

REVIEW

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## Reproduction and dispersal in aquatic hyphomycetes

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**Abstract** The conidia of aquatic hyphomycetes were discovered by C.T. Ingold some 60 years ago. They are typically multiradiate or sigmoid, relatively fragile, and produced in enormous numbers. Their main function seems to be the rapid colonization of a periodic superabundance of leaves common in most streams. Conidia are unlikely to survive adverse conditions and to be responsible for the apparently worldwide distribution of many aquatic hyphomycete species. It has repeatedly been suggested that meiospores are responsible for long-distance dispersal; however, to date, only some 10% of described species have been connected to a teleomorph. To determine additional connections, and to document the potential role of meiospores in long-distance dispersal of aquatic hyphomycetes, the application of modern molecular methods is essential.

**Key words** Biogeography · Conidia · Meiospores · Spore production

### Introduction

Aquatic hyphomycetes belong to the kingdom Fungi, subkingdom Dikarya (Hibbett et al. 2007). They are also known as freshwater hyphomycetes, amphibious hyphomycetes, or Ingoldian fungi (Bärlocher 1992a). Some species were described in the late 19th century from soil, and a few more from ponds, ditches, and marshy areas. The decisive breakthrough, however, was Ingold's (1942) observation of a large number of multiradiate (often tetra-radiate) or sigmoid fungal spores in foam trapped behind twigs. He made this discovery while looking for chytrids in an alder-lined stream near his house. Within a few weeks, he connected the conidia to mycelia growing and sporulating on alder and

willow leaves decaying in the stream. The spore shapes are attributed to convergent evolution with natural selection shaping them to optimize attachment to substrates (Webster 1959; Webster and Davey 1984; Dang et al. 2007; Kearns and Bärlocher 2007). Aquatic hyphomycetes are therefore an ecologically defined, polyphyletic group, primarily with ascomycetous affinities (Belliveau and Bärlocher 2005; Baschien et al. 2006; Campbell et al. 2006; Shenoy et al. 2007). Interestingly, members of another group of aquatic fungi with tetra-radiate spores but belonging to the Entomophthoromycotina were also first described from spores before their actual substrates were discovered (Webster 1992).

Allochthonous (imported) plant matter is often the major energy source of food webs of natural streams. In many temperate regions, autumn-shed leaves dominate. Kaushik and Hynes (1971) showed that during their decay in streams, the leaves accumulate nitrogen (at least some in the form of protein) and become more palatable and nutritious to leaf-feeding invertebrates. These and additional changes, summarized as conditioning, are connected to fungal colonization of the leaves. Primarily because of their copious production of striking and (for the most part) easily identifiable conidia, aquatic hyphomycetes were assumed to dominate fungal communities on leaves (Bärlocher and Kendrick 1974; Suberkropp and Klug 1976). While this is undoubtedly correct, recent molecular studies have revealed the consistent presence of fungi from other phyla (Nikolcheva and Bärlocher 2004).

The involvement of these fungi in food webs greatly stimulated interest among stream ecologists (Bärlocher 1992a, 2005). In many leaf decomposition studies it has become routine to estimate fungal biomass by measuring ergosterol, a fungal-specific indicator molecule (Gessner 2005), and fungal production by incorporation of <sup>14</sup>C-acetate into ergosterol (Newell and Fallon 1991; Suberkropp and Gessner 2005). Maximum levels of mycelial biomass can reach 17% of total detrital biomass (Gessner 1997), and in small woodland streams, annual fungal production can approach or greatly exceed that of bacteria and invertebrates (Suberkropp and Weyers 1996; Weyers and

