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Lentic and Lotic Habitats as Templets for Fungal Communities: Traits, Adaptations, and Their Significance to Litter Decomposition Within Freshwater Ecosystems

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Abstract

Decomposition of plant matter is a key ecosystem process and considerable research has examined plant litter decay processes in freshwater habitats. Fungi are common inhabitants of the decomposer microbial community and representatives of all major fungal phyla have been identified within freshwater systems. Development and application of quantitative methods over the last several decades have firmly established that fungi are central players in the decomposition of plant litter in freshwaters and are important mediators of energy and nutrient transfer to higher trophic levels. Despite the critical roles that fungi play in carbon and nutrient cycling in freshwater ecosystems, there are notable differences in the types and adaptations of fungal communities between lotic and lentic habitats. These differences can be explained by the wide range of hydrologic, physical, chemical and biological conditions within freshwater systems, all of which can influence the presence, type, and activity of fungal decomposers and their impact on litter decomposition. This following seeks to provide a brief overview of the types, adaptations, and role of fungi within lotic and lentic freshwater ecosystems, with a particular emphasis on their importance to litter decomposition and the key environmental conditions that impact their growth and decay activities. This discussion will specifically focus on fungal dynamics occurring on plant litter in forested headwater streams and emergent freshwater marshes, since published data concerning their role in these systems is considerably more abundant in comparison to other freshwater habitats.

Introduction

It is widely established that fungi are common inhabitants of the microbial community in freshwater ecosystems around the globe. Representatives of all major fungal groups (Chytridiomycota, Zygomycota, Ascomycota and Basidiomycota) and fungal-like organisms (Stramenopiles) have been identified in freshwater systems (Shearer, 1993; Tsui and Hyde, 2003; Nikolcheva and Bärlocher, 2004; Shearer et al., 2007; Wurzbacher et al., 2011; Duarte et al., 2015), and their corresponding life styles are an integral component of nearly every trophic level. Although important as pathogens, parasites and symbionts, a major functional role of fungi in freshwater ecosystems is the breakdown and mineralization of both allochthonous and autochthonous organic matter. Compelling evidence has accumulated over the last several decades that point to fungi as being key players in the decomposition of plant litter in freshwaters (Gulis et al., 2006b; Gessner et al., 2007; Kuehn, 2008; Krauss et al., 2011; Gulis et al., 2009). Furthermore, it is now widely accepted that fungal growth and biomass accumulation within decaying plant litter also represents a critical food resource for detritus feeding consumers (e.g., Bärlocher, 1985; Suberkropp, 1992; Bärlocher and Sridhar, 2014). Thus, fungi also serve as important mediators in the processing and flow of carbon, nutrients (N & P), and essential biochemical compounds to higher trophic levels within aquatic food webs (e.g., Cross et al., 2006; Arce-Funck et al., 2015).

Freshwater ecosystems are intimately coupled to, and controlled by, the hydrological cycle. As precipitation falls on the terrestrial landscape, surface waters will follow a drainage or collection pathway that is dictated by physical characteristics of the surrounding watershed (i.e., geomorphology). Many lotic ecosystems begin as small streams in upper elevations of the

watershed (headwaters), where water begins its journey down slope in response to gravity. These headwater streams eventually connect with other streams that flow into catchment basins forming lentic freshwater ecosystems, such as ponds, lakes, and inland wetlands, or eventually coalesce further to form larger rivers that flow into coastal regions forming lakes (e.g., oxbows), floodplain habitats, and tidal marshes as freshwater transitions into the marine environment. Along this freshwater continuum, there are marked changes in hydrologic, physical, chemical, and biologic conditions, all of which forms a habitat templet (e.g., Townsend and Hildrew, 1994) that influences the presence, types, adaptations, and decay activities of fungal decomposers.

Despite the critical roles that fungi play in carbon and nutrient cycling, there are notable differences in fungal communities between lotic and lentic freshwater habitats, which can be explained by the spatial and temporal heterogeneity in environmental conditions encountered within these systems. In streams and rivers, aquatic hyphomycetes are among the most well-recognized and extensively studied fungal group. These fungi comprise an ecological assemblage of ~300-320 species (Shearer et al., 2007; Duarte et al., 2013b) that typically dominate the fungal communities associated with decaying plant litter (Nikolcheva et al., 2005; Seena et al., 2008; Duarte et al. 2015), much of which is leaf litter and wood derived from riparian vegetation. Aquatic hyphomycetes complete their entire life cycle under submerged or amphibious conditions and are uniquely adapted to life in the lotic environment, where they produce asexual reproductive spores (conidia, Fig 1) that are morphologically adapted for dispersal and attachment to litter substrata in flowing water (Webster and Descals, 1981; Descals, 2005). In contrast to stream systems, fungal communities in lentic freshwater ecosystems, such as lakes, ponds and wetlands, are much more diverse and may comprise a variety of terrestrial and aquatic fungi (e.g., chytridiomycetes, ascomycetes, and basidiomycetes) depending on the habitat

(pelagic vs. littoral) and specific environmental decay conditions present (e.g., submerged vs. aerial standing litter) (Fig 1) (Gessner and Van Ryckegem, 2003; Tsui and Hyde, 2003; Wurzbacher et al., 2011). These fungi may colonize a wide variety of plant litter substrata, ranging from phytoplankton to submerged, floating-leaf, and emergent macrophytes as well as inputs of terrestrial plant litter.

Fungi and the decomposition process

The breakdown and decomposition of plant litter in freshwater ecosystems encompasses a complex array of biotic and abiotic processes that result in the production of decomposer biomass (microbial and invertebrate), release of CO_2 and nutrients (N and P) through organic matter mineralization, as well as the release of dissolved and fine particulate organic matter (Gessner et al., 1999; Kuehn, 2008). From a purely fungal perspective, the rates of these decay processes are strongly influenced by the response of fungal communities to the prevailing environmental decay conditions, the intrinsic quality of the detrital resources they are metabolizing, and the myriad of potential interactions that may occur within and between different decomposer groups within aquatic detrital food webs (Gulis et al., 2006b; Gessner et al., 2007; Kuehn, 2008; Gulis et al., 2009). For example, allochthonous or autochthonous plant litter entering freshwater environments may be quite diverse and vary in its chemical quality (e.g., C:N:P ratios, lignin content), physical characteristics, and the time when it becomes available to fungal decomposers. Likewise, plant litter in freshwater environments may be constantly submerged, intermittently flooded, or temporarily exposed to air, as in the case of standing emergent macrophyte litter within freshwater marshes and lake littoral zones. These types of hydrologic conditions as well as other environmental variables (e.g., temperature, pH,

oxygen availability) can significantly influence the colonization, growth, and decay activity of fungi on/within plant litter and the development and dispersal of their reproductive propagules.

The following review article seeks to provide a brief overview of the types, adaptations, and quantitative role of fungi in lotic and lentic freshwater habitats, with a particular emphasis on their importance and the key environmental conditions that impact their growth and decay activities. This discussion will specifically focus on fungal dynamics occurring on plant litter in forested headwater streams and emergent freshwater marshes, since published data concerning their role in these systems is considerably more abundant in comparison to other freshwater habitats, such as ponds and lake pelagic habitats. Although much less studied, recent research and reviews by Wurzbacher and colleagues (Wurzbacher et al., 2010; 2011; 2014) provide an excellent synthesis of our current knowledge of fungi and fungal-like organisms in lake pelagic zones.

Fungi in lotic ecosystems: headwater streams and aquatic hyphomycetes

In forested headwater streams, allochthonous organic matter originating from riparian vegetation (leaves, twigs and branches) forms the major source of organic matter input to the stream environment and prior studies have estimated that these inputs can contribute up to 99% of the carbon and energy budget of a stream (Webster and Meyer 1997). Decomposition of this plant material is widely accepted as a key ecosystem process, and a vast amount of research over the last several decades has focused on the decomposition of this plant detritus and its links to higher trophic levels in stream food webs (Webster and Benfield, 1986; Wallace et al., 1997; 1999; Gessner et al., 2010; Tank et al., 2010). This research has firmly established that fungal

decomposers and invertebrate consumers are critical players in the processing and decomposition of plant detritus in streams.

As indicated earlier, aquatic hyphomycetes or “Ingoldian fungi” (Webster and Descals, 1981; Descals, 2005) are arguably the best-known group of fungi associated with decaying plant litter in streams. These fungi are an ecologically well-defined but polyphylectic group, with nearly all members having phylogenetic affinities to different groups of ascomycetes (Shearer et al., 2007; Baschien et al., 2013; Duarte et al., 2013b). Although zoosporic fungi and stramenopiles have been identified from decaying plant litter in streams (Marano et al., 2011; Bärlocher et al., 2012), molecular-based analyses of natural litter samples from streams indicate that aquatic hyphomycetes typically dominate the litter-associated fungal communities (Nikolcheva et al., 2005; Seena et al., 2008; Duarte et al., 2015). At the global scale, many aquatic hyphomycete species are considered to be cosmopolitan (Wood-Eggenschwiler and Bärlocher, 1985; Bärlocher, 2009; Bärlocher and Marvanová, 2010; but see Duarte et al., 2012), however, the diversity appears to peak at temperate mid-latitudes and some taxa appear to be restricted to certain latitudes (Shearer et al., 2007; Jabiol et al., 2013).

