

10

Interactions Between Fungi and Other Microbes

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In all but the most sparsely inhabited environments (e.g. cold deserts or hot dry deserts), fungi continuously interact with other organisms. This can dramatically affect the size of the interacting populations or the fitness of interacting individuals. Commonly, several or many populations/individuals will interact with one another simultaneously but, for simplicity, it is usually only interactions between two species/individuals that have been studied. For the most part we will adopt this approach here, but it is essential to remember that the situation in the natural environment is far more complex. The overall effects on each member of the interacting pair of populations/individuals can be positive, negative, or neutral, resulting in six possible eventualities for the pair of interacting organisms (Table 10.1). This has been simplified to three scenarios: (1) the outcome of the interaction is beneficial to either or both, but detrimental to neither, (2) the outcome is detrimental to either or both, and (3) neither organism is affected. The last situation seems unlikely to occur very often if organisms are truly interacting, rather than passively coexisting.

Fungi participate in a wide range of interactions that result in benefit to one or both partners, especially when they are interacting with organisms from other kingdoms, for example, with plants (Chapter 7) as mycorrhizas and endophytes, with algae and cyanobacteria to form lichens (pp. 228–234), with invertebrates and ruminants (Chapter 9), and with some bacteria (pp. 356–357). However, no such intimate interactions have yet been described between different species of fungi in nature, although undoubtedly they exist. Mutualism can occur when physiological activity of a fungus and another organism are complementary, such as when one fungus synthesises or releases a compound which the other fungus requires but cannot otherwise obtain, and vice versa. For example, *Nematospora gossypii* and *Bjerkandera adusta* can grow in mixed culture in the laboratory, but not individually, on a medium lacking biotin, inositol, and thiamine. Whilst the former can synthesise thiamine, but not biotin or inositol, the latter can synthesise biotin and inositol but not thiamine. Another example might be the cogrowth of fungi which produce different cellulases, resulting in more rapid utilisation of cellulose. However, this might not necessarily be mutualism if more rapid utilisation

TABLE 10.1 Classification of the Possible Interactions Between Two Species/Individuals

Original scheme		Simplified scheme	
Effect on interacting species/individuals	Name of interaction		
++	Both are positively affected	Mutualism	Benefit to either or both, but detrimental to neither
+0	One is positively affected while the other is unaffected	Commensalism	
--	Both are negatively affected	Competition/combat	Detrimental to either or both
+-	One is positively affected to the detriment of the other	Parasitism/predation	
-0	One is negatively affected, while the other is unaffected	Amensalism	
00	Activities of neither have any effect on the other	Neutralism	Neither are affected

The effects, either positive (+), negative (-), or neutral (0), on population size, population growth rate or individual fitness of two interacting populations/individuals. EP Odum first used a scheme like that depicted on the left side of the table in the early 1950s. This was simplified (right hand columns) for fungi in the early 1980s by Alan Rayner & Joan Webber.

of the resource is not in keeping with a fungus' particular life strategy. Likewise, the induction of fruit body production and of cord or rhizomorph formation (pp. 58–60) by the presence of another organism have sometimes been considered to be examples of mutualism or neutralism, but these are more likely to occur as a result of deleterious action.

All fungi will interact negatively with other organisms at some time in their lives. For some it is a way of life, and the sole or main way of obtaining nutrition, for example, the parasites and pathogens of plants (Chapter 9), animals (Chapter 11), and other fungi (see below). For others it is also usually directly or indirectly related to obtaining food, a situation often described as competition. The definition of competition used for macroorganisms, and applicable to fungi, is the negative effects of one organism on another resulting from the consumption of a resource of limited availability, or from controlling access to a resource. Macroecologists consider two types of competition: interference competition and exploitation competition. Interference competition refers to the situation where one organism inhibits another by, for example, producing allelopathic chemicals or shading out slower growing or smaller plants. Exploitation competition, on the other hand, is the situation when one organism uses a resource and thereby reduces its availability to another organism. These terms have sometimes been used in relation to fungi; certainly some fungi do massively interfere with other microbes, as outlined later in this chapter. Also, fungal mycelia do sometimes directly compete with each other and with other microbes for dissolved nutrients, for example, while growing through soil. However, for saprotrophic or necrotrophic fungi that grow in solid plant tissues (e.g. wood or leaf litter), the idea of exploitative competition and interference competition are not easy to separate as these fungi gain access to nutrients by competition for space/territory. Thus, for them it is not sensible to use the terms interference and exploitation competition.

Competition between fungi in solid, organic resources can be divided into two types – primary resource capture and secondary resource capture. The former refers to the situation where a resource is uncolonised, and success in capturing this type of resource is determined by factors such as good dispersal, rapid spore germination and growth, as well as the ability

to use the substrates present. Such fungi are said to have R-selected or ruderal characteristics. Secondary resource capture refers to the situation where resources are already colonised by other fungi; aggressive antagonistic interactions (often called combat) are necessary to capture occupied territory or to defend it against aggressors.

This chapter begins by detailing negative interactions amongst fungi, brought about by antagonism at a distance and following contact – both mycoparasitism and larger scale mycelial interactions, including describing how morphology, biochemistry and gene expression changes, and how these affect physiology and ecology. We then go on to consider negative, positive, and mutualistic interactions of fungi with bacteria, archaea, viruses, and protists.

FUNGAL–FUNGAL INTERACTIONS

Fungal hyphae, mycelia, and yeasts can interact both with individuals of the same and different species ([Figure 10.1](#)). Intraspecific (i.e. between members of the same species) interactions, including those related to sexual reproduction and those that are not (i.e. somatic), are described in Chapter 4. Here we confine ourselves to **aggressive interspecific** interactions. These interactions can occur when fungi (1) are at a distance from each other (i.e. there is no contact between hyphae), (2) make contact at the hyphal level, or (3) when large parts of mycelia meet with other large mycelia. Overall there is a range of possible ultimate outcomes to antagonistic interaction between different fungal species, in terms of the territory that they occupy: (1) deadlock, where neither species gains headway, (2) replacement, where one species wrests territory from the other, (3) partial replacement, where one species captures some but not all of the opponent's territory, and even (4) mutual replacement, where one species obtains some of the territory formerly occupied by the other and vice versa ([Figure 10.2](#)). Aggressive interactions are not only major determinants of fungus community development, but are also of considerable interest because of the potential of some fungi to be used as bio-control agents of plant pathogenic fungi (Chapter 8).

Antagonism at a Distance

Antagonism between fungi that have not made physical contact occurs when one or other, or both of the opponents produces volatile and/or diffusible chemicals, including enzymes, toxins, other anti-fungal metabolites, or alters the pH of the environment. It is easy to see the effects of diffusible chemicals in agar culture, as colony size is reduced when opponents are not touching, and often mycelia are unable to meet. Effects of volatiles can be seen by taping a culture of a fungus above a culture of an antagonist and comparing growth with that of the same fungus above uncolonised medium. Reactions often vary depending on the species against which an antagonist is paired, suggesting a reciprocal exchange of chemical signals and subsequent recognition. Chemical signalling by volatile and/or diffusible organic compounds (VOCs and DOCs) plays a major role in fungal recognition systems. These chemicals can be termed infochemicals or semiochemicals.

Microorganisms produce a range of different VOCs, with some of the main compounds detected from soil listed in [Table 10.2](#). Different microbial species have characteristic VOC profiles, though these can vary in amount and composition depending on growth substrates (including amino acids), climate, and as the antagonistic interactions progress. It is

