Fungi

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Introduction

Aquatic fungi are microscopic organisms with mostly mycelial growth and hyphae developing on or within their typically submerged organic substrates of plant or animal origin. Resident aquatic fungi are able to complete their life cycle in freshwaters and often have special adaptations for growth, sporulation, and dispersal in aquatic environments. A number of so-called transient fungi that are blown in from terrestrial ecosystems are regularly reported from freshwaters, but they may or may not be metabolically active under submerged conditions. Emergent macrophytes (e.g., cattail or reed stands) also harbor terrestrial fungi, especially during the aerial standing-dead decomposition stage. These fungal assemblages will also be considered here because of their crucial importance in decomposing plant detritus in wetlands and lake littoral zones. Freshwater fungi are rather difficult to observe and study due to unusual character of the habitat and the intimate association of fungal hyphae with the substrate they colonize. As a result, they were often overlooked by both aquatic ecologists and mycologists alike. Since the 1940s, some interest in the systematics and evolutionary relationships among these fungi has emerged. Furthermore, development and application of quantitative methods within the last two decades have established that fungi play a key role in the decomposition of plant litter in freshwater environments and are important mediators of energy and nutrient transfer to higher trophic levels (e.g., shredding invertebrates). Even though some freshwater fungi or fungus-like organisms are economically or ecologically important parasites of aquatic animals and plants, most freshwater fungi depend on dead coarse particulate organic matter (CPOM), mostly plant litter, as their primary source of energy and nutrients. This dead plant material may be of autochthonous (e.g., submerged or emergent macrophytes) or of allochthonous origin (leaf litter and wood from the riparian zone). This chapter will focus on fungi associated with plant litter in two freshwater ecosystems that have received the most attention: streams and wetlands or marshes. Since fungal activity and fungi-mediated processes differ between the lotic and lentic ecosystems, they will be discussed separately.

Fungal Diversity in Freshwaters

About 2000 fungal species have been reported to date from submerged decaying substrates, as spores in water, parasites of aquatic plants or animals, or associated with decaying macrophytes in wetlands (Table 1). Overall, fungi are thought to be one of the largest groups of eukaryotes on Earth, second only to insects, with only about 5% of species described to date. True fungal diversity in freshwaters, therefore, is likely to be significantly higher than the 2000 species mentioned above. Representatives of all major taxonomic groups of fungi (Chytridiomycota, Zygomycota, Ascomycota, and Basidiomycota) have been observed, isolated, and described from freshwater habitats. Chytrids thrive in aquatic environments and are the only group of fungi producing zoospores and no true mycelium. Even though they are able to degrade recalcitrant compounds, such as chitin or cellulose, their functional role in organic matter decomposition has not been extensively studied. Some chytrid taxa are well-known parasites of algae or invertebrates. One species, *Batrachochytrium dendrobatidis*, has been recently identified as the etiological agent responsible for declines in amphibian populations worldwide. Very little is known about saprotrophic Zygomycota in freshwaters, although they can be detected on submerged substrates using molecular techniques. Representatives of one class within this phylum, the Trichomycetes, are quite common in freshwaters. These fungi are highly specialized obligate symbionts in the digestive tracts of arthropods and are often found in association with nymph or larval stages of aquatic insects. Apparently, aquatic environments have selected against basidiomycetes or their asexual (mitosporic) stages, since they are not commonly observed in freshwaters. The most common and ecologically significant group of fungi in freshwaters is ascomycetes and their anamorphs or mitosporic fungi, i.e., fungi whose sexual or meiosporic stages are unknown. The following discussions of fungal characteristics and processes and their importance in decomposition pertain largely to this group of fungi. Fungal-like organisms, the Oomycetes, are phylogenetically distant from the true fungi, but are traditionally studied by mycologists and are quite common in freshwaters as both saprotrophs on various organic

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Table 1 Some estimates of fungal diversity in freshwater habitats

Taxonomic or ecological group	*Number of species*
Chytridiomycota	576
Trichomycetes	148
Ascomycota (meiosporic)	ca. 500
Basidiomycota	11
Aquatic hyphomycetes (mitosporic)	ca. 300
Aero-aquatic fungi (mitosporic)	90
Miscellaneous mitosporic fungi	405
Fungi on emergent macrophytes	>600[a]
Freshwater or amphibious lichens	>100
Oomycota (Saprolegniales)[b]	138

[a]600 species have been recorded from a single species of emergent macrophyte, *Phragmites australis*.

[b]Oomycota are not true fungi but fungus-like heterotrophs of the Kingdom Stramenopila.

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substrates as well as parasites of fishes (*Saprolegnia*) and crustaceans (*Aphanomyces*). Their role in decomposition of plant litter is not well understood.

Fungi in Streams and Rivers

Headwater woodland streams receive about 90% of their carbon input from the riparian zone in the form of plant litter (leaves and wood), while in-stream primary producers, such as algae and macrophytes, play a greater role in large rivers or streams without a riparian canopy (e.g., grassland, desert, or tundra streams). Microbial decomposition of CPOM in lotic ecosystems is primarily carried out by fungi, while bacteria assume a greater role in the decomposition of fine particulate organic matter (FPOM, particle size < 1 mm) and dissolved organic matter (DOM). Aquatic hyphomycetes, which are mostly mitosporic ascomycetes, dominate on submerged leaf litter in streams, while both mitosporic fungi and ascomycetes colonize submerged wood. Currently, little is known about the diversity of fungi on submerged macrophytes in lotic waters and their role in litter decomposition.