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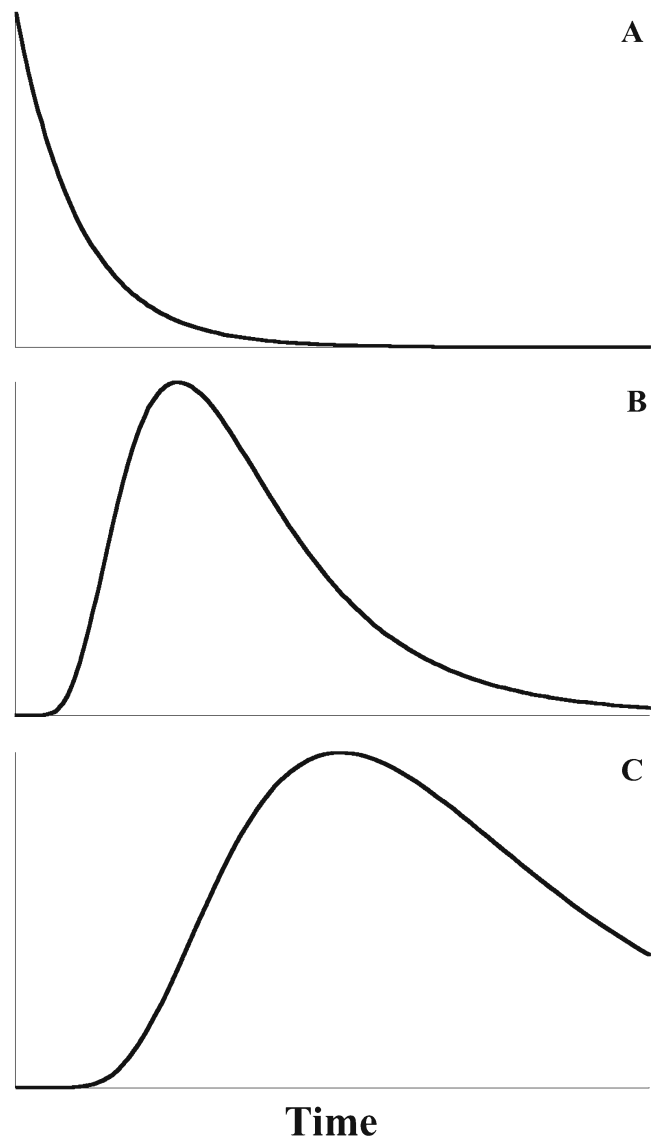
Suberkropp 1996; Suberkropp 1997; Carter and Suberkropp 2004).

### The boom–bust cycle of aquatic hyphomycetes

Without attached conidia, mycelia on leaves or other substrates cannot be identified with traditional methods (although it is becoming feasible with molecular techniques; Nikolcheva and Bärlocher 2004; Nikolcheva et al. 2005; Bärlocher 2007). Comparing fungal biomass on substrates to types and numbers of conidia carried in the water column has been facilitated by several approaches. Iqbal and Webster (1973) introduced a filtration technique: a predetermined volume of water is sucked through a membrane filter with a pore size of 5–8  $\mu\text{m}$ . The conidia will be retained on the filter and are stained (e.g., with 0.1% aniline or trypan blue in lactophenol). They are then counted and can usually be identified (although some require pure cultures or molecular techniques for unequivocal identification; Raviraja et al. 2005). Repeating this throughout the year demonstrates a common pattern in most temperate streams (Iqbal and Webster 1973; Webster and Descals 1981; Bärlocher 1992b). The number of conidia peaks at up to 30000/l a few weeks after leaf fall. The subsequent decline might be interrupted by a second, smaller peak caused by melting snow or spring rains (Bärlocher 2000). In summer, fewer than 10 conidia per liter may be present. This pattern may be modified by rainfalls throughout the year, which stimulate spore production by increased turbulence or washing-in of leaves near the streams, but in general, it clearly mimics leaf fall patterns in temperate regions (e.g., Weigelhofer and Waringer 1994).

Mycelia of aquatic hyphomycetes (as pure cultures or in naturally colonized substrates) can be induced to sporulate by incubating them in solutions with low concentrations of organic nutrients (Sridhar and Bärlocher 1997; Kempt et al. 2002) that are agitated either by placing the container on a shaker or by bubbling air through the solution (Gessner et al. 2003). Collecting, counting, and identifying these conidia (Bärlocher 1982) has been widely used to follow fungal successions on leaves exposed in streams. This approach is often combined with estimates of fungal biomass (based on ergosterol measurements; Gessner 2005) or growth (by measuring the incorporation of  $^{14}\text{C}$ -acetate into ergosterol; Suberkropp and Gessner 2005). Typically, the potential to produce conidia increases rapidly and peaks within a few weeks, followed by a rapid decline (Suberkropp 1991, 1995, 2001; Gessner and Chauvet 1994; Baldy et al. 1995; Suberkropp and Chauvet 1995; Maharning and Bärlocher 1996; Pascoal and Cássio 2004; Ferreira et al. 2006). The same pattern is shown by fungal productivity (incorporation of  $^{14}\text{C}$ -acetate into ergosterol; e.g., Suberkropp 1995, 2001; Gessner and Chauvet 1997; Baldy et al. 2002) and the quantities of small subunit (SSU) rDNA as estimated by quantitative real-time polymerase chain reaction (PCR) (M.A. Manerkar, unpublished observations). The buildup of biomass [based on ergosterol or adenosine triphosphate

