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*E. B. Gareth Jones, Kevin D. Hyde,
Ka-Lai Pang (Eds.)*

FRESHWATER FUNGI

AND FUNGAL-LIKE ORGANISMS

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Verónica Ferreira, Vladislav Gulis, Cláudia Pascoal and Manuel A. S. Graça

18 Stream pollution and fungi

18.1 The importance of aquatic hyphomycetes in woodland streams

Aquatic hyphomycetes are a group of freshwater fungi that includes asexual stages of ascomycetes and basidiomycetes. Even though aquatic hyphomycetes are a phylogenetically heterogeneous group, there are common characteristics to most species: (i) they are saprotrophs, using submerged leaves and wood as substrates and sources of carbon (Gulis et al. 2006b), (ii) they can obtain nutrients from both the water column and from organic substrates (Suberkropp 1995), (iii) they inhabit mostly well aerated and turbulent waters (Medeiros et al. 2009), and (iv) they produce large numbers of conidia (asexual spores) with distinct shapes and sizes (Gessner and Chauvet 1994; Gulis and Suberkropp 2003c; Ferreira et al. 2006a) (Fig. 18.1).

Aquatic hyphomycetes are important players in small woodland streams, where they facilitate a fundamental ecosystem-level process—the decomposition of allochthonous plant litter entering streams from the riparian zone, mostly as leaves (Webster et al. 1997). Once in water, leaves leach soluble compounds, particularly during the first 24–48 h of submersion and are colonized by a range of microbes. In temperate streams, aquatic hyphomycetes are often the main microbial colonizers of submerged litter contributing >90% to the total microbial biomass and production (Weyers and Suberkropp 1996; Hieber and Gessner 2002; Pascoal and Cássio 2004). After attachment to the leaf litter surface, aquatic hyphomycete conidia germinate (Tretton et al. 2004) and mycelia penetrate the leaf mesophyll (Canhoto and Graça 1999). Aquatic hyphomycetes macerate the leaf matrix with extracellular enzymes (Chamier and Dixon 1982; Arsuffi and Suberkropp 1984, 1988), mineralize organic carbon (Gulis et al. 2006b), or convert it into fungal biomass (Gessner and Chauvet 1994; Gulis et al. 2006b), and release large numbers of conidia (Gessner and Chauvet 1994; Gulis et al. 2006b; Ferreira et al. 2006a). The activities of aquatic hyphomycetes on leaf litter have been shown to correlate well with litter mass loss (Gessner and Chauvet 1994; Niyogi et al. 2003), and they can directly account for the loss of up to 39% of initial litter mass under field conditions (Hieber and Gessner 2002; Pascoal and Cássio 2004). The accumulation of fungal biomass and the maceration of litter also increase litter quality and palatability to invertebrate detritivores whose feeding activities lead to further litter mass loss (Canhoto and Graça 2008). Also, conidia released into the water column are used as food by the filter feeders (Bärlocher and Brendelberger