Aquatic Hyphomycetes

The most well-studied group of fungi in streams are aquatic hyphomycetes or Ingoldian fungi (Figure 1).

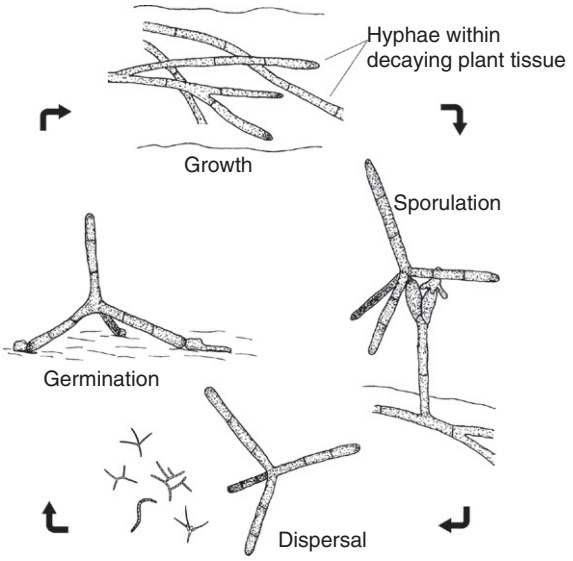

Figure 1 Life cycle of a typical aquatic hyphomycete (*Lemonniera aquatica*). Note that a few aquatic hyphomycetes may have sexual stages (not shown). Conidial shapes of several species of aquatic hyphomycetes are shown under 'dispersal.' Drawing by K. Suberkropp.

They produce large, distinctly shaped spores (conidia) (tetraradiate, sigmoid, or variously branched) that facilitate their dispersal and attachment to submerged substrates in lotic environments (Figure 2). Once conidia come in contact with the substrate, mucilage secretion, development of appressoria, and rapid germination (within a few hours) ensure their secure attachment and colonization of a new substrate. Fungal hyphae then grow mostly within the plant litter and finally give rise to conidiophores (conidia-bearing structures) that protrude from the substrate into the water and shed newly formed conidia. Once released, conidia are carried downstream by the current to colonize new substrates. Conidia may also become trapped and concentrated in foam at the air–water interface (neuston) where they can survive for weeks. As autumn-shed leaves or branches fall into the stream, they become colonized by conidia from neuston or by spores drifting in the water column.

Fungal Biomass, Production, and Reproduction

Current estimates of fungal biomass associated with plant litter are based on determining the concentration of ergosterol, a lipid specific to cell membranes of higher fungi. Fungal biomass associated with leaf litter in streams generally increases rapidly following colonization and peaks within 2–8 weeks depending on the type of substrate, temperature, stream water chemistry, and other environmental factors (Figure 3(a)). At its maximum, fungal biomass can comprise up to 23%

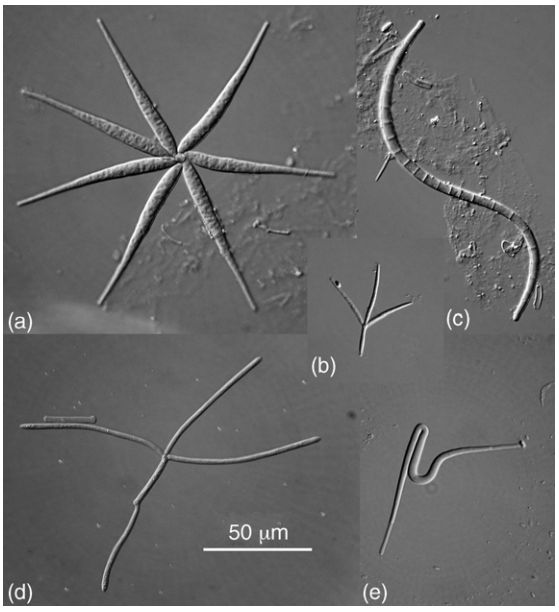

Figure 2 Spores of aquatic hyphomycetes. (a) *Flabellospora* sp., (b) *Alatospora acuminata* s.l., (c) *Anguillospora* sp., (d) unidentified conidium, and (e) *Condylospora* sp. All spores are from a single sample from a stream in Alabama. Differential interference contrast (DIC) micrographs by V. Gulis.

