H2.4. Biology and ecology of mycoparasitism

Peter Jeffries

Abstract: The term mycoparasitism applies strictly to those relationships in which one living fungus acts as a nutrient source for another, but fungicolous relationships may also be included in which nutrient exchange has not been shown. Fungicolous fungi have a constant but indeterminate association with another fungus, and it can be difficult to demonstrate a true parasitic relationship. Mycoparasitic relationships can be necrotrophic or biotrophic, and can be classified on the basis of the host—parasite interface as contact necrotrophs, invasive necrotrophs, haustorial biotrophs, intracellular biotrophs, or fusion biotrophs depending on the intimacy of the relationship. In natural ecosystems, it is proposed that mycoparasitic relationships play an important role in the development of fungal communities. Two specific examples have been chosen to illustrate the general principles of mycoparasitism: the necrotrophic invasion of spores of arbuscular mycorrhizal fungi and the biotrophic invasion of mucoralean hosts by haustorial mycoparasites.

Key words: mycoparasitism, fungicolous fungi, arbuscular mycorrhizal fungi, fungal ecology.

Résumé : Le terme de mycoparasitisme s'applique strictement aux relations dans lesquelles un champignon vivant sert de source de nourriture pour un autre, mais des relations fongicoles peuvent également être incluses dans lesquelles l'échange de nutriments n'a pas été démontré. Les champignons fongicoles montrent une association constante mais indéterminée avec un autre champignon, et il peut être difficile de démontrer une réelle relation parasitaire. Les relations mycoparasitaires peuvent être nécrotrophes ou biotrophes, et peuvent être classifiées sur la base de l'interface hôte—parasite comme nécrotrophes de contact, nécrotrophes avec envahissement, biotrophes avec haustéries, biotrophes intracellulaires ou biotrophe par fusion, selon l'intimité de la relation. Dans les écosystèmes naturels, l'auteur propose que les relations mycoparasites jouent un rôle important dans le développement des communautés fongiques. Il a choisi deux exemples spécifiques pour illustrer les principes généraux du mycoparasitisme: l'invasion nécrotrophe de spores de champignons arbusculaires et l'invasion biotrophe des hôtes mucoraléens par des mycoparasites à haustéries.

Mots clés : mycoparasitismes, champignons fongicoles, champignons mycorhiziens à arbuscules, écologie fongique.
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Introduction

There are many ways in which fungi can interact with each other such that the behaviour of one affects the development of another. When the interaction is competitive and results in one fungus gaining nutrients from another, the relationship is known as mycoparasitism, a term introduced by Butler (1954) to describe the relationship when one fungus parasitizes another. At one extreme, the host remains alive and the mycoparasitic fungus obtains nutrients from within the mycelium of its partner in a stable and balanced relationship termed biotrophic mycoparasitism. In contrast, necrotrophic mycoparasitism results in the death of the host, and the mycoparasite then preferentially utilizes the dead remains of the host as a nutrient source. In many cases, nutrient transfer via the mycoparasitic interface has not been demonstrated, but parasitism is assumed from morphological or physiological observations. In the strict sense a fungus should be consid-

ered as a mycoparasite only if it has been proved to obtain all or part of its nutrients from another fungus, thereby being detrimental to it. This proof, however, is often difficult to obtain and many quoted examples of mycoparasitism are presumptive (sensu Mulligan and Deacon 1992). The demonstration of phosphorus transfer from Rhizoctonia solani to the mycoparasite Arthrobotrys oligospora (Olsson and Persson 1994) is an exception and further work of this nature should be encouraged. Where relationships are relatively loose and two fungi often seem to grow as closely associated mycelia although no evidence for mycoparasitism is presented, the partners can be described as fungicolous (Hawksworth 1981). Fungicolous fungi are widespread, and there are numerous fungi that are obligately found in nature associated with the mycelium or sporomes of other fungi and that may be parasitic or commensal (for a more detailed discussion of these relationships see Jeffries and Young 1994). Although there is an immense number of fungi known to grow on other fungi, especially amongst the foliicolous tropical species, no overall estimate of the total exists. Hawksworth (1981) considered that there were not less than 1200 conidial fungi occurring on other fungi and perhaps 2000 fungi of all groups growing only on lichens (lichenicolous

Table 1. Some parasites of
R. solani (modified from
Jeffries and Young 1994).