(ATP)] often lags behind, and the subsequent decline is more gradual (Suberkropp 1991, 1995, 2001; Gessner and Chauvet 1994; Suberkropp and Chauvet 1995; Maharning and Bärlocher 1996; Ferreira et al. 2006). Oxygen uptake from decaying leaves (based on bacterial and fungal respiration) follows the pattern of ergosterol (Suberkropp 1991; Gulis and Suberkropp 2003; Gulis et al. 2004). Finally, the settling of conidia on newly exposed leaves seems to be best described by an exponential decay function, indicating that the substrate becomes increasingly less hospitable to new arrivals (Nikolcheva et al. 2005). These generalized patterns (presented in Fig. 1) tend to be more pronounced in fast-decomposing leaves, while external inorganic nutrients often accelerate and compress them into a smaller period. Organic nutrients or other pollutants generally inhibit



**Fig. 1.** Proposed patterns of aquatic hyphomycetes colonizing leaves exposed in a stream. **A** Rate of arrival of conidia on leaf. **B** Release of conidia, fungal growth rates, and quantities of fungal small subunit (SSU) rDNA. **C** Fungal biomass, respiration (includes bacteria)

conidium production (and species richness) to a greater extent than fungal growth (Sridhar and Bärlocher 1997; Sridhar et al. 2001; Pascoal et al. 2005a,b).

The strongly seasonal supply of discrete substrate units, their increasing attractiveness to leaf-shredding invertebrates due to fungal growth, and their rapidly deteriorating potential to sustain conidium production suggest that rapid colonization, reproduction, and dispersal rather than defense of acquired resources are crucial. Not surprisingly, aquatic hyphomycetes often invest in excess of 50% of their biomass production in the formation of conidia (Suberkropp 1984, 1991; Findlay and Arsuffi 1989; Maharning and Bärlocher 1996; Chauvet and Suberkropp 1998). When external N and P sources become scarce, existing mycelium may be converted to spores (Sridhar and Bärlocher 2000).

This emphasis on rapid reproduction clearly distinguishes aquatic hyphomycetes from cord-forming fungi, whose extended and long-lived mycelia (Smith et al. 1992) explore, capture, and defend resources (Boddy 1993; Boddy and Jones 2007). In aquatic hyphomycetes, there is extensive intermingling of colonies belonging to different species on leaves (Bärlocher and Kendrick 1974; Suberkropp and Klug 1976; Shearer and Lane 1983), suggesting limited interference. This idea has been confirmed with pure cultures: hyphal interference, the release of inhibitory substances, and invasion of a colony by the same or by other species is rare (Khan 1987; Bärlocher 1991). Interference is more pronounced among species growing on wood and during the earliest phase of colonization of freshly immersed leaves. Thus, *Tetrachaetum elegans* inhibits germination of *Flagellospora curvula* conidia (Tretton et al. 2004), and arrival and germination of new spores decline rapidly within a few days (Nikolcheva et al. 2005).

Colonization by conidia seems ideally suited to quickly respond to the regular cycle of superabundance and scarcity of discrete, ephemeral substrates common in many temperate streams. Similar conditions may prevail in subtropical or tropical regions with regular changes between wet and dry seasons.

Although a ruderal strategy applies to aquatic hyphomycetes as a group, there are undoubtedly species-specific differences. It is not uncommon to see reports of apparently clear and reproducible successions of different species during leaf decay, implying the existence of distinct niches or strategies, which may remain stable within a stream or a region (e.g., Gessner et al. 1993). However, an earlier review found no convincing evidence connecting the majority of species to a specific successional stage (e.g., early, middle, late, or throughout; Bärlocher 1992b), suggesting considerable phenotypic flexibility within most species. It is also generally accepted that most aquatic hyphomycete species can colonize and grow on a wide range of substrates (Bärlocher 1992b). Nevertheless, the relative frequencies of individual species are influenced by the substrate. For example, different species dominate on conifer needles than on deciduous leaves, and fungal communities of streams running through eucalypt stands are more similar to each other than to those running through mixed deciduous forest

(Bärlocher and Graça 2002). Such differences are particularly pronounced when leaves are compared to wood or to grasses (Gulis 2001).

