Some fungicolous fungi

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Farlow Herbarium

That fungi are phenomenally opportunistic heterotrophs and can be found in almost every ecological niche is no surprise. Of these numerous associations, those interactions with which most people are familiar include fungi as plant pathogens, important decomposers (e.g., forest ecosystems), and producers of foodstuffs (cheese, soy sauce, ethyl alcohol). Less familiar are fungus-fungus relationships which are known from almost every major fungal group, with the zenith in the Ascomycota ( Hawksworth, 1981). Though many fungi associate with other fungi, the exact nature of these complex interactions, however, is often obscure. It has always been difficult to distinguish the different degrees of interspecific fungal relationships. Hawksworth (1981) recommended that the broad term fungicolous be used to describe whenever two fungi are living together, whether or not a definite nutritional relationship has been demonstrated. According to Cooke and Rayner (1984), interfungal interactions can be categorized as competitive (the association can be deleterious to either or both of the participating fungi); neutralistic (neither beneficial nor harmful to either); or mutualistic (favorable to both).

This introductory article will concentrate only on those fungi that obtain nutrients at the expense of another fungus, whether by first killing the host (e.g., using exotoxins) then feeding saprophytically (a necrotrophic interaction); living directly on the host in a subtle physiological balance for an extended period (biotrophic interaction); or through out-competing the host for a resource. The terms biotroph and necrotroph were created (Barnett and Binder, 1973) to help categorize mycoparasitic relationships based on the mode of nutrition. These, however, are not necessarily mutually exclusive ways of life and a fungus may switch from one form to another as the association develops (Cooke and Rayner, 1984; Jeffries and Young, 1994). The degree of antagonism depends on the physiological states of the fungi involved and whether one or both species produce lytic enzymes, antibiotics, physically interferes with the other's hyphae or penetrates the cell wall of the host fungus (Jeffries and Young, 1994).

Necrotrophic interactions are distinguished by whether or not the host (hyphae, spores, sclerotia) is penetrated ( Jeffries and Young, 1994). Penetration may involve the production of specialized structures such as appressoria or fine penetration pegs. A generalized sequence of events is: 1) recognition of host hyphae by necrotroph, 2) attachment to host cell surface (may involve lectin), 3) hyphal tips of necrotroph may swell to form structures which will aid in mechanically breaching the host cell wall, 4) enzymatic degradation of host cell wall, 5) penetrating hyphae expands. Although some necrotrophs may be generalized (they can violate any host structure), most are specific and can attack only the hyphae, the sclerotia or the spores ( Jeffries and Young, 1994). This invasive type of necrotrophy can be considered
similar to saprotrophy because the compounds utilized are polymers rather than simple sugars and amino acids (Cooke and Rayner, 1984). An example of an invasive necrotroph is *Trichoderma*, in which some species were found to produce hyphal collings, appressoria, and hooks prior to the disintegration of host cytoplasm (Tong et al, 1990).

Unlike the “penetrating” necrotrophs, the contact (either directly touching or living less than 50 microns away from the host fungus) necrotrophs generally do not breach the host cell but rather interfere with growth rate and cause cytoplasmic disruption (Jeffries and Young, 1994). Interference, however, is limited only to the hyphae in contact with the necrotroph. Little work has been done on these particular fungal interactions so it is not surprising that the metabolites have not been identified nor what type of exchange (e.g. nutrients) between the antagonist and the host has occurred. It has also been assumed that many wood-inhabiting basidiomycetes probably use hyphal interference (Jeffries and Young, 1994). Interestingly, the diameter of the contact necrotroph may be as small as one-tenth of the host fungus. In SEM photographs of *Arthrobotrys* coiling around *Rhizoctonia* (Jeffries and Young, 1994), the hyphae of both taxa look approximately the same diameter.

It is not easy to distinguish which type of necrotrophic interaction is involved in an interfungal relationship. Different methods of attack by the antagonist, coupled with different levels of susceptibility by the host, have been observed within a single fungus-fungus relationship. Despite this, necrotrophic interfungal associations are gaining more attention today because, as antagonistic fungi, they could serve as biocontrol agents for plant pathogenic fungi. In order for a fungus to be considered a potential control agent, it must act quickly while eradicating or killing the host fungus. In addition, the potential biocontrol agent must not be pathogenic to other economically valuable organisms (Kendrick, 1992). Recent biocontrol research has centered around the widespread soil fungus, *Trichoderma*, which produces a series of antibiotics and fungal cell wall-degrading enzymes. Some of the fungi which *Trichoderma* are used against include: a fungus root disease in trees (*Armillaria*, a member of the Agaricales), another which causes root rot and stem canker of many crops (*Rhizoctonia*, anamorphic Aphyllorhorales), and the causitive agent of stem blight of peanuts, *Sclerotium* (asexual stage). Other important biocontrol fungi include the hyphomateous (i.e., fungi which produce conidia free on the mycelia) genera: *Arthrobotrys*, *Verticillium*, *Alternaria* and *Gliocladium*) which act on target hyphomycetes. *Peniophora* (Kendrick, 1992) and *Tremella* (Zugmaier et al, 1994) are basidiomycetes which have been shown to act against plant pathogenic basidiomycetes.