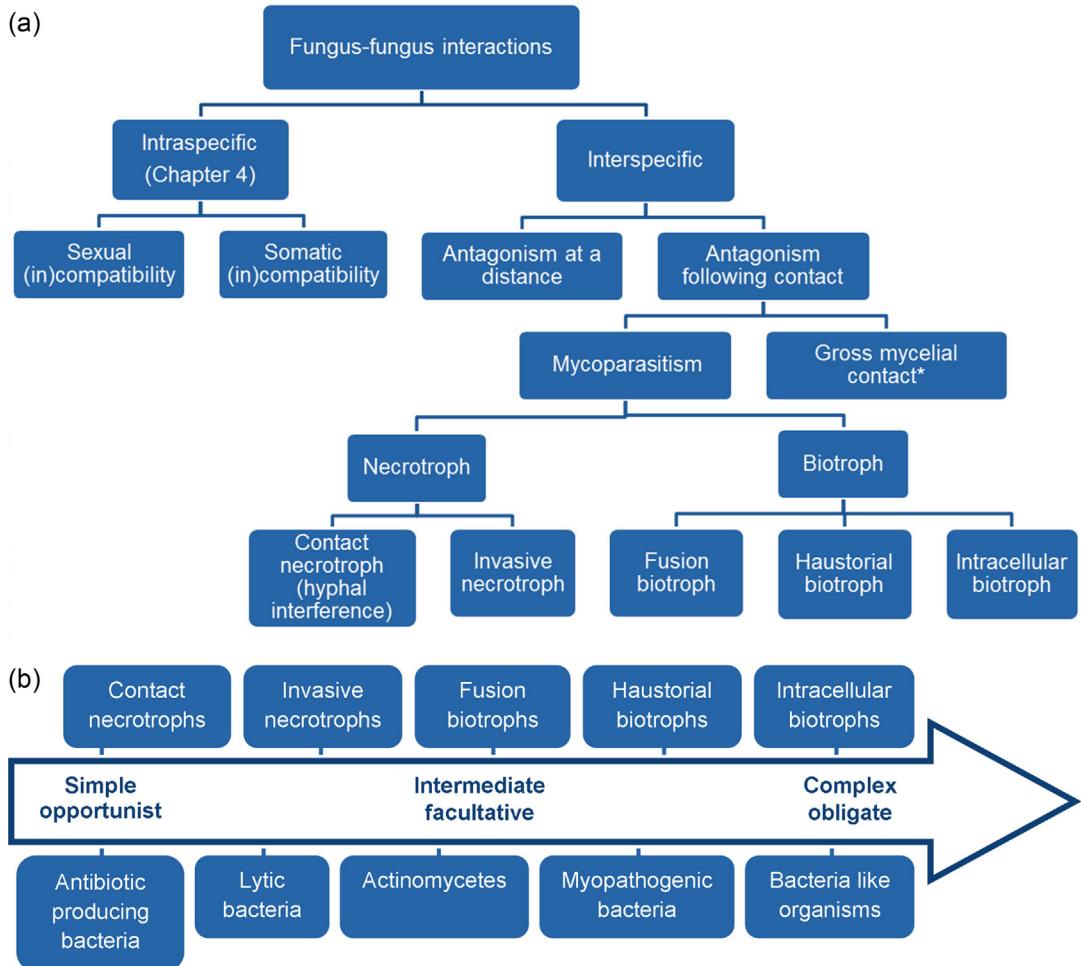


FIGURE 10.1 (a) Spectrum of fungus-fungus interactions. *The lack of further categories within gross mycelial contact reflects lack of knowledge and understanding rather than lack of complexity. (b) Evolution of fungus host-parasite interactions, showing mycoparasites on the top of the arrow, and bacterial antagonists beneath. *Source:* Panel (b) is based on Kobayashi and Hillman (2005).

not a single chemical that is responsible for recognition and antagonistic effects but several or many chemicals in the bouquet. Nonetheless, some classes of VOCs have greater effects than others. For example, aldehydes and ketones, including decanal, heptanal, 2-propanone, 2-methyl-1-butanol, and octanal, produced by *Trichoderma* spp. are particularly inhibitory to mycelial extension of wood decay basidiomycetes. VOCs affect gene expression, and can alter the profile of proteins produced by an affected fungus.

There are a wide variety of types of DOCs, including aromatic compounds. DOCs must operate over shorter distances than VOCs in soil and organic substrata. On artificial media they have been shown to affect spore germination, mycelial foraging, mycelial morphology,

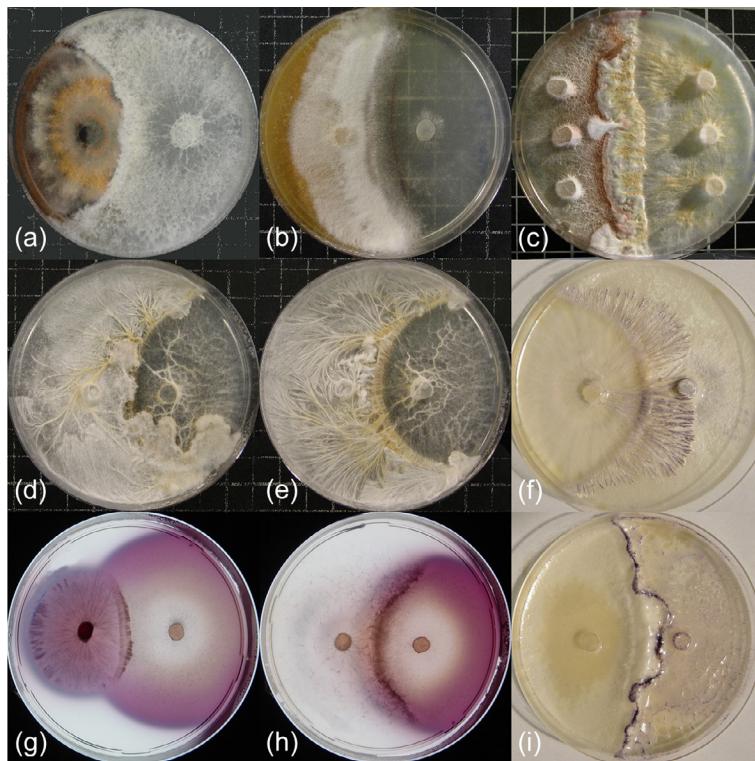


FIGURE 10.2 Examples of interspecific interactions between mycelia of wood rotting basidiomycetes (unless stated differently) in agar culture, showing mycelia barrages, fans and cords. (a) *Bjerkandera adusta* (right) starting to replace *Hypoxylon fragiforme* (Ascomycota); (b) *Trametes versicolor* (right) has almost completely replaced *Stereum gausapatum*; (c) *Hypholoma fasciculare* (right) replacing *Resinicium bicolor*. The reddish brown pigment is produced by *Resinicium bicolor*. (d) and (e) *Trametes versicolor* (left) and *Hypholoma fasciculare* (right). In (e) *Hypholoma fasciculare* has completely over grown *Trametes versicolor* as cords, and eventually completely replaces it, but in (d) while *Hypholoma fasciculare* has overgrown its opponent as cords in some places, *Trametes versicolor* is replacing *Hypholoma fasciculare* at the bottom right. (f) Production of superoxide by *Hypholoma fasciculare* (left) replacing *Trametes versicolor* (right), indicated by purple staining (nitroblue tetrazolium). Intense laccase activity during interactions between (g) *Hypholoma fasciculare* (left) and *Trametes versicolor* (right) and (h) *Bjerkandera adusta* and *Trametes versicolor*, indicated by purple staining (ABTS: 2,2'-azino-bis(3-ethylbenzothiazoline-6-sulfonic acid) diammonium salt). Source: Panel (c) © Timothy Rotheray; all other images © Jennifer Hiscox.

and to increase production of ligninolytic enzymes in some fungi. DOCs leaching from wood previously colonised by fungi sometimes inhibit and sometimes stimulate extension rates of other fungi. Release of DOCs by fungi in wood is likely to influence which fungi follow during community development (p. 254).

Antagonism Following Contact: Mycoparasitism

There is a spectrum of mycoparasitic relationships with biotrophs and necrotrophs at the two extremes, and many intermediate types between (Table 10.3, Figure 10.1). The biotrophs

TABLE 10.2 Volatile Organic Compounds (VOCs) Evolved from Soil Under Aerobic and Anaerobic Conditions

Alcohols	Aldehydes	Aromatics	Butyl, Ethyl and Methyl esters	Ketones	Sulphides
Butan-1-ol	2-Methyl-butan-1-al	Benzene	Acetic acid	Butan-2-one	Dimethyl sulphide
Butan-2-ol	3-Methyl-butan-1-al	Benzaldehyde	Butanoic acid	3-Hydroxy butan-2-one	Dimethyl disulphide
Ethanol		Dimethyl benzene	2-Methyl-butanoic acid	Pentan-2-one	Dimethyl trisulphide
2-Methyl propan-1-ol		Ethyl benzene	3-Methyl-butanoic acid	Pentan-3-one	2-Methyl propylsulphide
2 Methyl propan-2- ol		Trimethyl benzene	2-Methyl propanoic acid	Propane-2-one	
Propan-1-ol				4-Methyl pentan-2-one	
				5-Methyl heptan-2-one	

The organisms generating the VOCs include both fungi and bacteria.

From Wheatley, R.E., 2002. The consequence of volatile organic compound mediated bacterial and fungal interactions. *AAnoton v Leeu.* 81, 357–364.

and necrotrophs can be divided further, based on the physiological nature of the interactions. As with necrotrophic pathogens of plants and animals (Chapters 8 and 9), necrotrophic mycoparasites tend to have a broad host range, with relatively unspecialized parasitic mechanisms, and kill their host. In contrast, as with biotrophic relationships between fungi and other organisms (Chapters 7–9), the biotrophic relationships between one fungus and another are complex, controlled and relatively non-destructive, and often, but not always, with narrow host ranges that have co-evolved. Biotrophic mycoparasites are dependent on the host fungus for survival. Mycoparasitic species can often not be defined as causing a specific type of parasitism, as some change their behaviour towards the host as the mycoparasitic interaction progresses. For example, parasitism that is initially biotrophic can later change to necrotrophy. Some fungi grow biotrophically on certain hosts but necrotrophically on others, for example, *Hypomyces chrysospermus* is necrotrophic on fleshy fruit bodies of Basidiomycota, but it can grow biotrophically within *Botrytis cinerea* and *Trichothecium roseum* hyphae when they colonise a mushroom that it has already parasitized. Some mycoparasites form different hyphal structures when they contact different hosts, and can have different effects on different hosts, due to different mechanisms being employed and to differential sensitivity to toxins. *Trichoderma virens*, for example, produces an antibiotic, gliovirin, which is strongly inhibitory to the fungus-like *Pythium ultimum*, but not to the basidiomycete *Rhizoctonia solani* (= *Thanatephorus cucumeris*), nor to the zygomycete *Rhizopus arrhizus*, nor to the ascomycete *Verticillium dahliae*.

