17 Fungal Decomposers of Plant Litter in Aquatic Ecosystems

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I. Introduction

Fungi are ubiquitous in the biosphere – from glacial forefields in high mountain to the deep sea (Jumpponen 2003; Gessner and Robinson 2003; Damare et al. 2006) and from hot springs to the polar ice caps (Jones et al. 2000; Gunde-Cimerman et al. 2003; Magan, this volume). One of their basic functions in natural ecosystems is the decomposition of plant matter, such as leaves, wood and fruits (Harley 1971). The view that fungi are instrumental in plant litter decomposition has been a longstanding paradigm in terrestrial ecology (Dighton, this volume) but, for aquatic ecosystems, this notion has not gained wide acceptance. Nevertheless, there is now strong evidence that fungi are critically important, if not the predominant, decomposers of plant litter in marine and freshwater ecosystems (Newell 1993; Newell and Porter 2000; Gessner and Van Ryckegem 2003; Bärlocher 2005; Gulis et al. 2006b).

Fungal decomposers in aquatic ecosystems are particularly prominent at the interfaces between land and water, where dense growth of higher plants typically results in abundant litter supply when plants or plant parts senesce and die. These environments comprise coastal marine areas, inland wetlands such as mires (peatlands), freshwater swamps and marshes, including littoral zones of lakes and rivers, and forest ponds and streams, which receive plant litter from adjacent riparian vegetation. Plant matter decomposing in these environments may be constantly submerged, periodically or occasionally flooded, or permanently exposed to air as in the case of standing-dead shoots of emergent plants in salt and freshwater marshes. Since different types of plant matter may vary greatly in chemical composition, physical structure, particle size, and timing when they become available to microbial colonization, a range of opportunities exist for fungal development within these habitats. In contrast to terrestrial environments, the continual availability of water and, in many cases, the abundant supply of dissolved nutrients often create conditions that are particularly favourable for fungal growth and activity.

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To demonstrate that fungi act as important decomposers in a given environment, several conditions should be met:

1. Fungi must be present in the natural system, where they may be detected by direct observation or indirect methods involving chemical indicator molecules (Newell 1992; Gessner and Newell 2002; Tsui and Hyde 2003; Foster et al. 2004; Graça et al. 2005). Culturing techniques also may be useful, although they carry a greater danger of introducing bias.
2. Identified species must be able to grow and reproduce under conditions prevailing in the natural habitat, i.e. the available substrate and under the environmental conditions defined by abiotic factors such as humidity, salinity, oxygen concentration, and temperature.
3. They should elaborate the enzymes necessary to degrade plant tissues and to produce them in amounts sufficient to cause significant litter degradation.
4. These activities should result in mass loss of organic matter or, when species are growing only in mixed assemblages, in an acceleration of mass loss.
5. Finally, the fungi should be successful in competing with other organisms present in the system and thus either rapidly colonize a resource and grow at a competitive rate or be able to oust established species.

Ultimate proof of fungal participation in decomposition consists in demonstrating fungus-specific degradative activity. This may be indicated when activities of a fungus grown on litter in microcosms (Hicks and Newell 1984; Suberkropp 1991; Treton et al. 2004) are similar to the activities observed in situ. Careful application of antibiotics and fungal inhibitors (Padgett 1993), coupled with the kind of measurements given above, may also be useful, although this approach is loaded with potential pitfalls (Oremland and Capone 1988). More powerful and currently promising methods appear to be the quantification of mRNA and/or enzymes, both of which are likely to provide important insights in the future as transcriptomics and proteomics are eventually applied to microbial assemblages associated with decomposing plant litter.

Decomposition of plant remains involves a range of biotic and abiotic transformations that result in the formation of carbon dioxide and other mineral substances, dissolved organic matter (DOM), and fine particulate organic matter (FPOM), but also in the biomass production of microbial decomposers, such as fungi (Gessner et al. 1999). The rates of all these processes are governed by the response of decomposers to environmental conditions (external factors) and the intrinsic quality of litter (internal factors), and they are modulated by biotic interactions within and between different groups of decomposers and with other components of aquatic food webs. Outcomes can be divided into those affecting the decomposition process (Fig. 17.1, bottom left) and those affecting fungal performance (Fig. 17.1, bottom right). Outcomes pertaining to fungal performance relate to life-history patterns, often apparent as shifts in fungal community structure, mycelial growth, and allocation of resources to reproduction. Outcomes relevant at the ecosystem level include litter mass loss, nutrient dynamics including immobilization and mineralization, and generation of litter transformation products such as FPOM and DOM. Thus, plant litter decomposition may be viewed from an ecosystem process perspective or from a decomposer point of view (Fig. 17.1).

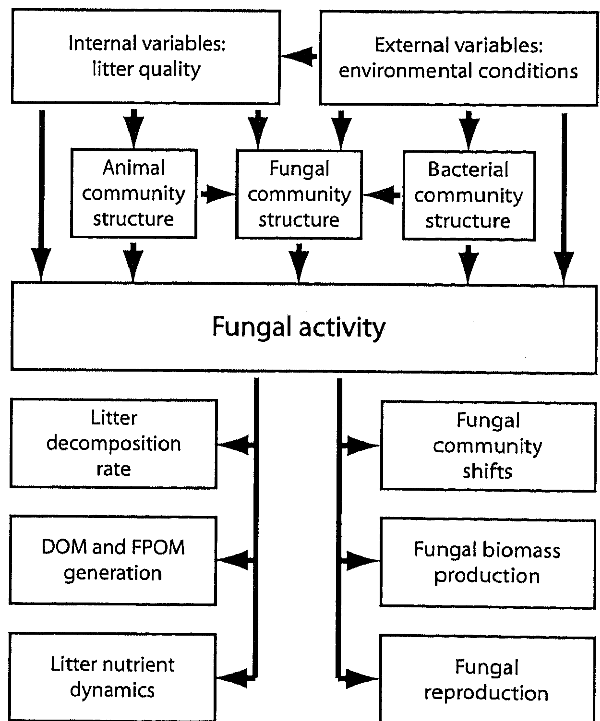

Fig. 17.1. Schematic representation of a fungus-dominated litter decomposition system as viewed from a process (*lower left cases*) and a fungal (*lower right cases*) perspective

This chapter will address both perspectives. Emphasis will be placed on two aquatic ecosystems in which fungal decomposers and plant litter decomposition have been studied to the greatest extent: standing-dead shoots of emergent vascular plants in salt and freshwater marshes (Sect. II.), and leaf litter that falls into forest streams from adjacent riparian vegetation (Sect. III). In addition, the importance of fungi as producers of biomass will be addressed at the ecosystem level; a comparison will be made with the biomass and production of bacteria, the other potentially important microorganisms associated with decomposing plant material; moreover, the role of fungi in decomposition budgets will be evaluated (Sect. IV.).

II. Fungal Decomposers in Salt and Freshwater Marshes

A. Marshes as Fungal Habitat

Salt and freshwater marshes are among the most productive ecosystems on the planet (Mitsch and Gosselink 2000). Emergent vascular plants, such as the smooth cord-grass *Spartina alterniflora* Loisel, the reed *Phragmites australis* (Cav.) Trin. ex Steud. and cattails (*Typha* spp.), are conspicuous features in these wetlands and often account for the greatest fraction of the total annual plant biomass produced (Dai and Wiegert 1996; Wetzel and Howe 1999). Since herbivore consumption is typically low (<1% of production; Wetzel and Howe 1999; Kreeger and Newell 2000), most of the plant biomass eventually enters into the detrital pool.

An important characteristic of most emergent wetland plants is that detachment of leaves and collapse of shoots does not immediately follow plant senescence and death (Newell 1993; Bärlocher 1997). Rather, shoots stay upright and leaves remain attached to the parent plant for extended periods, typically resulting in large amounts of standing-dead plant matter that accumulate in marshes (e.g. Asaeda et al. 2002). Fungi are a key component of the decomposer assemblage of this plant material (Newell 1993; Newell and Porter 2000; Gulis et al. 2006b), and may serve as an important food source for metazoan consumers (e.g. Silliman and Newell 2003). Thus, nutrient cycling and energy flow in these ecosystems are regulated to a significant extent by the metabolic activities of fungi associated with decaying plant material. The following section focuses on fungi in salt and freshwater marshes with special emphasis on fungal dynamics associated with standing-dead shoots of emergent wetland plants.

B. Fungal Diversity on Emergent Wetland Plants

Fungal communities associated with emergent plants in freshwater marshes are often taxonomically diverse. Early work by Saccardo (1898) reported 168 fungal taxa from shoots of a single species, *P. australis*, and a recent compilation of literature data now suggests that over 600 species have been recorded from this plant (Gessner and Van Ryckegem 2003). The most common fungal taxa identified from *P. australis* were members of the Ascomycota (94%, including 30% hyphomycetous and 22% coelomycetous anamorphs), with Basidiomycota (6%) occurring much less frequently. In a more limited survey, over 30 species were identified from standing-dead *Juncus effusus* (Kuehn and Suberkropp 1998a). Hyphomycetes and coelomycetes were the predominant taxa observed. However, examination of dead leaves attached to standing shoots in the field revealed large numbers of basidiomata of two white-rot fungi, *Panellus copelandi* and *Marasmiellus* sp., indicating that laboratory culturing techniques produced conditions that excluded sporulation of these and possibly other fungal species.

Several studies have reported successional changes of fungal taxa as shoot decomposition of emergent freshwater plants proceeds (Pugh and Mulder 1971; Apinis and Taligoola 1974; Van Ryckegem and Verbeken 2005). For example, based on observations of fruiting structures, Pugh and Mulder (1971) reported a succession of sporulating taxa during standing-dead and submerged decomposition of *Typha latifolia* leaves. Prevalent fungi observed during early decomposition stages (i.e. on standing-dead shoots) were similar to taxa observed on terrestrial plants, with primary colonization by phylloplane fungi such as *Aureobasidium pullulans*, *Cladosporium herbarum*, *Phoma typharum* and *Epicoccum nigrum*. This initial phase was followed by a secondary phase in which *Leptosphaeria* spp. were dominant. Predacious nematode-trapping fungi, such as *Arthrobotrys* and *Dactylaria* spp., were most prevalent during the final submerged stages of decomposition when plant matter had collapsed to the sediment surface.