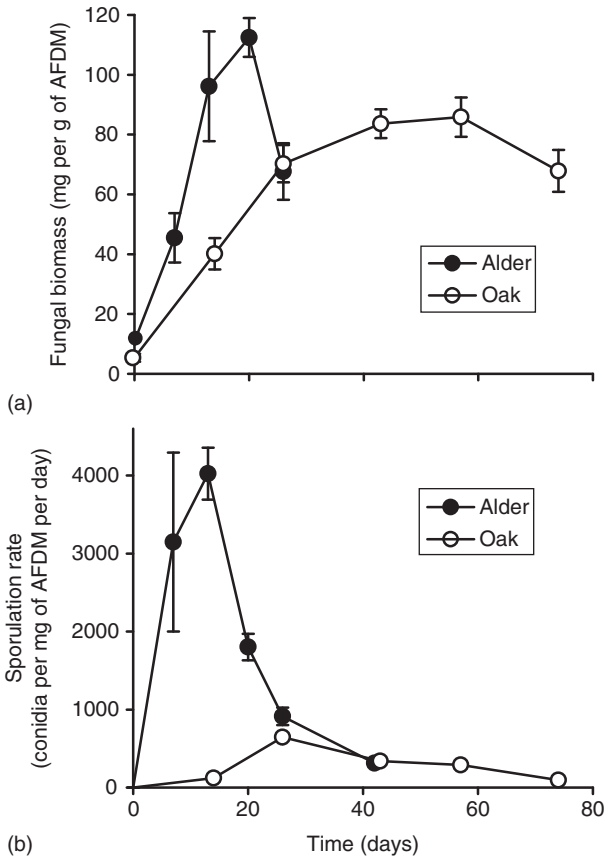

Figure 3 Dynamics of fungal biomass (a) and conidia production of aquatic hyphomycetes (b) associated with two types of decomposing leaf litter in a Portuguese stream. Symbols indicate means ± 1 SE ($n = 4$–8). On the basis of data from Gulis V, Ferreira V, and Graça MAS (2006) Stimulation of leaf litter decomposition and associated fungi and invertebrates by moderate eutrophication: Implications for stream assessment. *Freshwater Biology* 51: 1655–1669, and unpublished data by the same authors.

of total detrital mass; however, typical values are around 10% (Table 2). Fungal biomass usually declines during later stages of decomposition as considerable losses occur due to production of spores, senescence and death of hyphae, grazing by detritivores, and losses of mycelial fragments with or as FPOM. Fungal reproduction follows a similar pattern with maximum conidial production of aquatic hyphomycetes often occurring before the peak in biomass (Figure 3(b)). Up to 80% of fungal production may be allocated to conidia. This translates into 2–12% of leaf mass loss converted into fungal spores (or, in other terms, up to 7% of initial litter mass lost as conidia, e.g., Figure 4). Since massive numbers of conidia are released into the water column (up to 25 000 l^{-1} in some streams), they can be captured (membrane filtration of stream water), counted, and identified based on their unique morphologies. This approach has provided valuable information on diversity and reproductive activity of aquatic hyphomycetes from a variety of streams.

Fungal growth rates (as determined from radiolabelled ^{14}C-acetate incorporation into ergosterol) on submerged leaf litter can be as high as 0.42 per day, but are typically an order of magnitude lower. Fungal production on decomposing leaves in streams has been found to peak at 0.6–16 mg of fungal C per g of detrital C per day, though variation for randomly collected leaves at various stages of colonization can be very high. Even though fungal biomass on submerged wood may be almost as high as that on leaves, fungal growth rates and, consequently, production are about 5–10 times lower on wood than on leaves (Table 2). This can be explained by the poor oxygen supply to the inner layers of wood, the more recalcitrant nature of wood constituents (e.g., higher lignin content), and the lower nutrient (N and P) content of wood than leaf litter.

Fungal biomass and production associated with leaf litter (per m^2 of streambed) and concentration of aquatic hyphomycete conidia in water often show clear seasonal patterns in temperate streams. However, this seasonality is not directly driven by temperature, but rather by seasonal availability of the substrate (i.e., input of autumn-shed leaves). In

Table 2 Comparison of fungal and bacterial biomass and production associated with submerged plant litter in streams and rivers and emergent plant litter in freshwater marshes (standing-dead and submerged)

Parameter	*Fungi*	*Bacteria*	*Source*
Streams and rivers			
Leaf litter			
Biomass (mg of C per g of detrital C)	108–174	2–6	3
Biomass (mg of C per g of detrital C)	70–77	3–4	5
Biomass (mg of C per g of detrital C)	38–140	0.4–0.7	13
Production (mg of C per g of detrital C per day)	1.2–1.4	0.4	1
Production (mg of C per g of detrital C per day)	3.5–9	0.11–0.6	8,9
Production (mg of C per g of detrital C per day)	0.5–7.2	0.04–0.28	13
Wood			
Biomass (mg of C per g of detrital C)[a]	10–119	–	4
Biomass (mg of C per g of detrital C)[b]	2–55	0.4–3.8	11
Production (mg of C per g of detrital C per day)[a]	0.003–0.28	–	4
Marshes			
Emergent macrophytes			
Biomass (mg of C per g of detrital C)	5–34	0.002–0.05	2
Biomass (mg of C per g of detrital C)	8–50	0.1–0.5	6
Biomass (mg of C per g of detrital C)	2–62	0.1–1.7	7
Biomass (mg of C per g of detrital C)	7–63	0.3–0.4	10
Biomass (mg of C per g of detrital C)	20–124	0.02–2.1	12
Production (mg of C per g of detrital C per day)	0.02–1.4	<0.001–0.003	2
Production (mg of C per g of detrital C per day)	0.1–0.3	0.01–0.06	6
Production (mg of C per g of detrital C per day)	0.2–1.3	0.001–0.04	7
Production (mg of C per g of detrital C per day)	0.5–5.0	0.01–0.07	10
Production (mg of C per g of detrital C per day)	0.6–5.0	<0.001–0.005	12

Values are maximum biomass or production estimates from leaf litter decomposition experiments or from wood in streams (see notes) or ranges (min–max) for naturally decomposing emergent macrophytes in marshes.

[a]Data from randomly collected naturally occurring submerged small wood (<40 mm diam) collected seasonally over one year, n = 122.

[b]Data from submerged decaying wood veneers sampled only once in about 3 months after deployment.