It is not known when mycoparasitism first evolved, but it is likely an ancient mode of nutrition. *Glomus*-like spores have been found in the Lower Devonian Rhynie chert, from 400 million

years ago (mya). These contained chytrid-like structures within. The oldest known fossil of an agaric was found in amber from the Early Cretaceous (100 mya), and this contained not only a mycoparasite but a hypermycoparasite (i.e. the parasite of a parasite). Mycoparasitism of basidiomycetes likely extends much further back, but they have not fossilised well. It is often assumed that the relationship between obligate biotrophs and their hosts is evolutionarily more advanced than that of necrotrophs, because the former relationships are more complex, but this is not the case. Biotrophic endoparasitism is a way of life for some of the most primitive fungal groups, and may even be the ancestral mode of nutrition in fungi.

There are three main types of biotrophic relationships: (1) intracellular parasites, (2) haustoria-producing parasites, and (3) fusion parasites (Table 10.3, Figure 10.1). With both fusion and haustoria-producing biotrophs, intimate connections with the host are necessary, allowing nutrient transfer from host to parasite. Haustoria-producing biotrophs actually penetrate host hyphae, but fusion biotrophs do not, and the latter relationship may be less complex.

With the **intracellular parasites**, the entire fungal thallus enters the host fungus. For example, many aquatic mycoparasitic Chytridiomycota penetrate the host wall and discharge their entire cytoplasm into that of the host. Nutrients are absorbed directly through the host-parasite interface. The presence of some intracellular mycoparasites, such as *Ampelomyces* on powdery mildew (pp. 271–272), can be seen by the naked eye in the natural environment, and were first described in the early 1800s (Figure 10.3). *Ampelomyces* condia land on leaves and germinate; germination is inhibited at high spore concentrations, but stimulated by the presence of the host, and germ tubes grow towards the host. Germ tubes can form appressoria-like structures, and penetrate the hyphal or spore walls of powdery mildew species (Figure 10.3) using enzymatic and mechanical pressure. The parasite grows intracellularly as a biotroph initially, but kills the host mycelia after 5–8 days, after which time it produces pycnidia, containing conidia, within the hyphae, conidiophores and immature ascomata of the host. In moist environments, spores are released and can spread to other leaves and powdery mildew colonies by rain splash and water run-off. *Ampelomyces* conidia can also be spread for long distances in parasitized hyphal fragments and condia of the host. These powdery mildew conidia can sometimes germinate and give rise to new colonies with *Ampelomyces* already inside. As well as eventually killing its host, *Ampelomyces* suppresses asexual and sexual reproduction of the host by killing conidia and immature ascomata, though conidia can be produced after the mycelium has been invaded. Though host death is not rapid, *Ampelomyces* was among the first fungi to be tried as a biological control agent, with commercial formulations available today (p. 424).

Haustorial biotrophs form an appressorium on the host surface, from which a fine peg develops, that penetrates the host hypha (Figure 10.4). When it has passed through the wall, it branches to form a lobed haustorium that invaginates the host plasmalemma. The haustorium is the presumed site of nutrient transfer to the parasite. *Piptocephalis fimbriata* is a haustorial biotroph. Its conidia germinate in the absence of the host, but its germ tube makes limited growth unless a suitable Mucorales host mycelium is sufficiently close to enable chemotropically directed growth, with subsequent penetration and haustorium formation. **Fusion biotrophs** produce specialised hyphae or buffer cells, which are closely adpressed to those of the host hyphae. Direct contact of parasite and host is made through channels or micropores in the cell walls. The plasmalemma of the host and parasite make contact and fuse, making their cytoplasm contiguous.

TABLE 10.3 Types of Mycoparasitism (Including Fungus-Like Oomycota)

Type of parasitism	How the parasite interfaces with the host	Examples			
		Parasite species	Parasite (sub)phylum	Host species	Host (sub)phylum
Contact necrotroph (hyphal interference)	Parasite contacts but does not penetrate the host hyphae. Host cytoplasm degenerates and lysis may occur	<i>Phlebiopsis gigantia</i>	Basidiomycota	<i>Heterobasidion annosum</i>	Basidiomycota
		<i>Coprinellus heptemerus</i>	Basidiomycota	<i>Ascobolus crenulatus</i>	Ascomycota
		<i>Panaeolus sphinctrinus</i>	Basidiomycota	<i>Bolbitius vitellinus</i>	Basidiomycota
		<i>Cladosporium</i> sp.	Ascomycota	<i>Exobasidium camelliae</i> (basidia)	Basidiomycota
Invasive necrotroph	Following contact, the parasite penetrates and enters the host; host cytoplasm rapidly degenerates and hyphal lysis often occurs	<i>Rozella</i> species	Cryptomycota	<i>Allomyces</i> , <i>Chytridium</i> , <i>Rhizophlyctis</i> , <i>Rhyzophydiuum</i> , <i>Zygorrhizidium</i>	Chytridiomycota
		<i>Syncephalis californicus</i>	Zoopagomycotina	<i>Rhizopus oryzae</i>	Mucoromycotina
		<i>Nectria inventa</i>	Ascomycota	<i>Alternaria brassicae</i> (hyphae and conidia)	Ascomycota
		<i>Coniothyrium minitans</i> , <i>Talaromyces flavus</i>	Ascomycota	<i>Sclerotinia sclerotiorum</i> (sclerotia)	Ascomycota
		<i>Cladosporium uredinicola</i>	Ascomycota	<i>Puccinia violae</i> (uredospores)	Basidiomycota
		<i>Fusarium merismoides</i>	Ascomycota	<i>Pythium ultimum</i> (oospores)	Oomycota
		<i>Mycogone perniciosa</i>	Ascomycota	<i>Rhopalomyces elegans</i> (conidia)	Mucoromycotina
		<i>Mycogone perniciosa</i>	Ascomycota	<i>Agaricus</i> and <i>Pluteus</i> fruit bodies	Basidiomycota
		<i>Trichoderma</i> spp.	Ascomycota	Many, e.g. <i>Rhizoctonia solani</i> (= <i>Thanatephorus cucumeris</i>), <i>Corticium rolfsii</i>	Basidiomycota
		<i>Trichoderma harzianum</i>	Ascomycota	<i>Botrytis cinerea</i>	Ascomycota
	<i>Rhizoctonia solani</i> (= <i>Thanatephorus cucumeris</i>)	<i>Rhizoctonia solani</i> (= <i>Thanatephorus cucumeris</i>)	Basidiomycota		Mucoromycotina
		<i>Pythium acanthicum</i>	Oomycota	<i>Phycomyces blakesleeanus</i>	Mucoromycotina

Intracellular biotroph	Entire thallus of the parasite enters the hypha of the host; host cell remains functional	<i>Ampelomyces</i> spp.	Ascomycota	<i>Arthrocladiella mougeotii</i> , <i>Blumeria graminis</i> , <i>Sawadaea bicornis</i> (all powdery mildews)	Ascomycota
Haustorial biotroph	A short haustorial branch from a parasite hypha penetrates the host; host cell remains functional	<i>Piptocephalis</i> spp. <i>Dimargaris</i> spp. <i>Filobasidiella depauperata</i>	Zoopagomycotina Kickxellomycotina Basidiomycota	At least 20 genera of Mucorales <i>Verticillium lecanii</i>	Mucoromycotina Mucoromycotina Ascomycota
Fusion biotroph	Host and parasite are in intimate contact; micropore(s) form between the adpressed host and parasite hyphae, or from a short penetrative branch from the parasite hypha; host cell remains functional	<i>Gonatobotrys simplex</i> <i>Dicyma parasitica</i>	Ascomycota Ascomycota	<i>Alternaria alternata</i> <i>Physalospora obtusa</i>	Ascomycota Ascomycota

Abstracted from Jeffries (1995) and other sources.

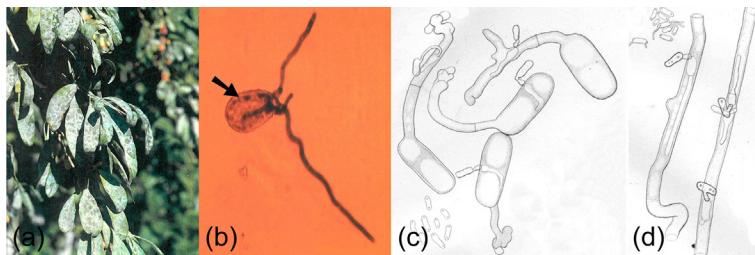


FIGURE 10.3 Intracellular mycoparasites. *Ampelomyces* species are initially biotrophic, though eventually they kill the host cell. *Ampelomyces* spp. are parasitic on powdery mildew fungi. (a) The brown patches are masses of intracellular pycnidia of *Ampelomyces* within white powdery mildew colonies, which are parasitic on *Lycium halimifolium* (Solanaceae). Hyphae of the mycoparasite penetrate into conidia (b, c) and hyphae (d) of the host. (b) Hyphae of *Ampelomyces* (stained with cotton blue) within (arrowed) and emerging from a conidium of *Erysiphe syringae-japonicae*. Source: (c, d) Drawings from early work on *Ampelomyces* by De Bary (1870), showing germ tubes extending from conidia (arrowed) and penetrating into (c) germ tubes of *Erysiphe heraclei* and (d) into hyphae of *Neoverisiphe galeopsidis*. From Kiss (2008).