A particularly marked shift in sporulating fungal taxa appears to coincide with the transition of decay of standing-dead shoots to decomposition of fallen or collapsed plant parts on the sediment (Van Ryckegem et al. 2007).

In addition to temporal shifts in community structure, fungi may exhibit distinct spatial distribution patterns on standing-dead shoots (Pugh and Mulder 1971; Apinis and Taligoola 1974; Poon and Hyde 1998; Van Ryckegem and Verbeken 2005). Different taxa may occupy specific plant parts, such as leaf blades, leaf sheaths, or the nodes and internodes of culms. In addition, fungal taxa associated with *P. australis* in tidal marshes showed distinct vertical distribution patterns in the plant canopy, which appeared to be a primary factor determining fungal community composition (Van Ryckegem and Verbeken 2005; Van Ryckegem et al. 2007). These small-scale distribution patterns on shoots may be a result of small-scale spatial variation in environmental conditions and/or differences in the resource quality of plant litter, such as varying amounts of recalcitrant compounds within different plant tissues.

In salt marshes, observations of fungal reproductive structures associated with standing-dead *S. alterniflora* revealed that ascomycete species of *Phaeosphaeria*, *Mycosphaerella* and *Buergenerula* are typically the most frequently encountered (Gessner 1977; Newell 1993, 2001a; Newell et al. 2000). Studies using molecular methods to describe fungal communities on decomposing wetland plants, such as ITS rDNA sequencing and terminal restriction fragment length polymorphism (T-RFLP), largely concur with observations based on traditional microscopic techniques (Buchan et al. 2002, 2003; Lyons et al. 2005; Torzilli et al. 2006). In particular, on leaf blades of standing-dead *Spartina* shoots in a South-Eastern U.S. salt marsh, analysis of ascospore expulsion rates, ITS clone libraries and T-RFLPs provided a similar picture of fungal community composition, with *P. spartinicola*, *Mycosphaerella* sp. and *P. halima* being the dominant taxa encountered (Buchan et al. 2002). Overall, these data suggest that fungal communities associated with *Spartina* are not particularly complex, with a single species accounting for most of the fungal biomass (Newell et al. 1989) and reproductive output (Newell and Wasowski 1995; Newell 2001a) in some salt marshes. This degree of species dominance appears to be in contrast with the often much more diverse fungal communities associated with standing-dead plants in freshwater marshes (see above), although strong dominance has also been found in freshwater marshes (Neubert et al. 2006).

Depending on characteristics of the habitat (i.e. degree and regularity of inundation by tides), fungi on standing-dead shoots in salt marshes may show vertical distribution patterns. Typical terrestrial fungi have often been observed on upper portions of standing-dead *S. alterniflora* shoots not exposed to tidal inundation (Gessner 1977), whereas marine taxa were most commonly observed on lower portions of plant shoots that were regularly submerged by tides (Gessner 1977). Similar observations have been reported for fungal communities on both standing-dead and collapsed plant parts of *P. australis* in a brackish tidal marsh (Poon and Hyde 1998; Van Ryckegem and Verbeken 2005; Van Ryckegem et al. 2007). Distinct fungal communities sporulated in different microhabitats (e.g. middle or basal canopy of standing-dead shoots), with greater numbers of terrestrial species associated with upper shoot portions. Flooding height and frequency influenced the vertical species distribution, presumably in response to not only water availability but also salinity.

C. Fungal Biomass and Production

In addition to the wealth of qualitative evidence showing pervasive fungal colonization of emergent wetland plants, the productivity and functional role of fungi has been assessed in several systems (e.g. Newell and Porter 2000; Gulis et al. 2006b). Historically, the lack of suitable methods to quantify fungal biomass and rates of biomass production has been a major impediment to obtaining such data. A particular problem has been the intimate association of fungi with decomposing plant tissue (Newell 1992) – hyphae penetrate the plant tissue, rather than adhere to its surface (Fig. 17.2; Newell et al. 1996b). Consequently, earlier estimates of fungal biomass based on measurements of hyphal length (Table 17.1), in particular after clearing of leaves, are likely to be severe underestimates (Newell 1992; Gessner and Newell 2002). However, these methodological problems have been largely overcome by the use of indicator molecules such as ATP, chitin, certain fatty acids in phospholipids and, particularly, the membrane lipid, ergosterol, which is likely to provide the most accurate estimates (Newell 1992; Gessner and Newell 2002). ATP is not specific for fungi but can be used as a re-

Table. 17.1. Some estimates of fungal biomass associated with decomposing plant litter in streams[a]

Fungal biomass ($mg\,g^{-1}$ detrital mass)	No. of streams	Litter type[b]	Method	Reference
0.12	1	LB(1)	Biovolume[c]	Iversen (1973)
8–49	1	LB(3)	Biovolume[d]	Findlay and Arsuffi (1989)
23	1	LB(1)	ATP	Findlay and Arsuffi (1989)
15–111	8[d]	LB(1)	ATP	Suberkropp and Chauvet (1995)
47–83	2	LB(2)	ATP	Suberkropp et al. (1993)
127–158	2	LB(2)	Ergosterol	Suberkropp et al. (1993)
61–155	1[e]	LB(7)	Ergosterol	Suberkropp et al. (1993), Gessner and Chauvet (1994)
78–226	4	LB(1)	Ergosterol	Methvin and Suberkropp (2003), Carter and Suberkropp (2004)
54–73	4	RCL	Ergosterol	Methvin and Suberkropp (2003), Carter and Suberkropp (2004)
1–175	10	WV	Ergosterol	Simon and Benfield (2001), Stelzer et al. (2003), Gulis et al. (2004)
2–25	4	WS	Ergosterol	Díez et al. (2002), Spänhoff and Gessner (2004)
24–86	2	RCWS	Ergosterol	Gulis et al. (unpublished data)

[a] Hyphal lengths were converted mycelial biomass by assuming an average hyphal diameter of 3 μm and a density of 500 $fg\,\mu m^{-3}$ (cf. Findlay and Arsuffi 1989; Newell 1992). ATP was converted fungal biomass assuming that fungal ATP accounted for 90% of the total ATP (cf. Findlay and Arsuffi 1989), at an average ATP concentration of 1.75 $mg\,g^{-1}$ mycelial dry mass (Suberkropp 1991; Suberkropp et al. 1993). Ergosterol was converted to fungal biomass assuming an average concentration of 5.5 $mg\,g^{-1}$ dry mass (Gessner and Chauvet 1993), unless more specific data were available

[b] LB, leaves in litter bags, with the number of leaf types in parentheses (maximum fungal biomass from decomposition experiments is given); RCL, randomly collected naturally occurring leaf litter (mean annual fungal biomass); WV, wood veneers and WS, wood sticks (range of fungal biomass from decomposition experiments); RCWS, randomly collected wood sticks (mean fungal biomass)

[c] Hyphal length determined after clearing of whole leaf material

[d] Hyphal length determined after grinding and collecting leaf fragments on membrane filters

[e] Different sites or years or both in the same stream

liable index of fungal biomass because, in terms of biomass, fungi commonly outweigh bacteria associated with plant litter (see Sect. IV.B.), and major sources of ATP other than bacteria are usually absent (Golladay and Sinsabaugh 1991; Suberkropp et al. 1993). Phospholipid fatty acid (PLFA) profiling has been used to quantify fungi in terrestrial habitats (e.g. Klamer and Bååth 2004) but has not yet been applied to fungi in aquatic habitats. Beyond the use of these biomass indicators, measurement of [^{14}C]acetate incorporation into ergosterol facilitates the determination of *in situ* fungal growth rates and production to assess the dynamics of fungal biomass accrual and loss (Newell and Fallon 1991; Gessner and Newell 2002).

Application of these and other quantitative methods has provided compelling evidence that fungi are a key component of microbial assemblages within standing-dead shoots of emergent wetland plants, suggesting an overall important contribution to carbon and nutrient cycling in marsh ecosystems (Gulis et al. 2006b). In pioneering studies involving a range of methods, fungal biomass in leaves of *S. alterniflora* ranged from 1.8% (microscopic determination of mycelial biovolume) to as much as 20% (immunosorbent assay, ELISA) of the total organic matter (Newell et al. 1989). Estimates based on the determination of ergosterol concentrations were intermediate (5%) but would have been about twice as high if a more realistic conversion factor (see Newell 1994) had been used. A large proportion of this biomass can be in the form of ascomata, which sometimes account for as much as 31% of the total fungal biomass in decomposing *Spartina* leaves (Newell and Wasowski 1995).

Assessment of multiyear patterns of fungal biomass associated with salt-marsh plants corroborates these earlier observations. Fungi associated with both standing-dead *S. alterniflora* (Newell 2001b) and *Juncus roemerianus* (Newell 2001c) accumulated substantial levels of biomass, with

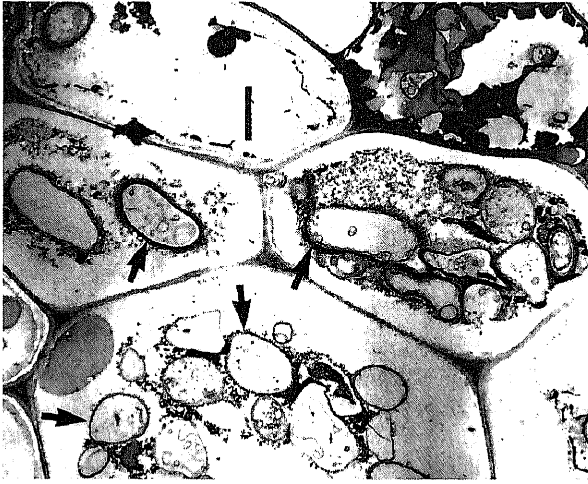

Fig. 17.2. Transmission electron micrograph of a cross-section of a yellow poplar leaf (*Liriodendron tulipifera* L.) that had been decomposing in a hardwater stream for 3 weeks. The leaf was fixed in 2% glutaraldehyde in 10 mM Na cacodylate, pH 7, immediately after it was removed from the stream. It was then post-fixed in 2% osmium tetroxide, dehydrated, embedded and sectioned. Note the masses of fungal hyphae within leaf cells. Four hyphae are indicated by *arrows*. Scale bar indicates 2 µm

estimated peak values exceeding 5% of the total organic mass of dead plant matter. On both plant species, fungal biomass was generally higher during the winter and spring and low during the summer, and *S. alterniflora* supported ~1.5-fold higher fungal biomass than *J. roemerianus*. In *S. alterniflora* leaves, ergosterol concentrations were negatively correlated with rainfall and tidal height (Newell 2001b), which supports findings from manipulative field experiments suggesting that prolonged water saturation has a negative effect on fungi associated with standing-dead wetland plants (Newell et al. 1996a).