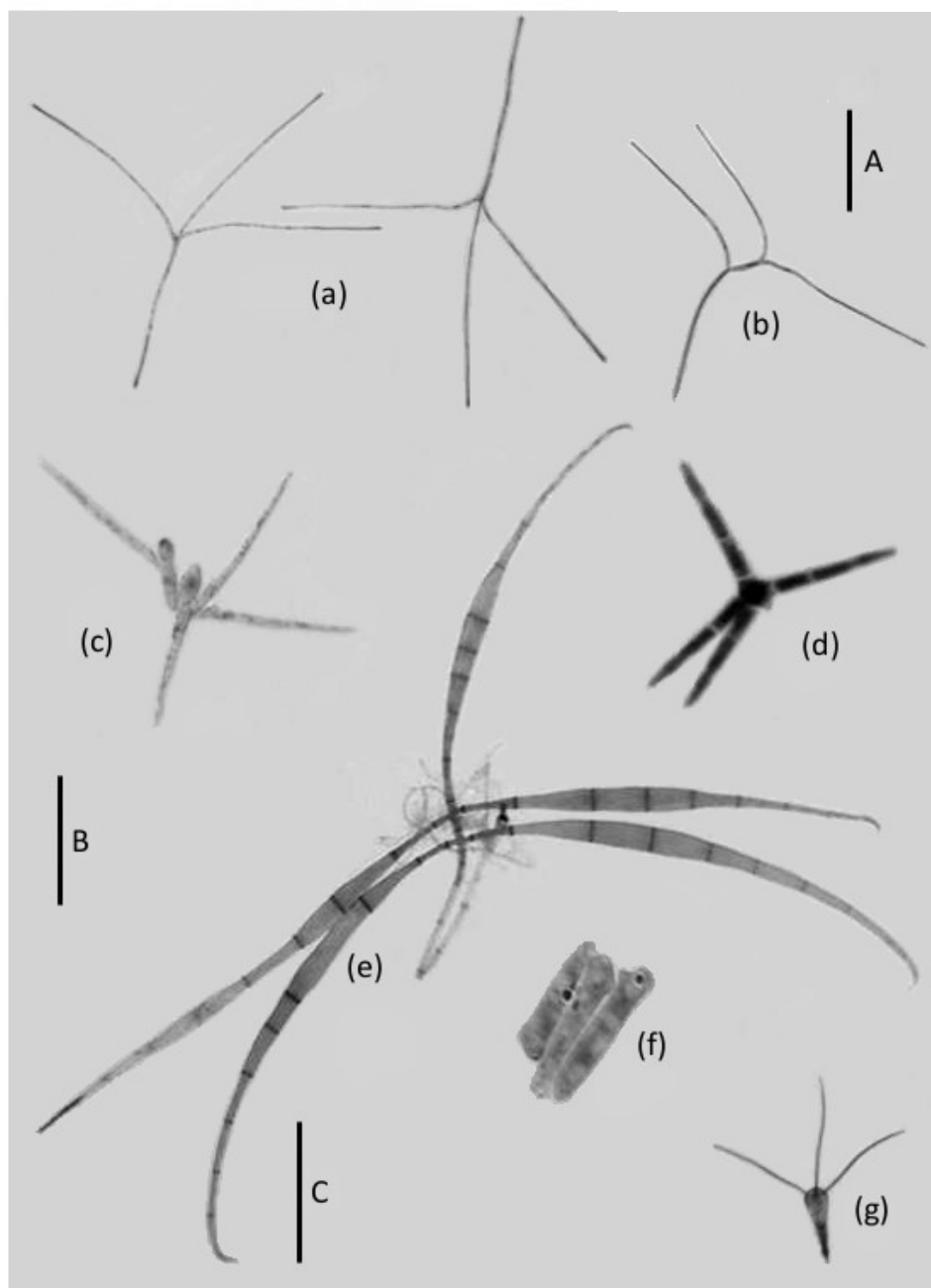


Fig. 18.1: Conidia of aquatic hyphomycetes. (a) *Tetrachaetum elegans*, (b) *Tricladium chaetocladium*, (c) *Tetracodium marchalianum*, (d) *Lemonnieria terrestris*, (e) *Casaresia sphagnum*, (f) *Heliscus lugdunensis* and (g) *Clavariopsis aquatica*. Scale bar A (species a, b, and g) = 50 μm , B (species c, d, and f) = 25 μm , C (species e) = 100 μm .

2004). Thus, aquatic hyphomycetes establish a link between dead organic matter and secondary invertebrate production.

Fungal community structure (species richness and identities) may also affect litter decomposition and invertebrate feeding (Arsuffi and Suberkropp 1984; Lecerf et al. 2005; Pérez et al. 2011). This can be attributed to species-specific differences in enzymatic activities (Zemek et al. 1985; Arsuffi and Suberkropp 1988) or elemental composition (Danger and Chauvet 2013), which suggests that litter colonized by certain fungal species will have distinct nutritive quality and could be preferentially consumed by detritivores.

Aquatic hyphomycete assemblages and activities are controlled by environmental conditions (e.g. nutrient availability, pH, temperature; Boyero et al. 2011; Cornut et al. 2012; Woodward et al. 2012). Therefore, human-induced changes in environmental conditions may affect fungal activity and community structure, fungi-driven litter decomposition and secondary production of invertebrates, and thus the functioning of woodland streams. Here, we address the effects of increases in nutrients, heavy metals, nanoparticle and xenobiotic concentrations, and water temperature, resulting from numerous human activities, on aquatic fungi.

18.2 Effects of nutrient enrichment on stream fungi

Pollution of streams and rivers due to agricultural or urban activities is often accompanied by increases in the concentration of dissolved organic and inorganic (nitrogen and phosphorus) nutrients, known as eutrophication. In addition to agricultural and urban runoff, atmospheric deposition of mostly nitrogen in highly industrialized regions of the world resulted in significant shifts from pristine oligotrophic conditions. Increased nutrient availability promotes the excessive growth of algae and heterotrophic organisms, such as bacteria and aquatic fungi (Vitousek et al. 1997; Carpenter et al. 1998). However, the majority of basic and applied studies dealt with the effects of nutrients on primary producers, while the heterotrophic pathways, including the effects of nutrients on fungal decomposers, received less attention (Dodds and Cole 2007).

The direct and indirect effects of dissolved organic nutrients on fungi are difficult to separate. Even though fungal growth in streams can be directly stimulated by readily available dissolved organic carbon (DOC) (Wilcox et al. 2005), prokaryotes generally outcompete fungi for dissolved labile C. The major indirect effects of organic pollution in streams and rivers are related to decreases in oxygen availability brought about by stimulation of bacterial respiration. Aquatic hyphomycetes are sensitive to dissolved oxygen concentration, and their growth, reproduction and diversity are negatively affected by oxygen deficiency (Medeiros et al. 2009). Several field studies have reported changes in fungal community structure in organically polluted reaches of streams or rivers, including increases in the relative abundances of

terrestrial fungi (Au et al. 1992b; Raviraja et al. 1998; Tsui et al. 2001). The activity of fungal decomposers and decomposition rate of plant litter are less sensitive to organic pollution than fungal diversity (Suberkropp et al. 1988; Raviraja et al. 1998), but can be negatively affected (Au et al. 1992a). However, the extent of organic pollution and the presence of other accompanying pollutants complicate the interpretation (Pascoal et al. 2003, 2005).

The effect of dissolved inorganic nitrogen (N) and phosphorus (P) on litter-associated fungi in streams has received considerable attention in the recent years. Aquatic hyphomycetes are capable of obtaining N and P from both the plant litter and from the water column (Suberkropp 1995). From the perspective of stoichiometric imbalance, since fungal biomass C:N and C:P ratios are considerably lower than that of plant litter (Danger and Chauvet 2013; Gulis et al. unpublished), fungi have to either retain N and P from the organic substrate more efficiently than C or immobilize inorganic nutrients from stream water. In addition, mining N and P from organic substrates requires considerable energy expenditures to produce extracellular enzymes to attack complex, often recalcitrant, organic molecules and eventually cleave amino or phosphate groups. Thus, based on microbial energetics, fungi should preferentially use dissolved inorganic nutrients from the water column. Indeed, increased availability of dissolved N and P in laboratory studies, whole-stream nutrient addition experiments or due to anthropogenic activities stimulates fungal activity and lead to nutrient immobilization (e.g. Gulis and Suberkropp 2003a; Ferreira et al. 2006a; Gulis et al. 2006a). The effects of dissolved nutrients on fungi are also greatest for low quality plant litter (i.e. low N and P, high lignin concentrations; e.g. rhododendron or oak leaves, wood) than for high-nutrient litter such as alder or maple leaves, as, for the former substrates, nutrient or carbon limitation of fungal growth can be alleviated or reduced by external inorganic nutrients (Stelzer et al. 2003; Gulis et al. 2004, 2008; Ferreira et al. 2006a).