Arthrobotrys oligospora
Botryotrichum piluliferum
Coniothyrium sporulosum
Dicyma olivacea
Gliocladium catenulatum
Gliocladium roseum
Gliocladium virens
Hormiactis fimicola
Laetisaria arvalis
Papulaspora stoveri
Penicillium vermiculatum
Pythium oligandrum
Stachybotrys chartarum
Stachybotrys elegans
Stachylidium bicolor
Talaromyces flavus
Trichoderma hamatum
Trichoderma harzianum
Trichoderma longibrachiatum
Trichoderma pseudokoningii
Trichoderma viride
Trichothecium roseum
Verticillium biguttatum
Verticillium chlamydosporium
Verticillium lamellicola
Verticillium lecanii
Verticillium nigrescens
Verticillium psalliotae
Verticillium tenerum
Volutella ciliata

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fungi). What is known, however, is that one species of fungus can act as host to several mycoparasites and *Rhizoctonia solani*, for example has been reported as a host of many (Table 1).

Antagonistic interactions of fungi can be mediated either by direct contact or at a distance. The former involves direct physical contact between the two organisms, while the latter refers to those instances in which one fungus releases materials such as antibiotics and lytic enzymes into the environment that induce a negative effect on the other. The boundary between indirect parasitism and competitive interactions involving primary resource capture can be very difficult to define, as parasitic individuals can benefit from the increased availability or release of nutrients consequent upon their activities and thus alleviate competition for primary nutrients. Some necrotrophic fungal parasites, such as *Trichoderma harzianum* and *Gliocladium virens*, are also able to grow well as saprotrophic competitors of other fungi, and the relative contributions of mycoparasitism and interference competition to this success can be difficult to distinguish. This is exacerbated by the fact that the antagonistic ability of a fungus can also be determined partly by its physiological state, so that changes in physiochemical or nutritional conditions associated with resource utilization will affect the outcome of interaction of combatants (Rayner

and Webber 1984). In this review emphasis will be placed on those relationships in which direct contact between partners occurs, and where clear morphological evidence of host invasion is evident.

The significance of mycoparasitism in the natural environment is certainly underrated, possibly because of the difficulties in making field observations, and interfungal parasitic relationships are likely to play an important role in the development of community structure. It is often difficult to obtain clear microscopical evidence of any fungal activity in soils, regardless of whether those fungi are mycoparasitic. Mycoparasitic relationships can sometimes be inferred in natural substrates when the mycoparasites cause distinctive growth abnormalities in the hyphae of the host, especially when such morphological alterations have also been noted in samples obtained directly from the field. Hyphal swellings in *Rhizopus oryzae* have been used in this way to infer mycoparasitic activity of the necrotrophic mycoparasite *Syncephalis californica* in both naturally and artificially infested agricultural soils (Hunter et al. 1977). Such cases are exceptional, however, and most mycoparasitic associations have only been demonstrated in the laboratory, usually after isolation of the host and parasite from the substratum on which they were growing. For this reason, the observations made on *S. californica* provide some of the most convincing evidence for the natural occurrence of mycoparasitism.