Similar to the consistent temporal pattern over several years, a large-scale comparative study along the eastern coast of North America revealed no significant latitudinal differences in fungal biomass in leaves of standing-dead *Spartina* or *Juncus* in salt marshes between 29 and 43°N latitude (Newell et al. 2000). This suggests that substantial fungal production derived from the aboveground primary production of these salt-marsh plants is the rule. However, Samiaji and Bärlocher (1996) found much lower fungal biomass associated with *S. alterniflora* leaves in the Bay of Fundy (Canada) at 45°N, indicating that harsher environmental conditions at more northern latitudes may begin to limit fungal biomass accrual in standing-dead shoots.

Substantial fungal biomass accumulations have also been reported from standing-dead shoots decaying in freshwater marshes (Newell et al. 1995; Bärlocher and Biddiscombe 1996; Kuehn and Suberkropp 1998a; Gessner 2001; Findlay et al. 2002a; Newell 2003; Welsch and Yavitt 2003). For example, in *Erianthus giganteus*, a reed-like grass, fungal biomass increased gradually during shoot senescence and early decomposition to reach 7 and 4% of total detrital mass in leaves and culms respectively (Kuehn et al. 1999). However, fungal biomass varied spatially along the culm axis of this plant, resulting in a maximum concentration in the lower portion of only about 1.5%.

The observed accrual of substantial fungal biomass in shoots of wetland plants is consistent with high rates of biomass production that fungi can exhibit in this type of habitat. Newell (2001b) reported production rates of 70–329 $\mu g\, g^{-1}$ organic mass h^{-1} on decomposing leaf blades of *S. alterniflora* over a 3-year period, corresponding to growth rates of ~0.1–0.3% h^{-1}. Higher rates were generally observed in winter and spring and lower rates during the summer, consistent with patterns of fungal biomass accrual. Similar dynamics were observed for fungi associated with *J. roemerianus* (Newell 2001c), where rates ranged from 66–366 $\mu g\, g^{-1}\, h^{-1}$ and were lower in summer than in spring and autumn. High rates of fungal production are not restricted to salt marshes in subtropical climate and, as with fungal biomass accrual, no significant latitudinal difference in production rates was observed in either *Spartina* or *Juncus* (Newell et al. 2000), suggesting that appreciable fungal production is a common feature of standing-dead plant shoots in salt marshes. On *S. alterniflora*, fungal production rates were negatively correlated with the C:N but not the C:P ratio of leaves (Newell 2001b), indicating that nitrogen may be the critical nutrient controlling fungal growth in this system (e.g. Newell et al. 1996a). In *J. roemerianus*, however, no significant relationship was observed between rates of fungal production and C:N or C:P ratios of the plant material.

Fungal production rates in freshwater wetlands can also be comparable to those measured in salt marshes (Newell et al. 1995; Kuehn et al. 2000; Findlay et al. 2002a; Su et al. 2007). For example, fungal production rates on leaves of standing-dead *T. angustifolia* ranged from 12 to 359 $\mu g\, g^{-1}\, h^{-1}$ (Fig. 17.3), corresponding to growth rates of ~0.02–0.2% h^{-1} (K.A. Kuehn et al., unpublished

data), very similar to the ranges reported by Newell (2001b, c). Fungi associated with *Typha* stems showed similar seasonal patters in biomass production but rates were only 11–108 $\mu g\,g^{-1}\,h^{-1}$ (corresponding growth rates $\sim$0.05–0.4% h^{-1}), consistent with a much lower fungal biomass in stems (Fig. 17.3). Similar fungal production rates were observed for *Typha* and *Phragmites* stems (between 2 and 70 $\mu g\,g^{-1}\,h^{-1}$) in a tidal freshwater marsh (Findlay et al. 2002a). These data indicate that fungal production rates on standing-dead shoots of emergent wetland plants may vary significantly, depending on both environmental conditions and the intrinsic quality of plant litter.

Detachment of leaf blades from their parent plant, or collapse of standing-dead shoots to the sediments or overlying surface waters often lead to distinct changes in the biomass and productivity of the fungi associated with this plant material. In a study with *J. effusus*, fungal biomass and production rates declined rapidly following submergence of plant material colonized during the standing-dead phase (Kuehn et al. 2000). Similar declines of fungal biomass have been observed for fungi on the salt-marsh grass *S. alterniflora* (Newell et al. 1989), and the emergent freshwater plant *P. australis* in both lakes (Tanaka 1991; Komínková et al. 2000) and a tidal freshwater marsh (Van Ryckegem et al. 2007). These concordant patterns suggest that fungi colonizing standing-dead shoots of wetland plants are poorly adapted to the abrupt changes in environmental conditions associated with the transition of plant material from an aerial, standing-dead to an aquatic or semi-aquatic decay phase. However, despite the strong decline in fungal biomass following collapse or detachment of the plant material, fungi continued to account for a major portion of total microbial biomass (Newell et al. 1989; Sinsabaugh and Findlay 1995; Komínková et al. 2000; Kuehn et al. 2000; Su et al. 2007).

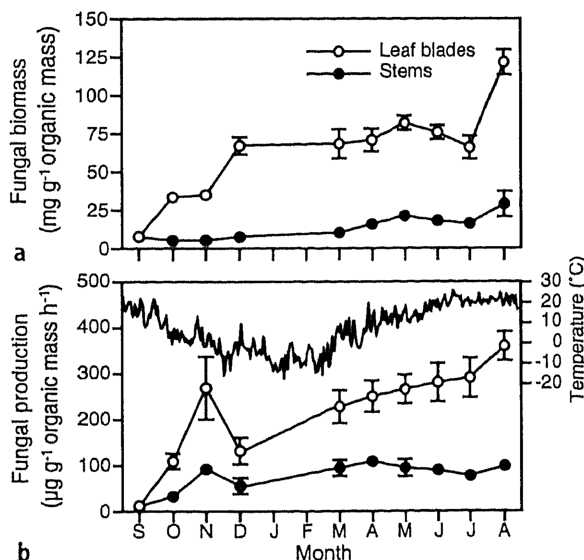

Fig. 17.3. Fungal biomass (**a**) and temperature trend and fungal production (**b**) associated with standing-dead shoots of *T. angustifolia* in a temperate littoral marsh (K.A. Kuehn et al., unpublished data). Symbols indicate means±1 SE ($n = 6$)

D. Enzymatic Capabilities

Fungi associated with emergent wetland plants can produce a variety of extracellular enzymes that are involved in the degradation of plant cell walls (Gessner 1980; Torzilli 1982; Pointing and Hyde 2000). Much of the current knowledge comes from laboratory-based studies of fungi isolated from decomposing shoots of the salt-marsh grass *S. alterniflora*. These isolates have typically been found to produce enzymes that degrade cellulose and hemicelluloses, including those containing xylose and arabinose (Gessner 1980; Torzilli 1982). Mixed results have been obtained concerning the ability of isolates to degrade pectin. Gessner (1980) found that only five of 20 isolates tested produced polygalacturonases. Torzilli (1982) detected pectinolytic activity when assays were carried out at pH 8 (pectin lyase) for all three species tested, but only one species produced pectinolytic activity when assayed at pH 5 (polygalacturonase). When four fungal species were provided with isolated cell walls from *S. alterniflora*, all of them grew, and filtrates from these cultures caused release of reducing sugars, indicating that these fungi were able to degrade polysaccharides embedded in native cell walls (Torzilli 1982). Three species grown in culture also caused losses of both the cellulose and hemicellulose fractions but not the lignin fraction of *Spartina* tissue (Torzilli and Andrykovitch 1986).

Although less efficient than typical terrestrial white-rot fungi (Basidiomycota), there is evidence that fungal decomposers associated with emergent wetland plants are often capable of degrading lignin. When provided with *Spartina* lignocellulose in which the lignin had been specifically radiolabelled, the ascomycete *Phaeosphaeria spartinicola* caused a loss of 6% (3.3% mineralized and 2.7% solubilized) in the lignin fraction within 45 days (Bergbauer and Newell 1992). In the same

time interval, *P. spartinicola* caused 26% loss in total lignocellulose (22% mineralized and 4% solubilized). Further, transmission electron micrographs of decaying *Spartina* leaves collected in the field revealed symptoms of soft rot from each of four ascomycete species examined, demonstrating the fungal ability to degrade cell wall material in its native state (Newell et al. 1996b). In line with this enzymatic and microscopic evidence, a high diversity of DNA sequences encoding laccase, a key enzyme in lignin degradation, has been demonstrated within the natural fungal community on *S. alterniflora* (Lyons et al. 2003). Laccase sequences amplified directly from decaying leaf blades were dominated by sequences characteristic of *P. spartinicola*, *Mycosphaerella* sp. and *P. halima*, which were previously identified as the principal fungal colonizers of standing *S. alterniflora* leaves (Newell 1993; Buchan et al. 2002, 2003). Thus, dominant fungi colonizing standing-dead *S. alterniflora* have the enzymes needed to degrade lignocellulosic tissues and can elaborate these enzymes when growing in their natural habitat. Fungi on other emergent wetland plants, both in salt and freshwater marshes, may have similar enzymatic capabilities, given the frequent occurrence of Ascomycota, including their anamorphs, on plant matter in these habitats.