In temperate forested regions, organic matter inputs to headwater streams often enter as a pulse during autumn leaf fall, where it is rapidly colonized by aquatic hyphomycetes and other microbial assemblages. Attachment of reproductive conidia to litter substratea is a critical step for aquatic hyphomycete colonization and these fungi produce large, uniquely shaped conidia (tetraradiate, sigmoid or variously branched), which are considered an evolutionary adaptation for their dispersal and attachment to litter substrata in flowing water (Fig 1) (Webster, 1987). Conidial traits (i.e., size and morphology), water flow, and litter surface topography, can significantly influence the attachment and colonization success of aquatic hyphomycetes

(Harrison et al., 1988; Read et al., 1991; Dang et al., 2007; Ferreira and Graça, 2006; Kearns and Bärlocher, 2008), which together with other factors, such as litter chemical composition (e.g., Canhoto and Graça, 1999), may explain why some litter substrata support specific aquatic hyphomycete assemblages (Thomas et al., 1992; Gulis, 2001).

Once attached to the litter substratum, conidial germination is initiated within a few hours via the production of one or more germ tubes that form appressoria, which ensure their attachment and colonization of the new litter substratum (Harrison et al., 1988; Read et al., 1991; Au et al., 1996). Fungal hyphae will then enter and grow pervasively within the litter matrix, where they produce and secrete an array of extracellular enzymes (e.g., cellulases, xylanases, pectinases) that allow the digestion and assimilation of plant litter structural polysaccharides (Suberkropp et al., 1983; Chamier, 1985; Zare-Maivan and Shearer, 1988). This fungal growth and enzymatic digestion results in the softening or maceration of leaf-litter tissue (Suberkropp and Klug, 1980; Chamier and Dixon, 1982) and the increased “microbial conditioning” of leaf detritus, which benefits invertebrate consumers. Certain aquatic hyphomycete species increase the palatability and nutritional quality of plant litter for leaf-feeding macroinvertebrate consumers (shredders) (Suberkropp, 1992; Jabiol and Chauvet, 2012; Bärlocher and Sridhar, 2014; Gonçalves et al., 2014), which is critical for macroinvertebrate growth and development (Arsuffi and Suberkropp, 1986; Chung and Suberkropp, 2009). This fungal conditioning of leaf detritus and subsequent invertebrate feeding also contributes to the production and release of fine particulate organic matter (FPOM) (e.g., Tant et al., 2015), which has additional impacts on other stream dwelling consumers that utilize FPOM as a primary food resource (collector-gatherers, see Wallace and Webster, 1996).

Aquatic hyphomycetes: fungal biomass, production, and sporulation

Once established, the biomass, growth, and secondary production of aquatic hyphomycetes in plant litter can been estimated using ergosterol-based methods (Gessner 2005, Suberkropp and Gessner, 2005). Since their development, these methods have been increasingly used within a variety of ecosystems, where they have been useful in allowing the quantitative assessment of fungal contributions to the cycling of carbon and nutrients. Application of these methods in stream ecosystems (Suberkropp and Weyers, 1996) has yielded a large body of evidence that aquatic hyphomycetes are quantitatively important members of the decomposer microbial community (Gulis et al. 2006b; Gessner et al., 2007; Gulis et al., 2009).

Studies in natural streams and in controlled laboratory stream microcosms observed that litter-associated fungal biomass (ergosterol) increases rapidly following litter submergence, with peak fungal biomass typically being attained within 2-10 weeks (Fig 2), depending on the type of leaf litter, its intrinsic chemical characteristics (e.g., nutrients), and the external environmental decay conditions (Suberkropp et al., 1993; Gessner and Chauvet, 1994; 1997; Suberkropp 1995; Baldy and Gessner 1997; Weyers and Suberkropp, 1996; Suberkropp, 2001; Mathuriau and Chauvet, 2002; Ferreira et al., 2006b; Gulis et al., 2006a). During this time, the accrual of fungal biomass within decaying leaf litter can be significant, with peak biomass typically accounting for ~10-20% of the total detrital weight (Table 1). Following this initial increase, fungal biomass usually declines during later stages of leaf decomposition (Fig 2) as losses in biomass occur due to the production of conidia, senescence and death of hyphae, and from the grazing activity of invertebrate detritivore consumers.

The growth and production rates of fungi associated with decaying leaf litter, as determined from rates of ^{14}C-acetate incorporation into ergosterol, follows a similar pattern with

peaks occurring soon after litter submergence (Fig 2) (e.g., Suberkropp, 1995; Baldy and Gessner, 1997; Weyers and Suberkropp, 1996; Suberkropp, 2001; Pascoal and Cássio, 2004). Estimates of fungal growth rates from decaying leaf litter range from <0.01 to 0.64 d^{-1} and typically peak when fungal biomass concentrations are still relatively low (Gessner and Chauvet, 1997). Corresponding rates of fungal secondary production peak between 0.6 and 16 mg fungal C g^{-1} detrital C d^{-1} (Table 1). Data on fungal dynamics associated with submerged wood in streams is exceedingly scarce, but a few studies indicate that fungal biomass concentrations on small wood (<40 mm diameter) can be almost as high as that observed on leaves (Findlay et al., 2002b, Gulis et al., 2008), while fungal growth and production rates are typically 5-10 times lower (Table 1, see Gulis et al., 2008).

Although fungal growth rates are typically lower than bacterial growth rates, fungal production is often much higher than corresponding bacterial production when both groups have been examined simultaneously (Table 1) (Weyers and Suberkropp, 1996; Baldy et al., 2002; Pascoal and Cássio, 2004; Pascoal et al., 2005; Suberkropp et al., 2010; but see Baldy and Gessner, 1997). These findings result from the much higher fungal biomass concentrations usually observed in decaying leaf litter, which often accounts for greater than 90% of total microbial biomass.

A notable life history feature of aquatic hyphomycetes is that initial hyphal growth within decaying litter is closely followed by the production of conidiophores, which protrude from the litter substratum and shed newly formed conidia into the flowing water column. Once released, these conidia are carried downstream to colonize new litter substrata, potentially captured by filter-feeding invertebrates (e.g., Bärlocher and Brendelberger, 2004), or become trapped in foam (neuston) at the air-water interface where they can survive for a short time (Sridhar and

Bärlocher, 1994). Sporulation of aquatic hyphomycetes often occurs in as little as 1-3 weeks following litter submergence, which typically peak before or during periods of increasing fungal biomass (Fig 2) (Suberkropp, 1991; 1995; Weyers and Suberkropp, 1996; Maharning and Bärlocher, 1996; Mathuriau and Chauvet, 2002; Ferreira et al., 2006a; Gulis et al, 2006a; Bärlocher, 2009). These observations reveal that aquatic hyphomycetes allocate considerable resources into early reproduction. Previous studies have estimated that these fungi can invest up to 46-80% of their biomass production in the formation of conidia (Suberkropp, 1991) and can convert up to ~7% of the initial plant litter carbon into spores (Suberkropp, 1991; Hieber and Gessner, 2002; Ferreira et al., 2006a). Because of their rapid and copious production, the concentration of aquatic hyphomycete conidia in many forested streams can reach 20,000 spores/l^{-1} or greater during the autumn (Suberkropp, 1991; 1997; Bärlocher, 2000), which coincides with the seasonal timing of allochthonous leaf-litter inputs from riparian vegetation. In contrast, conidial concentrations during the summer season in temperate streams are low, as a result of diminishing detrital substratum availability.

The rapid colonization, reproduction and dispersal of aquatic hyphomycete conidia appears to be a key life history strategy that distinguishes them from other fungal groups, which may tend to colonize, capture and retain acquired resources within mycelial biomass (Bärlocher, 2009). Termed a “boom-bust cycle” by Bärlocher (2009), aquatic hyphomycetes appear to be ideally suited to life in the lotic environment where they can quickly respond to the seasonal cycle of ephemeral detrital inputs that are characteristic of many temperate forested streams. Interestingly, the life cycles and secondary production of many detritivorous invertebrates (e.g., shredders) are also timed to take advantage of these peaks in organic matter availability (Wallace et al., 1999; Cross et al., 2006; Walther and Whiles, 2011), most likely resulting from the

increased palatability and nutritional quality of detrital resources via aquatic hyphomycete colonization (Arsuffi and Suberkropp, 1986; Chung and Suberkropp, 2009). Similar "boom-bust" life history strategies may also prevail among stream fungi in subtropical and tropical regions, which, in contrast to temperate streams, may be more strongly influenced by the seasonal fluctuation in water availability (i.e., wet and dry season) versus the availability of detrital substrata (Bärlocher, 2009).