Biotrophic fungi are considered ecologically obligate parasites (Alexopoulos et al, 1986), which have restricted host ranges and specialized infection structures. Although the host remains alive for an extended period, its normal metabolic functions are probably suppressed, and the antagonistic fungus serves as a nutrient sink. As in necrotrophic relationships, the biotrophic association can be further categorized based upon the intricacies of the physical and chemical interface. Jeffries and Young (1994) classified these interfungal interfaces into the following three groups: 1) haustorial, 2) fusion, and 3) intracellular. In the first category the antagonist's “body” remains external to the host. After the initial recognition between parasite and host, penetration (via a penetration/infection peg) of the host cell may be direct or occur after a contact structure known as an appresorium has formed. Sometimes the host fungus tries to “defend” itself by forming papillae to stop the penetration pegs (Urbasch. 1989). After penetration, specialized branched hyphae (haustoria) develop inside the host cell for nutrient uptake. Those mycoparasites that “employ” this strategy are found in the Zygomyctota. Brefeld (1872) illustrated two members of this group, *Chaetocladium* (fig. 1) and *Piptocephalis* (fig. 2) within the host. With fusion biotrophs, the host is not penetrated with infection pegs but rather open channels (small or large) form between both “partners”. Fusion biotrophic relationships are unusual, however. Unlike the previous two biotrophic relationships, the entire intracellular biotroph enters the hyphae of the host cell. Examples of this
type are found in the Chytridiomycota (organisms with zoospores).

Fig. 1. Chaetocladium (stippled mycelia) on *Mucor* from Brefeld, 1872, fig. 8.

The most numerous fungus-fungus associations, however, are those in which the biology of the interaction is not known.

Fig. 2. *Piptocephalis* growing (a) on *Mucor* from Brefeld, Taf. V, fig. 17.

The majority of these interfungal relationships are found in the Ascomycota, including the "imperfect" fungi. For example, many species of the ascomycete *Hypomyces* are found on the basidiomata of members of the hymenomycetes. The subiculum of the aggressive fungus may cover not only the hymenium but also the stipe and pileus. The colors range from buff, to brick red or black. A bright orange species (*Hypomyces lactifluorum*) is even considered delicious if found on an edible mushroom (e.g. *Lactarius deliciosus*).

There are also numerous examples of fungicolous heterobasidiomycetes but relatively few members in the homobasidiomycetes (Jeffries and Young, 1994). It is quite easy to find examples of fungicolous relationships since the large fruiting structures of ascomycetes and basidiomycetes provide ample substrates (e.g., this fall I found a *Boletus* sp. with the *Hypomyces* imperfect *Sepeodonium*, covering 2/3 of the cap). According to Hawksworth (1981), there are approximately 44 species in 23 genera of hyphomycetes that are obligately or predominantly lichenicolous. The lichenicolous fungi (fig. 3), may occur on the thallus or on the apothecia of the mycobiont. Jeffries and Young (1994) also report that the mycobiont may be displaced by the invading fungus and a new lichen association established.

There are many keys to fungicolous cup-fungi as well as other ascomycete taxa to aid in your discoveries (e.g., Ellis and Ellis, 1988; Hawksworth, 1980). Fungicolous fungi may have limited or wide ranges of fungal hosts. Some genera may be strictly fungicolous, such as the tiny *Callorioropsis*, *Micropyxis* (Pfister, 1976) and *Parenteola* (Zhuang, 1988). While others, such as the large genus *Cordyceps*, have relatively few (three) mycetophilous species.

References


F. A. Harrington is a postdoctoral fellow with D. H. Pfister

ABLS Award

Annually, the American Bryological and Lichenological Society recognizes distinguished papers in those subjects published in the Society's journal, The Bryologist, with two awards: the William Starling Sullivan Award and the Edward Tuckerman Award. Papers published in The Bryologist are nominated by members of the Society, and the awards are granted by the Society's Awards Committee. This year, Samuel Hammer, professor at Boston University's College of General Studies, and a Farlow Associate, was awarded the Edward Tuckerman Award for his paper, "Prothallus Structure in Cladonia," The Bryologist 99(2), pp. 212-217. For his thesis work, Dr. Hammer, Harvard 1993, studied the Cladoniases of the western United States. Now a Cambridge resident, Dr. Hammer's focus has shifted to our northeastern species of Cladonia. The establishment, growth and form of the lichen thallus are of special interest to Dr. Hammer as are the soil binding properties of the terricolous Cladinas and Cladoniases. Using scanning electron microscopy, Hammer investigates the structural, nutritional and reproductive roles of the prothallus, studies originally undertaken by E. Vainio in his late 19th century work on Cladonia. Vainio undoubtedly would have read Hammer's article with great interest, and, we hope, it will bring you, our FoF members, into our library as well.