New experimental approaches are needed to study the phenomenon; for example, the development of precolonized plate techniques to isolate presumptive mycoparasites has demonstrated the widespread occurrence of several of these fungi in British soils (Mulligan and Deacon 1992). Using a range of bait fungi, these authors detected *Pythium oligandrum*, *Gliocladium roseum*, *Trichoderma* spp., and a *Papulaspora* sp. in 18, 28, 24, and 21, respectively, of a total of 28 soils. In contrast to the status of field observations, there are many examples where mycoparasitism has been described from laboratory investigations. The unequivocal demonstration of a mycoparasitic association under laboratory conditions, however, cannot be taken as proof that a similar parasitic relationship occurs in the field. Such studies are often carried out in pure mixed culture under favourable environmental conditions and nutrient excess. Under field conditions the situation will be very different and microbial competition and nutrient limitation will place a premium on those attributes that give an advantage in antagonistic interactions. Characteristics that enhance the ability of a fungus to compete for carbon and nitrogen sources or help the fungus to withstand the antagonistic behaviour of other fungi will increase the share of primary or secondary resources available to that fungus. In this respect, the ability to antagonize and utilize other fungi as nutrients must be a powerful attribute, and thus it is likely that mycoparasitism occurs more widely than is currently appreciated. It is difficult, however, to make field observations of mycoparasitism in situ, but there are examples where the significance of mycoparasitism can be gauged from observations of field-collected material. Necrotrophic mycoparasitism of the spores of arbuscular mycorrhizal fungi (AMF) offers a good example and some recent observations will be considered in more detail later. Other results concerning haustorial mycoparasites will also be discussed. Our inability to grow these

Table 2. Types of mycoparasite and the respective host—parasite interface.

Type of relationship	Host—parasite interface
Contact necrotroph	Fungi in contact; no penetration of host mycelium by parasitic hyphae; cytoplasm of the host degenerates and hyphal lysis may occur
Invasive necrotroph	Fungi in contact; hyphae of the parasite penetrate and enter the host; degeneration of host cytoplasm occurs rapidly, often followed by hyphal lysis
Intracellular biotroph	Complete thallus of mycoparasite enters the hypha of the host; cytoplasm of the host remains healthy
Haustorial biotroph	Hypha of the host is penetrated by a short haustorial branch from the hypha of the parasite; host cytoplasm remains healthy
Fusion biotroph	Fungi in close contact; micropore(s) develop between the adpressed hyphae, or from a short penetrative hyphal branch of the parasite; host cytoplasm remains healthy

obligate mycoparasites axenically is taken as unequivocal evidence that they exist in nature in the parasitic form. Before describing these examples, however, it is necessary to describe the range of types of mycoparasite and to outline the main mechanisms of mycoparasitism.

Types of mycoparasites

Interfungal relationships can be split into a number of categories. Firstly, there are the intraspecific interactions that involve mycelia from within a single species. These can have a sexual basis and are essential for plasmogamy and karyogamy as part of the sexual reproductive cycle. Alternatively, they may involve asexual or vegetative interactions of mycelia, which can determine individuality amongst mycelia and can regulate the degree of anastomosis and heterokaryosis within a hyphal network. Finally, intraspecific interactions can involve competition between different individual mycelia within a species resulting in antagonism at the contact zone between opposed mycelia. In extreme cases, destruction of one mycelium by the other can result in the transfer of nutrients, and hence, mycoparasitism can occur during these intraspecific interactions.

Interspecific fungal relationships, on the other hand, are much more widely documented, as neutralistic, mutualistic or as competitive interactions (Cooke and Rayner 1984). Competitive interactions are detrimental to one or both fungi and involve antagonism mediated at a distance or on contact of the respective mycelia. Many such interactions result in the capture of nutrients by the most aggressive fungus from the other. The aggressor is, therefore, acting as a mycoparasite in the broad sense of the term. Problems of terminology can arise, however, particularly when the parasitic relationship is loose or when nutrient transfer is not implicit. As mentioned earlier, the use of the term fungicolous fungi overcomes this difficulty and embraces the broad range of associations of two fungi found living together even when the biological nature of the association is obscure. Barnett and Binder (1973) realized that true mycoparasites could be divided into two very distinct groups, the necrotrophs and the biotrophs, as was common for phytopathogenic fungi. Necrotrophic or destructive mycoparasites kill their hosts as a result of their parasitic activity, while biotrophic mycoparasites obtain their nutrients directly from the living mycelium of their hosts.