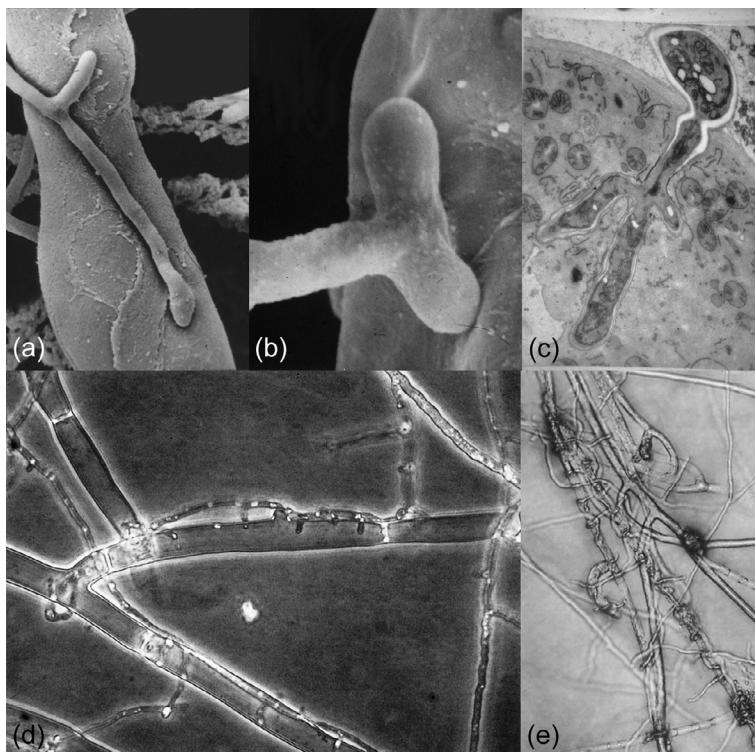


FIGURE 10.4 Mycoparasitism. (a, b) Scanning and (c) Transmission Electron Micrographs of *Piptocephalis unispora* parasitizing *Cokeromyces recurvatus*. (a) Narrow hyphae of *Piptocephalis unispora* closely adpressed to the surface of its host, and bulging at the tip to form an appressorium. (b) An appressorium developing lateral hyphae. (c) An appressorium (top right) on the surface of the host, with haustorial apparatus developing inside the host. (d) *Trichoderma virens* hyphae penetrating into large hyphae of *Rhizoctonia solani*. (e) Hyphae of *Trichoderma virens* coiling around the larger hyphae of *Rhizoctonia solani*. Coiling of hyphae around a host is often a feature of mycoparasitism. Source: Panels (a, b) © Peter Jeffries; (c) from: Jeffries, P., Young, T.W.K., 1976. Ultrastructure of infection of *Cokeromyces recurvatus* by *Piptocephalis unispora* (Mucorales). *Arch. Microbiol.* 109, 277–288; (d, e) from Howell (2003).

While for some fungi, mycoparasitism is the major or only way in which nutrition is obtained, for many necrotrophs it is more opportunistic. Parasitism can also be temporary, serving as a means to obtain a different food source (see below). Necrotrophic mycoparasites acquire nutrients from hosts in a much less controlled way than biotrophic mycoparasites, and are hence more destructive, and have broad host ranges, as seen with *Trichoderma* species and *Pythium* species (oomycetes). Necrotrophic parasites can be invasive or non-invasive.

Non-invasive (contact) necrotrophic mycoparasites make contact or almost (within a few micrometre) contact host hyphae. This type of parasitism is sometimes called **hyphal interference** and was first described by John Webster and colleagues in the early 1970s for *Coprinellus heptemerus*. Hyphal interference is most effective at the hyphal tips of the mycoparasite, and the affected fungus is also most sensitive in the tip region. Hyphal extension of the fungus being interfered with slows dramatically, membrane function is impaired, organelles lose contents, the plasmalemma invaginates, and the contacted hyphal compartment dies. Death of the whole mycelium will occur if multiple contacts are made. A single hypha of *Panaeolus sphinctrinus* can prevent a colony of *Bolbitius vitellinus* from advancing in agar culture. Hyphal interference is so effective in causing death of the opponent that *Phlebiopsis gigantea* is used as a biocontrol agent against the conifer tree pathogens *Heterobasidion annosum* and *Heterobasidion parviporum*. cDNA analysis of interference of *Heterobasidion parviporum* by *Phlebiopsis gigantea* showed up-regulation of expression of genes encoding a wide range of proteins, including those important for nutrient acquisition and use, enzymes involved in glycolysis and gluconeogenesis, breakdown of pectic compounds, and in nitrogen metabolism. Hydrophobins were up-regulated, and these are implicated in cell wall assembly and the monomers may act as toxins.

With **invasive necrotrophs**, hyphae of the mycoparasite contact those of the host, sometimes coiling around and often penetrating. *Trichoderma* species are examples of invasive necrotrophs, and their parasitic ability and bio-control ability has been studied since the 1930s. Mycoparasites are often able to sense the presence of a potential host and direct their growth towards it (e.g. *Trichoderma* spp. towards *Rhizoctonia solani*), and the presence of a potential host can stimulate spore germination (e.g. conidia of *Coniothyrium minitans*) are stimulated by the presence of sclerotia of *Sporidesmium sclerotivorum*. After contact, recognition, binding and morphological changes occur. *Trichoderma* spp. hyphae typically coil around those of the host ([Figure 10.4](#)) and in some penetrate into the host (e.g. *Trichoderma virens* penetrates the hyphae of *Rhizoctonia solani*) ([Figure 10.4](#)). Both *Trichoderma* spp., and some of its hosts (e.g. *Corticium (Sclerotium) rolfsii*), produce lectins which interact with carbohydrates on the surface of the opposing fungus and are involved in recognition and differentiation of structures involved in the parasitism. Signals from the host are recognised by receptors on the surface of the mycoparasite. This elicits an internal signal transduction cascade causing transcription of genes relevant to parasitism. With *Trichoderma* spp., heterotrimeric G proteins of the parasite transmit signals from G-protein-coupled receptors, to the cAMP and the MAP kinase pathways, which govern production of antifungal metabolites, lytic enzymes, and infection structures. Host cytoplasm is then completely disrupted ([Figure 10.4](#)). When *Trichoderma* (= *Gliocladium*) *roseum* attacks *Botrytis* species, for example, vacuolation occurs and hyphal walls and organelles are then lysed. *Trichoderma* spp. are such vigorous necrotrophs because of the toxic substances and enzymes, including chitinases, glucanases, and proteases, that they produce.

Some fungi are **temporarily parasitic** on others. They first obtain nutrition by parasitizing a host and then, more importantly, taking over the resource occupied by the host. When the parasite has killed its host and occupied its resource, it can then defend and expand its territory by non-parasitic, antagonist interactions with adjacent fungi. This occurs with several wood decomposing species. For example, *Lenzites betulina* is temporarily mycoparasitic on *Trametes* species, and *Trametes gibbosa* on *Bjerkandera* species. In both cases the mycoparasite is relatively uncommon, while the host is very common, occupying large volumes of decomposing wood which, following death of the host becomes available to the temporary mycoparasite.

Not only can vegetative hyphae be parasitized or killed, but so too can **hyphae within fruit bodies**. *Hypomyces aurantius* parasitizes *Trametes versicolor* and other wood-decay basidiomycetes, by producing a powerful toxin, which causes destruction of host organelles and coagulation of cytoplasm. Initially lipid bodies accumulate, then mitochondria and cisternae of the endoplasmic reticulum swell, and the plasma membrane invaginates, shrinking away from the cell wall. Other presumed parasites of fruit bodies include the basidiomycetes *Asterophora lycoperdoides* and *Pseudoboletus parasiticus* that fruit on *Russula nigricans* and *Scleroderma citrinum* respectively, and *Spinellus fusiger* (Mucoromycotina) on *Mycena* species (Figure 10.5). The basidiomycete *Squamanita odorata* reduces the fruiting tissues of its basidiomycete host *Hebeloma mesophaeum* to unrecognisable galls. Most, perhaps all, species of Tremellales (Basidiomycota) are mycoparasitic, including on the hymenia of basidiomycete mushrooms, brackets and Dacrymycetales, and the ascocarps and stromata of pyrenomycetes (Ascomycota). Parasitic *Tremella* species form haustoria with micropores connecting the cytoplasm of host and parasite.