There is a puzzling discrepancy, however, between the continued high level of fungal biomass (measured by ergosterol) at later stages of leaf decay with low conidium production potential (see Fig. 1). This finding suggests that only some of the mycelium is easily converted to conidia. Barring systematic errors of ergosterol to biomass conversion, this could indicate a bet-hedging life history. Rather than risking the entire biomass in instantaneous reproduction (which may be lost to filter-feeding invertebrates; Bärlocher and Brendelberger 2004), some of it may be held back to be expended more slowly over an extended period of time, or may be diverted to sexual reproduction (although this is more common on wood than on leaves; Webster 1992). Alternatively, it could be converted to a form better able to survive hostile environments, such as guts of leaf-eating invertebrates (Bärlocher 1981). Molecular techniques may allow us to follow changes in the expression of genes initiating conidiogenesis and relate these to ambient conditions (Fang and Bidochka 2006).

Conidia are relatively fragile and quickly lose their ability to germinate, even under benign conditions (Sridhar and Bärlocher 1994). They are therefore unlikely to be involved in long-distance dispersal. Even within a stream, 50% of newly released conidia are removed from the water column after 300 to 800 m of downstream displacement (Thomas et al. 1991a,b; Bärlocher 1992a).

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### Surviving substrate scarcity and long-distance dispersal

A common problem of stream-dwelling organisms is their unidirectional displacement by the water current, which threatens their continued occurrence in a given stream reach. Animals can overcome this by active movement, but it is not an option for aquatic hyphomycetes. Potential compensatory mechanisms include the extension of aquatic hyphomycete habitat into stream sediments (hyporheic zone and groundwater: Krauss et al. 2005; Bärlocher et al. 2006) and the surrounding terrestrial environment (some mycologists therefore prefer the term “amphibious hyphomycetes”). Most likely, they survive in these locations not as conidia but as mycelia or resistant, dormant structures associated with plant detritus. In addition, several aquatic hyphomycete species are endophytes in tree roots (Bärlocher 2006), and one species has even been isolated from needles of *Picea mariana* (Sokolski et al. 2006).

Another (perhaps the most likely) possibility is the formation of meiospores (primarily ascospores), which are smaller and appear more robust than aquatic hyphomycete conidia. Their formation has been demonstrated in approximately 10% of described aquatic hyphomycete species. Generally, the sexual state is found on moist but not submerged wood (Webster 1992), and is believed to be rare on leaves. However, some ascocarps are very small and incon-

spicuous and may be missed by cursory inspections (Shearer 1992).

Aquatic hyphomycetes have been isolated and described from all over the world, resulting in the early recognition that many (morpho) species are cosmopolitan, although some appear to be restricted to certain latitudes. Even if they were around before Pangaea split up some 200 million years ago, it seems unlikely that they would have remained morphologically undistinguishable on the various continents without fairly regular genetic exchanges, implying long-distance movements of viable inoculum. In geologically young islands, this would be an absolute necessity. For example, the currently existing Hawaiian islands originated between 1 and 5 million years ago, and the nearest land mass is 2000 miles away. In a total of three studies, (Anastasiou 1964; Goos 1970; Ranzoni 1979), with the most intensive survey restricted to a 10-week period, a total of 28 aquatic hyphomycete species were documented, none of them endemic. To explain their presence on these remote islands, Ranzoni (1979) mentions accidental introductions by Polynesians or whaling ships and aerial dispersal of meiospores.

However, basing species recognition on morphology, especially in primarily (or exclusively?) asexually reproducing taxa, can be misleading. In several morphospecies (e.g., *Neurospora discreta*), multilocus sequence data revealed a number of phylogenetic species (Taylor et al. 2000; Dettman et al. 2006) with distinct geographic distributions (Taylor et al. 2006). This result suggests that microfungi do have a biogeography; i.e., most (phylogenetic) species do not occur “everywhere,” as has been suggested for other eukaryotic microbial (morphological) species (Fenchel and Finlay 2004). There are exceptions, such as *Aspergillus fumigatus*: its ubiquitous distribution and lack of local adaptation have been tentatively attributed to its occurrence in composting vegetation, the geographic distribution of which has been greatly expanded by human activity (Taylor et al. 2006).

## Conclusions

The basic mechanisms regulating asexual reproduction in aquatic hyphomycetes are reasonably well known. Conidia are clearly the dominant propagules responsible for the rapid expansion of fungal populations after the annual leaf fall in temperate streams. Major gaps exist in our understanding of their role in allowing species to persist during the seasonal scarcity of substrates, and to what extent they participate in exchanges among communities at scales ranging from different reaches within a stream, to neighboring streams and catchments, to continents. In these processes, an involvement of meiospores seems likely. To go beyond mere speculations, molecular data are essential.

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