Fungal contributions to litter decomposition in streams

Fungal activity (e.g., peak biomass, sporulation) associated with leaf litter and wood in streams is positively correlated with the litter decay rates (e.g., Gessner and Chauvet, 1994, Gessner et al., 2007), which implies that a large fraction of the plant litter carbon is likely channeled into and through litter-inhabiting aquatic fungi. Investigations in laboratory stream microcosms using pure cultures of aquatic hyphomycetes and in natural stream systems have estimated that fungal assimilation (production + respiration) of plant litter substrata can account for 23-56% of plant carbon loss (Gessner and Chauvet, 1997; Gulis and Suberkropp, 2003a; 2003b; Pascoal and Cássio, 2004; Ferreira and Chauvet, 2011a), depending on temperature and dissolved nutrient availability (see below). For example, Pascoal and Cássio (2004) quantified rates of microbial production (bacteria and fungi) during the decomposition of alder leaf litter in four Portugal streams that varied in the degree of anthropogenic pollution. Microbial production was dominated by fungi (>94%) and estimates of total fungal assimilation accounted for 29-39% of the observed losses in leaf litter carbon. In contrast, bacterial decomposers contributed only between 4 and 13%, lending support to the idea that bacteria assume a more important role in detrital processing when organic matter undergoes greater fragmentation (e.g., FPOM) or

becomes dissolved (Findlay et al., 2002b; Tant et al., 2013). Estimates of fungal contributions given above are likely conservative, since fungal-mediated losses of DOM and FPOM were not taken into account. When these losses are incorporated, fungal contributions to total leaf mass loss can often be significantly higher (see Baldy et al., 2007).

The impact of aquatic hyphomycete diversity on fungal community performance (e.g., biomass and sporulation) and litter decomposition in streams has been the subject of considerable research in the last decade. Several studies have observed a positive relationship between fungal species richness and leaf decomposition (Bärlocher and Corkum, 2003; Duarte et al., 2006; Pascoal et al., 2010; Fernandes et al., 2011), whereas others have reported no clear diversity effect at all (Dang et al., 2005; Geraldes et al., 2012; Ferreira and Chauvet, 2012). However, it appears that the functional impacts of aquatic hyphomycete diversity is largely dependent on species identity, as certain aquatic hyphomycete species possess traits that have a greater influence on ecosystem processes than level of species diversity alone (Bärlocher and Corkum, 2003; Duarte et al., 2006; Geraldes et al., 2012). Furthermore, prior investigators have shown that environmental decay conditions (e.g., temperature, nutrients) can significantly alter the impacts of aquatic hyphomycete diversity on litter decomposition (Bärlocher and Corkum, 2003; Dang et al., 2009; Ferreira and Chauvet, 2011a; 2011b; Fernandes et al., 2012; Duarte et al., 2013a; but see Geraldes et al., 2012).

When integrated on an areal basis (m^{-2}), the amount of fungal biomass and production associated with plant litter in streams is not trivial, and illustrates the quantitative importance of stream fungi when viewed at the ecosystem scale. In forested headwater streams, areal estimates of fungal biomass associated with leaf litter ranged from <1 to 23 g C m^{-2} and displayed a highly seasonal pattern due to the timing of leaf litter inputs (autumn) and the overall retentiveness of

the stream environment (Suberkropp, 1997; Methvin and Suberkropp, 2003; Carter and Suberkropp, 2004; Suberkropp et al., 2010). To date, only two published studies have estimated areal fungal biomass associated with wood in streams (Findlay et al., 2002b; Gulis et al., 2008). In contrast to leaf litter, Gulis et al. (2008) observed that fungal biomass associated with small wood (7-40 mm diameter) averaged 4-7 g C m^{-2} in two North Carolina streams with very little seasonal variation throughout the year.

Rates of annual fungal production on an areal basis have also been quantified in a limited number of streams. Annual fungal production associated with leaf litter in five streams exhibiting low leaf litter retention ranged from 8 to 23 g C m^{-2} yr^{-1} (Suberkropp, 1997; Methvin and Suberkropp, 2003; Carter and Suberkropp, 2004). Assuming a fungal growth efficiency of 33% (see Suberkropp 1991; Gulis and Suberkropp, 2003b) and taking into account annual leaf litter input, annual fungal assimilation (production + respiration) in these streams accounted for 10-29% of annual litter input. In contrast, annual fungal production reached 49-290 g C m^{-2} in two small highly retentive streams with high litter inputs (Suberkropp et al., 2010). In these streams, estimated fungal assimilation was significantly higher, ranging from 35% to >100% of the annual leaf litter input. Corresponding estimates of annual fungal production associated with small woody debris within these same two streams were much lower (13 - 17 g C m^{-2} yr^{-1}), but still translated into a fungal assimilation of 45-57% of annual wood inputs to these streams (Gulis et al., 2008).

Key factors affecting fungal activities and litter decomposition in streams

A variety of factors can strongly influence fungal activities and plant litter decomposition in stream ecosystems, which may include, but are not limited to, the type and chemical quality of

the litter substratum being metabolized, biotic interactions within the decomposer food web, and a wide range of external environmental conditions, such as water chemistry, temperature, water inundation and flow, and oxygen availability. The intrinsic chemical quality of the plant litter substratum, specifically the lignin and nutrient content of litter, has been widely documented as an important factor influencing fungal activity and litter decomposition in streams (Gessner and Chauvet, 1994; Stelzer et al., 2003; Ferreira et al., 2006b; Gessner et al., 2007). In general, fungal activities (sporulation, growth, biomass accrual) are negatively affected by high lignin contents and high C:nutrient ratios of plant litter substrata. Because of their organo-osmotrophic lifestyle, a central feature of fungal metabolism is their reliance on external digestion of complex organic matter (e.g., lignocellulose) by extracelluar enzymes, which facilitates the acquisition and assimilation of carbon and nutrients (N & P) from detrital substrata. The production and release of extracellular enzymes is a substantial energy cost for fungi and other osmotrophic microorganisms, such as bacteria. As a consequence, fungi and bacteria will regulate the production and release of extracellular enzymes in accordance with detrital resource availabilities (C, N, P), which serves to optimize their assimilatory return on investment (Sinsabaugh and Follstad-Shah, 2012; Sinsabaugh et al., 2014). Collectively, this regulation will strongly affect outcomes related to fungal community performance (Sinsabaugh et al., 2015) and hence the rates of plant litter decomposition.

Because plant litter C:N and C:P ratios are considerably higher than C:nutrient ratios of fungal biomass (Danger and Chauvet, 2013; Grimmett et al., 2013), fungal activity is typically limited by the availability of nutrients. In streams, aquatic hyphomycetes can alleviate this substratum nutrient limitation by taking up dissolved N and P from the overlying surface waters. Prior experiments conducted in laboratory stream mesocosms and whole-stream nutrient addition

experiments under field conditions have shown that increases in dissolved nutrients can stimulate aquatic hyphomycete activities (growth, sporulation, biomass, respiration, cummulative production) and rates of plant litter decomposition (Suberkropp, 1995; 1998; Gratten and Suberkropp, 2001; Gulis and Suberkropp, 2003a; 2003b; 2003c; Gulis et al., 2004; Suberkropp et al., 2010; Ferreira and Chauvet, 2011b). Even small increases in exogenous nutrients stimulated fungal activities and were generally more pronounced for lower quality plant litter substrata (low N and P, high lignin), such as wood (Stelzer et al., 2003; Gulis et al., 2004; 2008; Ferreira et al., 2006a). Collectively, these findings underscore that eutrophication can have profound effects on organic matter processing in stream ecosystems (Woodward et al., 2012; Rosemond et al., 2015), and a recent review by Ferreira et al. (2015) provides compelling evidence that stimulation of microbially-mediated litter decomposition by dissolved nutrients is a globally widespread phenomenon. Although, note that excessive nutrient pollution may also have a negative impact on fungal activity and litter decomposition (e.g., Pascoal and Cássio, 2004).

In addition to dissolved nutrients, other chemical parameters of stream water, such as alkalinity, pH, and pollution, can also affect fungal activity and litter decomposition in streams Krauss et al., 2011; Ferreira et al., 2014). Aquatic hyphomycete diversity is typically higher in softwater streams (Bärlocher and Rosset, 1981, Wood-Eggenschwiler and Bärlocher, 1983). Despite this increased diversity, fungal activity and litter decomposition is usually greater in hardwater versus softwater streams (Jenkins and Suberkropp, 1995; Suberkropp and Chauvet, 1995). This has been attributed to the greater production and activity of pectin lyase in hardwaters (higher pH, presence of Ca+ ions), which contributes to the softening and maceration of leaf litter (Suberkropp and Klug, 1980; Chamier and Dixon, 1982; Jenkins and Suberkropp, 1995). While aquatic hyphomycetes do not appear to be overly sensitive to low pH (Krauss et al.,

2011), the presence of acidic conditions in combination with other dissolved constituents, such as metal ions (e.g., Al, Zn), appear to have combined effects that inhibit the decay activities of fungi in streams. Anthropogenic acidification of headwater streams is well documented (e.g., Mullholland et al., 1987) and known to severely impact aquatic biota (e.g., shredders, fungi) and leaf litter processing through a reduction in pH, increases in stream water metal concentrations, and decrease in base cation availability (Niyogi et al., 2001; Dangles et al., 2004; Cornut et al., 2012; Clivot et al., 2013; 2014). Increasing concentrations of Al are known to negatively alter aquatic hyphomycete activities on decaying leaf litter (Dangles et al., 2004; Clivot et al., 2014; Pacioglu et al., 2015). Furthermore, recent studies have provided evidence that elevated Al concentrations may also alter the phosphorus cycle in acidified streams, which could induce P limitation of microbial (fungal) decomposers and affect their litter decay activities (Clivot et al., 2013; 2014).