E. Respiratory Activities on Standing-Dead Wetland Plants

If fungi are the dominant component of microbial assemblages associated with standing-dead wetland plants, as comparative estimates of fungal and bacterial biomass and productivity suggest (see below), then general microbial activities, such as CO_2 release resulting from microbial respiration, should largely be attributable to fungi (e.g. Kuehn et al. 2004). The rationale behind the arguments and conclusions in this section are based on this premise.

As in most terrestrial ecosystems, moisture availability is the single most important factor limiting microbial activity on and, thus, mineralization (CO_2 evolution) of dead emergent wetland plants (Gallagher et al. 1984; Newell et al. 1985; Kuehn and Suberkropp 1998b; Kuehn et al. 2004). Fungi are well adapted to this situation due to their ability to respond quickly (within 5 min or less) to wetting, permitting them to take advantage of even short favourable periods in an environment characterized by strongly fluctuating environmental conditions (Newell et al. 1985; Kuehn and Suberkropp 1998b; Kuehn et al. 1998, 2004). During desiccation stress, these fungi survive by accumulating intracellular compatible solutes (polyols and trehalose; Kuehn et al. 1998). As a result of these adaptations, microbial assemblages associated with standing-dead wetland plants, particularly fungi, are capable of mineralizing a significant portion of the plant carbon before the collapse of leaves or shoots to the sediment (Kuehn et al. 2004).

Respiratory activities of microbial assemblages associated with standing-dead *S. alterniflora* and *J. roemerianus* shoots fluctuate rapidly after exposure to wetting or drying conditions (Newell et al. 1985). During periods of desiccation (i.e. water content <30%, < -6.0 MPa, see Newell et al. 1991), CO_2 is released at very low rates (<10 μg CO_2-C g^{-1} dry mass h^{-1}). However, upon exposure to water (water content >50%, < -2.5 MPa), rates of CO_2 evolution increase greatly (to >100 μg CO_2-C g^{-1} h^{1}) and are maintained at high rates until exposure to drying conditions (Newell et al. 1985). Frequent wetting of standing *S. alterniflora* shoots had a negative effect on fungal growth and ascomata production of the dominant fungal species (*P. spartinicola*) colonizing leaves. This counter-intuitive result suggests that fungi on *S. alterniflora* shoots are specifically adapted to fluctuating water availability, and are dependent upon the cyclic episodes of desiccation and wetting for optimal growth and reproduction (Newell et al. 1996a).

Similar respiratory patterns have been reported for microbial assemblages associated with standing-dead plant shoots in freshwater marshes (Kuehn and Suberkropp 1998b; Kuehn et al. 1998, 1999, 2004; Welsch and Yavitt 2003). For example, rates of CO_2 evolution from standing-dead *P. australis* exhibited a pronounced diel periodicity, with the highest rates occurring at night when cooling increased relative humidity (to the point of dew formation) and thus water potentials of the plant material (Fig. 17.4). By contrast, respiratory activities virtually ceased during the day as a result of desiccation. This indicates that diel fluctuations in water availability play a key role in controlling microbial metabolic activities during the standing-decay phase of emergent vascular plants (Kuehn et al. 2004). Results of this study in a temperate wetland were remarkably similar to earlier observations from *J. effusus* in a subtropical freshwater marsh (Kuehn and Suberkropp 1998b), suggesting

that pronounced diel shifts in microbial carbon mineralization of standing-dead wetland plants may be a geographically widespread phenomenon.

As with fungal biomass and production (Fig. 17.3), large differences in microbial respiration patterns have been observed among plant litter types (species and organ) in terms of microbial colonization and metabolic response to water availability. Respiration rates associated with different *P. australis* shoot fractions varied considerably (Kuehn et al. 2004). Maximum respiration rates from standing-dead leaf blades were 24–42% higher than those from leaf sheaths under the same environmental conditions, and maximum respiration rates from standing-dead culms were always an order of magnitude lower. These differences in respiration rates were consistent with differences in water absorption patterns, known structural characteristics (e.g. lignocellulose concentration), and degree of fungal colonization among shoot fractions (Kuehn et al. 2004). Maximum rates of microbial respiration were positively correlated ($r = 0.72, p < 0.001$) with litter-associated fungal biomass. Similar correlations were found for rates of microbial CO_2 evolution from decaying standing *J. effusus* shoots ($r = 0.65$; Kuehn and Suberkropp 1998b), and a variety of other plant species from salt and freshwater marshes ($r = 0.77$, Newell 2003). These consistent patterns suggest that fungi are likely to be responsible for most of the respiratory carbon release from standing-dead marsh plant shoots.

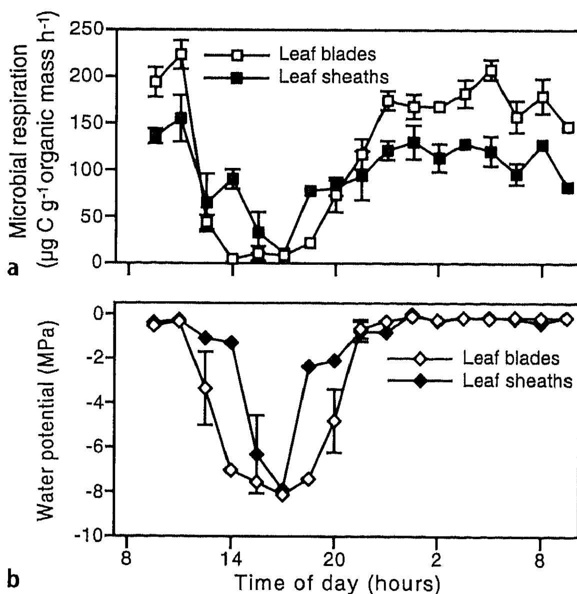

Fig. 17.4. Diel changes in rates of CO_2 evolution from leaf blades and sheaths on standing-dead *P. australis* (a) and leaf blade and sheath water potential (b) in a temperate littoral marsh (data from Kuehn et al. 2004). Symbols indicate means±1 SE ($n = 3$)

III. Fungal Decomposers in Streams

A. Streams as Fungal Habitat

The most striking feature of stream and river ecosystems is the unidirectional flow of water. Streams and rivers have therefore long been considered mere transport systems – for water, solutes and particulate matter. Current concepts emphasize, however, that running waters are actively metabolizing ecosystems with strong longitudinal and vertical coupling and intimate terrestrial linkages (e.g. Fisher et al. 2004). In forest streams, much of the resources available to decomposers and consumers enter the wetted channel in the form of leaf litter and wood derived from riparian vegetation (Webster and Meyer 1997). Total litter inputs are typically on the order of 500 g dry mass m^{-2} $year^{-1}$ but may exceed 2000 g m^{-2} $year^{-1}$ (Webster and Meyer 1997; Abelho 2001). Decomposition of this organic matter is a key process in streams that is driven by both microorganisms and invertebrates (Webster and Benfield 1986; Maltby 1992; Suberkropp 1998b; Gessner and Van Ryckegem 2003). Fungi rapidly establish as key components of decomposer assemblages on submerged litter (Bärlocher and Kendrick 1974; Suberkropp and Klug 1976), thus mediating to a large extent not only litter decomposition (Gessner and Chauvet 1994) but also the transfer of energy and nutrients to other trophic levels in stream food webs (Bärlocher 1985; Suberkropp 1992a; Graça 2001). This section focuses on fungal decomposers of leaf litter in streams. Emphasis is placed on a particularly important and well-studied group commonly referred to as aquatic hyphomycetes but also known as Ingoldian fungi or amphibious hyphomycetes (Webster and Descals 1981; Bärlocher 1992).

B. Fungal Diversity on Decomposing Litter

The fungi associated with decomposing plant litter in streams have received more attention than any other fungi in aquatic ecosystems. Representatives of all major fungal phyla (Chytridiomycota,

Zygomycota, Ascomycota and Basidiomycota), in addition to the fungus-like Oomycota (Kingdom Stramenopila), can be detected on submerged leaves or wood by means of both traditional and molecular techniques (e.g. Tsui and Hyde 2003; Nikolcheva and Bärlocher 2004; Shearer et al. 2007). Casual observations suggest that Chytridiomycota, Zygomycota and Oomycota probably play a minor role as decomposers of plant litter, while Ascomycota and their anamorphs, particularly hyphomycetes, assume the greatest importance (Bärlocher 1992). Using phyla-specific primers for the ITS region of rDNA, Nikolcheva and Bärlocher (2004) found that fungal communities of submerged leaves and wood were consistently dominated by Ascomycota in terms of species numbers and abundance, followed by Basidiomycota (on wood) and Chytridiomycota (in winter). With such a molecular approach, the Ascomycota also included most of the mitosporic fungi or anamorphs commonly detected by conventional methods, i.e. aquatic and terrestrial hyphomycetes, the majority of which appear to have ascomycetous affinities (Webster 1992). Although a diverse assemblage of Ascomycota (over 500 species) is associated with wood in freshwaters, sexual (teleomorphic) stages of Ascomycota are uncommon on decomposing leaves in streams (Shearer 1993; Cai et al. 2003). Terrestrial hyphomycetes are part of the phylloplane microbiota in plant canopies and thus colonize leaves before they enter streams (Bärlocher 1992). Their role in decomposition once leaves have fallen into streams is not certain, but their activity appears to be limited at the low winter temperatures that prevail in temperate regions after leaf fall (Bärlocher 1992; Maltby 1992). Dematiaceous and other hyphomycetes that do not produce intricately shaped conidia are less common on leaves in streams but are frequently isolated from submerged wood (Goh and Tsui 2003).

The most active fungal decomposers of leaf litter in streams are the aquatic hyphomycetes (Webster and Descals 1981; Bärlocher 1992; Suberkropp 1998b). The group includes at least 320 species (Descals 2005). Aquatic hyphomycetes are well adapted to the stream environment (Bärlocher 1992; Suberkropp 1992b; Gessner and Van Ryckegem 2003), and produce tetraradiate, sigmoid or variously branched conidia that have been interpreted as traits that facilitate attachment to the substrate in flowing water (Webster and Descals 1981; Webster 1987; Descals 2005; Dang et al. 2007). These fungi are able to quickly colonize ephemeral resources, such as leaf litter in streams, to grow and rapidly produce spores, and thus to complete their life cycle within a few weeks. At the low water temperatures prevailing after leaf fall in temperate climates, they are also able to outcompete other fungi, mainly of terrestrial origin (Bärlocher 1992).