Experiments in laboratory microcosms simulating stream conditions (i.e. using plant litter as a substrate, providing aeration and realistic nutrient concentrations) (e.g. Sridhar and Bärlocher 1997; Suberkropp 1998; Gulis and Suberkropp 2003a, b; Ferreira and Graça 2007; Ferreira and Chauvet 2011) showed that even moderate increases in dissolved nutrient concentrations typically stimulate fungal biomass accrual, fungal production, sporulation, respiration, growth efficiency and, ultimately, litter decomposition. Fungal sporulation rate or total reproductive output are most sensitive to nutrient availability and often increase by one to two orders of magnitude under elevated nutrient conditions.

Whole-stream nutrient addition experiments provide additional realism to the interpretation of the effects of dissolved nutrients on fungi. Short-term studies in temperate, Arctic and Mediterranean streams (Stelzer et al. 2003; Benstead et al. 2005; Ferreira et al. 2006a) demonstrated that N or N + P additions increased fungal biomass accrual, sporulation and decomposition of leaf litter and wood veneers. A 5-year whole-stream nutrient addition (N + P) experiment in southern Appalachians

(USA) showed that increased dissolved nutrient availability stimulated fungal biomass accrual, fungal growth rate and production, microbial (mostly fungal) respiration and sporulation rate of aquatic hyphomycetes associated with decomposing leaf litter and wood, and resulted in increases in concentration of fungal spores in transport (Gulis and Suberkropp 2003c, 2004; Gulis et al. 2004, 2008; Suberkropp et al. 2010). In addition, the direct effect of dissolved nutrients on fungi led to important ecosystem-level consequences. Nutrient enrichment altered storage and fluxes of detrital carbon by accelerating organic matter decomposition and carbon export as CO₂ and as fine particulate organic matter downstream, and decreasing carbon storage (Benstead et al. 2009). This affected higher trophic levels by changing production and biomass of detritivorous invertebrates and the flow of microbially immobilized N and P to these consumers (Cross et al. 2006, 2007; Greenwood et al. 2007).

Increases in dissolved inorganic nutrients in whole-stream nutrient enrichment experiments also affected fungal community structure. For example, Gulis and Suberkropp (2003c, 2004) reported changes in dominance patterns and relative abundances of aquatic hyphomycetes associated with decomposing leaf litter. Specifically, following nutrient addition, species that produced relatively large conidia (*Anguillospora filiformis*, *Terachaetum elegans*, *Tricladium chaetocladium*) assumed dominance, whereas species with smaller conidia dominated before the nutrient addition and in the reference stream. A somewhat similar pattern has been observed by Artigas et al. (2008). This trend implies that production of conidia with higher biovolume requires additional N and P supply and that these additional nutrients may be indeed shunted largely to reproduction (Suberkropp 1998).

Correlative studies based on natural or anthropogenic gradients of dissolved inorganic nutrients showed mixed results. Studies performed in streams across a natural (geological) nutrient gradient (e.g. Suberkropp and Chauvet 1995; Rosemond et al. 2002) or affected by moderate agricultural land use (e.g. Niyogi et al. 2003; Gulis et al. 2006a; Bergfur et al. 2007) demonstrated stimulation of fungal biomass accrual, sporulation of aquatic hyphomycetes and/or microbial respiration associated with decomposing plant litter by dissolved nutrients. However, in streams that experience high levels of eutrophication, factors other than nutrients, e.g. oxygen deficiency, accumulation of fine sediments or toxic pollutants (pesticides, heavy metals, etc.), may override the positive effects of nutrients on fungal activity. As a result, fungal activity and microbially mediated plant litter decomposition may be inhibited in highly polluted streams despite high nutrient availability (Pascoal and Cássio 2004; Duarte et al. 2009; Woodward et al. 2012). Likewise, even though some studies reported increased fungal diversity in moderately eutrophied streams, it decreased in highly eutrophied streams (Pascoal et al. 2005; Duarte et al. 2009; Sridhar et al. 2009); the latter effect is probably attributable to other accompanying pollutants rather than elevated dissolved inorganic nutrients.

Whole-stream nutrient addition experiments and correlative studies in streams suggest that fungal nutrient demands are met at relatively low concentrations of

dissolved inorganic N and P, and the relationship between nutrient availability and fungal activity and/or fungi-driven plant litter decomposition often follows asymptotic saturation-type models (e.g. Michaelis-Menten) (Rosemond et al. 2002; Ferreira et al. 2006a; Gulis et al. 2006a, b). The half saturation constants (i.e. concentration at which half of the maximum rate of activity is achieved) for nitrate-N and soluble reactive phosphorus (SRP) were estimated at 16–303 and 7–21 $\mu\text{g/L}$, respectively. This type of data together with the information on the responses of primary producers (Dodds 2007) can be useful for establishing nutrient criteria in streams. As mentioned earlier, due to potentially negative effects of other pollutants on fungi in highly impacted streams, the relationship between dissolved nutrient availability and microbial-driven decomposition on a continental scale (Europe) is rather unimodal (bell shaped) (Woodward et al. 2012).