Temperature is widely accepted as an important parameter influencing the metabolic activities of organisms and consequently a considerable body of research has focused on examining the effects of temperature on aquatic hyphomycetes. This is particularly relevant as global climate change is predicted to alter the thermal regime of streams and rivers worldwide, with subsequent impacts on important ecological processes like litter decomposition (Ferreira and Chauvet, 2011a; 2011b; Ferreira et al., 2014). The response of aquatic hyphomycetes to temperature largely depends on the species in question, with many species exhibiting a relatively narrow range of optimal tempertures that are suitable for its growth and sporulation (Webster et al., 1976; Chauvet and Suberkropp, 1998; Duarte et al., 2013a). For example, some aquatic hyphomycete species exhibit much greater rates of growth and sporulation at lower temperatures (15˚C), whereas other species exhibit much greater rates of growth and sporulation at higher

temperatures (25˚C) (see Table 18.1 in Ferreira et al. 2014). This differential pattern in temperture optima among "cold- and warm-water" species (Ferreira et al., 2014) is an important factor influencing their geographic distribution and the seasonal pattern of aquatic hyphomycete reproduction in streams (Suberkropp, 1984; Wood-Eggebschwiler and Bärlocher, 1983; 1985; Nikolcheva and Bärlocher, 2005).

Laboratory studies examining single or mixed species responses to temperature have shown that growth and sporulation rates are stimulated by increases in temperature up to a thermal optimum, whereas further temperature increases had either no effect or inhibited biomass production and/or sporulation rates (Chauvet and Suberkropp, 1998; Fernandes et al., 2009; Geraldes et al., 2012; Duarte et al., 2013a). Observations of a thermal optimum threshold of ~12-15˚C for natural stream fungal communities (Bärlocher et al., 2013), suggest that the optimal temperature patterns for many species may be influenced by the presence of other species. Recent research has documented that temperature increases and/or oscillations in temperature can significantly alter the interspecific relationship among aquatic hyphomycete communities in regards to growth and sporulation (Dang et al., 2009; Fernandes et al., 2009; 2012; Geraldes et al., 2012; Duarte et al., 2013a), which could alter successional patterns and lead to shifts in fungal species dominance (Dang et al., 2009; Ferreira and Chauvet, 2011a; 2011b; Fernandes et al., 2012). The magnitude of temperature effects may also be complicated by additional factors, such as the quality of the litter substratum (Bärlocher et al., 2013), the availability of dissolved nutrients (Ferreira and Chauvet, 2011a), and the presence of metal contamination (Batista et al., 2012; Ferreira et al., 2012). Collectively, these findings underscore that elevated temperatures, as a result of global climate change, may have significant impacts on

aquatic hyphomycete communities and hence energy flow and nutrient cycling within stream detrital food-webs.

Due to the hydrologic nature of lotic environments, many of the world's small streams and some rivers are temporary and experience a periodic interruption in flow or at the extreme a complete drying of the stream channel (Larned et al., 2010). This flow intermittency has both a temporal and spatial dimension, resulting in an expansion, contraction and/or fragmentation of the stream environment in response to inundation and drying events. As a consequence, many temporary streams and rivers are a shifting mosaic of differing lotic, lentic and terrestrial habitats, which can influence biotic communities (e.g., fungi and detritivores) and rates of organic matter decomposition (Lanhans et al., 2008). Low water flow and dissolved oxygen conditions can significantly reduce the diversity, growth, and sporulation of aquatic hyphomycetes (Chergui and Pattee, 1988; Pascoal and Cássio, 2004; Medeiros et al., 2009), possibly favoring a shift to aero-aquatic hyphomycetes that are better adapted to slow-flowing stagnant conditions. In addition to low flow, drying of the stream channel can also significantly impact aquatic hyphomycete performance. For example, Bruder et al. (2011) observed that the intensity and timing of drying events had a significant influence on alder litter decomposition and litter associated biomass and sporulation of aquatic hyphomycetes in a 3rd order stream in Southwestern France. The highest sporulation rates were noted on alder litter that was continually submerged. Likewise, fungal biomass accrual was nearly three-fold higher in continually submerged leaf-litter compared to leaf-litter that experienced a single drying event (Bruder et al., 2011; but see Mehring et al., 2015). Earlier research by Langhans and Tockner (2006) demonstrated that the duration of drying events, but not the frequency, can be an important factor influencing aquatic hyphomycete activity and litter decomposition in streams.

Their data suggested that if drying-rewetting cycles are short in duration, then alternating dry-wet cycles may have only a small impact on fungal decomposers, since fungi can rapidly regain their decay activity once water becomes available and flow resumes. Similar rapid metabolic responses have also been observed for fungal decomposers in freshwater marshes (see below, Kuehn et al., 1998; Kuehn and Suberkropp, 1998b; Kuehn et al., 2004), which lends support to an expanded view of Bärlocher's (2009) boom-bust cycle concept, where decomposer fungal activities (i.e., growth, respiration and/or sporulation) can rapidly respond when either detrital inputs and/or conducive environmental conditions become available.

Fungi in lentic ecosystems: freshwater marshes and the diversity of fungi

Freshwater marshes, including lake littoral zones, are considered important ecotones between terrestrial and aquatic ecosystems, which are know for their high biodiversity and extensive food webs (Mitsch and Gosselink, 2007). Emergent hydrophytic plants (Tiner, 1991), such as *Typha*, *Juncus* and *Phragmites*, are common within freshwater marshes where they often account for a large fraction of the plant biomass produced (Wetzel, 2006; Yu et al., 2010). These plants exhibit very prolific rates of growth and nutrient sequestration (e.g., nitrogen and phosphorus), with estimates of aboveground biomass production alone frequently exceeding 1000 g dry mass/m^{-2}/yr^{-1}. As a consequence, these plants embody an important reservoir of carbon and nutrients, and are usually depicted as the primary carbon and nutrient pools in most marsh wetland elemental budgets (e.g., Hopkinson 1992).

In freshwater marshes, most of this plant biomass enters the detrital pool, where microbial decomposers and detritus-feeding animals play an important role in its breakdown and mineralization. Despite the well-recognized occurrence and abundance of plant detritus in

marshes (Mitsch and Gosselink, 2007), we still lack a full understanding of *natural* decomposition processes within these habitats and the associated role of fungal decomposers. To date, most studies examining emergent plant decomposition in freshwater marshes have focused on microbial decay processes occurring at or within the surface sediments (e.g., Rothman and Bouchard, 2007; Fennessy et al., 2008), which has resulted from, and continues contributing to, the false perception that emergent plant litter decomposition takes place solely at/within the marsh sediments by bacterial decomposers. As a result, fungal participation in wetland biogeochemical cycles has not yet gained wide recognition by most wetland researchers, and their contributions remain absent from nearly all extant conceptual and quantitative models describing wetland carbon and nutrient flow pathways (Mitsch and Gosselink, 2007; Reddy and Delaune, 2008; Kayranli et al., 2010; Batzer and Sharitz, 2014).

Although frequently overlooked, a key phenologic detail to consider in emergent wetland plants is both the spatial and temporal conditions under which plant litter naturally decomposes (Kuehn, 2008). In most emergent plants, abscission and collapse of plant material to the sediments or overlying surface waters does not typically occur following shoot senescence and death. As a result, large amounts of standing-dead plant litter tend to accumulate in wetland marshes and lake littoral habitats (Asaeda et al., 2002; Christensen et al., 2009), where it undergoes initial stages of decomposition in an upright aerial position. Thus, the *natural* progression of plant decay in emergent marshes is a sequential process, which begins under aerial terrestrial-like conditions and eventually transitions to an aquatic or sediment environment following the collapse of standing litter. When studies have closely simulated these natural conditions, fungi have been found to be an important contributor to emergent plant decomposition (Gulis et al., 2006b; Gessner et al., 2007; Kuehn, 2008; Gulis et al., 2009).

A substantial body of evidence has accumulated for over a century (Saccardo 1898) that fungi pervasively colonize and reproduce on and within both standing and collapsed litter of emergent marsh plants (Pugh and Mulder, 1971; Apinis and Taligoola, 1974; Apinis et al., 1975; Farr et al., 1989; Poon and Hyde, 1998; Tsui and Hyde, 2003; Gessner and van Ryckegem, 2003; van Ryckegem and Verbeken, 2005a; 2005b; 2005c; van Ryckegem et al., 2007). In contrast to streams, fungal communities colonizing emergent plant litter typically comprise a more taxonomically diverse group of fungi (Fig 1). For example, Gessner and van Ryckegem (2003) reported that over 600 species of fungi have been recorded from the common reed (*Phragmites australis*). The most common taxa were members of the Ascomycota (94%, including anamorphic hyphomycetes 30% and coelomycetes 22%), with Basidiomycota (6%) being observed much less frequently. Several studies have reported distinct temporal changes in fungal assemblages during litter decomposition (Pugh and Mulder, 1971; Apinis and Taligoola, 1974; Van Ryckegem and Verbeken, 2005a; 2005b; Van Ryckegem et al., 2007). Terrestrial fungi are commonly observed during the initial standing phase of decomposition and are replaced by aquatic fungi when plant litter collapses to the marsh sediments or overlying surface waters. In addition to these temporal shifts, fungi colonizing standing-dead litter may also exhibit spatial distribution patterns within decaying plant litter (Apinis et al., 1975; Poon and Hyde, 1998; Van Ryckegem and Verbeken, 2005c; Van Ryckegem et al., 2007), where certain fungal taxa occupy specific plant parts, such as leaves, sheaths or culms. These temporal and spatial patterns in fungal colonization are most likely reflected in the intrinsic quality of the plant litter substratum as well as the diverse range of environmental conditions that decaying litter experiences throughout the decomposition process.