Fungal spores are also parasitized. **Mycoparasitism of spores** has been mostly studied on those of arbuscular mycorrhizal fungi (AMF, pp. 206–215), which are the largest within kingdom Fungi. Many, often the majority, of AMF spores extracted from soil have walls perforated by fine canals where mycoparasitic fungi, or sometimes amoebae (p. 358), have penetrated. These canals are commonly associated with ingrowths similar to the papillae produced in response to the entry of penetration pegs of *Piptocephalis* spp. on Mucorales. *Spizellomyces* and *Pythium*-like zoosporic oomycetes are common on Glomales spores, sporulating on the surface or within. Many genera of Ascomycota (e.g. *Trichoderma* and *Verticillium*) that parasitize hyphae have species that parasitize spores. Older spores and less melanised spores appear to be less able to resist invasion than younger, darker spores of Glomales.



FIGURE 10.5 Fruit bodies of mycoparasitic fungi on fruit bodies of basidiomycete hosts. (a) *Spinellus fusiger* (Mucoromycotina) on *Mycena* sp. (b) *Asterophora lycoperdoides* on *Russula nigricans*. (c) *Pseudoboletus parasiticus* on *Scleroderma citrinum*. Source: Panels (a, b) © Penny Cullington and (c) © Alan Hills.

Mycoparasitism of sclerotia – survival structures – is also common, and of particular interest when the host is a plant pathogen, as again there is potential for biocontrol. For example, hyphae of *Sporodesmium sclerotivorum* and *Teratosperma oligocladium* penetrate the rind of *Sclerotinia sclerotiorum* and *Sclerotinia minor* and then proliferate intercellularly within the medulla, but not within sclerotial cells. The parasites probably use glucose and other monosaccharides released from hyphae within the medulla of the sclerotium. Subsequently, hyphae of the mycoparasite grow to the surface of the sclerotium and sporulate profusely.

Antagonism Following Contact: Gross Mycelial Contact

Mycoparasitism can clearly ultimately affect the whole mycelium of the parasitized fungus and, in agar culture, the mycelium of the mycoparasite can sometimes be seen macroscopically, advancing unhindered through the colony of the host. The rather imprecise term, gross mycelial contact, is used to describe the situation where dramatic changes, obvious to the naked eye, occur when mycelia of different species meet. The growth of one or both mycelia slow, the morphology of the mycelium changes, pigments are often produced and zones of lysis are sometimes seen. These changes are particularly evident in interactions between basidiomycetes and also xylariaceous ascomycetes on nutrient rich agar media and also on the surface of soil, where morphological changes such as 'barrages' of mycelium resistant to invasion, invasive mycelia fans and aggregated mycelia structures – cords and rhizomorphs – can be seen ([Figure 10.2](#)). These morphological shifts are often accompanied by redistribution of mycelial biomass from elsewhere, with a reduction in hyphal density distant to the interaction zone, which can result in greater susceptibility to invasion if the opposing mycelium reaches this area.

Interactions, or at least the site of interactions, can be seen in natural organic resources as 'interaction zone lines' ([Figure 10.6](#)). In wood, these appear in cross section as narrow, often dark-coloured though sometimes brightly coloured (e.g. orange with *Oudemansiella mucida*), lines in cross section. These lines are pseudosclerotial plates (PSPs; p. 61). They often extend many centimetres longitudinally and completely surround the territory occupied by the decay fungus that produced them. A narrow (one or a few wood cells thick) 'no man's land' is present between PSPs surrounding the territory of adjacent fungal individuals. This region is often occupied by small colonies of dematiaceous ascomycetes (e.g. *Chaetosphaeria myriocarpa* and *Rhinocladiella* spp.), which may partly explain the vast number of different DNA sequences revealed by high throughput sequencing of colonised wood. These barriers can sometimes be breached by decomposer fungi occupying large adjacent territories, and the fungus that produced them can be replaced. This can be seen in wood as 'relic' zone lines (i.e. PSPs) that have been partly decomposed. Mycelial biomass is often unevenly distributed within decay columns in the wood. This can be seen when wood is incubated in moist conditions; prolific mycelial outgrowth occurs at the edges of decay columns close to interaction zone lines, while outgrowth from inner regions is often sparser.

There are likely to be many different mechanisms covered by this single catch-all term, gross mycelial interactions. Indeed, a fungus may operate different combative mechanisms against different opponents. These mechanisms involve the release of enzymes, toxins, and

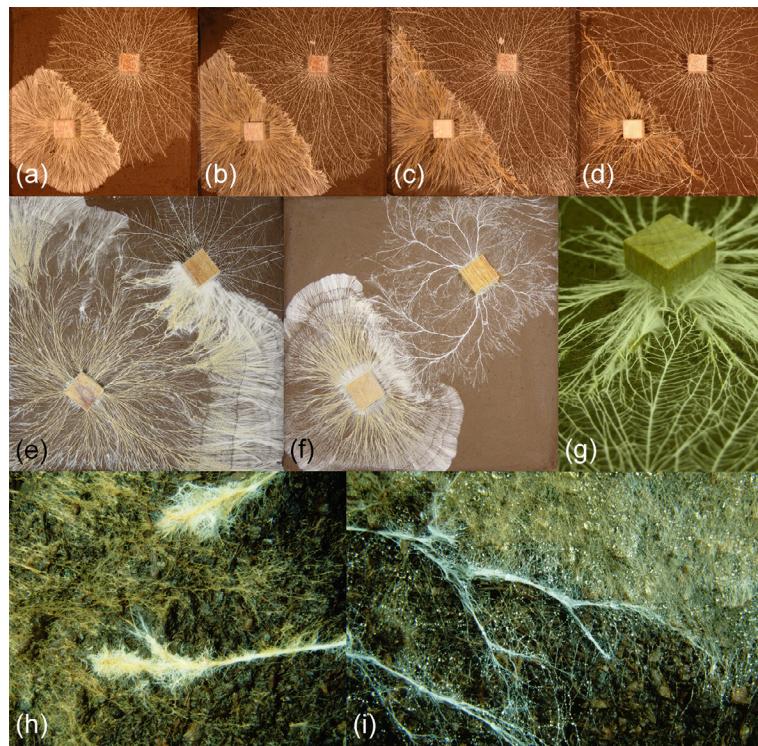


FIGURE 10.6 Interactions between basidiomycete mycelia in soil and wood. (a–d) Mycelium of *Hypholoma fasciculare* (left) extending from a colonised wood block interacting with that of *Phallus impudicus* on the surface of compressed, non-sterile soil in 24 × 24 cm trays, 2 (a), 10 (b), 32 (c), and 84 days (d) after contact, respectively. After 32 days cords of *Phallus impudicus* have managed to pass the defences of *H. fasciculare* and to grow over it. By 84 days *Phallus impudicus* has reached the wood block colonised by *H. fasciculare*, and from then on interaction occurs within the wood block. Damage to the *Phallus impudicus* mycelium, resulting from grazing by invertebrates (Collembola) is evident at 84 days in regions away from the opponent. (e) A different strain of *H. fasciculare* (left) replacing *Phallus impudicus*. (f) *Hypholoma fasciculare* (left) being replaced by *Phanerochaete velutina*. Note that in some interactions replacement of mycelium occurs by a fungus as it progresses across soil (f) whereas in others (d) overgrowth occurs first. (g) Close up of mycelium of *Phallus impudicus* (bottom) replacing *Resinicium bicolor*. (h) Mycelial cords of *Phanerochaete velutina* overgrowing (from the right) extraradical mycelium of the ectomycorrhizal *Paxillus involutus*. Tips of *Phanerochaete velutina* cords are truncated (cf. with cords on soil in (f), so are also being affected antagonistically). (i) Cords of *Phanerochaete velutina* (bottom) preventing access to territory by the extraradical mycelium of the ectomycorrhizal *Paxillus involutus* (top). Source: Panels (a–g) © Timothy Rotheray; (h, i) © Damian Donnelly.

other antifungal compounds (see below). Which species ultimately dominate in antagonistic interactions is determined by the relative abilities of the opponents to capture and defend territory. Fungi exhibit a hierarchy of combative ability, some species being more aggressive than most, others being replaced by most antagonists, and the combative ability of many others in between (Figure 10.7). Further, some fungi are good at ‘defence’, others at ‘attack’, and others at both. This is similar to the concepts of competitive effect and competitive response in plant ecology, the former being able to suppress resource levels for other plants, and the latter

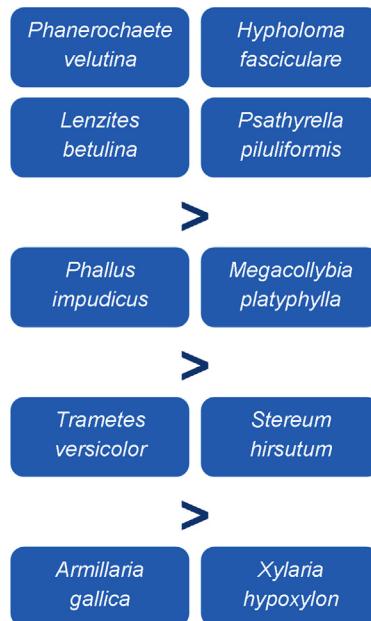


FIGURE 10.7 The hierarchy of combative ability for some of the dominant fungi involved with decomposition of felled beech (*Fagus sylvatica*) wood.

having the ability to tolerate suppression. So within the spectrum of combative abilities there are: (1) transitive hierarchies, where species A is more combative than species B, which in turn is more combative than species C (i.e. A>B>C); and (2) intransitive hierarchies, where species A is more combative than species B, and species B is more combative than species C, but species C is more combative than species A (i.e. A>B, B>C, C>A). Such intransitivity may result from different species employing different combative and defensive mechanisms. This hierarchy of combative ability is a bit like a sports league, in which the team at the top of the league table beats most of the others, but it can, too, occasionally be beaten. Likewise, teams at the bottom of the league sometimes beat teams higher up and are occasionally ‘giant killers’, beating the very best teams. The situation is further complicated by the fact that outcomes between particular combinations of species vary depending on abiotic regime (e.g. temperature, water potential, nutrient status), fungal strain, size of territory already held, location of the interaction (e.g. wood or soil), presence of other microorganisms and invertebrate grazing, and even sometimes under apparently identical conditions.