18.3 Effects of heavy metals and acidification on stream fungi

Humans have been mining for metals for millennia. For instance, ancient mining in Rio Tinto, Spain, dating from circa 3000 BC, has led to a river with pH of 2.2 and red colour (“tinto” in Spanish). Worldwide mining has resulted in thousands of active and abandoned mines. The exposure of sulphide minerals to weathering results in the formation of sulphuric acid and the release of metal ions. Some metals such as Al and Fe may form hydroxides that precipitate and give sediments an orange color. Drainage waters from mines commonly have low pH and high concentration of metals, whereas benthic substrates in impacted streams are often coated with metal hydroxides (e.g. Hogsden and Harding 2013). Acidification of streams can also be caused by acid rain. The burning of fossil fuels results in the formation of sulphate and nitrous oxides that end up in streams *via* atmospheric deposition, with the consequent decrease in water pH (Allan and Castillo 2007). Other sources of heavy metals in the environment are the industry and agricultural practices (e.g. Corbi et al. 2006; Duan and Tan 2013). Because heavy metals are highly reactive and retained by living organisms, they are highly toxic (e.g. Nagajyoti et al. 2010). The biological effects of acid waters and metals on the biota include reduced biodiversity with the predominance of few tolerant species, decreased production and shortened food webs (Gray 1998; Hogsden and Harding 2013).

Increased concentrations of heavy metals reduce growth and sporulation of aquatic hyphomycetes under laboratory conditions (Miersch et al. 2001; Azevedo and Cássio 2010; Medeiros et al. 2010), with sporulation often being more sensitive to heavy metals than fungal growth (Abel and Bärlocher 1984). Low levels of heavy metals and acidity may lead to decreases in sporulation with no effect on fungal biomass (Duarte et al. 2004; Baudoin et al. 2008; Clivot et al. 2013). Suppression of reproduction or growth results in organisms channelling energy for maintenance, if stress conditions do not affect energy intake. This may explain why Gonçalves et al.

(2011) found higher microbial respiration rates on leaves from an uranium contaminated site than on leaves from a reference site. However, if environmental stress interferes with energy intake or expenditure, respiration rates are likely to decrease (Bermingham 1996; Dangles et al. 2004; Niyogi et al. 2009, 2013).

Heavy metals and acidification may also affect fungal community structure and ecosystem functioning. Stress conditions can cause changes in community structure (e.g. relative abundances of species) with no major changes in species richness on plant litter exposed to Zn (Duarte et al. 2004). In other studies, decreases in biodiversity with no changes in plant litter decomposition rates (Medeiros et al. 2010) or decreases in biodiversity and decomposition (Bermingham 1996; Baudoin et al. 2008; Niyogi et al. 2009; Clivot et al. 2013) have been reported. Decomposition rates were also reported to decrease with increased acidity (Dangles et al. 2004; Simon et al. 2009; Cornut et al. 2012). Hydroxide precipitation in streams affected by acid mine drainage may create a physical barrier for microbial colonization of plant litter and negatively affect decomposition (Schlief and Mutz 2005; Niyogi et al. 2013).

Several species of aquatic hyphomycetes have been often found in highly polluted streams (Sridhar et al. 2000, 2001; Krauss et al. 2001), which suggests some degree of tolerance or adaptation to high metal concentrations. Evidence to support this assumption comes from reports of higher tolerance to metals in fungal strains isolated from contaminated sites compared to conspecific strains from unpolluted streams (Chamier and Tipping 1997; Miersch et al. 1997; Baldrian and Gabriel 2002; Fernandes et al. 2011), and evidence of morphologic (Ferreira et al. 2010) and enzymatic differences between strains (Braha et al. 2007).

The effects of metals and acidification on aquatic hyphomycetes can have repercussions for higher trophic levels given the dependence of invertebrates on fungi to access the energy and nutrients locked in plant litter (Suberkropp 1992; Graça 1993; Canhoto and Graça 2008). Gonçalves et al. (2011) reported that although there were no differences in fungal biomass accrual between leaves incubated in uranium polluted and clean waters, the shredder *Sericostoma vittatum* discriminated between leaf types and preferentially consumed leaves from the non-polluted site. Similar pattern was found by Medeiros et al. (2008) in a stream receiving waters from an abandoned gold mine; fungal biomass and decomposition rates were similar between polluted and reference sites, but the shredder *Allogamus ligonifer* preferentially fed on leaves from the reference site.

18.4 Ecological and toxicological effects of engineered nanoparticles on stream fungi

The advances in nanotechnology have raised concerns about the potential impacts of the enormous amounts of nanomaterials that were produced over the past decade. Indeed, engineered nanoparticles (ENPs) have become part of our daily life in the form

of cosmetics (Perugini et al. 2002), antimicrobial paints (Kaegi et al. 2008), textile fabrics (Zhang et al. 2009) and electronic devices (Luechinger et al. 2008). Natural waters are likely to serve as a final repository of natural and engineered nanoparticles *via* waste release, soil runoff and atmospheric deposition (Klaine et al. 2008).

Nanomaterials are generally defined as materials that are < 100 nm in at least one dimension. A common difficulty in assessing their properties and behavior arises because nanomaterials can exist in many forms and sizes (Bernhardt et al. 2010). The surface properties of ENPs are of essential importance for their aggregation behaviour, and thus for their mobility and interaction with biota. The aggregation into larger particles and deposition in aquatic systems are determined by the ENP surface properties, which are mainly dependent on parameters such as temperature, ionic strength, pH, particle concentration and size (Navarro et al. 2008).

A major gap that influences the research of the environmental behavior of nanoparticles is the lack of analytical methods for their analysis at low and environmentally relevant concentrations (Hassellöv et al. 2008). Although ENPs have been already detected in aquatic environments (e.g. TiO₂ ENPs leached from the paint of house facades into a stream; Kaegi et al. 2008), their potential impacts on ecosystem health are largely unknown. The vast majority of ecotoxicological studies of ENP effects to date have looked at model organism responses to pure solutions/suspensions of ENPs. Such studies, though essential, are insufficient to predict the ecological impacts of the much wider range of likely exposure scenarios (Bernhardt et al. 2010).

