Marren & Harper 2001). It is not known whether these sites are in any way unusual, each has simply become the focus for repeated collection by leading experts whose lists have been augmented by increasing numbers of visiting taxonomic specialists. On a larger scale, one of the best-recorded and most important sites for fungi in the UK is the New Forest. Over a century of fungal recording in this mosaic of habitats has been published, mainly covering macrofungi and including lichens, and the compiled mycota details over 2,600 species (Dickson & Leonard 1996).

5.2 Distribution of fungi

Even in the most mycologically well-studied regions of the world, such as northern Europe, there is no macrofungal species whose distribution is completely known. In addition to the constraints listed above, there is also the consideration that in practice we rely entirely on the highly conservative estimation of fungal distribution based solely on observations of fruit body production. No sites have been subjected to *sufficient* survey intensity by *sufficient* specialists over a *sufficient* timescale (which seems unlikely to be less than a decade) to yield a confident estimate of the number of macrofungal species present. The curve of accumulation of species plotted against visits showed no sign of levelling off for one Caledonian pinewood site intensively recorded for agarics and boletes for 21 years. Even with such a prolonged and intense search effort and a total of 502 species recorded, the authors concluded that 21 years was insufficient for producing a reliable estimate of the fungal diversity of the site (Tofts & Orton 1998). The longer a site is surveyed, the more pertinent the questions “how many species used to be present but have long gone, how many have gone and returned and how many are recent arrivals?”

Distribution dot maps, based on hectads (10 km squares), have been produced for some species based on records of fruiting and these are housed in the national database (British Mycological Society Fungal Records Database) and available online at: <http://194.203.77.69/fieldmycology/BMSFRD/bmsfrd.htm>

However, much of the raw dataset requires careful editing, interpretation, standardisation of site details and addition of estimated grid references to improve the value of the derived maps. Historically, the maps have been voluntarily produced as a demonstration of the potential value and use of the stored data and to very good effect. Unfortunately, they are becoming out of date and further development is needed.

The true distribution of fungi, ie of fungal mycelia, is unknown. It is highly likely that the mapped 'fruiting distribution' of a species is only a subset of a much larger 'mycelial distribution' area which extends beyond the fruiting zone into regions where, for various reasons, fruiting does not occur after mating and the mycelia remain sterile and undetected. To add further complexity and realism, it is also possible that there are many unmated basidiomycete mycelia whose distribution is currently not mapped because they are unable to fruit without a compatible partner. Hence the familiar 'tip of the iceberg' analogy is applicable not only to a single fruit body indicating a hidden mycelium, but also to a fruit body distribution map indicating a hidden distribution of mycelia.