In necrotrophic relationships the antagonistic action of the mycoparasites is strongly aggressive and the mycoparasite dominates the association. Hyphae of the parasite contact and grow in association with those of the host, sometimes coiling around them and frequently penetrating. Secretion of hyphal wall degrading enzymes or exotoxins may cause the death of the cytoplasm of the host prior to hyphal contact, or alternatively, cytoplasmic death may not occur until after contact has been established. Necrotrophic mycoparasites tend to have a broad range of host fungi and are relatively unspecialized in their mechanism of parasitism. For example, they often release toxins and lytic enzymes into the environment, are overtly destructive, and usually lack specialized infection structures. In this way their behaviour parallels that of the necrotrophic fungi that parasitize plants.

In a biotrophic mycoparasitic relationship, the living host supports the growth of the parasite for an extended period of time and may not appear diseased, and its growth rate, sporulation, and metabolism may appear overtly to be little affected, at least in the early stages of the relationship. The parasitic relationship is physiologically balanced and the parasite appears to be highly adapted to this mode of life. Biotrophic mycoparasites tend to have more restricted host ranges than necrotrophs and often form specialized infection structures or host—parasite interfaces. Exotoxin production has not been demonstrated in any biotrophic mycoparasitic interaction. Although it is convenient to group mycoparasitic relationships on the basis of their physiology into necrotrophic and biotrophic categories, it is apparent that there several further groupings of mycoparasites based on the structure of the host—parasite interface.

Host—parasite interfaces

Host—parasite interfaces during mycoparasitism have recently been reviewed (Jeffries and Young 1994) and a new scheme of nomenclature proposed (Table 2). In necrotrophic relationships there preferably needs to be direct contact between partners so that a channel for nutrient exchange is established that is not easily accessible to competing microorganisms. In the simplest examples, nutrient transfer takes place through the hyphal wall of an antagonist where it is attached to that of its partner fungus. These are the contact necrotrophs and are distinctive in that penetration of the mycelium of the host has not been recorded. The hyphae of

Table 3. Examples of invasive necrotrophs.

Structure	Parasite	Host attacked
Hyphae	*Nectria inventa*	*Alternaria brassicae*
	Pythium acanthicum	*Phycomyces blakesleeanus*
	Rhizoctonia solani	Mucorales
	Syncephalis californicus	*Rhizopus oryzae*
Sclerotia	*Coniothyrium minitans*	*Sclerotinia sclerotiorum*
	Talaromyces flavus	*Sclerotinia sclerotiorum*
Spores	*Cladosporium uredinicola*	*Puccinia violae* (uredospores)
	Eudarluca filum	*Puccinia graminis* (uredospores)
	Fusarium merismoides	*Pythium ultimum* (oospores)
	Humicola fuscoatra	*Phytophthora megasperma* (oospores)
	Mycogone perniciosa	*Rhopalomyces elegans* (conidia)
	Nectria inventa	*Alternaria brassicae* (conidia)

the two fungi often grow in close contact; those of the aggressor may coil around those of the host, in which destructive effects are usually observed prior to eventual breakdown and lysis. In the second type of necrotrophic relationship, direct penetration of one fungus by another occurs, accompanied almost immediately by the degeneration and death of the invaded cytoplasm. This has been called invasive necrotrophy and it is widespread in nature. Often, however, nutrient uptake has not been proven and such examples may represent an aggressive form of antagonism that does not involve one fungus obtaining nutrients directly from the mycelium of another.