Given the critical role of microorganisms in organic matter and nutrient cycling in aquatic ecosystems, ENPs can potentially alter ecosystem productivity and biogeochemistry by affecting aquatic fungi. Indeed, the exposure to nanoparticulate silver (nano Ag) or copper oxide nanoparticles (nano CuO) led to a reduction in fungal sporulation and leaf decomposition (Pradhan et al. 2011). These effects have been accompanied by shifts in the composition of leaf-associated fungal assemblages based on fungal spore morphology and DNA fingerprints. The dominant fungal species *Articulospora tetracladia* was stimulated, while the co-dominant species *Flagellospora* sp. was inhibited by exposure to nano or ionic metals, being replaced by *Heliscus lugdunensis* (Pradhan et al. 2011). *Articulospora tetracladia* and *Heliscus lugdunensis* are reported to occur in metal contaminated streams (Jaekel et al. 2005; Pascoal et al. 2005) and some strains of these species were found to be resistant to high concentrations of metals in their ionic (Braha et al. 2007) or nano form (Pradhan et al. 2013). Results for aquatic microorganisms are in agreement with those obtained for terrestrial microbial assemblages. Exposure to nano Ag decreased the biomass of soil microbes in concert with changes in the activity of both leucine aminopeptidase and phosphatase (Coleman et al. 2013), which are extracellular enzymes often used as indicators of the microbial potential to decompose organic matter.

Effects on microbial decomposers are expected to translate to higher trophic levels. Uptake or incorporation of metal ENPs into microbial biomass suggests the potential for trophic transfer of these contaminants (Coleman et al. 2013). A significant

inhibition of leaf consumption rate (up to 47%) and growth rate of invertebrate detritivores (up to 46%) was observed when invertebrates were exposed to sublethal concentration of nano CuO (75 mg/L) through either contaminated stream water or pre-contaminated food (Pradhan et al. 2012), which is possibly related to the food avoidance behavior. Moreover, the exposure to increased concentration of nano CuO via water or pre-contaminated food led to accumulation of Cu in the larval body (Pradhan et al. 2012). Thus, the stress induced by nanoparticles may affect the invertebrates directly or indirectly through its effects on microbes.

The toxicity of ENPs can be attributed to physical characteristics, metal ions released by dissolution of metal ENPs, or production of reactive oxygen species. For instance, Ag antimicrobial activity is most often attributed to the dissolved cation rather than to the high surface area and low solubility of nonionic metallic nanoparticle (Klaine et al. 2008). Consistently, effects of metal nanoparticles are generally less pronounced than those of the respective metal ions (Pradhan et al. 2011, 2012). However, some studies reported that leached metal ions are insufficient in explaining the toxicity of nanoparticles due to low solubility of some metal ions (e.g. Griffitt et al. 2008). A differential response of aquatic microbial communities to nanoparticulate form of metals and their respective ionic form suggests different modes of action.

In a study with pure cultures of fungi, nano CuO expressed its toxicity by inhibiting fungal biomass production and altering the mycelium morphology in a dose- and time-dependent manner (Pradhan et al. 2013). Nano CuO was more toxic to fungi isolated from non-polluted than from metal-polluted streams (Pradhan et al. 2013), suggesting adaptive mechanisms underlying the tolerance/resistance against metal nanoparticles as found for several metal ions in aquatic fungi (Jaekel et al. 2005; Azevedo et al. 2007; Guimarães-Soares et al. 2007; Krauss et al. 2011).

Overall, the data obtained so far point to the toxicity of nanoparticles to freshwater organisms which potentially places at risk fungal diversity and stream ecosystem processes. However, further studies are needed to identify the bioavailable forms of nanoparticles and effects of different metals. Moreover, ENPs themselves may serve as pollutant carriers because of interactions of nanoparticles with other pollutants (Bernhardt et al. 2010), further complicating predictions of their behavior in the environment. Furthermore, new ENPs are being developed, such as carbon-based nanoparticles, and their effects on fungi and fungi-driven ecological processes are yet unknown.

18.5 Effects of organic xenobiotics on stream fungi

Organic xenobiotics are man-made compounds that are not naturally found in the environment. Their effects depend on the nature of the compound, its mode of action and the target organism (Proia et al. 2012). Effects can be acute or chronic depending on the exposure time and concentration. There is no direct evidence of the

mineralization of organic xenobiotic pollutants by freshwater fungi. However, aquatic hyphomycetes can be affected by or bioaccumulate xenobiotics or their metabolites. For instance, dichloro-diphenyl-trichloroethane (DDT, an insecticide) at concentrations between 0.1 and 60 µg/mL enhanced the growth of several fungal species (Hodkinson 1976). Within 2 weeks, *Heliscus submersus* was able to convert 27% and 8% of DDT into 1,1-dichloro-2,2-bis(4'-chlorophenyl)ethane (DDD) and 1,1-dichloro-2,2-bis(4'-chlorophenyl)ethylene (DDE), respectively, whereas *Clavariopsis aquatica* transformed 6% of DDT into these metabolites (Hodkinson 1976). The fungicides mancozeb and carbendazim did not inhibit fungal growth or reproduction at concentrations up to 5 mg/L or conidial germination up to 1 mg/L (Chandrashekar and Kaveriappa 1994). In contrast, Bärlocher and Premdas (1988) reported a linear negative relationship between conidium production and concentration of the fungicide pentachlorophenol (0.0001–10 mg/L).

The contamination of alder leaves with the herbicide mecoprop reduced the biomass of *Heliscus lugdunensis* and inhibited leaf consumption by the shredder *Gammarus pseudolimnaeus* (Birmingham et al. 1998). The major factor affecting food choice was the concentration of mecoprop that the leaves were exposed to, not the mecoprop-mediated effects on fungal biomass. On the other hand, antibiotic mixtures, at concentrations typical of streams receiving wastewater treatment plant effluents, had no effects on bacterial assemblages but led to stimulation of fungal biomass on leaves, which increased leaf palatability to shredders (Bundschuh et al. 2009).