Currently, much of our knowledge of fungal biodiversity in freshwater marshes comes from traditional microscopic studies, where fungal reproductive structures (e.g., ascoma, basidioma) were detected and identified either directly from field collected plant litter or after employing various culture techniques within the laboratory. The advancement of molecular-based methods promises to improve our ability to assess fungal diversity and processes in both lotic and lentic freshwater ecosystems (Duarte et al. 2013b); however, to date, very few published studies have applied these modern techniques to fungal decomposers in marshes (Neubert et al., 2006; Buesing et al., 2009).

Freshwater marshes: fungal biomass and production

Despite the well-documented evidence indicating fungal colonization of emergent plant litter, very few studies have examined the quantitative role of fungi in litter decay or their potential contribution to marsh ecosystem carbon and nutrient cycling. As a consequence, our understanding of fungal functional processes in freshwater marshes has lagged appreciably behind the body of data for other microbial groups, such as bacteria. However, as in stream ecosystems, application of ergosterol-based methods in both temperate and subtropical marshes has provided compelling evidence that fungi are an important microbial assemblage involved in plant litter decomposition, particularly during the initial standing decay phase (Gulis et al., 2006b; Gessner et al., 2007; Kuehn, 2008; Gulis et al., 2009). Significant accumulation of fungal biomass has been reported in standing emergent plant litter, with peak values accounting for as much as 5-10% of the total detrital mass (Table 1) (Newell et al., 1995; Bärlocher and Biddiscombe, 1996; Kuehn and Suberkropp, 1998a; Kuehn et al., 1999; Gessner, 2001; Findlay et al., 2002a; Newell, 2003; Welsch and Yavitt, 2003; Ohsowski, 2008; Kuehn et al., 2011; Su

2014). For example, Kuehn et al. (2011) and Su (2014) documented significant increases in fungal biomass concentrations in decaying standing *Typha angustifolia* and *T. domingensis* leaves, which revealed the rapid colonization of *Typha* leaf litter by fungal decomposers following plant senescence (Fig 3A). Analogous to observed spatial patterns in fungal diversity, differences in fungal biomass have also been noted among specific plant parts (e.g., leaves *vs.* culms). Earlier, Kuehn et al. (1999) observed significantly higher fungal biomass concentrations in leaf versus culm litter of the emergent plant *Erianthus giganteus* (Fig 3B). These differences were consistent with the chemical quality of the litter substrate, where culm tissues had much lower concentrations of nutrients (higher C:N and C:P ratios) and were more recalcitrant (lignin) than corresponding leaf tissues.

In addition to accumulating large quantities of biomass, fungal communities inhabiting standing litter can also exhibit appreciable rates of secondary production (Newell et al., 1995; Findlay et al., 2002a; Verma et al., 2003; Kuehn et al., 2011; Ohsowski, 2008; Su 2014). In the few studies conducted to date, fungal growth rates associated with both standing and collapsed emergent plant litter are typically lower than those reported in streams, ranging from ~0.01 to 0.12 d^{-1}. Corresponding rates of fungal secondary production are also lower and have been observed to peak at ~5.6 mg fungal C g^{-1} detrital C d^{-1} (Table 1). As noted with fungal biomass, rates of fungal production also differ among specific plant tissues, with higher rates of production being observed in leaf versus culm/stem litter (e.g., Komínková et al. 2000, Ohsowski, 2008). Thus, like fungal biomass, fungal activities (production and respiration) may also vary considerably depending on intrinsic quality of the plant litter substratum.

Collapse of standing-dead litter to the sediments or overlying surface waters is often accompanied by a notable shift in the environmental decay conditions (e.g., increased water

availability), which lead to shifts in litter-associated fungal communities (see above) and concomitant changes in fungal biomass and activity. For example, Kuehn et al. (2000) observed a rapid decrease in litter associated ATP concentrations, fungal biomass (ergosterol), and production rates after the movement of standing *Juncus effusus* leaf litter to a submerged environment. This initial decline was followed by an increase in fungal biomass and production rates during later stages of submerged litter decomposition, which suggests a possible shift to fungal taxa better adapted for an aquatic or semi-aquatic existence (see also Komínková et al., 2000; Van Ryckegem et al., 2007). Despite litter submergence and initial declines in fungal biomass and production, fungi continue to be a quantitatively important microbial group on and within decaying plant litter. Simultaneous estimates of fungal and bacterial biomass reveal that fungal decomposers often account for >90% of the total microbial biomass associated with submerged plant litter (Table 1) (Newell et al., 1995; Sinsabaugh and Findlay, 1995; Komínková et al., 2000; Kuehn et al., 2000; Findlay et al., 2002b; Su et al., 2007; Kuehn et al., 2014). Furthermore, studies have reported that rates of fungal production are often comparable to or exceed corresponding rates of bacterial production (Newell et al., 1995; Kuehn et al., 2000; Findlay et al., 2002a; Su et al., 2007; Ohsowski, 2008; Kuehn et al., 2014; but see Buesing and Gessner, 2006).

Fungal contribution to litter decomposition in marshes

Observations of appreciable fungal biomass accrual in both standing and collapsed emergent litter suggest that fungal decomposers are effective in enzymatically transforming and assimilating detrital C and nutrients (e.g., N and P) to support their pervasive growth. Similar to aquatic hyphomycetes, increases in litter-associated fungal biomass (ergosterol) are significantly

correlated with concomitant losses in standing leaf C mass (Gessner, 2001; Kuehn et al., 2011; Su et al., 2015), suggesting that a considerable fraction of the plant litter C is likely channeled into and through inhabitant fungal decomposers. Earlier, Kuehn et al. (2011) constructed a partial decay budget to assess the contribution of fungal decomposers to standing leaf litter mass loss in the emergent marsh plant, *T. angustifolia*. Estimated cumulative fungal production during *Typha* leaf decay totaled 123 $mgCg^{-1}$ initial leaf C, indicating that 22% of the observed *Typha* leaf C lost was transformed and assimilated into fungal biomass (i.e., fungal yield) in the standing litter environment. Similar findings were also recently reported by Su et al. (2015), where estimated cumulative fungal production accounted for ~11% of the observed carbon loss during standing *T. domingensis* leaf decomposition. Furthermore, corresponding estimates of cumulative microbial respiration from decaying *T. domingensis* leaves totaled 133 mg Cg^{-1} initial detrital C, which concurs with other studies (Kuehn and Suberkropp, 1998b; Kuehn et al., 2004) that a significant fraction of standing dead plant litter is also mineralized by litter-associated microbial communities, most likely fungal decomposers. Fungal contributions to leaf litter mass loss can also be significant following the collapse of standing litter (Komínková et al., 2000; Kuehn et al., 2000). For example, Kuehn et al. (2000) estimated that cumulative fungal production accounted for 68% of the observed litter mass loss during submerged *J. effuses* decomposition. In contrast, bacterial contributions to *J. effuses* decomposition accounted for only 11% of the observed mass loss.

To date, only a few studies have attempted to estimate the ecosystem-scale contribution of fungi to carbon and nutrient cycling in freshwater marshes (Buesing and Gessner, 2006; Ohsowski, 2008; Su, 2014; Kuehn and Gessner, unpublished data). Despite this paucity of data, when estimates of fungal biomass and production per gram of detritus have been accompanied

by areal (m^{-2}) estimates of plant litter standing crop, the importance of fungi at the ecosystem scale can be sizeable. Recently, Su (2014) estimated annual fungal biomass and production and microbial respiration associated with naturally-occurring standing-dead litter in a subtropical freshwater tidal marsh dominated by *Cladium jamaicense*. Fungal biomass per gram of plant litter remained fairly constant over the annual study period, averaging 30 mg Cg^{-1} detrital C. Because of appreciable accumulation of standing *C. jamaicense* litter in this marsh (annual mean 643±103 gCm^{-2}), corresponding standing stock estimates of fungal biomass were considerable, averaging 18 $gCm-^{2}$ over the annual study period.