Biotrophic relationships, in sharp contrast, involve the formation of stable interfaces between partners. These range from the complex multilamellate barriers between the haustorial mycoparasites and their hosts through to the absolute fusion of the protoplasts of the partner fungi. Broadly speaking the interfaces can be categorized into three groups based on the infection structures that are formed. First, there are those in which the entire thallus of the parasite enters the hyphae of the host fungus. These are the intracellular biotrophs and include chytridiaceous and oomycete organisms. Many of the aquatic mycoparasitic Chytridiomycota, for example, penetrate their host and discharge the complete protoplast into the cytoplasm of the host where it remains viable and presumably absorbs nutrients directly through the host–parasite interface. In the other two groups most of the thallus of the parasite remains external to the host. In the haustorial biotrophs, specialized hyphae form during the interaction. An appressorium develops once the parasite contacts the host, and a narrow infection peg develops and penetrates the hypha below. Once the peg has breached the wall it grows into a lobed haustorium that invaginates the plasmalemma of the host so establishing the mature host–parasite interface. Nutrients are presumed to be absorbed from the cytoplasm of the host via the haustorium. The third interface type found in biotrophic relationships is very unusual and involves the formation of channels of direct contact between closely appressed partner hyphae. Specialized hyphae or buffer cells are formed that contact the hyphae of the host but do not penetrate them. These contact elements serve as the interface for transfer of nutrients from the cytoplasm of the host to that of the parasite. Electron microscope

studies of the interface have shown that the plasmalemma of the host and that of the parasite come into direct contact in the buffer zone and fuse; thus, the cytoplasm of the parasite becomes contiguous with that of the host. Mycoparasites with this form of symbiotic interface are the fusion biotrophs, a term which emphasizes this extraordinary phenomenon. Barnett (1963) had previously termed these the contact biotrophs, but the term fusion biotroph stresses the intimate nature of the interface more strongly. A number of tremellaceous mycoparasites, previously thought to form typical haustorial interfaces, are now known to form micropores connecting the cytoplasm of the haustorium and that of the host cell (Zugmaier et al. 1994), thus demonstrating a more widespread occurrence.

Ecology of mycoparasitism

As discussed earlier, the evidence of mycoparasitic activities in the field is limited. Most refers to the occurrence of invasive necrotrophs within host structures extracted from natural environments. Some invasive necrotrophs invade any of the host structures that they encounter, but most are specialized and colonize vegetative hyphae, sclerotia, or spores of their respective hosts. Examples of each are given in Table 3. Because of the ease with which certain large fungal spores can be sieved from soils, there is now an extensive literature on the presumptive mycoparasites found within these structures. Mycoparasitism of fossil spores has also been observed and taken as evidence that this phenomenon was established early in the evolution of the terrestrial biota (Hass et al. 1994). To illustrate ecological aspects of mycoparasitism, two examples have been chosen: (*i*) necrotrophic mycoparasites of spores of AMF and (*ii*) the biotrophic haustorial mycoparasites.

Mycoparasitism of spores of AMF

The invasion of spores of AMF has been taken here as a typical example of necrotrophic mycoparasitism that can influence population dynamics of fungal communities in the field. For example, parasitism of spores of AMF by Chytridiales is probably a widespread phenomenon and may limit the populations of mycorrhizal fungi in wet soils (Sylvia and Schenck 1983). In contrast, some mycoparasitic fungi appar-

ently do not affect the natural mycorrhizal populations. For example, a lack of antagonism has been reported between *Gliocladium virens* and AMF (Paulitz and Linderman 1991). This is particularly significant because *G. virens* is a potential biocontrol agent that has already received approval for use in commercial agriculture.

The colonization of the roots of plants by AMF represents one of the most interesting obligate associations of fungi with higher plants. This dual association of plant roots and certain soil fungi is ubiquitous in natural ecosystems and responsible for the nutritional well-being of many plants. The fungi involved are related to the Zygomycetes and include the genera *Acaulospora*, *Glomus*, *Gigaspora*, *Scutellospora*, and *Sclerocystis*. They are grouped in the Glomales, on the basis of vegetative and reproductive morphology, but this may constitute an order of taxonomically heterogeneous fungi. Whatever their taxonomic affinities, they are certainly an ancient group of fungi and recent molecular analysis indicates that *Glomus* may have evolved around 400–450 million years ago, prior to the emergence of most higher plant families (Berbee and Taylor 1993; Simon et al. 1993). The presence of endobiotic chytridlike structures on *Glomus*-like spores from the Lower Devonian Rhynie chert (400 million years old), along with the observation of papillae and fine radial invasion channels in their walls (Hass et al. 1994), indicates that mycoparasitism has coevolved with these organisms.