- EJK

Summer Meetings & Forays

The Farlow Herbarium and Friends were well represented on forays and at conferences this past summer and early fall. Philip May attended the meeting of the International Association of Lichenologists in Salzburg, Austria, in early September. About 320 lichenologists attended the five-day symposium. Prior to the symposium, Phil went on one of the associated four-day field excursions in the Alps. Josef Hafellner and Helmut Wittman led the excursion, which was aimed at collecting lichens--mostly crusts--on or near the summits of various mountains. Ropes were needed for one collecting site!

Elizabeth Kneiper went on the ABLS forays to the Olympic Peninsula and Central Cascades led by Katherine Glew of the University of Washington and Judy Harpel of the University of British Columbia. Clear skies and gorgeous scenery made the Blomquist Foray, led by Lewis Anderson out of Highlands, North Carolina, a perfect weekend for Elisabeth Lay and Elizabeth Kneiper. More locally, the A. E. Andrews Foray, led by Richard Andrus and Nancy Slack, was held in the southeastern Catskills region and included the special ecosystems of Shawangunk Mountain.

Talks on a wide range of topics were given by FoF members at the 47th Annual Meeting of the American Institute of Biological Sciences, held in Seattle, Washington this past August. The
developmental progression of establishment of soredia of *Cladonia grayi*, presented by John Blackmer, currently a Harvard undergraduate, was praised for its originality. Samuel Hammer's "Form in *Cladonia*: Does it Matter?" explored the role of form in the classification in this variable lichen genus. David Hibbett (last year's FoF annual meeting guest speaker) organized and presided over a Botanical Society of America Symposium: "Recent Advances in Mycology for Undergraduate Botany Teachers." David's presentation of the work he and H.U. Herbartia Director Michael Donoghue are doing on the evolution of homobasidiomycetes, fossil mushrooms in amber, and the evolution of homobasidiomycetes, is undoubtedly of interest to many of our FoF members. In her talk, "Habitat-focused Lichen Mini-courses," Elizabeth Kneiper described the short courses in lichenology she offers at the New England Wild Flower Society to participants in the Teaching Session of the American Institute of Biological Sciences.

**New Farlow Graduate Student**

Karen Hansen, who has just completed a master's thesis on Pezizales from the University of Copenhagen, is a visiting graduate student working with Donald Pfister. She is working on various discomycete groups and also learning molecular techniques working with David Hibbett on his project on species and speciation of the shiitake.

**MSA Presidential Farewell**

Donald H. Pfister served as President of the Mycological Society of America for 1995-1996. He delivered the Presidential Address on Castor, Pollux, and life histories of fungi, discussing teleomorphic-anamorphic connections in the Orbiliaceae.

**FoF Web Page Address Change**

The FoF Fellowship Web Page is now accessible through a new address: HTTP://WWW.BIO.UMASS.EDU. This gets you to the U. Mass. Dartmouth Biology Department web page. Click on "Resources" and the FoF Fellowship should be there.

**Diatom Display**

In keeping with the FoF annual lecture, this year's guest speaker Robert K. Edgar and his graduate student, Stacey McBride Ginnetty, have mounted an exhibit at the Cabot Science Library, "Vignettes of Diatom Diversity: Two Centuries through a Looking Glass." This display outlines the history of our understanding of the biology and ecology of three diatom species from their original descriptions in the 1800's to the present. These species are interesting also because they are important components in freshwater, southern ocean, and salt marsh ecology. Copies of the original illustrations of the species along with more current illustrations (including electron micrographs) are featured.

**FoF Financial Report**

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Friends of the Farlow is an international group of amateur and professional botanists concerned with supporting the programs and resources of the Farlow Reference Library and Herbarium of Cryptogamic Botany of Harvard University. Membership categories are: Associate member, $10-$24; Full member, $25-$49; Sponsor, $50-$99; Benefactor, $1000 or more. To join, please make your check payable to the Friends of the Farlow and send to the address below. The membership year runs from January 1st to December 31st. Members receive a discount on Farlow publications and services, participate in book sales, annual meetings and other events, and receive a special welcome at the Farlow. This newsletter is published twice a year, in the spring and fall. For more information, contact the Farlow Herbarium, 20 Divinity Avenue, Cambridge, MA 02138, USA (Tel. 617-495-2368; Fax. 617-495-9484).