Interaction Chemistry and Gene Expression

As well as changes in mycelial morphology during contact between mycelia, up-regulation of genes involved in antagonism results in the production of additional chemicals (pp. 339–341) in hyphae, which are released into the surrounding environment as volatile or diffusible organic compounds (VOCs and DOCs), as already mentioned in the section on ‘Antagonism at a distance’ (pp. 339–341). The production of antibiotic compounds by fungi (e.g. penicillin) has

long been known, but the extent of production and scale over which they exert an effect in the natural environment is still unclear. Some antimicrobial compounds are definitely persistent; large quantities of methylbenzoates are produced *in vivo* in wood decayed by *Sparassis crispa* – a brown rot (pp. 147–152) basidiomycete that is a tree pathogen – and persist for many years. Production of such high concentrations represents a significant biosynthetic commitment by the fungus, implying considerable benefit to it. Other antifungal chemicals have also been readily detected in wood, including lipid-soluble compounds from the majority of fungi isolated from stumps of Sitka spruce (*Picea sitchensis*). The activity of these compounds, however, varied against other fungi. For example, three compounds from culture of *Stereum sanguinolentum* on artificial medium were antifungal to *Cladosporium cucumerinum*, but only one of them inhibited mycelial growth of *Hypholoma fasciculare*, *Heterobasidion annosum*, and *Resinicum bicolor*.

Enzyme activity varies in different regions of interacting mycelia. Some enzymes are hugely up-regulated in the interaction zone, with small increases in activity in other regions of the mycelia. Production of reactive oxygen species, phenoloxidases and sometimes β -glucosidase increase widely in mycelia, whereas laccases and manganese-dependent lignin peroxidases increase in the contact zones between interacting wood decay-causing species. The laccases may well have a defensive role, since they are involved in the production of melanins and similar compounds which are frequently formed during interspecific interactions. Chitinases also play a role since they cause cell lysis and release sequestered nitrogen from the hyphae of fungi whose territory is being taken over.

Antagonistic Effects on Physiology and Ecology

In the natural environment, fungi almost always exist in multispecies communities, so interspecific mycelial interactions and competition for resources occur continually. Not only do interactions occur between mycelia of saprotrophs, but also between saprotrophs and mycorrhizal fungi (Chapter 7), and amongst mycorrhizal fungi. Many key enzyme systems are common to ectomycorrhizal (ECM) and saprotrophic basidiomycetes, and since their mycelia are often found together in wood at very late stages of decay, and in organic soil, they will inevitably compete. In Boreal forests, however, there may be separation of niches which reduces competition, with saprotrophs dominating upper, organic soil horizons and ECM fungi dominating in lower, mineral layers.

During interactions between saprotrophic fungi, CO_2 evolution sometimes increases, reflecting an increase in metabolic cost when defending territory or wresting it from an opponent. Movement and partitioning of carbon within mycelia is also affected; in wood when one species replaces another, the replacing fungus can switch from reliance on carbon available in the originally occupied resource to that available in the captured territory, including use of the mycelium of the fungus that has been killed. When saprotrophic basidiomycetes interact with ECM basidiomycetes, there are marked effects on allocation of photosynthetically derived carbon to the ECM mycelium growing from the roots (Figure 10.8). Carbon exchange between mycelia can also occur; during antagonistic interactions carbon compounds leak from damaged hyphae in the interaction zone, even where there is deadlock, and these can be absorbed opportunistically by the opponent.

Mineral nutrient uptake, movement, partitioning, and release are altered by interspecific mycelial interactions. As with carbon, mineral nutrient exchange between mycelia occurs, probably via leakage in the interaction zone. Nutrients also move within mycelia during

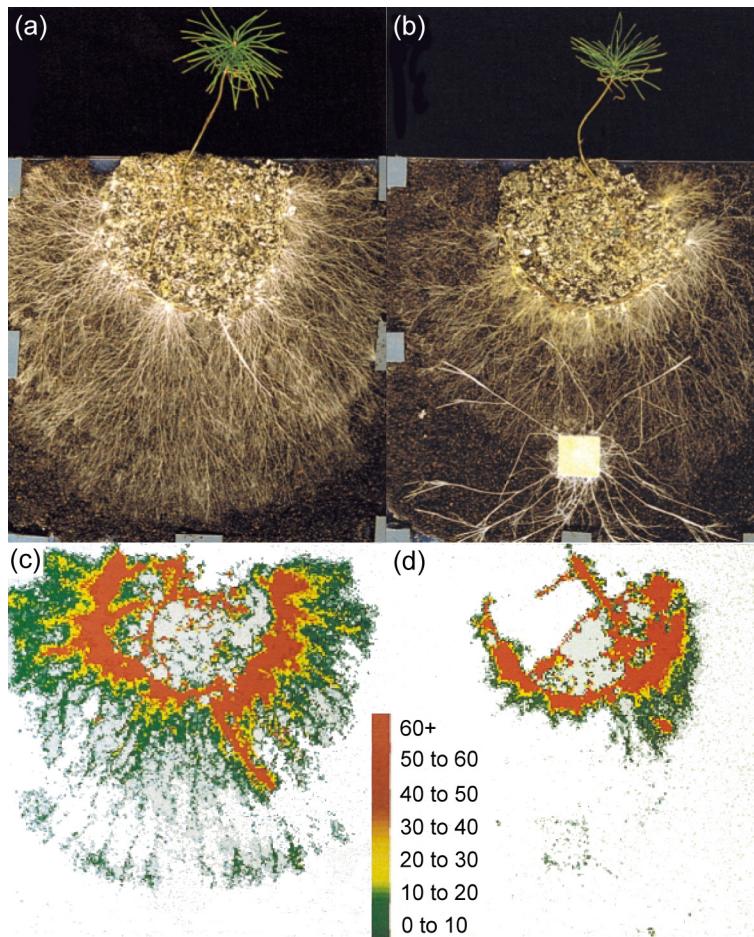


FIGURE 10.8 Saprotofrophic basidiomycetes can dramatically affect ectomycorrhizal mycelial spread and allocation of carbon to the extraradical mycelium of the mycorrhizal fungus. Here the wood decay fungus *Phanerochaete velutina*, growing from a piece of wood, is interacting with mycelium of *Suillus bovinus* in association with *Pinus sylvestris* in soil microcosms. (a) and (b) show, respectively, ectomycorrhizal mycelial growth in the absence and presence of the saprotroph. Plants were pulse-labelled with ^{14}C , and this was quantified in a $20 \times 24\text{ cm}$ below-ground area by digital autoradiography (c, d). The colour scale represents counts mm^{-2} over 45 min. Very little carbon from the host plant is allocated to ectomycorrhizal mycelium in the area of territorial combat, and its growth is inhibited. There was a 60% reduction in ^{14}C allocated to mycelium of *Suillus bovinus* when interacting with *Phanerochaete velutina*, up to 30 h after pulse labelling. Presence of ^{14}C (0.03 %) was detected in *Phanerochaete velutina* after 5 days. Source: Modified from: Leake, J.R., Donnelly, D.P., Saunders, E.M., Boddy, L., Read, D.J., 2001. Carbon flux to ectomycorrhizal mycelium following ^{14}C pulse labelling of *Pinus sylvestris* L. seedlings: effects of litter patches and interaction with a wood-decomposer fungus. *Tree Physiol.* 21, 71–82. By permission of Oxford University Press.

interactions. In some cases there is movement of phosphorus towards the interaction zone and in others away from it, the latter probably occurring when a mycelium is losing a confrontation. During interactions, nutrients are not only released in the interaction zone, but the whole mycelium can become 'leaky', and this is probably one of the main ways by which nutrients are released from mycelia into the soil.

Interspecific Interactions and Fungal Community Development

The outcomes of fungal interactions are often the major causes of change in fungal communities. This has been studied most intensively in decaying organic matter, especially wood, but also in respect of establishment of mycorrhizas. Position in the hierarchy of combative ability (pp. 349–351) is broadly, but not completely, correlated with position of fungi in community succession. Initial colonisers of dead organic resources do not have to be successful combatants to gain territory, and hence access to resources, but those which arrive later do have to be, as other fungi are already present. Combative interactions are not, however, always the main drivers of community change. Disturbance or environmental stress can alter communities. Thus, certain fungi can be poor combatants, but have characteristics that allow them to cope with the disturbance or stress, and thus to dominate.