Extensive evidence from pot trials and field work shows that AMF are beneficial to the development of the plant principally by improving phosphorus uptake in nutrient-poor soils. The fungus benefits from such an association by obtaining organic carbon substrates from the plant, and as most angiosperm plants have arbuscular mycorrhizal associations, the implications for agriculture and forestry are enormous (Jeffries 1987). The spores of some AMF are the largest known within the fungal kingdom and they can easily be extracted from field soils by a simple wet-sieving procedure. In any sample of extracted spores there is usually a proportion, often the majority, that appear to be parasitized. Examination of individual spores shows that the wall may be perforated by many fine radial canals. These are extremely common in field-collected spores and have been described many times previously. For example, they were well illustrated in *Glomus microcarpum* by Malençon (1930). In some of the early original descriptions of spores of these fungi the papillae and penetration canals have been recorded as morphological features of the spores themselves. The canals are usually said to arise through penetration of the wall by the hyphae of mycoparasitic fungi and, indeed, hyphae are occasionally seen to penetrate the canals. In some cases, however, it has been suggested that amoebalike organisms could also be responsible (Boyetchko and Tewari 1991), especially when no bacteria or fungi can be seen inside the perforated spores. The radial canals in the wall of the spores are often associated with ingrowths on the inner surface of the spore wall that are reminiscent of the papillae induced by the penetration pegs of *Piptocephalis* species on mucoralean hosts (Jeffries and Young 1978). The ingrowths are synthesized as an invading hypha penetrates the spore wall, indicating that the spore must have been alive at the time of attack. There are few data that record the relative proportions of parasitized to intact spores in field soils, but it is likely that a large number of these spores are attacked. For example, during an assessment of the arbuscular mycorrhizal status of various crops in different agricultural soils of northern Greece, AMF were found to be associated with most crops (Jeffries et al. 1988). Spore types, number, and distribution were also determined and it was found that a consistent feature of all soils was the presence of large numbers of empty spores (ghosts), which usually outnumbered intact spores by a factor of one to five. The ghosts were always perforated by fine radial canals, often with associated papillae, and this was taken to indicate attack by other soil fungi.

Several zoosporic fungi are able to attack the spores of members of the Glomales and either sporulate within the spores themselves or on the outer surface. Indeed, the most frequently observed propagules within spores of AMF are members of the Oomycota, including *Spizellomyces* and *Pythium*-like fungi (Boyetchko and Tewari 1991), but this observation may reflect the ease by which these structures can be recognized. The colonization of these spores in this manner may enhance the survival and dispersal of the mycoparasites in a way analogous to that suggested for *Verticillium psalliotae* infecting *Rhopalomyces elegans* (Dayal and Barron 1970). Other nonsporulating fungi may also be common inside the spores but may not be recognized without culturing. Mycoparasites can be easily isolated from the spores of AMF and appear to be facultative, with some degree of saprotrophic ability and not dependent on the presence of the spores for survival (Paulitz and Menge 1986). An extensive study of mycoparasitism of spores of *Gigaspora gigantea* was reported by Lee and Koske (1994). Fungi and actinomycetes were isolated monthly from spores of this fungus recovered from a maritime sand dune. From 272 isolates cultured from crushed, surface-disinfected spores of *G. gigantea*, 44 species of fungi were recorded. The five most frequently isolated organisms were *Acremonium* sp., *Chrysosporium parvum*, *Exophiala werneckii*, *Trichoderma* sp., and *Verticillium* sp. Thirty-one of these isolates were tested for their ability to parasitize healthy spores of *G. gigantea* in vitro or to invade dead spores killed by hot water treatment. Twenty-two species were able to invade the spores, forming fine radial canals with or without associated papillae. Papillae were not formed during penetration of heat-killed spores. Mycoparasitic species were more frequently isolated from healthy spores, while species originally isolated from dead or dying spores from the field (e.g., *Fusarium* sp., *Gliomastix* sp., *Mortierella ramanniana*) were typically not pathogenic. These results indicated the importance of mycoparasitism in the natural decline of spore abundance of *G. gigantea* in sand dunes during spring and summer (Lee and Koske 1994). Older spores of AMF appear to be more susceptible to mycoparasitism, which may relate to a decreased ability to resist invasion. It has also been suggested that the degree of melanization of the wall of the spore can influence its resistance to mycoparasitism (Daniels and Menge 1980). *Glomus macrocarpum*, for example, was observed to be more susceptible to parasitism than the darker-coloured *Gigaspora gigantea* (Ross and Ruttencutter 1977). In contrast, a white-spored species of *Gigaspora*, *G. candida*, appeared to be very susceptible to parasitism (Bhattacharjee et al. 1982). Several other examples have been reported; for