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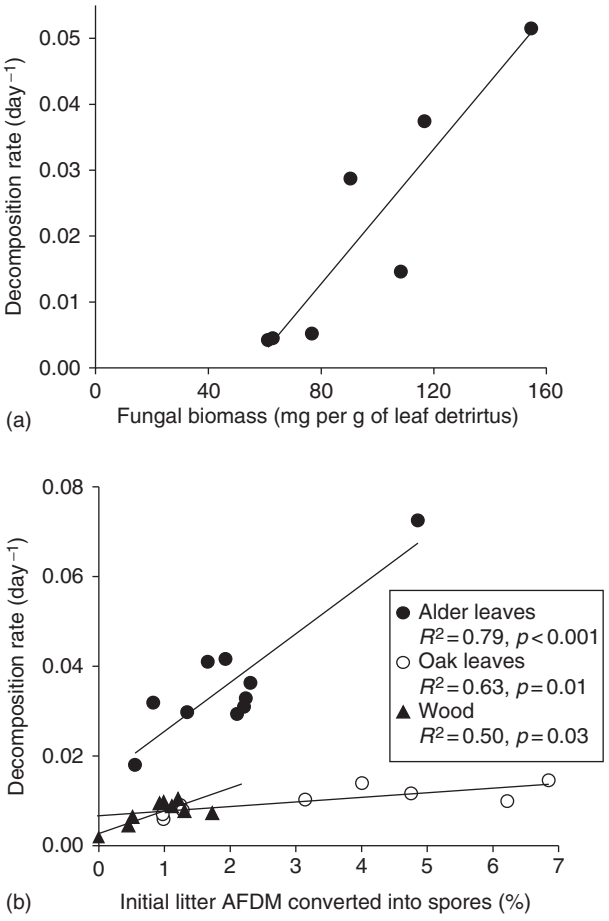

Figure 4 Relationships between the peak fungal biomass associated with 7 types of leaf litter and their decomposition rates (a) and between the cumulative aquatic hyphomycete spore output (as % of initial litter mass) and decomposition rates of leaf litter and wood (b). Data for panel (a) are from Gessner MO and Chauvet E (1994) Importance of stream microfungi in controlling breakdown rates of leaf litter. *Ecology* 75: 1807–1817. Data for panel (b) are from Ferreira V, Gulis V, and Graça MAS (2006) Whole-stream nitrate addition affects litter decomposition and associated fungi but not invertebrates. *Oecologia* 149: 718–729, and unpublished data by the same authors.

temperate streams, a major peak in fungal activity occurs in late autumn–early winter when the water temperatures are quite low. Interestingly, the life cycles of many detritivorous invertebrates (shredders) are timed to take advantage of these peaks in substrate availability, fungal activity and, hence, enhanced nutritional quality and palatability of litter.

Fungi associated with leaf litter typically account for 95–99% of total microbial biomass, whereas the biomass of bacteria is very low (Table 2). Fungi also dominate microbial communities of leaf litter in terms of production, even though bacteria have higher growth and turnover rates than fungi. Fungal production is comparable to or exceeds bacterial production from leaf litter by a factor of 1–627. Fungi also appear to dominate microbial communities colonizing submerged wood in streams (67–97% in terms of biomass). There are some indications that the relative importance of bacteria on submerged macrophytes may be higher than that on leaves and wood. However, more studies of these substrates are needed.

Fungal Role in Decomposition of Submerged Organic Matter and Their Importance at the Ecosystem Scale

Aquatic hyphomycetes have enzymatic capabilities to degrade the major constituents of plant litter. Extracellular enzymes produced by these fungi include enzymes that hydrolyze cellulose (endo- and exoglucanases, exoglucosidase) and hemicelluloses, pectin (polygalacturonase and pectin lyase), proteins, and lipids. Some laboratory studies have shown degradation of lignin or its derivatives by some aquatic fungi. However, ligninolytic activity has not been demonstrated under natural situations. In contrast, activities of multiple enzymes involved in degradation of other plant constituents have been reported from decomposing leaf litter in streams and have been correlated with fungal metabolic activities. Pectin degradation by fungi is probably a key process in the breakdown of leaf litter in streams, since it facilitates leaf maceration and FPOM release.

Fungal activity (e.g., peak biomass, sporulation) associated with leaf litter and wood in streams is positively correlated with final decomposition rates, indicating that fungi play a key role in CPOM dynamics (Figure 4). The activity of shredding invertebrates and mechanical fragmentation of leaf litter in streams often depends on the extent of fungal colonization. Increases in N and protein contents of leaf litter and partial digestion of refractory plant polymers due to fungal activity render leaf material a more nutritious and palatable food resource for invertebrate consumers. In feeding experiments, most shredding invertebrates show clear preference for fungal-colonized leaf material versus uncolonized leaves. As softening due to fungal enzymatic activity and shredding by invertebrates continue, leaf litter becomes more susceptible to mechanical fragmentation by water current and abrasion by sediments.

In some studies, fungal diversity has been shown to have a positive effect on fungal biomass and leaf litter decomposition rates; however, the magnitude of these effects is small, suggesting relatively high functional redundancy among species of aquatic hyphomycetes. Interestingly, some shredders show preferences for leaf litter colonized by a particular fungal species.