Colonization of leaf litter by aquatic hyphomycetes is initiated by the impacting and trapping of conidia on leaf surfaces after the leaves enter a stream. Subsequent germination is rapid, within 2–6 h in most species (Read et al. 1992). Once established, the fungal hyphae extend inside the leaf matrix (Fig. 17.2), so that significant quantities of mycelial mass are built up within a few weeks after leaf colonization (Fig. 17.5a, see below). A striking feature of aquatic hyphomycete life cycle is that mycelial growth is closely followed by the production of conidiophores, which may start to release conidia in as little as 6–10 days after leaves are submerged. This has been demonstrated both in microcosm experiments (Suberkropp 1991; Gulis and Suberkropp 2003b; Treton et al. 2004) and under field conditions where sporulation rates of natural communities often peaked earlier than fungal biomass (Fig. 17.5b; Suberkropp et al. 1993; Baldy et al. 1995; Gulis and Suberkropp 2003c; Ferreira et al. 2006a). Sporulation rates rapidly

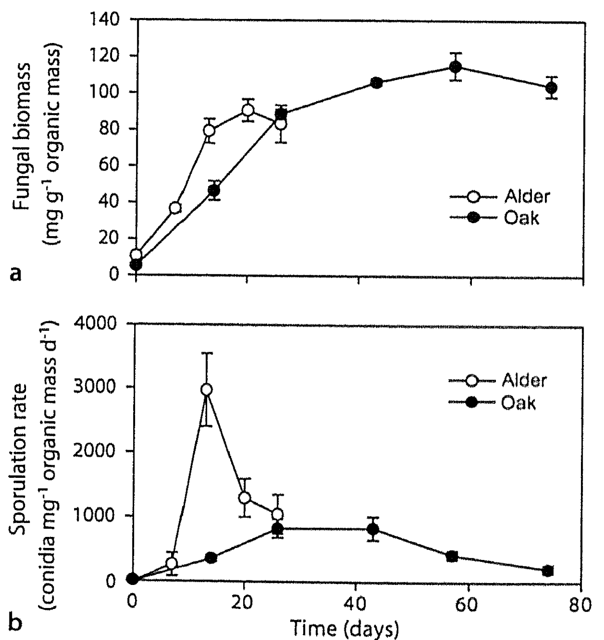

Fig. 17.5. Fungal biomass (a) and sporulation rates of aquatic hyphomycetes (b) associated with alder and oak leaves decomposing in a Portuguese woodland stream (data from Ferreira et al. 2006a). Symbols indicate means±1 SE (n = 4 to 6)

increase to maxima and then decline (Fig. 17.5b). Maximum rates can reach seven conidia μg^{-1} litter dry mass day^{-1}, although rates of at least an order of magnitude lower are frequently observed (Bärlocher 1982; Suberkropp et al. 1993; Gessner and Chauvet 1994; Suberkropp and Chauvet 1995; Bärlocher et al. 1995). The maximum rates of sporulation are controlled by both internal factors, such as litter quality (Gessner and Chauvet 1994; Ferreira et al. 2006b), and external factors such as temperature, alkalinity, pH and nutrient availability in stream water (e.g. Jenkins and Suberkropp 1995; Suberkropp and Chauvet 1995; Sridhar and Bärlocher 1997; Chauvet and Suberkropp 1998; Gulis and Suberkropp 2003c; see Sect. III.D. for nutrient effects).

Identification of many aquatic hyphomycetes is facilitated by characteristic conidial shapes. Diversity and community structure of these fungi is therefore often inferred from the relative abundances of released conidia that are captured either after incubation of leaf material in the laboratory, by filtering stream water or by examining foam collected from streams, in which conidia tend to be trapped (Suberkropp 1992b; Gessner et al. 2003; Bärlocher 2005). This approach is based on the assumption that sporulation rates correlate with the biomass of fungal species inside a leaf. Although this is not necessarily the case, much of the current knowledge on aquatic hyphomycete communities in streams has been derived from these types of studies. Individual leaves are colonized by typically 4–10 and up to 23 species (Shearer and Webster 1985; Suberkropp 1992b). On a stream scale, richness varies dramatically from just a few to >70 species, depending on collection effort and stream characteristics (Bärlocher 2005). A range of factors affect the composition of aquatic hyphomycete communities. These include latitude and altitude, season, water chemistry (pH, alkalinity, concentrations of inorganic nutrients, degree of pollution), composition of riparian vegetation, possibly interspecific competition, competition with and predation by invertebrates, and type of substrate. These factors are discussed in greater detail elsewhere (Bärlocher 1992, 2005; Suberkropp 1992b; Gessner and Van Ryckegem 2003).

Alternative approaches to studying aquatic hyphomycete communities make use of immunological or molecular techniques. Monoclonal antibodies raised against individual species and detected by enzyme-linked immunosorbent assay (ELISA) or immunofluorescence enable in situ identification and, to some extent, quantification of mycelial biomass of individual species (Bermingham et al. 1996, 1997). Even though the technique is highly specific and gives different insight into species abundances than the traditional approach based on counting conidia, it has not been developed to a point where it is practical for ecological investigations. Antibodies need to be available for each species in a community but to date they have been developed for only four species. DNA-based approaches to analyse aquatic hyphomycete communities include development of fluorescently labelled oligonucleotide probes for in situ detection of fungal mycelia (FISH) (Baschien et al. 2001; McArthur et al. 2001) and PCR-based techniques. Denaturing gradient gel electrophoresis (DGGE) and T-RFLP analyses of amplified fungal DNA from submerged leaf litter indicate that dominant phylotypes belong to aquatic hyphomycetes. These analyses also suggest higher species richness during the initial stages of decomposition than have been detected with the traditional microscopic identification of conidia, and some decline in the number of phylotypes as decomposition progresses (Nikolcheva et al. 2003, 2005). These results corroborate previous conclusions that aquatic hyphomycetes replace phylloplane/terrestrial fungi during early stages of decomposition (Bärlocher and Kendrick 1974; Suberkropp and Klug 1976), and they also suggest that some germinated aquatic conidia are unable to establish long-lasting viable colonies (Nikolcheva et al. 2005), pointing to a possible role of interspecific competition in structuring fungal communities on decomposing leaves in streams.

C. Fungal Biomass and Production

Following submergence of leaves in streams, fungal biomass usually increases gradually during a few weeks to months and then levels off or decreases slightly (Fig. 17.5a). The rate of fungal biomass accrual and maximum values attained largely depend on plant litter quality and stream water chemistry, and can vary dramatically among systems (Table 17.1). From a stoichiometric perspective, the lower C:N or C:P ratio of fungal biomass in comparison to leaf litter, and especially wood, should result in better fungal growth on substrates high in N and P (Stelzer et al. 2003; Gulis et al. 2006b). Indeed, slower fungal biomass accrual on low-N oak than high-N alder leaves (Fig. 17.5a; Gessner

and Chauvet 1994; Nikolcheva et al. 2003; Gulis et al. 2006a), on wood than on leaves (Nikolcheva et al. 2003; Stelzer et al. 2003), and generally lower levels attained on wood (Table 17.1) support this idea. However, both oak leaves and wood have high lignin concentration, which could be more important in determining fungal activity and decomposition rates than C:N or C:P ratios. In line with this argument, initial lignin rather than N or P concentration of leaf litter was strongly correlated with litter decomposition rate in a comparative study across seven leaf species, as were maximum fungal biomass and sporulation rate of aquatic hyphomycetes (Fig. 17.6), suggesting that leaf litter decomposition was controlled through a kinetic carbon limitation of fungal growth (Gessner and Chauvet 1994).

Estimates of fungal growth rate and production (Suberkropp and Weyers 1996; Gessner and Chauvet 1997) give a better understanding of carbon flow from plant litter through fungal compartment than estimates of fungal biomass alone, since losses of fungal biomass as conidia or mycelial fragments, through respiration or as a result of detritivore feeding and hyphal death can be extensive. Growth rate (or ratio of daily production to biomass, P:B) and production of fungi colonizing leaves during decomposition in litter bags peak very early following leaf submergence in streams when fungal biomass is still relatively low, and gradually decrease as decomposition progresses (Suberkropp 1995; Weyers and Suberkropp 1996; Baldy and Gessner 1997; Suberkropp 2001; Baldy et al. 2002). Growth rates attain maxima of 0.01 to 0.42 day^{-1} in decomposition experiments with litter placed in mesh bags, and vary from 0.01 to 0.17 day^{-1} from randomly collected leaf litter where the stages of decomposition are unknown (Suberkropp 1997; Methvin and Suberkropp 2003; Carter and Suberkropp 2004). In decomposition experiments with litter bags, fungal production has been found to peak at 0.6–16 mg g^{-1} organic litter mass day^{-1} (Suberkropp 1995, 2001; Weyers and Suberkropp 1996; Baldy and Gessner 1997; Pascoal and Cássio 2004; Pascoal et al. 2005), very similar to the range (0.8–10 mg g^{-1} day^{-1}) observed on randomly collected leaves in streams (Suberkropp 1997; Methvin and Suberkropp 2003; Carter and Suberkropp 2004). While average fungal biomass in randomly collected leaves is relatively constant throughout the year, fungal growth rates and production on a leaf mass basis (mg g^{-1} organic litter mass day^{-1}) are seasonal and peak in summer, probably in response to elevated temperature. Fungal biomass and daily production calculated on an areal basis (g m^{-2} of stream bed) peak in autumn and winter following leaf fall in temperate regions and sharp increases in the amounts of litter in stream channels (Suberkropp 1997; Methvin and