example, the hyphae of mycoparasitic fungi such as *Humicola fuscoatra* and *Anguillospora pseudolongissima* have been detected within and isolated from the spores of *Glomus fasciculatum* and *G. versiforme* grown in glasshouse pot culture (Daniels and Menge 1980). A high percentage of these spores were determined to be infected by inoculation on tapwater agar or became so when placed in sterile sand containing these mycoparasites.

Some of the observations of spores described as being parasitized do not indicate whether the spores were viable or dead when attacked. In the absence of papillae, this is not always clear. *Spizellomyces punctatum* has been shown to invade nonviable spores of *Gigaspora margarita* (Paulitz and Menge 1984) and it was suggested that this invader is primarily a saprotroph that attacks dead spores. This evidence suggests that some previous reports of *Phlyctochytrium* species as mycoparasites of spores may need reinterpretation. For example, treatment of agricultural soil used for growing peanuts and soybeans with the fumigant methyl bromide resulted in the enhanced development of *G. macrocarpum* in the roots and the soil during the growing season (Ross and Ruttencutter 1977). During the following season, however, a decline in the population of *G. macrocarpum* chlamydospores appeared to be correlated with an increase in mycoparasitism by *Phlyctochytrium*. It is not clear whether this reflects an increase in necromass of the AMF that provided a suitable substrate for *Phlyctochytrium*, on whether the chytrid was directly responsible for the decline of the *Glomus*. Another chytridiaceous fungus occasionally observed associated with the spores of *Glomus* is *Rhizidiomycopsis stomatosa* reported as a parasite of *G. versiforme*. More detailed information is available for the antagonism of spores of *Gigaspora margarita* by *Stachybotrys chartarum* (Siqueira et al. 1984). This fungus was found as a frequent contaminant of pot cultures of inoculum of this fungus. *Stachybotrys chartarum* colonizes the spores and produces conidiophores over the surface. Sometimes, hyphae were seen to penetrate the host spore, but it is not known if only dead spores were penetrated.

The population dynamics of an AMF in a natural soil has been studied by Paulitz and Menge (1986), who investigated the effects of *Anguillospora pseudolongissima* parasitizing spores of *Glomus deserticola*. *Glomus deserticola* was associated with the roots of onion plants and was responsible for improved growth of the crop especially in soil in which the availability of phosphorus was low. A preparation of soil, pieces of root, and spores was chopped and air-dried for 7 days prior to incubation with the mycoparasite to kill the hyphae and leave the spores as the main source of the inoculum. Dilutions of the inoculum were mixed with various dilutions of the mycoparasite in sandy loam planted with onion seeds and the plants were harvested from 40 to 100 days later. The results showed that the primary effect of *A. pseudolongissima* was to reduce the number of effective propagules of *Glomus* resulting in a delay and reduced incidence of root colonization. At low propagule densities, *A. pseudolongissima* was responsible for reducing (by up to 50%) the effective propagule density to the point at which colonization of host plants no longer occurred. The mycoparasitic activity thus indirectly affects the crop yield as the timing of colonization of the roots by the fungus is delayed,