Fungal production can be significant in stream ecosystems and is of the same order of magnitude as bacterial and secondary invertebrate production. Estimates of fungal production associated with leaf litter in small streams range from 8 to 96 g of C per m^2 of streambed per year and are positively correlated with mean annual standing crop of leaf litter. Consequently, annual fungal production on an areal basis should be lower in larger streams and rivers, which receive lower CPOM inputs and are less retentive. Losses of leaf litter carbon as CO_2 due to microbial respiration (mainly fungal) can also be significant and have been estimated to account for 17–56% of total leaf C loss during decomposition. On the basis of production data and fungal growth efficiencies of 24–60% or direct respiration measurements, fungal assimilation can be calculated. Fungal assimilation (production plus respiration) accounted for 5–40% (in one instance as much as 97%) of the annual leaf litter input in several headwater streams. Indirect fungi-mediated losses of DOM and FPOM during decomposition have not been accounted for in these estimates, and the downstream transport of leaf litter in less retentive streams can be significant. Fungal activity on submerged wood is considerably lower than that on leaves. The available estimates of annual fungal production on small wood (<40 mm diam) from two streams are 4–6 g of C per m^2 of streambed per year. Nevertheless, fungi can assimilate a considerable proportion of annual small wood input to these streams (15–20%).

Factors Affecting Fungal Activity and Microbially Driven Plant Litter Decomposition in Lotic Ecosystems

Fungal activity associated with plant litter is controlled by characteristics of the substrate, environmental variables, and biotic interactions. Fungal reproduction, i.e., sporulation rate of aquatic hyphomycetes, is typically affected to a much greater extent than biomass accrual. The type of leaf litter or wood and, more specifically, the lignin, nitrogen, and phosphorus concentrations can exert strong control over fungal growth and reproduction. Lignin is difficult to degrade enzymatically due to its refractory structure. Hence, plant litter of low carbon quality (high lignin) supports low fungal activity and decomposes slowly. High N and P concentrations in plant litter often stimulate fungal activity. Thus, for a given substrate, fungal activity largely depends on the interplay of these intrinsic factors (i.e., lignin to nutrient ratios). To complicate the matter further, fungal activity is also affected by dissolved inorganic N and P concentrations in stream water, since fungi are capable of taking up N and P from both the substrate and the overlaying water column. A number of laboratory and field studies have shown that when fungi are limited by N and P supply from the substrate or the water column (e.g., in pristine low-nutrient streams), even small experimental increases in dissolved inorganic nutrients result in considerable increases in fungal biomass, production, and reproduction, and, consequently, accelerated plant litter decomposition. From an environmental perspective, eutrophication of rivers and streams often leads to stimulation of fungal activity, faster plant litter disappearance, and, consequently, reduced resource availability (amount and timing) to higher trophic levels (e.g., shredding invertebrates).

Apart from the dissolved nutrients, other chemical parameters, such as pH, alkalinity, oxygen, pollution, etc., also affect fungal activity in streams. Aquatic hyphomycete diversity is typically higher in soft water streams, while fungal activity and leaf litter decomposition rates are usually greater in hard water streams. Such differences may be due to the greater activity of fungal pectin lyase in hard water streams and, consequently, faster leaf litter softening, maceration, and overall leaf litter mass loss. Organic pollution and sedimentation may also negatively affect fungal diversity and activity through oxygen limitation. Coal mine effluents and elevated heavy metal concentrations in water typically reduce fungal diversity and slow plant litter decomposition. However, some species of aquatic hyphomycetes appear to be resistant to high concentrations of heavy metals in chronically polluted streams or at least are more tolerant than aquatic invertebrates. Decomposition in these streams is generally slow, but this is more likely the result of a decreased presence of shredding invertebrates.

Elevated stream water temperatures positively affect fungal growth and litter degrading activity. Therefore, increasing temperatures as predicted from global climate change scenarios might lead to increased fungal activity and concomitant increases in litter decomposition rates. Such responses may have negative consequences that propagate through higher trophic levels as mentioned earlier for the effects of nutrients.

Diversity of riparian vegetation has a positive but rather small effect on aquatic fungal communities by affecting the diversity of resources available to fungi. Biotic interactions of fungi with stream inhabitants include interactions with bacteria and detritivores.

Fungi obviously compete with bacteria for detrital resources. Some aquatic hyphomycetes produce antibiotics that limit bacterial growth. However, interactions of fungi with bacteria are not well understood. Interactions with shredding invertebrates include direct competition for resources (plant litter), grazing by invertebrates, and direct ingestion of spores, which can pass undamaged through the digestive system facilitating fungal dispersal.

Fungi in Freshwater Marshes and Lake Littoral Zones

Freshwater marshes, including the littoral zone of lakes, are unique transitional habitats that occur at the interface between the terrestrial and aquatic environments. Emergent plants, such as cattails (*Typha*) or common reed (*Phragmites*), are common inhabitants of freshwater marshes. These plants often have very high rates of primary production, making freshwater marshes among the most productive ecosystems on the planet. Most of the living plant biomass is not consumed by herbivores in these ecosystems. Instead, the bulk of the plant material enters the detrital pool following plant senescence and death. Consequently, microbial decomposers (fungi and bacteria) and detritus-feeding consumers (macroinvertebrates) are important groups of organisms involved in the breakdown and mineralization of this plant matter in wetlands.

Characteristics of Emergent Plant Decomposition

Important aspects to consider when examining emergent plant decomposition are the spatial and temporal conditions under which plant litter naturally decomposes. In many emergent plants, abscission and collapse of leaves and culms to the sediments or overlying surface waters does not occur immediately after plant shoot senescence and death. A significant portion of the dead plant mass often remains in an aerial standing-dead position. As a result, the decomposition sequence of emergent plants typically involves two distinct spatial phases separated in time: an initial phase that occurs under aerial standing-dead conditions followed by a second phase that occurs under submerged conditions or on surface sediments. When litter decomposition studies have closely simulated natural decay conditions (i.e., standing-dead initially), fungi have been found to play a dominant role in decomposition in these environments.