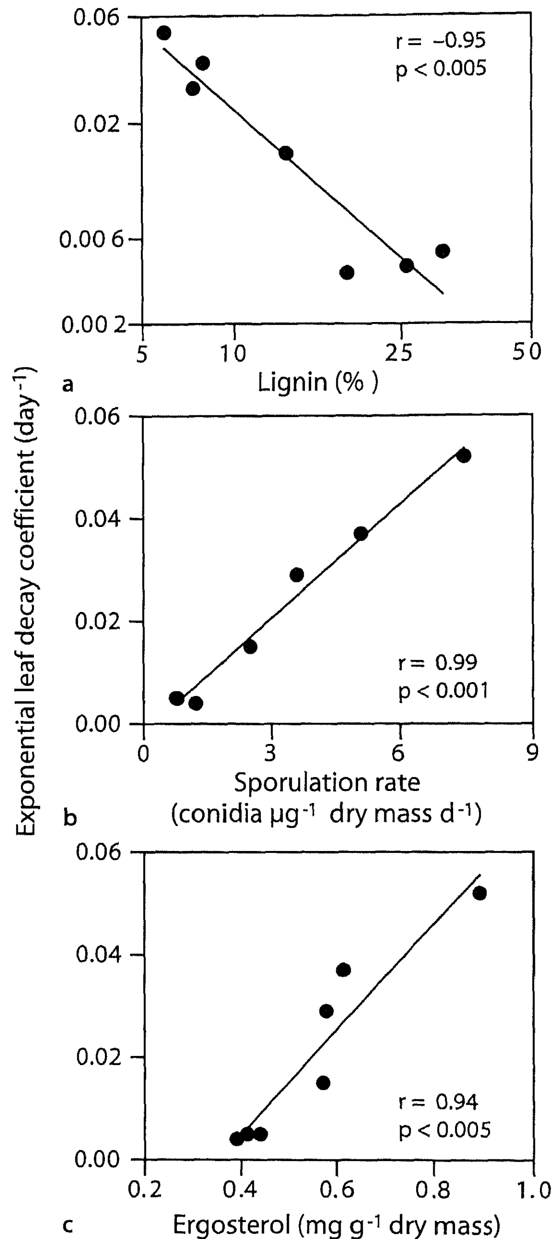

Fig. 17.6. Relationships between decay coefficients of litter from seven deciduous leaf species and concentrations of refractory leaf constituents (**a**), maximum sporulation rates of aquatic hyphomycetes on leaves (**b**), and maximum fungal biomass in leaves expressed as ergosterol concentration (**c**) (data from Gessner and Chauvet 1994). Symbols indicate means±1 SE ($n = 3$)

Suberkropp 2003; Carter and Suberkropp 2004). Similar data on fungi associated with submerged wood are scarce, but a recent estimate from randomly collected wood sticks suggests that both fungal growth rate and production (mg g^{-1} detrital mass d^{-1}) are about an order of magnitude lower than those on leaves in the same streams, while biomass is only about twofold lower (Gulis et al., unpublished data).

Increases in fungal biomass associated with leaf litter often correlate with increases in nitrogen concentration, suggesting that fungi immobilize N from the stream water (Gulis et al. 2006b). Phosphorus concentration of leaf litter also often increases during decomposition, concomitant with fungal biomass accrual (e.g. Robinson and Gessner 2000; Gulis et al. 2006a; Stallcup et al. 2006). These increases in fungal biomass and elemental concentrations enhance the palatability and nutritional quality of litter as a food source for stream invertebrates (Bärlocher 1985; Suberkropp 1992a).

D. Responses of Fungal Decomposers to Dissolved Nutrients

A variety of factors influence fungal activity and decomposition of plant litter in aquatic ecosystems. The most important ones are plant litter quality (e.g. concentrations of nutrients and refractory and inhibitory plant constituents), biotic parameters (e.g. fungal community structure, presence of detritivores), and environmental variables (e.g. temperature, pH, oxygen availability, and dissolved nutrient concentrations) (Fig. 17.1). The critical importance of dissolved nutrients in regulating fungal activity and fungal-mediated decomposition in streams was recognized about a decade ago (Suberkropp and Chauvet 1995), following earlier discovery that elevated nutrient concentrations can stimulate litter decomposition (e.g. Elwood et al. 1981), and has received much attention in recent years (e.g. Robinson and Gessner 2000; Rosemond et al. 2002; Gulis and Suberkropp 2003c; Ferreira et al. 2006b). Stream fungi can obtain inorganic nutrients (e.g. N and P) from both the plant litter they grow in and stream water (Suberkropp and Jones 1991; Suberkropp 1995). Since plant litter is typically low in N and P (i.e. C:N and C:P are much higher than those of mycelium), fungi are often nutrient-limited in oligotrophic streams, and their activity is significantly higher in streams with high dissolved nutrient concentrations (Suberkropp and Chauvet 1995) or following experimental nutrient addition (Grattan and Suberkropp 2001; Gulis and Suberkropp 2003c; Ferreira et al. 2006b). Strong positive correlations between dissolved nitrogen and/or phosphorus concentrations and fungal biomass, sporulation of aquatic hyphomycetes, respiration and/or exponential decay rates of leaves have been observed in various streams (e.g. Suberkropp and Chauvet 1995; Niyogi et al. 2003; Gulis et al. 2006a). In addition to this correlational evidence, microcosm studies have clearly shown stimulation of fungal activity and litter decomposition by dissolved N and/or P (Sridhar and Bärlocher 1997; Suberkropp 1998a; Gulis and Suberkropp 2003a, b). The most convincing results on the importance of dissolved nutrients, however, came from whole-stream nutrient enrichment experiments that demonstrated stimulation of microbial activity, and acceleration of leaf and wood decomposition in a variety of streams in different geographic settings (Gulis and Suberkropp 2003c; Stelzer et al. 2003; Gulis et al. 2004; Benstead et al. 2005; Ferreira et al. 2006b; Stallcup et al. 2006).

A few studies have not found evident effects of nutrient addition on either fungal activity or litter decomposition. This could happen when background levels of dissolved nutrients in streams are high and therefore not limiting to fungi (Royer and Minshall 2001; Simon and Benfield 2001), or when a non-limiting nutrient such as N is experimentally added to streams (Newbold et al. 1983) when another nutrient such as P is limiting (Elwood et al. 1981). Furthermore, fungal activity in nutrient-poor streams may be co-limited by N and P and, thus, the addition of either nutrient alone has no effect (Tank and Webster 1998; Grattan and Suberkropp 2001).

The shape of the dose-response curve between dissolved nutrient concentrations in water and fungal activity or litter decomposition rate depends on the range of concentrations examined. Studies in streams with low to moderate N and P concentrations strongly support a linear relationship (Suberkropp and Chauvet 1995; Niyogi et al. 2003). However, as the range of dissolved nutrient concentrations is increased to include high-nutrient streams, the relationship with fungal biomass, sporulation rate of aquatic hyphomycetes, microbial respiration, and leaf litter decomposition rather follows a Michaelis-Menten-type saturation model (Fig. 17.7; Rosemond et al. 2002; Ferreira et al. 2006b; Gulis et al. 2006a, b; Baldy et al. 2007).

Therefore, the linear responses observed in earlier experiments are likely to represent only the rising limb of the saturation model.

Nutrient stoichiometry of plant litter may modify the response of fungi to dissolved nutrients. A stimulating effect of exogenous nitrogen, for example, would be less pronounced when fungal demands can be met by nitrogen sources within decomposing plant material. Consistent with this idea, the effect of stream water nutrients appears to be greater on wood, which has very high C:N and C:P ratios, than on leaves (Stelzer et al. 2003; Gulis et al. 2004; Ferreira et al. 2006b). However, nutrient availability, whether external or internal, would be less critical when labile carbon is in limited supply, as may often be the case in leaf species with high concentrations of refractory carbon compounds such as lignin (Gessner and Chauvet 1994). Thus, the regulation of fungal activity and plant litter decomposition by dissolved nutrients may vary according to the relative impact and interactions of a range of controlling factors, both external ones related to the environment and factors intrinsic to the decomposing plant material.

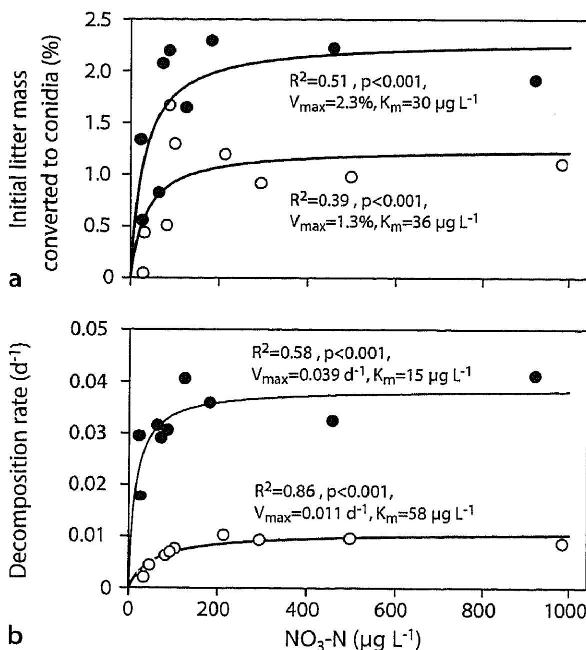

Fig. 17.7. Relationship between nitrate concentrations in stream water and percentage of initial litter mass converted into aquatic hyphomycete conidia (**a**) or litter decomposition rate (**b**). Data are fitted to a Michaelis-Menten saturation-type model: $V=V_{max}[S]/(K_m+[S])$, where V_{max} is the maximum parameter value, K_m is the nutrient concentration at which half of the maximum parameter value is achieved, and [S] is the nutrient concentration. *Open symbols* denote high-nutrient leaf litter (alder) and *closed symbols* indicate low-nutrient balsa wood veneers (data from Ferreira et al. 2006b)

E. Enzymatic Capabilities

Aquatic hyphomycetes produce a variety of extracellular enzymes that degrade the structural polysaccharides of leaves (Chamier 1985; Suberkropp 1992b). Enzymes that hydrolyze cellulose (endoglucanases, exoglucanases and exoglucosidase) and hemicelluloses (xylanases, xylosidase and arabinosidase) are produced by a number of species in culture growing on pure substrates or leaf material. Aquatic hyphomycetes also typically produce several enzymes that degrade pectin (Suberkropp and Klug 1980; Chamier and Dixon 1982). Pectin degradation leads to the softening and maceration of plant tissue, resulting in the release of mesophyll cells (Chamier 1985; Suberkropp 1992b). Both polygalacturonase and pectin lyase depolymerize pectin, and both are produced by aquatic hyphomycetes, but the latter appears to play a greater role in leaf maceration (Suberkropp and Klug 1980; Jenkins and Suberkropp 1995). Since aquatic hyphomycetes also produce enzymes to degrade proteins and lipids (Zemek et al. 1985; Zare-Maivan and Shearer 1988; Abdullah and Taj-Aldeen 1989), it appears that most plant polymers can be metabolized by the majority of these fungi.