the rate of colonization is reduced, and fewer plants are colonized, which results in an overall reduction in the dry weight of the plants. These effects are most marked when the effective propagule density of the mycorrhizal symbiont in soil is low, for example, under conditions of anaerobiosis or after a fumigation treatment, when the inoculum density of the mycopathogen is high, and when the soil is deficient in available phosphorus. Phosphorus-deficient soils are likely to occur where significant leaching or binding of this element takes place as in the acid-infertile soils of the tropics, and it is not suprising that most of the benefits of mycorrhizal inoculation have been realized in these situations. A thorough study of the significance of mycoparasitism in such ecosystems would be appreciated by exponents of low-input sustainable agriculture, as a buildup of a mycoparasitic community might have detrimental effects on the use of mycorrhizal technology to improve crop yields.

Biotrophic haustorial mycoparasites
The highly specialized nature of the biotrophic haustorial mycoparasites, coupled with the difficulty encountered in inducing them to grow in the laboratory in the absence of the host, leaves little doubt that they normally grow as parasites in nature. Where the parasite can be observed growing together with the host on the natural substratum, (e.g., species of *Piptocephalis* and *Dimargaris* on living mucoralean hosts on the dung of herbivorous animals), the natural parasitic relationship seems clear. *Piptocephalis* species are also extremely common in many soils and can be readily isolated providing a suitable baiting technique is employed (Jeffries and Kirk 1976), but owing to their biotrophic nature it is often concluded that they do not have any marked effects on the population ecology of their host communities. Richardson and Leadbeater (1972) reported that this genus could be frequently isolated from litter and A horizon soil samples, especially from woodland and pasture habitats. It has been suggested that the occurrence of *Piptocephalis* on dung samples is not the result of the suitability of dung as a habitat for the parasite, but a combination of the ability of dung to support a rich mucorine flora and the invasion of already-established *Piptocephalis* from the underlying soil and litter (Richardson and Leadbeater 1972).

Conclusion

In summary, these two examples are clear evidence of the frequent occurrence of mycoparasitic relationships in nature. In some cases, as the former example has illustrated, necrotrophic associations can have far-reaching effects. In contrast, biotrophic relationships and fungicolous associations may be common but by their very nature are assumed not to affect the behaviour of other hosts in any drastic manner. Perhaps because of this the phenomenon of mycoparasitism has sometimes been regarded as a curiosity by some biologists and its significance thus underrated. We badly need further studies on the ecology of mycoparasitism that are not solely geared to their exploitation as biocontrol agents of plant pathogens. For example, in a competitive situation, does biotrophic mycoparasitism really not affect the host fungus to any major degree? In the case of some of the biotrophic mycoparasites of rust pustules it is clearly evident

that the population ecology of the host fungi is affected through a decreased level of sporulation. When nutrient resources are limited, even a small drain to a mycoparasitic fungus might be of great significance in reducing the ecological fitness of the host. Differential labelling techniques such as those described by Olsson and Persson (1994) offer an opportunity to quantify nutrient fluxes in vitro, while dual culture studies using a substrate normally unavailable to the mycoparasite can be used to demonstrate the creation of a nutrient sink by the mycoparasite (van den Boogert and Deacon 1994). Further studies using these techniques are required. There is also the possibility that relationships that involve the fusion biotrophs may also allow the transfer of genetic material as well as nutrients between the interacting fungi. Pararecombinants has recently been suggested (Kellner et al. 1993) as a term to describe recombinant intergeneric chimeras that are generated as a consequence of mycoparasitism. This natural gene transfer mechanism might have an important evolutionary context. Mycoparasitism is not just a mycological curiosity, it represents a diverse and interesting example of a microbial interaction that deserves wider attention.

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