Interactions between saprotrophs and ECM fungi depend on the species, suppression of either sometimes occurring. For example, there are reports of *Suillus variegatus* and *Paxillus involutus* ectomycorrhizal with pine seedlings being antagonistic against the wood decaying cord-forming basidiomycete *Hypholoma fasciculare*, whereas *Hypholoma fasciculare* can inhibit *Pisolithus tinctorius* ectomycorrhizal with chestnut. *Hypholoma fasciculare* can inhibit root colonisation by *Pisolithus tinctorius*, if present at the time when colonisation begins, and even influences the mycorrhizas formed when arriving 30 days after the start of root colonisation by the ECM fungus.

INTERACTIONS BETWEEN FUNGI AND BACTERIA

Interactions between fungi and bacteria are many and varied, and they can affect the growth, survival, and virulence of each other. These effects can be negative, positive or mutualistic to the interacting organisms, and can result from fungi being sources of nutrition for bacteria, and vice versa, as well as other stimulatory and inhibitory effects.

Negative Interactions Between Bacteria and Fungi

Some fungi are bacterivores, for example, the cultivated mushroom, *Agaricus bisporus*, utilises bacteria as a major source of nitrogen from the microbe-rich compost on which it is grown. Those fungi that are able to lyse bacteria appear to be attracted to bacterial colonies. On the other hand, some bacteria are mycophages – parasites/pathogens of fungi. Some filamentous *Streptomyces* strains can coil around and penetrate hyphae (e.g. of *Aspergillus niger*) and also parasitize spores of the arbuscular mycorrhizal fungus *Gigaspora gigantea*. Non-filamentous bacteria can also attack hyphae; *Collimonas* strains attack hyphal tips using a combination of chitinases and antibiotics; myxobacteria destroy yeasts and penetrate hyphae of soil fungi, including plant pathogenic *Rhizoctonia* species.

Bacterial parasitism of cultivated mushroom species has been known for almost 100 years. There is a range of mushroom diseases of fruit bodies, but brown blotch disease of *Agaricus bisporus*, caused by *Pseudomonas tolaasii*, has been most studied. The bacterium grows in soil and compost, but can also attack fungal hyphae and fruit bodies. Zones of attack are seen as brownish spots; tolaasin and, to a lesser extent, other secondary metabolites cause membrane disruption which releases nutrients from within fungus cells. A cascade of events follows, resulting ultimately in the production of melanins and quinones that form chemical barriers to protect inner fruit body tissues from becoming infected. Soft rots are another set of fruit body diseases caused by bacteria, with symptoms such as pitting, sticky blotches, and even complete dissolution. Rapid soft rot of the cap and stipe are caused by *Burkholderia gladioli* pv. *agricicola* and *Janthinobacterium agaricidamnosum*, while a *Pantoea* sp. causes a soft rot accompanied by water-soaked lesions in *Pleurotus eryngii*. Mummy disease has very different symptoms (fruit bodies fail to reach maturity but, rather than decomposing, become mummified) but the cause has not yet been verified by fulfilling Koch's postulates, though several *Pseudomonas* species have been implicated. As well as there being a range of pathogenic bacteria, there is also variation in the diseases caused by the same species. *Pseudomonas agaricus* causes: a mild blotch disease of *Agaricus*; yellow blotch disease of *Pleurotus* species, characterised as yellow droplets on the surface of fruit bodies; and dippy gill disease which manifests itself as exudates from longitudinal splits in the stipe where bacteria colonise inter- and intra-cellularly.

There are many examples of bacterial pathogens of fungi seen in agriculture, not least because of the possibility of using these as biocontrol agents of plant pathogenic fungi. *Lysobacter enzymogenes* is pathogenic on a diverse range of fungi as well as on nematodes, bryophytes, and other organisms. Following attachment, it infects its hosts colonising intracellularly, it replicates and is subsequently released. Enzymes produced during pathogenesis include chitinases, β -1,3-glucanases and proteases, which are involved in cell wall degradation. It also employs antibiotics, including a heat-stable antifungal factor, and it uses a type III secretion system (a protein appendage used to secrete proteins into the host) in pathogenesis of some organisms. As well as lytic enzymes and antibiotics, a well-characterised virulence mechanism during bacterial pathogenesis of fungi is the T4 pilus (a filamentous projection that aids in attachment to the host).

Communication has a critical role in pathogenesis, as shown by the pathogenic capabilities of *Pseudomonas aeruginosa* on *Candida albicans*. *Pseudomonas aeruginosa* produces quorum sensing molecules, which prevent *Candida albicans* switching from the yeast to the mycelial phase (p. 167), but it is only pathogenic on the mycelial stage. In the yeast phase, *Candida albicans* can produce its own quorum sensing molecule – farnesol – that self-regulates conversion to the mycelial phase, and prevents *Pseudomonas aeruginosa* from producing its quorum sensing signal quinolone and other virulence factors. The human bacterial pathogen, *Acinetobacter baumannii*, also inhibits *Candida albicans* from forming a mycelial phase, which is an important feature of *Candida albicans* pathogenicity to humans (pp. 306–307).

Clearly, production of lytic enzymes and antibiotics are important pathogenic mechanisms, though they are also employed during transient, non-specific interactions conducted at a distance. Bacteria tend to produce mixtures of antagonistic metabolites rather than single antibiotics, which prevents development of resistance in the target. Some fungi do have defence mechanisms against some antibiotics, and may employ different mechanisms in concert. Such mechanisms

include the ability to detoxify and degrade antibiotics. Transport by membrane bound efflux pumps enables release of toxic compounds from the fungus cell (e.g. *Botrytis cinerea* uses the efflux pump BcAtrB to expel the antifungal compound 2,4-diacetylphloroglucinol (DAPG); *B. cinerea* uses tannic acid as a mediator for DAPG degradation). In contrast, *Fusarium oxysporum* converts DAPG to a less toxic derivative. *Fusarium* species also produce fusaric acid, which inhibits the production of DAPG and other antifungal compounds by bacteria, as well as being toxic to bacteria and eukaryotes. However, the situation becomes yet more complex as some biocontrol bacteria (e.g. *Pseudomonas fluorescens* WCS365) are attracted to fusaric acid-producing *Fusarium oxysporum*, and so colonise the fungus.

Competition between bacteria and fungi for nutritional resources that they both need is another negative interaction. Not only do they compete for simple carbon compounds, but also for products of extracellular digestion of lignocellulolysis. Because they lack the appropriate extracellular enzymes, bacteria are unable to breakdown complex lignocellulose-rich resources, but many fungi can, releasing water-soluble sugars and phenolic compounds that form carbon and energy sources for the fungus (pp. 146–152). Intense bacterial competition for breakdown products could deprive the fungus of these soluble resources. Bactericidal effects have not surprisingly, therefore, evolved widely in fungi, some of which have already been mentioned. Fungi produce many antibacterial compounds – not least penicillin, cephalosporins, and griseofulvin – that are widely used in medicine (pp. 418–421). Other anti-bacterial strategies include extra production of hydroxyl radicals and acidification of the environment. The extremely hydrophobic nature of the mycelium of some fungi (e.g. *Pleurotus* species) can also prevent bacteria from penetrating colonised substrata.

Another widespread negative effect of microbes on fungi is the ubiquitous phenomenon of mycostasis (also called fungistasis), whereby the majority of fungal spores that land on soil fail to germinate. Mycostasis is correlated with microbial activity, and can be alleviated if soil is sterilised and/or easily available energy sources are added. The effect is, thus, probably mediated by soil microbes rapidly sequestering any soluble nutrients that become available in soil and also by the production of inhibitory metabolites. Susceptibility of spores to mycostasis may actually be advantageous to fungi, preventing germination until local microbial activity is reduced and substrates are available.

Positive and Mutualistic Effects

Despite the anti-bacterial effects mentioned above, bacteria are commonly present on the surface of hyphae and spores, including species in the genera *Pseudomonas*, *Burkholderia*, and *Bacillus*, and non-culturable Archaea. Bacterial attachment is regulated by species specificity and fungal vitality, but the molecular and biochemical controlling mechanisms are largely unknown. Organic acids, oxalic acid, and antibiotics may all have a selective role, as do lectins, which have been shown to be produced by truffle (*Tuber*) species and bind *Rhizobium* sp. to them. As well as the negative effects alluded to in the previous section, bacteria can have positive effects on fungi, the most well-known being the so-called mycorrhiza helper bacteria (MHB). Some pseudomonads, bacilli, paenibacilli, and streptomycetes stimulate ectomycorrhiza formation (pp. 215–220). The mechanisms involved include effects on the fungus and on the host plant. The bacteria detoxify antagonistic substances in soil, inhibit competitors/antagonists, and produce growth factors that stimulate spore germination and mycelial growth.