Some freshwater fungi, including *Clavariopsis aquatica*, have shown the ability to degrade xenobiotics, such as xenoestrogen nonylphenol (Junghanns et al. 2005), polycyclic musks (Martin et al. 2007) and synthetic azo and anthraquinone dyes (Junghanns et al. 2008). This has been related to the activity of extracellular laccases that are involved in biodegradation of polyphenols and lignin found in plant tissues. Also, *Heliscus lugdunensis* showed the ability to metabolize polycyclic aromatic hydrocarbons such as naphthol (Augustin et al. 2006). *Heliscus lugdunensis* was consistently found among the top-ranked fungal species identified at different highly polluted sites (Krauss et al. 2001; Sridhar et al. 2005), which suggests a potential for some aquatic hyphomycetes to affect the fate of pollutants in aquatic ecosystems.

18.6 Effects of thermal pollution on stream fungi

Temperature is a major environmental factor shaping the activity of individual organisms, species distribution (Parmesan and Yohe 2003; Brown et al. 2004; Thackeray et al. 2010) and, therefore, affecting key ecosystem processes (Brown et al. 2004; Traill et al. 2010). Alterations of the thermal regimes can have serious effects on aquatic biota since most organisms have limited optimal thermal ranges (Ward and Stanford 1984; Lehtonen 1996). Alterations of the thermal regime of streams and rivers can result from human activities such as urbanization, forest clearance, thermal

discharges, and flow modification, which presently affect many streams worldwide (Poole and Berman 2001; Cassie 2006). These activities will likely intensify over this century as a result of human population growth and concomitant needs for housing, food, water and energy (Vörösmarty et al. 2000). Thus, the number of streams and rivers affected by changes in thermal regime will probably increase in the future. In addition to these local or regional effects, global warming is predicted to affect thermal regimes of streams and rivers worldwide. Current climate models considering a doubling in atmospheric carbon dioxide concentration predict increases in mean global air temperature of 1.1°C–6.4°C by 2100 (IPCC 2007), which may translate into increases in stream water temperature of up to 0.6°C–0.9°C for each degree in air temperature (Pilgrim et al. 1998; Morrill et al. 2005). Further changes to the thermal regime of streams and rivers will result from the interaction between stressors (Stefan and Sinokrot 1993). Laboratory experiments have shown that responses of fungal growth and reproduction to increases in temperature depend on species identity, background temperature, and their interaction (Tab. 18.1). Fungal growth on solid media in the laboratory is stimulated by increases in temperature until the optimum of 10°C–30°C (species specific) is reached; any further increase in temperature leads to lower rates of colony extension (Koske and Duncan 1974; Webster et al. 1976; Graça and Ferreira 1995; Chauvet and Suberkropp 1998; Rajashekhar and Kaveriappa 2000; Dang et al. 2009; Duarte et al. 2013) (Tab. 18.1). For any given species, reported thermal optimum range is relatively narrow (<10°C), and the precision of the estimate depends on the number of temperature treatments and strain chosen. The increase in temperature also stimulates the reproductive activity in microcosm experiments up to the thermal optimum, which differs depending on species (Webster et al. 1976; Chauvet and Suberkropp 1998; Ferreira et al. 2012). For instance, *Lunulospora curvula* exhibits high spore production at high temperatures (25°C) and is therefore known as a warm-water species, while *Flagellospora curvula* has the highest spore production at lower temperatures (15°C) and is known as a cold-water species (Tab. 18.1). The different temperature optima of individual species partially determine seasonal patterns of conidia abundance in individual streams (Suberkropp 1984; Thomas et al. 1989; Gessner et al. 1993; Nikolcheva and Bärlocher 2005) and biogeographic distribution (Wood-Eggenschwiler and Bärlocher 1985; Ferreira et al. 2006b).

In experiments with fungal assemblages in laboratory microcosms, the increase in water temperature from low background levels (<15°C) stimulated biomass build-up and fungal sporulation on decomposing leaf litter (Ferreira and Chauvet 2011a, b; Bärlocher et al. 2013), while increases in water temperature from higher background levels (>15°C) generally had no effect or inhibited fungal growth and/or reproductive activity (Fernandes et al. 2009, 2012; Batista et al. 2012; Geraldine et al. 2012; Bärlocher et al. 2013). This apparent temperature threshold for fungal assemblages around 15°C is somewhat lower than the optimal temperatures for many species when grown in pure cultures (Tab. 18.1). Indeed, Webster et al. (1976) have shown that the sensitivity of individual species to warming depends on the presence of other species. They

Tab. 18.1: Effect of temperature on colony growth and spore production in 29 species of aquatic hyphomycetes (only studies that tested individual species using at least three temperatures were included).