In addition to accumulating large quantities of biomass in standing *C. jamaicense* litter, fungal decomposers also exhibited high rates of biomass production on an areal basis. When integrated over the study period, Su (2014) estimated that rates of fungal secondary production in and microbial respiration (CO_2 evolution) from standing litter totaled 90 and 124 $gCm-^{2}yr^{-1}$, respectively, providing evidence that a sizeable fraction (~33%) of mean annual standing litter carbon pool flows into and potentially through litter-inhabiting fungal decomposers. Rates of microbial respiration were significantly correlated with litter-associated fungal biomass (ergosterol) and production, implying that a large portion of the observed respiratory flux from standing litter was likely due to fungal metabolic activities (see also Kuehn and Suberkropp, 1998b, Kuehn et al., 2004). Similar findings from other freshwater marsh ecosystems (Ohsowski, 2008; Kuehn and Gessner, unpublished data) highlight that fungal processes during standing litter decomposition are a significant pathway of ecosystem carbon flow before the collapse and subsequent decay of plant litter at the marsh sediments or overlying surface waters.

Substantial rates of carbon flow can also occur through fungal communities colonizing benthic plant detritus (Buesing and Gessner, 2006; Ohsowski, 2008). For example, Buesing and

Gessner (2006) estimated annual production rates of both bacterial and fungal communities associated with submerged *P. australis* litter in a temperate lake littoral marsh. Annual fungal production totaled 93 $gCm^{-2}y^{-1}$, which equated to ~15% of the annual aboveground *P. australis* production (603 $gCm^{-2}y^{-1}$). However, in contrast to fungi, annual bacterial production was reported to be 7 times higher (661 $gCm^{-2}y^{-1}$), indicating that litter-associated bacterial decomposers may assume a more important role in carbon flow pathways once standing litter collapses to the marsh sediments (see also Ohsowski, 2008). Although, note that the very high bacterial production estimate reported earlier by Buesing and Gessner (2006) may well be an overestimate caused by leucine concentration used in their bacterial production assay (see Gillies et al., 2006).

Key factors affecting fungal activities and litter decomposition in marshes

As in stream ecosystems, fungal activities in marsh ecosystems are strongly influenced by a variety of physical and chemical conditions. These conditions differ markedly for fungal communities inhabiting standing versus collapsed plant litter, as changes in the litter decay environment (i.e., standing to aquatic) are often accompanied by major shifts in both physical and chemical conditions. As noted earlier, differences in litter associated fungal biomass and production have been observed among plant litter organs (leaves *vs.* culms). As a consequence, the intrinsic chemical quality of the plant litter substrate, specifically the nutrient content of litter, can have a significant influence on fungal activity and the resulting rate of litter decomposition. For example, both Kuehn et al. (2011) and Su et al. (2015) observed rapid increases in fungal biomass during standing leaf litter decomposition in *T. angustifolia* and *T. domingensis*, respectively (Fig 3A). Despite similar patterns of increase, peak fungal biomass accumulation in

standing *T. angustifolia* leaf litter (106±7 mg Cg^{-1} detrital C) was considerably higher than in *T. domingensis* leaf litter (37±4 mg Cg^{-1} detrital C). Furthermore, corresponding rates of fungal production (daily and cumulative) were also markedly higher in standing *T. angustifolia* litter (data not shown), which was consistent with the greater rate of mass loss observed in *T. angustifolia* (55%) versus *T. domingensis* (37%) leaf litter. The contrasting performance and contribution of fungal decomposers to *Typha* leaf decay in these studies may be reflected, in part, to the differing litter nutrient concentrations observed between these two *Typha* species. Kuehn et al. (2011) observed that C:N and C:P ratios in standing *T. angustifolia* leaf litter averaged 67 and 2583, respectively, throughout the post-senescent stages of standing litter decomposition. In contrast, Su et al. (2015) observed much higher C:N and C:P ratios in standing *T. domingensis* leaf litter, which averaged 88 and 4352, respectively. Collectively, fungal biomass concentrations in both *T. angustifolia* and *T. domingensis* leaf litter were negatively correlated with litter C:N and C:P ratios, which implies that fungal communities inhabiting standing *T. domingensis* leaf litter may have been limited by N and P to a greater extent. Similar to aquatic hyphomycetes (above), this nutrient limitation significantly impacts the ability of fungi and other microbial decomposers (bacteria) to meet their stoichiometric demands for growth and reproduction, which can limit their overall participation and impact on the litter decomposition process (Sinsabaugh et al., 2014; 2015).

As in most terrestrial ecosystems (Borken and Matzner, 2009), water availability has been identified as a critical factor influencing microbial activities in standing plant litter within freshwater marshes. A number of laboratory and field studies have established these microbial communities, particularly fungi, are well adapted to life in the aerial standing litter environment, where they can rapidly shift their metabolism from an inactive to fully active state when

sufficient water becomes available (Kuehn and Suberkropp, 1998b; Kuehn et al., 1998; Kuehn et al., 2004). For example, early laboratory studies by Kuehn et al. (1998) observed that rates of microbial respiration (CO_2 evolution) from standing *Juncus effuses* litter increased rapidly following exposure to wetting conditions (from <5 to ~100 µg CO_2-C g^{-1} AFDM hlr^{-1} within 5 min), and continued at high rates until plant litter became dry. Under natural field conditions and in the absence of precipitation, rates of microbial respiration from standing *J. effusus* litter exhibited a distinct diel periodicity, with the highest rates occurring at night and in the early morning hours when water becomes available to litter inhabiting microorganisms via dew condensation (Fig 4A). In contrast, microbial respiration virtually ceases during the day as a result of increased daytime temperatures, decreased litter water potentials (i.e., water availability), and ensuing microbial desiccation stress (Fig 4B and 4D). Similar respiration patterns observed in other emergent marsh ecosystems (Kuehn et al., 2004) suggest that temperature-driven increases in nighttime relative humidity and dew condensation on standing litter surfaces is the primary mechanism underlying the cyclical increases in microbial water availability and hence their decay activities.

This extreme metabolic plasticity may be a key physiological strategy for fungal growth and survival in the harsh standing litter environment, whereby fungal decomposers can rapidly take advantage of even short-term periods of moisture availability to exploit detrital resources (e.g., boom and bust cycle, Bärlocher, 2009). Because fungi and other microorganisms possess no active cross-membrane transport mechanism for water, they must raise their intracellular water potential relative to the external environment in order to meet the physiological demands for cellular maintenance and growth (Papendick and Mulla, 1986). In fungi, intracellular turgor pressure is a critical factor controlling the rate of hyphal extension and hence provides the key

driving force for pervasive mycelial growth within plant detritus (Money, 1994; 1995). In fungi, the degree of intracellular turgor pressure is controlled by a complex osmoregulatory system that closely regulates the internal cytoplasmic osmotic potential. This osmotic regulation is achieved by the uptake or export of inorganic ions across the cell membrane (K^+, Na^+), and by the biosynthesis or degradation of intracellular "compatible" solutes, such as sugar alcohols (i.e., polyols) and trehalose (Brown, 1990; Blomberg and Alder, 1992). Prior studies have shown that these compounds are important carbohydrate storage products in fungi (Jennings, 1995), as well as the dominant osmotic solutes produced in response to increased water stress (Brown, 1990). Fungal decomposers in standing litter also adjust their intracellular compatible solute concentrations in response to fluctuating water availability. Under natural field conditions, Kuehn et al. (1998) observed that concentrations of polyols and trehalose within standing *J. effusus* litter exhibited a contrasting diel pattern with rates of microbial respiration, with the highest concentrations occurring during periods of low water availability (Fig 4C). Concentrations of these osmotic solutes within plant litter were negatively correlated with both rates of carbon dioxide evolution and plant litter water potentials, suggesting that with fluctuations in water availability and microbial activity there is a concomitant regulation of the internal osmotic potential within fungal hyphae.

In addition to regulating the osmotic potential of fungal hyphae, the presence of polyols and trehalose has also been shown to increase the physical stability of cellular structures to the adverse effects of dehydration and thermal denaturation. Polyols, trehalose and other sugars can interact and replace water around the polar groups of membrane phospholipids and proteins, which increases their stability during periods of thermal desiccation (Crowe et al., 1984; 1988). Additional studies have also documented the role of trehalose and polyols in stabilizing soluble

enzymes from both thermal and desiccation related denaturation (Carpenter and Crowe, 1988; Lozano et al., 1994). As a consequence, these compatible solutes may serve a dual role in both osmotic regulation and cellular protection of fungi. The ability of fungal decomposers to rapidly synthesize, accumulate, and degrade these solutes implies that fungal communities in standing litter are physiologically well tuned to the cyclic changes in temperature and dessication, which may be a key adaptive strategy that allows their survival and predominance in the standing litter habitat.

In addition to facilitating microbial growth, cyclic episodes of water availability in standing litter may also be a key factor influencing the production and dissemination of fungal spores. Kuehn and Suberkropp (1998b) observed that airborne fungal spore concentrations above decomposing *J. effuses* litter followed a similar diel pattern as microbial respiratory activities, with the highest atmospheric concentrations occurring at night following dew formation on standing litter. In the absence of precipitation, airborne fungal spore concentrations above the *J. effuses* canopy were negatively correlated with light and temperature and positively correlated with relative humidity, indicating that fungal decomposers of *J. effuses* litter may require dark conditions and/or increases in nighttime moisture (i.e., dew formation) for the formation and optimal release of spores. Increasing water availability is known to influence spore release in a number of fungal species (Ingold, 1971).