Fungi Associated with Emergent Plant Litter

Current knowledge of fungal diversity associated with emergent plant litter largely comes from traditional microscopic studies where fungi associated with litter have been detected and identified by direct observation of reproductive structures (e.g., ascomata) either directly from field collected material or by subsequent culturing techniques in the laboratory. Ascomycetes are the most common fungal taxa encountered, including both hyphomycetous and coelomycetous anamorphs (mitosporic fungi). Basidiomycetes have also been observed on decaying emergent plant litter, but are much less frequent than ascomycetes.

Distinct spatial and temporal changes in fungal taxa have been observed during the decomposition of emergent plant litter. Terrestrial taxa are commonly observed during the initial stages of decomposition (standing-dead). These taxa are frequently replaced by fungi adapted to aquatic environments when shoots collapse to the sediments or surface waters. In addition to temporal shifts, fungi colonizing standing-dead litter also exhibit distinct spatial distribution patterns within the litter canopy. Different fungal taxa may occupy specific plant parts, such as leaves, sheaths, or the nodes and internodes of culms. These colonization patterns may be a result of spatial variation in environmental conditions within the litter canopy (temperature, water availability, etc.) and/or differences in the intrinsic quality of the plant litter substrate, such as the amounts of recalcitrant compounds (lignin) or available nutrients (N and P) within different plant tissues.

Fungal Biomass and Production

As plant litter decomposes, fungal hyphae pervasively invade the substrate, producing a suite of extracellular enzymes that enable fungi to degrade plant polymers, absorb, and assimilate plant litter carbon and nutrients into fungal biomass. In addition, fungi convert plant litter carbon into CO_2 as a result of their respiration. Despite well-documented evidence indicating fungal colonization of emergent plant litter, few studies have quantified the role of fungi in litter decay or their overall importance in wetland carbon and nutrient cycling. The use of the biochemical marker, ergosterol, to estimate litter-associated fungal biomass in freshwater marshes has provided compelling evidence that fungi are quantitatively important in decomposing emergent plant litter and play a pivotal role in marsh carbon and nutrient cycling. Fungal

biomass associated with decaying litter increases gradually during shoot senescence and early standing-dead decomposition, with peak fungal biomass often accounting for as much as 10% of the total detrital mass. Differences in fungal biomass have been observed between plant organs (e.g., leaves vs. culms), with generally higher biomass being observed in leaf litter than culms (Figure 5). In addition, fungal biomass associated with standing-dead culms has been observed to vary spatially along the culm axis, with higher fungal biomass occurring in the upper portions of culms (Figure 5). These differences in fungal biomass between plant organs are likely due to the more recalcitrant nature (lignin concentration) and the lower amounts of nutrients (higher C:N and C:P ratios) in culm tissues compared to leaf tissues.

Significant changes in litter-associated fungal biomass often occur following the collapse of standing-dead litter. Fungal biomass rapidly decreases after submergence. This initial decline is followed by an increase in fungal biomass during later stages of submerged litter decay, possibly reflecting a shift to aquatic or semiaquatic fungal taxa. Despite changes in the environment, fungal decomposers typically account for a major portion of total microbial biomass associated with decaying litter. Simultaneous estimates of litter-associated fungal and bacterial biomass indicate that fungi typically account for >90% of the total microbial biomass on both standing and collapsed litter.

Fungal growth rates associated with both standing and collapsed plant litter are also significant, with peak growth rates as high as 0.10 per day.

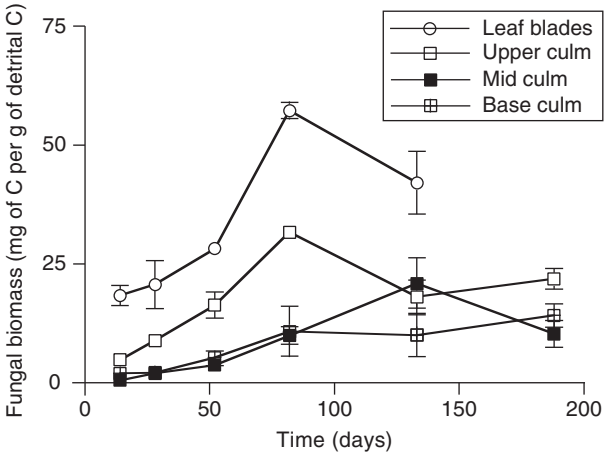

Figure 5 Fungal biomass associated with standing-dead leaf and culm litter of the freshwater emergent macrophyte *Erianthus giganteus*. Symbols indicate means ± 1 SE ($n = 3$). Data from Kuehn KA, Gessner MO, Wetzel RG, and Suberkropp K (1999) Standing litter decomposition of the emergent macrophyte *Erianthus giganteus*. *Microbial Ecology* 38: 50–57.

Corresponding fungal production has been found to peak at 1.0–3.0 mg of fungal C per g of detrital C per day. As observed with fungal biomass (above), fungal production also differs between plant organs, with higher production being observed in leaf than culm litter. Thus, like fungal biomass, fungal production may also vary depending on plant litter quality (lignin and nutrient concentrations). In addition, fungal production associated with emergent plant litter greatly exceeds bacterial production, accounting for >93% of the total microbial production when both microbial groups have been quantified simultaneously.