Fungal species	Temperatures (°C) tested	Optimal temperature (°C) for colony growth ^a	Optimal temperature (°C) for spore production ^a	Reference
<i>Alatospora acuminata</i>	2–24 (17 temperatures)	20–24		Dang et al. (2009)
<i>Alatospora acuminata</i>	5–25 (at 5° intervals)	20		Koske and Duncan (1974)
<i>Anguillospora filiformis</i>	15, 20, and 25	25	20 = 25	Chauvet and Suberkropp (1998)
<i>Anguillospora longissima</i>	15, 20, and 25	25	20	Chauvet and Suberkropp (1998)
<i>Articulospora tetracladia</i>	15, 20, and 25	20	20	Chauvet and Suberkropp (1998)
<i>Articulospora tetracladia</i>	11, 13, 16, 21, and 27	13 = 16		Duarte et al. (2013)
<i>Articulospora tetracladia</i>	5–30 (at 5° intervals)	10–15		Graça and Ferreira (1995)
<i>Articulospora tetracladia</i>	5–25 (at 5° intervals)	20		Koske and Duncan (1974)
<i>Dactyliella aquatica</i>	5–35 (at 5° intervals)	25		Rajashekhhar and Kaveriappa (2000)
<i>Flagellospora curvula</i>	15, 20, and 25	20	15	Chauvet and Suberkropp (1998)
<i>Flagellospora penicillioides</i>	5–35 (at 5° intervals)	25		Rajashekhhar and Kaveriappa (2000)
<i>Flagellospora saccata</i>	5–35 (at 5° intervals)	30		Rajashekhhar and Kaveriappa (2000)
<i>Gyoeffrella craginiformis</i>	5–25 (at 5° intervals)	20		Koske and Duncan (1974)
<i>Heliomyces</i> sp.	5–35 (at 5° intervals)	25		Rajashekhhar and Kaveriappa (2000)
<i>Heliopus lugdunensis</i>	2–24 (17 temperatures)	20–24		Dang et al. (2009)
<i>Heliopus lugdunensis</i>	5–30 (at 5° intervals)	20–25		Graça and Ferreira (1995)
<i>Heliopus submersus</i>	11, 13, 16, 21, and 27	27		Duarte et al. (2013)
<i>Lemonnieria aquatica</i>	5–30 (at 5° intervals)	20–25		Graça and Ferreira (1995)
<i>Lemonnieria terrestris</i>	5–30 (at 5° intervals)	10		Graça and Ferreira (1995)
<i>Lunulospora curvula</i>	15, 20, and 25	25	25	Chauvet and Suberkropp (1998)
<i>Lunulospora curvula</i>	11, 13, 16, 21, and 27	27		Duarte et al. (2013)

(continued)

Tab. 18.1: (continued)

Fungal species	Temperatures (°C) tested	Optimal temperature (°C) for colony growth ^a	Optimal temperature (°C) for spore production ^a	Reference
<i>Lunulospora curvula</i>	5–35 (at 5° intervals)	25	25	Rajashekhar and Kaveriappa (2000)
<i>Lunulospora curvula</i>	5–30 (at 5° intervals)	20	25	Webster et al. (1976)
<i>Margaritipora aquatica</i>	5–25 (at 5° intervals)	25	25	Koske and Duncan (1974)
<i>Phalangi-spora constricta</i>	5–35 (at 5° intervals)	25	25	Rajashekhar and Kaveriappa (2000)
<i>Tetrachaetium elegans</i>	15, 20, and 25	20	20 = 25	Chauvet and Suberkropp (1998)
<i>Tetracladium marchalianum</i>	15, 20, and 25	20	25	Chauvet and Suberkropp (1998)
<i>Tetracladium marchalianum</i>	2–24 (17 temperatures)	20	20	Dang et al. (2009)
<i>Tetracladium setigerum</i>	5–25 (at 5° intervals)	20	20	Koske and Duncan (1974)
<i>Tetracladium setigerum</i>	5–35 (at 5° intervals)	25	25	Rajashekhar and Kaveriappa (2000)
<i>Tricellula aquatica</i>	5–25 (at 5° intervals)	20	20	Koske and Duncan (1974)
<i>Tricellula aurantiaca</i>	5–25 (at 5° intervals)	20	20	Koske and Duncan (1974)
<i>Tricellula curvatis</i>	5–25 (at 5° intervals)	20	20	Koske and Duncan (1974)
<i>Tricellula inaequalis</i>	5–25 (at 5° intervals)	25	25	Koske and Duncan (1974)
<i>Tricladium chaeocladium</i>	15, 20, and 25	25	15 = 20 = 25	Chauvet and Suberkropp (1998)
<i>Tricladium chaeocladium</i>	5–30 (at 5° intervals)	15	25	Webster et al. (1976)
<i>Tricladium splendens</i>	5–25 (at 5° intervals)	20	20	Koske and Duncan (1974)
<i>Varicosporium elodeae</i>	11, 13, 16, 21, and 27	27	27	Duarte et al. (2013)
<i>Vermispora cauveriana</i>	5–35 (at 5° intervals)	30	30	Rajashekhar and Kaveriappa (2000)
<i>Wiesneriomyces laurinus</i>	5–35 (at 5° intervals)	30	30	Rajashekhar and Kaveriappa (2000)

^a indicates no difference between temperatures

demonstrated that the optimum temperature for reproduction of *Lunulospora curvula* and *Tricladium chaetocladium* was 15° and 10° lower, respectively, when both species were incubated together compared to monocultures (Webster et al. 1976). This suggests that the optimum temperatures estimated for individual species in the laboratory are likely overestimates compared to those under field conditions, where species form diverse communities. The magnitude of the stimulation of fungal growth and reproduction by warming is also modulated by other factors such as substrate type, stage of decomposition, structure of the fungal assemblage (Bärlocher et al. 2013), metal contamination (Batista et al. 2012), and nutrient availability (Ferreira and Chauvet 2011a).

Increases in water temperature also affect the relative contribution of individual fungal species to the overall spore output (Dang et al. 2009; Fernandes et al. 2009, 2012; Ferreira and Chauvet 2011a, b; Batista et al. 2012; Geraldès et al. 2012), and in some cases this translates into shifts in the dominance pattern (Dang et al. 2009; Ferreira and Chauvet 2011a, b; Fernandes et al. 2012). Generally, the contribution of cold water species (e.g. *Articulospora tetracladia*, *Flagelospora curvula*) to the cumulative spore output decreases while that of warm-water species (e.g. *Lunulospora curvula*, *Lemonniera aquatica*) increases under elevated temperature (Fernandes et al. 2012).

Fungal respiration rates, as a surrogate for overall metabolism, are stimulated by warming both in experiments with monocultures (Ferreira et al. 2012) and multi-species assemblages (Ferreira and Chauvet 2011a, b) in laboratory microcosms. This indicates that increases in temperature stimulate carbon mineralization with the probable consequence of increased litter mass loss. In fact, fungi-driven litter decomposition is generally stimulated by temperature increases in the laboratory (Fernandes et al. 2009, 2012; Ferreira and Chauvet 2011a, b; Batista et al. 2012; Ferreira et al. 2012; Geraldès et al. 2012).