In addition to chemical and physical factors (above), fungal decay activities in freshwater marshes may also be influenced by the myriad of biotic interactions that can occur on and within decaying plant litter (Gessner et al., 1999; 2007). For example, plant litter submerged in freshwater marshes will often develop complex microbial biofilms (Battin et al., 2007), which can harbor diverse communities of both autotrophic (algae) and heterotrophic microorganisms

(bacteria, fungi and protists). The close spatial proximity of these diverse microbial groups on and within decaying litter suggests the potential for a wide range of biotic interactions among microbial inhabitants (Mille-Lindblom and Tranvik, 2003; Francoeur et al., 2006; Mille-Lindblom et al., 2006; Kuehn et al., 2014). For example, Kuehn and colleagues recently identified novel metabolic couplings between autotrophic and heterotrophic microbial assemblages associated with submerged wetland plant litter (Francoeur et al., 2006; Kuehn et al., 2014). In the presence of periphytic algae, both litter-associated bacterial and fungal production and extracellular degradative enzyme activities were rapidly stimulated by short-term exposure to UV-free light (400 µmol m^{-2} s^{-1} PAR), presumably in response to active algal photosynthesis. In addition, experimental incubations of decaying plant litter with ^{14}C- and ^{13}C-bicarbonate demonstrated trophic-level transfer of carbon between litter-associated autotrophs and heterotrophs, thus establishing the potential for algal "priming" of heterotrophic microbial activities. First recognized in terrestrial soils (Blagodatsky et al., 2010; Kuzyakov, 2010), the priming effect describes a change, either positive or negative, in the decomposition of recalcitrant soil organic matter through the input of labile organic matter. These labile carbon inputs produce hotspots and hot moments of microbial activity, where microbial heterotrophs are provided energy-rich compounds that increase their metabolic capabilities to degrade and mineralize refractory organic matter. Similar observations in stream ecosystems (Rier et al., 2007; 2014; Danger et al., 2013; Hotchkiss et al., 2014) strengthen the contention that the priming effect phenomenon may be relevant within a wide range of aquatic ecosystems (Guenet et al., 2010). Collectively, these observations suggest that algal stimulation of microbial decomposers, especially fungi, is an important and largely unrecognized interaction within the detrital microbial landscape, which may transform our current conceptual understanding of

microbial-mediated litter decomposition in aquatic ecosystems.

Conclusion and research outlook

At the global scale, freshwater habitats are quite diverse and vary considerably in regards to their biotic (plants and consumers) and abiotic environmental conditions (e.g., hydrology, temperature, nutrient availability). In freshwater ecosystems, inputs of allochthonous or autochthonous plant litter provide critical basal resources in aquatic food webs, where microbial decomposers (fungi and bacteria) serve as important mediators in the flow of both carbon and nutrients (N & P) to higher trophic levels. The diversity of fungi in freshwaters is high, and representatives of all major fungal phyla have been identified from plant detritus. The microscopic nature and intimate association of fungi with detrital substrata makes their detection, identification, and ecological impacts difficult to assess. However, development of biochemical and molecular techniques over the last several decades has greatly improved our ability to detect and assess fungal contributions to ecosystem carbon and nutrient cycling. In a few types of freshwater ecosystems, particularly streams and marshes discussed in this review, application of these methods has established that fungi are important decomposers of plant detritus and play key roles in detrital food webs. Although the role of fungi in plant litter decomposition is becoming more widely recognized, major gaps in our knowledge of freshwater fungi remain. These gaps include, but are not limited to:

1. The need for wider application of modern biochemical and molecular techniques (i.e., omics) to identify and understand fungal involvement in litter decomposition (e.g., proteome analysis, see Schneider et al., 2010)

2. Our lack of data on how other microbial groups associated with plant detritus (algae, bacteria, and protists) potentially interact and impact fungal decay processes under natural conditions (e.g., priming effects, see Danger et al., 2013; Kuehn et al., 2014).
3. Limited data on the effects of detrital resource stoichiometry and water chemistry on fungal stoichiometry and its resulting impacts on fungal community structure, fungal physiology and their litter decay activities (see Danger et al., this issue).
4. Poor understanding of the contribution of chytrids to plant litter decomposition in freshwater environments.
5. Our limited data concerning the relative importance of fungi and bacteria in the decomposition of submerged wood and wetland macrophytes.
6. The paucity of data on freshwater fungi from polar and tropical regions.
7. Our lack of data concerning the effects of chronic vs. pulse nutrient enrichment on fungi and fungi-driven processes.
8. Our lack of large quantitative and modeling studies to understand the effects of global climate change (temperature, precipitation, sea-level rise) on fungi and fungi-driven processes.

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References

Apinis A.E., Chesters, C.G.C., Taligoola, H.K., 1975. Microfungi colonizing nodes and internodes of aerial standing dead culms of *Phragmites communis* Trin. *Nova Hedwigia* 26, 495-507.

Apinis, A.E., Taligoola, H.K., 1974. Biodegradation of *Phragmites communis* Trin. by fungi, in: Kilbertus, G., Reisinger, O., Concela Da Fonseca, J.A. (Eds), Biodegradation et humification. Sarreguemines, Pierron, pp. 24-32.

Arce Funck, J., Bec, A., Perrière, F., Felten, V., Danger, M., 2015. Aquatic hyphomycetes: a potential source of polyunsaturated fatty acids in detritus-based stream food webs. *Fungal Ecology* 13, 201-210.

Arsuffi, T.L., Suberkropp, K., 1986. Growth of two stream caddisflies (Trichoptera) on leaves colonized by different fungal species. *Journal of the North American Benthological Society* 5, 297-305.

Asaeda, T., Nam, L.H., Hietz, P., Tanaka, N., Karunaratne, S., 2002. Seasonal fluctuations in live and dead biomass of *Phragmites australis* as described by a growth and decomposition model: implications of duration of aerobic conditions for litter mineralization and sedimentation. *Aquatic Botany* 73, 223-239.

Au, D.W.T., Jones, E.B.J., Moss, S.T., Hodgkiss, I.J., 1996. The role of muscilage in the attachment of conidia, germ tubes, and appresoria in the saprobic aquatic hyphomycetes *Lemonniera aquatica* and *Mycocentrospora filiformis*. *Canadian Journal of Botany* 74, 1789-1800.

Baldy, V., Chauvet, E., Charcosset, J.Y., Gessner, M.O., 2002. Microbial dynamics associated with leaves decomposing in the mainstem and floodplain pond of a large river. *Aquatic Microbial Ecology* 28, 25-36.

Baldy, V., Gessner, M.O., 1997. Towards a budget of leaf litter decomposition in a first-order woodland stream. *Comptes Rendus de l'Académie des Sciences Paris, Series III* 320, 747-758.

Baldy, V., Gobert, V., Guérold F, Chauvet, E., Lambrigot, D., Charcosset, J.Y., 2007. Leaf litter breakdown budgets in streams of various trophic status: effects of dissolved inorganic nutrients on microorganisms and invertebrates. *Freshwater Biology* 52, 1322-1335.

Bärlocher, F., 1985. The role of fungi in the nutrition of stream invertebrates. *Botantical Journal of the Linnean Society* 91, 83-94.

Bärlocher, F., 2000. Water-borne conidia of aquatic hyphomycetes: seasonal and yearly patterns in Catamaran Brook, New Brunswick, Canada. *Canadian Journal of Botany* 78, 157-167.

Bärlocher, F., 2009. Reproduction and dispersal in aquatic hyphomycetes. *Mycoscience* 50, 3-8.

Bärlocher, F., Biddiscombe, N., 1996. Geratology and decomposition of *Typha latifolia* and *Lythrum salicaria* in a freshwater marsh. *Archiv für Hydrobiologie* 136, 309-325.

Bärlocher, F., Brendelberger, H., 2004. Clearence of aquatic hyphomycete spores by a benthic suspension feeder. *Limnology and Oceanography* 49:2292-2296.

Bärlocher, F., Corkum, M., 2003. Nutrient enrichment overwhelms diversity effects in leaf decomposition by stream fungi. *Oikos* 101, 247-252.

Bärlocher, F., Kebede, Y.K, Gonçalves, A.L., Canhoto, C., 2013. Incubation temperature and substrate quality modulate sporulation by aquatic hyphomycetes. *Microbial Ecology* 66, 30-39.

Bärlocher, F., Marvanová, L., 2010. Aquatic hyphomycetes (Deuteromycotina) of the Atlantic Maritime Ecozone, in: McAlpine, D.F., Smith, I.M. (Eds), Assessment of species diversity in the Atlantic Maritime Ecozone. NRC Research Press, Ottawa, pp. 71-104.

Bärlocher, F., Rosset, J., 1981. Aquatic hyphomycete spora of two Black Forest and two Swiss Jura streams. *Transactions of British Mycological Society* 76, 479-483.

Bärlocher, F., Sridhar, K.R., 2014. Aquatic hyphomycetes and invertebrates, in: Gareth Jones, E.B., Hyde, K.D. (Eds), Freshwater fungi and fungus-like organisms. De Gruyter, New York, pp. 413-441.

Bärlocher, F., Stewart, M., Ryder, D.S., 2012. Processing of *Eucalyptus viminalis* leaves in Australian streams – importance of aquatic hyphomycetes and zoosporic fungi. *Fundamental and Applied Limnology* 179, 305-319.