Factors Affecting Fungal Activity and Microbially Driven Plant Litter Decomposition in Marsh Ecosystems

As in streams, fungal activity associated with emergent plant litter in marsh ecosystems is controlled by a variety of physical and chemical conditions. These conditions are markedly different for fungi inhabiting standing-dead and submerged/sediment litter, as changes in the litter decay environment are accompanied by major shifts in both physical and chemical conditions. As indicated earlier, differences in litter-associated fungal biomass and production are often observed among plant litter organs (leaves vs. culms). Leaf litter typically contains lower concentrations of recalcitrant compounds (lignin) and higher concentrations of both nitrogen and phosphorus than corresponding culm litter. Thus, for a given litter substrate, fungal activity may depend on a combination of these internal factors (i.e., lignin to nutrient ratios, C:N:P ratios, etc.). To date, no studies have examined the potential influence of exogenous nutrient inputs (i.e., eutrophication) on fungal diversity or activity in freshwater marsh systems.

A number of laboratory and field studies have established that water availability is a key factor controlling the metabolic activities of microbial (fungal and bacterial) assemblages in standing-dead litter. Microbial respiration (CO_2 evolution) associated with standing-dead litter fluctuates rapidly upon exposure to wetting or drying conditions. Under laboratory conditions, rates of microbial respiration increase rapidly following addition of water to plant litter (from 10 to >200 μg of CO_2–C per g of AFDM per h within 5 min after being wetted). Respiration continues at high rates until plant litter is exposed to drying conditions. Under natural field conditions, rates of microbial respiration from standing-dead litter exhibit a cyclical diel periodicity (Figure 6), with the highest rates occurring at night when water becomes available (i.e., high relative humidity, dew formation) to litter inhabiting microorganisms. In

contrast, microbial respiration virtually ceases during the day as a result of increased desiccation stress. These diel patterns suggest that temperature-driven increases in relative humidity and subsequent dew formation are important controlling mechanisms underlying the nighttime increases in water availability and associated microbial respiration in standing litter.

Distinct differences in patterns and rates of microbial respiration have been observed among plant organs (leaves vs. sheaths vs. culms). Maximum respiration rates observed from standing leaf litter are considerably higher (>24%) than rates from corresponding sheath litter experiencing identical environmental conditions (Figure 6(a)). Furthermore, maximum respiration rates from standing culm litter are often an order of magnitude lower than rates from both leaf and sheath litter. Variation in rates of microbial respiration from litter substrates can be attributed to differences in litter water absorption patterns, litter quality characteristics, and the extent of fungal colonization (biomass). Maximum rates of respiration among litter fractions are positively correlated with litter-associated fungal biomass (e.g., $r > 0.65$), suggesting that fungi are likely responsible for a major portion of the respiratory carbon release from standing-dead litter.