Bacteria associated with fungi can also influence formation of fruit bodies and production of spores. With *Agaricus bisporus*, fruit body initiation depends on the presence of *Pseudomonas putida*, and the latter also promotes mycelial growth and fruit body formation. However, though as humans we may view these responses as beneficial to the fungus, fruiting and increased mycelial extension rate can occur as a result of stress. Though bacteria commonly inhibit spore germination (p. 356), some spore-associated bacteria can stimulate germination, perhaps as a result of volatiles, breakdown of germination-inhibiting compounds and/or by enzymatic weakening of the spore wall.

As in plants, animals, and protists, bacteria are found living within fungal cells (i.e. as endosymbionts). These have been most studied in arbuscular mycorrhizal (AM) fungi. Sequence analysis of the 16S rDNA has shown that the unculturable bacteria-like organisms (BLOs) within *Gigasporaceae* are related to the genus *Burkholderia*. They can occur in groups or singularly, often within vacuoles, in both hyphae and spores. Loss of these bacteria severely affects hyphal elongation and branching. Endobacteria of other fungi also have major effects on their host: *Rhizopus microsporus*, a fungal pathogen of rice, owes its pathogenicity to an endosymbiotic *Burkholderia* strain. In contrast, a biocontrol strain of *Fusarium* becomes pathogenic when its endosymbionts are removed.

The fungus cell wall is a physical barrier that largely prevents entry of bacteria. The wall is, however, not rigid at the hyphal tip (p. 37) and bacterial acquisition could take place there. *Geosiphon pyriforme* (Glomeromycota) incorporates primordia of free-living *Nostoc* (cyanobacteria) at the hyphal tips, which then swell to form bladders containing *Nostoc* cells that photosynthesise. *Burkholderia* sp. can invade germinating AM spores via weakened fungal germ tubes (e.g. by bacterial lytic enzymes). Acquisition of the endosymbionts by *Gigasporaceae*, however, appears to have been a unique event that occurred in an ancestral fungus; the bacteria are now spread vertically through generations, and are probably obligate endosymbionts.

Fungal-bacterial interactions can have positive effects on bacteria, in addition to the nutritional effects previously mentioned. As single cells that can only move in water films, bacterial movement across air gaps in soil is extremely difficult. This is not a problem for fungal hyphae, and some bacteria use hyphae to 'hitchhike' through soil (e.g. species of *Burkholderia*, *Dyella*, and *Ralstonia* on a *Lyophyllum* sp.). It is not that bacteria simply attach to a hyphal wall and move through soil as a hypha grows; because hyphae grow from the tips, the bacteria must move actively along the hyphae as they grow, and probably do so in a biofilm on the surface of hyphae.

VIRUSES OF FUNGI

Viruses are widespread in fungi in all phyla, though the host range of a virus type is very narrow, and frequency of infection within a species is variable, but sometimes over 80%. They were first discovered in the early 1960s, as the cause of La France disease, which causes malformed fruit bodies of the cultivated mushroom *Agaricus bisporus*. Soon after, they were found to be responsible for the production of interferon in the culture filtrates of some *Penicillium* species. Though mycoviruses have been relatively little studied, they occur in fungi that feed in all ways, including saprotrophs, plant and animal pathogens, endophytes, mycorrhizal fungi, and lichens. Most mycoviruses are spherical, have double-stranded RNA

(dsRNA) genomes with isometric particles, 25–50 nm diameter, and are found in three families, based on the number of genome segments – *Chrysoviridae*, *Partitiviridae*, and *Totiviridae*. Mycoreoviruses (family *Reoviridae*), however, have double-shelled particles, 80 nm diameter. Fungi do not usually contain large molecules of dsRNA, so presence of the latter is a sign of viral infection.

Mycoviruses are intracellular within the fungus, are transmitted between hosts by cell-to-cell contact/fusion, and can be disseminated within spores. No natural vectors are known. Transmission within a species is often restricted by vegetative incompatibility (pp. 102–104). Transmission between species is even less common, though phylogenetic analyses have revealed that it does occur. Also, infection experiments show that transmission between species can occur within genera (e.g. *Aspergillus*, *Cryphonectria*, and *Heterobasidion*). There has probably also been horizontal transfer between plants and plant pathogenic fungi, since Partitiviruses that infect fungi and plants are closely related taxonomically. Also, there are some homologs of partitivirus and totivirus genes in some plants and fungi. To be a true mycovirus, infection between fungi must occur; so, as many dsRNA elements are not transmissible, they are referred to as virus-like particles.

Most viruses cause few or no obvious symptoms, but sometimes effects are severe, and both beneficial and adverse effects have been reported. In plant pathogenic fungi, some mycoviruses lead to increased fungal virulence (hypervirulence) and some to decreased virulence (hypovirulence), including in *Cryphonectria parasitica* (cause of chestnut blight), *Botrytis cinerea*, *Helminthosporium victoriae* and *Sclerotinia sclerotiorum*. The hypovirus CHV1 is now used successfully to control chestnut blight. Viruses have effects other than on virulence. In a three-way symbiosis, the presence of the virus CThTV in *Curvularia protuberata* endophytic within a tropical grass (*Dichanthelium lanuginosum*) allows the plant and fungus within to grow at the high soil temperatures found in Yellowstone National Park. Single virus strains can sometimes have different effects on different species of fungi, and different effects on the same species in different situations. For example, virus HetRV3-ec1 increases, decreases or has no effect on the competitive ability of various species of *Heterobasidion* against other fungi.

INTERACTIONS BETWEEN FUNGI AND PROTISTS

Protists and fungi are likely to encounter each other often in soil, aquatic ecosystems and in the guts of ruminants, but interactions between them have received little attention. There is certainly evidence of protists feeding on fungi. Some testate amoebae (e.g. *Geococcus vulgaris*), fasten to the walls of fungal spores and hyphae and suck out the contents. There is also evidence that protists may reduce ectomycorrhizal colonisation of roots and reduce the amount of mycorrhizal mycelium in the mycorrhizosphere. Considerable interactions between fungi and protists occurs in the rumen (pp. 329–330) – ciliate protozoa ingest Neocallimastigomycota zoospores, and their predatory activity can reduce overall cellulolytic activity and alter the fermentation products formed.

Plasmodia of myxomycetes have been shown to consume fungi in lab culture, the susceptibility of the latter varying between species of myxomycetes and fungi. Plasmodia will feed on mycelia mats that emerge from wood under moist conditions, and on resupinate fungal fruit

bodies. The fungi in decay columns extending for many centimetres through wood can be completely devoured by plasmodia. For example, *Badhamia utricularis* has been seen to consume the ascomycete *Xylaria hypoxylon*, and *Comatricha nigra* consumes the basidiomycete *Stereum hirsutum*. Myxomycetes can be prevalent in wood; in one study myxoflagellates emerged from about 50% of fallen dead angiosperm branches sampled, having been active vegetatively or having emerged rapidly from microcysts; *Stemonitis fusca* was particularly common.

The tables are turned, however, by *Dactylella passalopaga*, amongst others, which produces bulbous outgrowths which trap testate amoeba. Several Zoopagales (zygomycete) adhere to amoeba and feed on them. Also, some isolates of *Heteroonium chaetospira* (a dark septate root endophyte; pp. 238–239) can control clubroot disease of Brassicaceae, caused by the soil-borne protozoan *Plasmodiophora brassicae*. The fungus infects root epidermal cells, but the mechanism of disease control is unclear.

Some fungi colonise the fruit bodies of myxomycetes. Hyphae penetrate the spore masses and kill the spores. Other fungi (e.g. the ascomycete *Gliocladium album*), parasitize the calcium-rich fruit bodies of the Physarales; *Nectriopsis violacea* is even more specific, only colonising species of *Fuligo*. Others are specific to non-calcareous myxomycetes, yet others colonise a wide host range, *Nectria exigua* being recorded on all of the major myxomycete groups. In lab culture on agar, the hemiascomycete yeast, *Dipodascus utricularis*, is able to live in the slime trail of *Badhamia utricularis*. If the yeast is ingested it is not digested and lives parasitically, multiplying within the myxomycete plasmodium.

From a medical mycology viewpoint, interactions between amoebae and fungi which are saprotrophic in the natural environment, but which can cause systemic infection in humans (pp. 303–309) and other mammals, are of particular interest. The yeast form of the pathogens *Blastomyces dermatidis*, *Cryptococcus neoformans*, *Histoplasma capsulatum*, and *Sporothrix schenckii* are ingested by amoebae, but inhibit amoebal growth or kill them. Outcomes of interactions, however, vary depending on the combination of species interacting. For example, growth of *Candida albicans* is enhanced by the amoeba *Hartmannella vermiformis* but killed by *Acanthamoeba castellanii*. Similarly, spores of *Aspergillus fumigatus* (p. 306) are ingested by amoebae; the spores can germinate within the cytoplasm and the fungus is released to the environment. These interactions between amoebae and yeasts and spores are similar to those with human macrophages, and the interaction of these saprotrophic fungi with amoebae in the natural environment over evolutionary time has been described as a ‘training ground’ for overcoming the macrophage defences of vertebrates.

Further Reading

General Text

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