Taking advantage of the experimental warming of the hyporheic zone of a 1st order stream, Bärlocher et al. (2008) compared the number of litter fragments buried in the sediment and their fungal colonization. The average 4.3°C warming resulted in a decrease in the number of leaf fragments suggesting faster decomposition. Fungal species richness on leaf litter, but not on other litter types (e.g. grass, wood), was lower and the amount of fungal spores produced was higher under warming than at ambient temperature (Bärlocher et al. 2008). This agrees with laboratory results suggesting that warming may alter fungal diversity and community structure while promoting reproductive activity and fungi-driven litter decomposition. In another field experiment, the decomposition of oak leaf litter was followed in both halves of a small mountain stream monthly over 1 year, one stream half being at ambient temperature and the other being continually warmed by ~3°C above ambient temperature (Ferreira and Canhoto 2013). Results show stimulated microbially-mediated litter decomposition rates in the coldest, but not the warmest, months. This can be partially attributed to higher temperature sensitivity of enzymatic activity at low background temperature (Brown et al. 2004), and together with the results from

laboratory experiments suggests higher sensitivity of cold water than warm water streams to increases in temperature.

Litter breakdown rates are also higher in warmer than colder streams across geographical thermal gradients (Irons et al. 1994; Fabre and Chauvet 1998; Friberg et al. 2009; Boyero et al. 2011), which can be attributed to enhanced microbial activity at warmer sites (Irons et al. 1994; Fabre and Chauvet 1998). This suggests that increases in temperature stimulate fungal activity, which translates into changes in ecosystem functioning. However, Gonçalves et al. (2006, 2007) found faster fungi-driven litter decomposition in a temperate stream than in warmer Mediterranean and tropical Cerrado streams. This may have resulted from higher fungal colonization of litter in the temperate stream, as suggested by the higher fungal biomass accumulation and sporulation rates in the temperate compared to the Mediterranean and tropical streams (Gonçalves et al. 2006, 2007). Ferreira et al. (2012a) also reported faster fungi-driven litter decomposition in a temperate stream than in a tropical rain-forest stream, which was also explained by higher fungal colonization of litter in the temperate stream. This suggests that the contribution of fungi to litter decomposition in different climate zones is shaped not only by temperature but other factors as well (e.g. biogeography, oxygen availability), and that when fungal activity is low and/or background temperature is already high, further increases in temperature may not necessarily translate into measurable stimulation of litter decomposition.

When seasonal temperature gradients are considered, fungi-driven litter decomposition rates and associated fungal biomass and reproductive activity per gram of plant litter are higher in the warm spring/summer than in the cold autumn/winter (Nikolcheva and Bärlocher 2005; Ferreira et al. 2013). However, at an areal basis (whole stream scale), higher standing stock of fungal biomass, higher fungal production and spore output are found in autumn/winter in temperate streams due to higher standing crop of submerged litter resulting from the litter fall (Suberkropp 1997; Suberkropp et al. 2010). Thus, the increase in temperature may have stronger ecosystem-level effects on fungal parameters and fungi-driven litter decomposition during the colder season when litter and fungal standing stocks are greatest.

18.7 Effects of the interaction among factors on stream fungi

The stimulating effect of increased water temperature on fungal activity (provided that it is still below the thermal optimum) may be modified by the concomitant changes in other environmental factors. For instance, the increase in water temperature resulting from water abstraction for agriculture or from forest clearance may be accompanied by an increase in nutrient concentrations, which may interact either synergistically to stimulate (Ferreira and Chauvet 2011a) or antagonistically to reduce (Piggott et al. 2012) fungal activity and fungi-driven litter decomposition compared to that expected from the effect of each individual factor. Nutrient enrichment is often accompanied

by decreases in dissolved oxygen concentration; in addition, oxygen solubility decreases as water temperature rises. As aquatic hyphomycetes prefer well aerated waters (Medeiros et al. 2009), oxygen depletion may counteract the potentially stimulating effects of nutrient enrichment or warming on fungal activity.

The increase in water temperature and nutrient availability in an agricultural landscape may also be accompanied by increases in the concentration of pesticides, which may be toxic to aquatic fungi (Bärlocher and Premda 1988) and can interact antagonistically with warming and nutrients to reduce fungal activities. The release of thermal effluents may be accompanied by the release of biocides used to control biofouling, which can pose additional stress on aquatic communities (Cooke and Schreer 2001). Increases in water temperature may exacerbate the toxicity of pollutants to fungi, while heavy metal pollution may in turn increase the sensitivity of fungi to warming (Batista et al. 2012). The relationship between temperature and fungi-driven litter decomposition in metal polluted streams can be further complicated if we consider that fungal strains in metal polluted streams may have adapted to these harsh conditions at the cost of reduced performance and therefore may have a reduced ability to cope with additional stressors (Ferreira et al. 2010, 2012a).

18.8 Conclusions

Aquatic hyphomycetes occupy a key position in aquatic food webs by establishing the link between terrestrial-derived organic matter and higher trophic levels. Therefore, changes in fungal community structure and/or activity can have strong impacts on ecosystem functioning (e.g. carbon and nutrient cycling), secondary production of invertebrates and fishes, and ecosystem services (e.g. water quality, food provision). The available literature shows that aquatic hyphomycetes are highly sensitive to environmental change, and several authors have suggested their potential utility as bioindicators of ecosystem health (Castela et al. 2008; Lecerf and Chauvet 2008; Solé et al. 2008). However, significant gaps still exist in our understanding of the effects of new pollutants (e.g. nanoparticles, pharmaceuticals) and interactions of multiple stressors affecting aquatic fungi at organismal, community and, especially, ecosystem scales.

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