Lignin may be an important exception. Evidence from laboratory studies indicates that aquatic hyphomycetes can degrade lignin-like substrates (Fisher et al. 1983; Zemek et al. 1985; Zare-Maivan and Shearer 1988; Abdullah and Taj-Aldeen 1989), and some freshwater fungi have been reported to solubilize lignin in wood (Bucher et al. 2004). However, ligninolytic capabilities of aquatic hyphomycetes appear to be limited, and the general difficulty to assess lignin degradation still hinders our understanding of this process under natural circumstances (Chamier 1985).

The general picture that emerges is, aside from quantitative difference in activity (Suberkropp et al. 1983), an apparent lack of specialization among species in terms of enzymatic capabilities. This indicates that aquatic hyphomycetes are a rather homogenous and generalist group with respect to nutritional niche breadth (Suberkropp 1992b), even though some substrate preferences and quite distinct communities associated with

leaves vs. wood have been reported (Gulis 2001; Bärlocher 2005; Ferreira et al. 2006b).

Little information is available on fungal enzyme activities associated with plant litter in streams, because fungi are not the only microbes colonizing this material. Nevertheless, since fungi typically dominate microbial biomass and production on leaf litter (see Sect. V.B.), they are likely to make a substantial contribution to the enzymatic activities associated with decomposing leaves in streams. For example, Golladay and Sinsabaugh (1991) found that exocellulase activity on maple leaves was closely correlated with fungal biomass, suggesting this hydrolytic activity was due to fungi. Similarly, the activity of four lignocellulose-degrading enzymes on wood showed generally positive relationships with fungal biomass (Tank et al. 1998). However, in another study, leaf-associated activities of three hydrolytic enzymes (xylanase, endocellulase and galacturonase) were lower in a hardwater than a softwater stream, whereas leaf softening and decay were faster, and fungal biomass accrual and sporulation of aquatic hyphomycetes were higher in the hardwater stream (Jenkins and Suberkropp 1995). It was therefore concluded that the hydrolytic enzymes examined were poor indicators of decomposition. Pectin lyase activity, by contrast, was higher in the hardwater stream, concomitant with faster leaf breakdown and greater fungal activity (Jenkins and Suberkropp 1995). These and similar results by Griffith et al. (1995) suggest that pectin degradation mediated by fungi is a key mechanism promoting leaf decomposition in streams (Suberkropp and Klug 1980; Chamier and Dixon 1982).

F. Significance of Fungal Diversity for Leaf Decomposition

In view of possible consequences of species extinction to ecosystem processes, the effects of fungal diversity on litter decomposition in streams have been examined in several studies. Results from field surveys suggest that species-poor fungal communities in streams affected by forestry practices or water pollution do not result in altered leaf decomposition rates (Raviraja et al. 1998; Bärlocher and Graça 2002). Similarly, varying species richness of aquatic hyphomycetes in microcosms had no effect on average leaf decomposition rates in mixed communities with up to eight species (Dang et al. 2005; Duarte et al. 2006). This points to a high degree of functional redundancy among aquatic hyphomycetes.

However, mixed cultures of two early colonizers enhanced decomposition by 73% compared to values expected from decomposition rates of single-species cultures (Treton et al. 2004). This outcome, in contrast to results from multispecies experiments (Dang et al. 2005; Duarte et al. 2006), is strong evidence of niche complementarity resulting in faster litter decomposition. In a similar vein, Bärlocher and Corkum (2003) reported a tendency towards faster decomposition with increasing fungal richness (1–5 species), although mixed communities never caused greater mass loss than the most effective species alone. Raviraja et al. (2006) also found that both species richness and identities affected leaf mass loss in microcosms, although again the most effective fungal species degraded leaves faster than did species mixtures.

There is also evidence that richness of aquatic hyphomycete communities can indirectly enhance decomposition through a positive effect on resource quality for invertebrate detritivores (Lecerf et al. 2005). Further, ecosystem processes other than litter decomposition (e.g. fungal biomass production) may be enhanced by diverse communities (Duarte et al. 2006). Lastly, even when average rates of decomposition are independent of species richness, variability of rates has been found to strongly decline with increasing fungal richness, as predicted from theoretical models (Dang et al. 2005). All else being equal, this should lead to higher predictability of litter decomposition rates when aquatic hyphomycete communities in streams are diverse.

IV. Importance of Fungal Decomposers in Aquatic Ecosystems

A. Fungal Biomass and Production at the Ecosystem Scale

When periodic estimates of fungal biomass or production per gram of litter are accompanied by data on the amount of plant litter present per m^2 of habitat, then fungal importance can be estimated at the ecosystem scale. Such estimates of fungal production in streams range from 16 to 193 $g\,m^{-2}\,year^{-1}$, and are generally comparable with estimates of bacterial and macro invertebrate

production (Suberkropp 1997; Methvin and Suberkropp 2003; Carter and Suberkropp 2004; Gulis et al. 2006b). Fungal production on an areal basis correlates well with the mean annual amount of leaf litter in streams. Amounts of benthic litter, in turn, are a function of litter input, downstream transport, and decomposition by microbes and invertebrates. Small woodland streams receive high litter input per m^2 of stream bed because they are intimately linked to their riparian zones, and also often retain litter effectively during high flows, because they are shallow and tend to have rough stream bottoms and other retention structures. Accordingly, annual fungal production per m^2 in these streams is particularly high (Gulis et al. 2006b).

Consistent with generally lower fungal activity on submerged wood than on leaves, fungal production on wood (randomly collected naturally occurring sticks, 5–40 mm in diameter) in two headwater streams was estimated at 9–11 $g\,m^{-2}\,year^{-1}$ (Gulis et al., unpublished data). Depending on stick size and stream water nutrient concentration, this translates into 2–13% of wood carbon assimilated by fungi per year, which is considerably lower than the estimated amounts of leaf carbon assimilated by fungi. However, taking into account the longer residence times of wood compared to leaves, the importance of wood-colonizing fungi in many streams is likely to be significant as well.

Fungal production associated with standing-dead plants in marshes is also sizeable and further points to the quantitative significance of fungi at the ecosystem scale. For example, in a subtropical coastal salt marsh, fungal biomass on standing-dead shoots of *S. alterniflora* ranged from 9 (summer–autumn) to 37 $g\,C\,m^{-2}$ of marsh area (winter–spring) (assuming 43% C in fungal dry mass). Estimated annual fungal production totalled 230 $g\,C\,m^{-2}\,year^{-1}$, equivalent to roughly 40% of the annual plant production (Newell 2001b). This estimate is based on the assumption that fungal communities of standing-dead *S. alterniflora* shoots are metabolically active (i.e. released from water stress) for 12 h per day (see Sect. II.E. above). Even if this were an overestimate, it indicates that conversion of plant biomass to fungal biomass can be substantial.

Substantial fungal production has also been observed in freshwater wetlands. Annual fungal biomass and production associated with leaf blades and stems of standing-dead *T. angustifolia* shoots in a north-temperate lake littoral marsh was 70 and 45 $g\,C\,m^{-2}\,year^{-1}$ respectively (K.A. Kuehn et al., unpublished data). This production estimate takes into account the diel periodicity in water availability (i.e. dew formation) that regulates microbial activities (see Sect. II.E. above). Substantial additional fungal production can occur on submerged litter in freshwater marshes. An annual production of nearly 100 $g\,C\,m^{-2}$ has been estimated in the submerged litter layer of another littoral marsh dominated by *P. australis* in a temperate lake (Buesing and Gessner 2006). Thus, all systems studied so far (i.e. submerged leaf litter in streams, and both submerged litter and standing-dead shoots in salt and freshwater marshes) have revealed very high potential for fungal production, suggesting a great importance of fungi in food webs and organic matter turnover at the ecosystem scale.

B. Fungal vs. Bacterial Biomass and Production

Studies in diverse streams (Sanzone et al. 2001; Findlay et al. 2002b) and salt and freshwater marshes (Sinsabaugh and Findlay 1995; Newell and Porter 2000) suggest that fungal biomass exceeds bacterial biomass on coarse submerged organic particles such as leaves, wood and other plant litter, whereas bacteria assume greater importance on finer organic particles and possibly on decaying floating-leaved macrophytes (Mille-Lindblom et al. 2006). In streams, fungi typically account for 88–99.9% of the microbial biomass (i.e. the combined fungal and bacterial biomass) developing on decomposing leaves (e.g. Findlay and Arsuffi 1989; Baldy et al. 1995; Weyers and Suberkropp 1996; Baldy and Gessner 1997; Hieber and Gessner 2002; Gulis and Suberkropp 2003a). Given these ratios of fungal and bacterial biomass, and the experimentally demonstrated preference of stream detritivores for fungal-colonized leaf patches (Arsuffi and Suberkropp 1985; Suberkropp 1992a), fungi appear to play a much greater role than bacteria in altering the palatability and food quality of decaying leaf litter in streams, and provide a much larger fraction to the nutrition of invertebrate detritivores (Suberkropp 1992a). Fungi appear to dominate microbial communities also on submerged wood in streams (67–97% in terms of biomass; Findlay et al. 2002b; Stelzer et al. 2003) but information is still very limited at present.