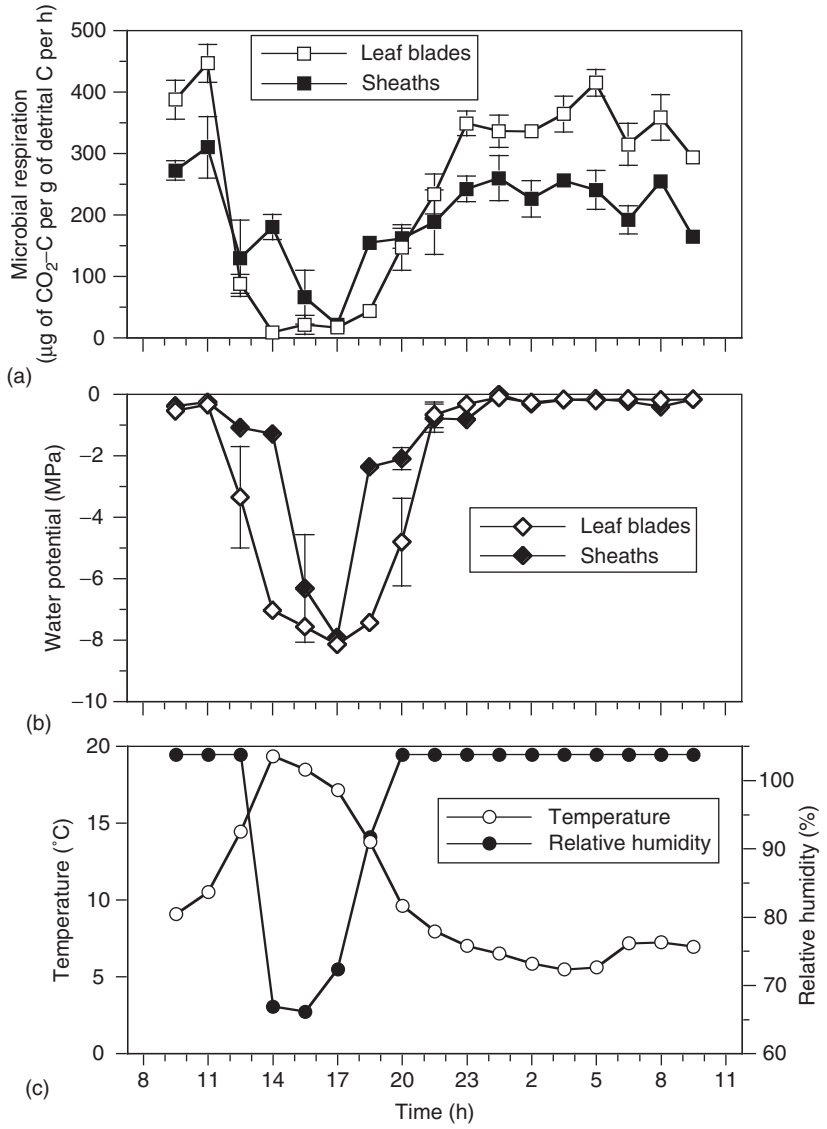

Figure 6 (a) Diel changes in rates of microbial respiration (CO_2 evolution) from standing-dead litter of *P. australis* within a temperate freshwater lake littoral marsh. Corresponding diel changes in plant-litter water potential (b) and temperature and relative humidity (c) are also illustrated. Symbols indicate means ± 1 SE ($n = 3$). Data from Kuehn KA, Steiner D, and Gessner MO (2004) Diel mineralization patterns of standing-dead plant litter: Implications for CO_2 flux from temperate wetlands. *Ecology* 89: 2504–2518.

Fungal Role in Decomposition of Emergent Plant Litter and their Importance at the Ecosystem Scale

When seasonal estimates of fungal biomass and production per gram of detritus are accompanied by areal (m^{-2}) estimates of emergent plant litter standing crop, the importance of fungi at the ecosystem scale can be estimated. Very few studies have attempted to quantify the impact of fungi at this scale. However, initial data suggest that fungal biomass and annual fungal production associated with wetland emergent plant litter per m^2 can be sizable when compared to other consumers. Because of considerable litter accumulation in freshwater marshes, annual standing stock of fungal biomass can average as much as 18 g of C per m^2. Substantial fungal production on areal basis have also been observed. For example, annual fungal production estimates associated with standing-dead *Typha angustifolia* leaf and stem litter totaled 70 and 45 g of C per m^2 per year, respectively. When combined, these annual production estimates indicated that roughly 10% of the annual aboveground *Typha* production was transformed and assimilated into fungal biomass. The loss of detrital carbon due to microbial (fungal) respiration (CO_2 evolution) associated with emergent standing litter is also a significant pathway of carbon flow in freshwater marshes. When integrated on an areal basis, estimated daily flux rates of between 1.4 and 3.3 g of C per m^2 per day have been reported for microbial assemblages inhabiting standing-dead *Juncus effusus* litter in a subtropical wetland. These flux rates were similar to or greater than CO_2 flux rates from the wetland sediments. Similarly, daily CO_2 flux rates reported from standing-dead *Phragmites australis* litter in a north temperate freshwater marsh were lower (51–570 mg of C per m^2 per day), but within the range of CO_2 flux estimates reported from wetland sediments in this type of climates. Although few in number, these studies provide some evidence that fungi likely play a key role in wetland carbon and nutrient cycles.

Conclusions

Fungal diversity in freshwaters can be high and includes representatives from all major fungal phyla, with the Ascomycota exhibiting the highest diversity and the Basidiomycota being underrepresented in comparison to terrestrial environments. The microscopic size, intimate association of fungi with their substrates, and scarcity of aquatic mycologists make detection and reliable identification of aquatic fungi difficult. However, the development and application of biochemical and molecular techniques in recent decades has greatly improved our ability to detect and quantify fungi associated with different substrates. These methods should greatly increase our understanding of the occurrence and importance of fungi in freshwater ecosystems in the future. Even though the key role of fungi in decomposition of CPOM and, hence, carbon and nutrient cycling in streams and wetlands is now widely recognized, these aquatic organisms are clearly understudied in comparison to other groups, such as algae or invertebrates.

Major gaps in our knowledge about fungi in freshwaters include

1. the virtual absence of data on freshwater fungi from polar and some tropical regions,
2. a lack of understanding of the relative contribution of chytrids to the decomposition of plant litter in freshwater environments,
3. a lack of data on the relative importance of fungi and bacteria in decomposition of submerged macrophytes and wood,
4. fungi associated with and decomposition of submerged and floating-leaf macrophytes are poorly understood, and
5. more quantitative and modeling studies are needed to understand the effects of global change (temperature, elevated nutrient loading, precipitation) on fungi and fungi-driven processes in freshwaters.

See also: Bacteria, Attached to Surfaces; Benthic Invertebrate Fauna; Carbon, Unifying Currency; Coarse Woody Debris in Lakes and Streams; Ecology and Role of Headwater Streams; Ecology of Wetlands; Eutrophication; Littoral Zone; Microbial Food Webs; Nitrogen; Natural Organic Matter; Nutrient Stoichiometry in Aquatic Ecosystems; Protists; Streams; Streams and Rivers as Ecosystems.

Further Reading

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Relevant Websites

http://aftol.org – Assembling the Fungal Tree of Life.

http://mycology.cornell.edu – Extensive directory of mycology internet resources.

http://www.life.uiuc.edu/fungi – Freshwater Ascomycete Database (also includes some data on mitosporic fungi).

http://www.indexfungorum.org – Index Fungorum (check current fungal names, search bibliography of systematic mycology).

http://www.msafungi.org – Mycological Society of America.

http://www.nhm.ku.edu~fungi – Trichomycetes, including online monograph.

http://www.botany.uga.edu/zoosporicfungi – Zoosporic Fungi Online.