Fungal dominance of microbial biomass (typically >90%) associated with standing-dead plant

shoots and submerged litter in freshwater marshes (Sinsabaugh and Findlay 1995; Newell et al. 1995; Komínková et al. 2000; Kuehn et al. 2000; Findlay et al. 2002a; Su et al. 2007) and salt marshes (Newell 1992, 1993; Newell and Porter 2000) is well established. For example, microbial biomass associated with naturally standing-dead shoots of the freshwater sedge, *Carex walteriana*, was dominated by fungi, with bacterial biomass often less than 0.5% that of fungi (Newell et al. 1995). Bacterial biomass increased significantly once standing-dead plant material fragmented and fell to the sediment surface. However, despite the change in decay conditions, fungal biomass still accounted for 97% of the total microbial biomass (Newell et al. 1995).

Bacteria may have higher growth rates and shorter turnover times than fungi, suggesting that comparisons between both groups are more meaningful on the basis of production than biomass. However, outcomes of both types of comparisons have generally been similar. In particular, fungal production greatly exceeded bacterial production (1–627×) associated with leaves in streams in all studies when both microbial groups were followed simultaneously (Suberkropp and Weyers 1996; Weyers and Suberkropp 1996; Baldy et al. 2002; Pascoal and Cássio 2004; Pascoal et al. 2005). This consistent finding further emphasizes the key importance of fungi colonizing leaf litter in stream ecosystems. One exception from the general pattern is an experiment with fresh green leaves collected in summer where fungal and bacterial production estimates were comparable (Baldy and Gessner 1997).

Similar findings have been reported for fungi colonizing standing-dead shoots and submerged litter in salt and freshwater marshes, where fungal production accounted for >93% of the total microbial production (Newell et al. 1995; Newell and Porter 2000; Kuehn et al. 2000; Findlay et al. 2002a; Su et al. 2007). By contrast, bacterial production outweighed fungal production (>8:1) on submerged *P. australis* litter in a littoral marsh of a lake (Buesing and Gessner 2006). The inverse relationship between fungi and bacteria in this marsh was due to a particularly high bacterial production (average of 660 g C m^{-2} $year^{-1}$), rather than a low fungal production (93 g C m^{-2} $year^{-1}$), and it is possible that this very high bacterial production was an overestimate caused by the high concentration of leucine used to determine protein synthesis rates as a measure of bacterial production (Gillies et al. 2006).

C. Decomposition Budgets

Estimates of the different fates of decomposing plant material in addition to conversion into fungal and bacterial biomass have been made in several aquatic ecosystems. However, most budgets considering these fates are partial and have been calculated for a particular period, usually advanced decomposition stages. Consequently, they do not reflect the dynamic changes that characterize the entire decomposition sequence. Since much of the fungal biomass produced during litter decomposition is transient and eventually lost as CO_2 or in other forms (Gessner et al. 1999; see below), fungi often appear more important when budgets are calculated at the time of maximum fungal biomass, rather than at final decomposition stages when the remaining mycelial biomass is relatively low (e.g. in streams, 0.5–3.9% of the initial organic litter mass; Gessner et al. 1997). Aquatic hyphomycetes on leaves in streams channel a substantial proportion of their production (1.0–7.3% of initial organic litter mass) into the formation of conidia (Findlay and Arsuffi 1989; Suberkropp 1991; Baldy et al. 1995; Hieber and Gessner 2002; Ferreira et al. 2006b), and two species grown on leaves in microcosms even allocated 46 and 81% of their production to conidia, equivalent to 7 and 12% of leaf mass loss respectively (Suberkropp 1991).

Estimates of fungal reproductive output are also available for fungi growing on standing-dead *Spartina* shoots in a salt marsh. Like aquatic hyphomycetes in streams, these salt-marsh fungi allocate substantial amounts of fungal biomass to reproductive structures (ascomata of *Phaeosphaeria spartinicola* and *Mycosphaerella* sp.). During periods of leaf wetness, an average of 59 ascospores per hour were found to be released per cm^2 of the upper two thirds of decaying leaf blades attached to standing-dead shoots. This value was conservatively estimated to represent 7.5 g fungal biomass per m^2 of salt marsh per year, and nearly 5% of the total mycelial production in these leaves (Newell 2001a). Since fungal spores typically contain high concentrations of nutrients (Dowding 1976), spore release is likely to be a more significant pathway of N and P loss from decomposing leaves than of carbon loss.

CO_2 fluxes from standing-dead plant shoots as a result of microbial (presumably, mostly fungal) respiration can represent an important pathway of carbon flow in wetlands (Kuehn and Suberkropp 1998b; Kuehn et al. 2004). Taking

into account diel fluctuations in respiration rates (see Sect. II.E.) and estimates of litter standing crops, daily fluxes from standing-dead *J. effusus* were estimated at 1.4–3.6 g C m^{-2} (Kuehn and Suberkropp 1998a), which generally exceeded CO_2 fluxes from sediments in the same wetland (0.12–2.4 g C m^{-2} day^{-1}; see Roden and Wetzel 1996). CO_2 fluxes from standing-dead *P. australis* shoots were lower (0.05–0.57 g C m^{-2} day^{-1}) but still within the range of those from wetland sediments in north-temperate climates (Kuehn et al. 2004). As a result, fungi and, to a smaller extent, other microorganisms could mineralize a significant portion of *J. effusus* leaf (~28%), and *Phragmites* leaf (~8%) and sheath (~29%) annual production under standing-dead conditions (Gulis et al. 2006b). CO_2 fluxes from decomposing leaf litter in streams are also sizeable, and were estimated in decomposition experiments to range from 17 to 56% of total leaf carbon losses (Elwood at al. 1981; Findlay and Arsuffi 1989; Baldy and Gessner 1997; Gulis and Suberkropp 2003c).

Estimates of the fraction of litter assimilated by fungi can be calculated as the sum of fungal production and respiration, or from fungal production when fungal growth efficiency is known. For stream fungi, growth efficiency ranges from 24 to 60% (Suberkropp 1991; Gulis and Suberkropp 2003b). This translates into a fungal assimilation of 5 to 97% of the annual leaf input (Gulis et al. 2006b). Estimates for freshwater marshes suggest that at least ~10% of the annual aboveground *Typha* production (K.A. Kuehn et al., unpublished data) and 15% of aboveground *Phragmites* production (Buesing and Gessner 2006) go into the production of fungal biomass. Both estimates consider only part of the fungal production per m^2 of marsh, because either the standing-dead or submerged decomposition phase was ignored. Total fungal production therefore is likely to be much higher in both cases.

One of the fates of leaves degraded by fungi in streams is the conversion to dissolved and fine particulate organic matter (DOM and FPOM; Suberkropp and Klug 1980; Gessner et al. 1999; Baldy et al. 2007). The ratio of released DOM to FPOM is variable but typically greater than one (Gessner et al. 1997), and the amounts of the two released fractions combined (FPOM+DOM; 36% of leaf mass loss in Findlay and Arsuffi 1989, and 8% in Baldy and Gessner 1997) may be on the order of the fraction released as CO_2 (40 and 17% respectively). Greater release of DOM compared to FPOM (barely detectable) has been reported from *Phragmites* leaves, with DOM representing some 39% of the initial leaf mass (Komínková et al. 2000). FPOM and DOM can also be generated by feeding, and defecation or excretion by leaf-shredding macroinvertebrates (Wallace and Webster 1996). However, even where detritivore-mediated leaf conversion to other forms of organic matter and CO_2 is high (e.g. >50% of total leaf mass loss vs. 14–18% for fungi; Hieber and Gessner 2002), fungi may significantly contribute to litter conversion in an indirect way by stimulating litter consumption by detritivores (Suberkropp 1992b).

V. Conclusions

A diversity of aquatic habitats occurs at land–water interfaces where the productivity of plants is often high and large amounts of plant matter enter the detrital pool. Environmental conditions (e.g. temperature, salinity, nutrient availability) vary widely within and across these systems where different types of plant matter from both aquatic and terrestrial sources are decomposing. The diversity of fungi present and potentially active in these systems is high. However, given the paucity of data for many systems, the overall importance of fungi as decomposers across aquatic ecosystems remains difficult to assess. Identification of the fungi present, by either traditional or molecular methods, is a prerequisite but not sufficient to ascertain an important functional role of these organisms in ecosystems. However, quantitative data are becoming increasingly available to evaluate the significance of fungi as agents of decomposition and nutrient cycling, producers of biomass, and mediators of organic matter transfer in aquatic food webs.

In a few types of aquatic ecosystems, particularly the marshes and streams discussed in this chapter, the role of fungi as decomposers of organic matter and producers of biomass has been demonstrated to be substantial. Fungi are clearly the key decomposers of standing-dead emergent plants in freshwater wetlands and salt marshes, and of terrestrial leaf litter in streams. The dominant species in these ecosystems possess the enzymatic potential necessary to degrade the structural compounds of litter, although fungal lignin degradation in streams is not well documented. Fungal biomass associated with decomposing plant material can easily exceed 10% of total litter mass in these systems, and typically outweighs bacterial biomass.

Comparisons of fungi and bacteria on a production basis generally yield similar results. Fungal biomass production at an ecosystem scale varies among systems and sites but can approach and even surpass 100 g C m^{-2} $year^{-1}$. Evidence from various sites suggests, furthermore, that fungal activity can be responsible for a large proportion of leaf mass loss during decomposition, leading to the mineralization of plant organic matter to CO_2 as well as conversion into DOM and FPOM.

Fungal activity and, consequently, leaf decomposition rates are regulated both by internal (e.g. litter nutrient concentration and carbon quality) and external (e.g. temperature, dissolved nutrient concentrations) factors. As fungi grow in leaf litter, their production is partitioned between the mycelium and reproductive structures. A significant fraction of biomass is ultimately channelled into spores. Fungi growing in decomposing leaves can immobilize nutrients such as nitrogen and phosphorus, thereby increasing the palatability and nutritional value of plant litter to invertebrate consumers. Thus, fungal decomposers assume multiple key roles in the aquatic ecosystems presented in this chapter. In other aquatic ecosystems, fungi may be important as well. However, these have not received sufficient attention to make assessments with any confidence, especially in view of some data (e.g. from mangrove swamps, seagrass beds or floating-leaved macrophytes; Gessner et al. 1997; Mille-Lindblom et al. 2006) that suggest notable differences may exist among aquatic systems in the roles of fungal litter decomposers.

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