Baschien, C., Tsui, C.K.M., Gulis, V., Szewzyk, U., Marvanová, L., 2013. The molecular phylogeny of aquatic hyphomycetes with affinity to the Leotiomycetes. *Fungal Biology* 117, 660-672.

Batista, D., Pascoal, C., Cássio, F., 2012. Impacts of warming on aquatic decomposers along a gradient of cadmium stress. *Environmental Pollution* 169, 35-41.

Battin, T.J., Sloan, W.T., Kjelleberg, S., Daims, H., Head, I.M., Curtis, T.P., Eberl, L., 2007. Microbial landscapes: new paths to biofilm research. *Nature Reviews Microbiology* 5, 76-81.

Batzer, D.P., Sharitz, R.R., 2014. Ecology of freshwater and estuarine wetlands, 2nd Edition. University of California Press, Berkley.

Blagodatsky, S., Blagodatskaya, E., Yuyukina, T., Kuzyakov, Y., 2010. Model of apparent and real priming effects: linking microbial activity with soil organic matter decomposition. *Soil Biology and Biochemistry* 42, 1275-1283.

Blomberg, A., Adler, L., 1992. Physiology of osmotolerance in fungi. *Advances in Microbial Physiology* 33, 145-212.

Borken, W., Matzner, E., 2009. Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils. *Global Change Biology* 15, 808-824.

Brown, A.D., 1990. Microbial water stress physiology: principles and perspectives. John Wiley and Sons, Chichester.

Bruder, A., Chauvet, E., Gessner, M.O., 2011. Litter diversity, fungal decomposers and litter decomposition under simulated stream intermittency. *Functional Ecology* 25, 1269-1277.

Buesing, N., Filippini, M., Bürgmann, H., Gessner, M.O., 2009. Microbial communities in contrasting freshwater marsh microhabitats. *FEMS Microbiology Ecolology* 69, 84-97.

Buesing, N., Gessner, M.O., 2006. Benthic bacterial and fungal productivity and carbon turnover in a freshwater marsh. *Applied Environmental Microbiology* 72, 596-605.

Canhoto, C., Graça, M.A.S., 1999. Leaf barriers to fungal colonization and shredders (*Tipula lateralis*) consumption of decomposing *Eucalyptus globulus*. *Microbial Ecology* 37, 163-172.

Carpenter, J.F., Crowe, J.H., 1988. Modes of stabilization of protein by organic solutes during desiccation. *Cryobiology* 25, 459-470.

Carter, M.D., Suberkropp, K., 2004. Respiration and annual fungal production associated with decomposing leaf litter in two streams. *Freshwater Biology* 49, 1112-1122.

Chamier, A.C., 1985. Cell-wall-degrading enzymes of aquatic hyphomycetes: a review. *Botanical Journal of the Linnaean Society* 91, 67-81.

Chamier, A.C., Dixon, P.A., 1982. Pectinases in leaf degradation by aquatic hyphomycetes: the enzymes and leaf maceration. *Journal of General Microbiology* 128, 2469-2483.

Chauvet, E., Suberkropp, K., 1998. Temperature and sporulation of aquatic hyphomycetes. *Applied Environmental Microbiology* 64, 1522-1525.

Chergui, H., Pattee, E., 1988. The dynamics of hyphomycetes on decaying leaves in the network of the River Rhone (France). *Archiv für Hydrobiologie* 114, 3-20.

Christensen, J.R., Crumpton, W.G., van der Valk, A.G., 2009. Estimating the breakdown and accumulation of emergent macrophyte litter: a mass-balance approach. *Wetlands* 29, 204-214.

Chung, N., Suberkropp, K., 2009. Contribution of fungal biomass to the growth of the shredder, *Pycnopsyche gentilis* (Trichoptera: Limnephilidae). *Freshwater Biology* 54, 2212-2224.

Clivot, H., Charmasson, F., Felten, V., Boudot, J.P., Guérold, F., Danger, M., 2014. Interactive effects of aluminium and phosphorus on microbial leaf litter processing in acidified streams: a microcosm approach. *Environmental Pollution* 186, 67-74.

Clivot, H., Danger, M., Pagnout, C., Wagner, P., Rousselle, P., Poupin, P., Guérold, F., 2013. Impaired leaf litter processing in acidified streams. *Microbial Ecology* 65, 1-11.

Cornut, J., Clivot, H., Chauvet, E., Elger, A., Pagnout, C., Guérold, F., 2012. Effect of acidification on leaf litter decomposition in benthic and hyporheic zones of woodland streams. *Water Research* 46, 6430-6444.

Cross, W.F., Wallace, J.B., Rosemond, A.D., Eggert, S.L., 2006. Whole-system nutrient enrichment increases secondary production in a detritus-based ecosystem. *Ecology* 87, 1556-1565.

Crowe, J.H., Crowe, L.M., Carpenter, J.F., Rudolph, A.S., Wistrom, C.A., Spargo, B.J. Anchordoguy, T.J., 1988. Interactions of sugars with membranes. *Biochimica et Biophysica Acta* 947, 367-384.

Crowe, J.H., Crowe, L.M., Chapman, D., 1984. Preservation of membranes in anhydrobiotic organisms: The role of trehalose. *Science* 223,701-703.

Dang, C.K., Chauvet, E., Gessner, M.O., 2005. Magnitude and variability of process rates in fungal diversity-litter decomposition experiments. *Ecological Letters* 8, 1129-1137.

Dang, C.K., Gessner, M.O., Chauvet, E., 2007. Influence of conidial traits and leaf structure on attachment success of aquatic hyphomycetes on leaf litter. *Mycologia* 99, 24-32.

Dang, C.K., Schindler, M., Chauvet, E., Gessner, M.O., 2009. Temperature oscillation coupled with fungal community structure shifts can modulate warming effects on litter decomposition. *Ecology* 90, 122-131.

Danger, M., Chauvet, E., 2013. Elemental composition and degree of homeostasis of fungi: are aquatic hyphomycetes more like metazoans, bacteria or plants? *Fungal Ecology* 6, 453-457.

Danger, M., Cornut, J., Chauvet, E., Chavez, P., Elger, A., Lecerf, A., 2013. Benthic algae stimulate leaf litter decomposition in detritus-based headwater streams: a case of aquatic priming effect? *Ecology* 94, 1604-1613.

Dangles, O., Gessner, M.O., Guérold, F., Chauvet, E., 2004. Impact of acidification on litter breakdown: implications for assessing ecosystem functioning. *Journal of Applied Ecology* 41, 365-378.

Descals, E., 2005. Diagnostic characters of propagules of Ingoldian fungi. *Mycological Research* 109, 545-555.

Duarte, S., Bärlocher F., Trabulo, J., Cássio, F., Pascoal, C., 2015. Stream-dwelling fungal decomposer communities along a gradient of eutrophication unraveled by 454 pyrosequencing. *Fungal Diversity* 70, 127-148.

Duarte, S., Fernandes, I., Nogueira, M.J., Cássio, F., Pascoal, C., 2013a. Temperature alters interspecific relationships among aquatic fungi. *Fungal Ecology* 6, 187-191.

Duarte S, Pascoal C, Cássio, F., Bärlocher F., 2006. Aquatic hyphomycete diversity and identity affect leaf litter decomposition in microcosms. *Oecologia* 147, 658-666.

Duarte, S., Seena, S., Bärlocher, F., Cássio, F., Pascoal, C., 2012. Preliminary insights into the phylogeography of six aquatic hyphomycete species. *PLOS one* 9, e45289.

Duarte, S., Seena, S., Bärlocher, F., Pascoal, C., Cássio, F., 2013b. A decade's perspective on the impact of DNA sequencing on aquatic hyphomycete research. *Fungal Biology Reviews* 27, 19-24.

Farr, D.F., Bills, G.F., Chamuris G.P., Rossman, A.Y., 1989. Fungi on plants and plant products in the United States. APS Press, St. Paul.

Fennessy, M.S., Rokosch, A., Mack, J., 2008. Patterns of plant decomposition and nutrient cycling in natural and created wetlands. *Wetlands* 28, 300-310.

Fernandes, I., Pascoal, C., Cássio, F., 2011. Intraspecific traits change biodiversity effects on ecosystem functioning under metal stress. *Oecologia* 166, 1019-1028.

Fernandes, I. Pascoal, C., Guimarães, H., Pinto, R., Sousa, I., Cássio, F., 2012. High temperature reduces the effects of litter quality on decomposition by aquatic fungi. *Freshwater Biology* 57, 2306-2317.

Fernandes, I. Uzun, B., Pascoal, C., Cássio, F., 2009. Response of aquatic fungal communities on leaf litter to temperature-change events. *International Reveiw Hydrobiology* 94, 410-418.

Ferreira, V., Castagneyrol, B., Koricheva, J., Gulis, V., Chauvet, E., Graça, M.A.S., 2015. A meta-analysis of the effects of nutrient enrichment on litter decomposition in streams. *Biological Reviews* 90, 669-688.

Ferreira, V., Chauvet, E., 2011a. Future increases in temperature more than decrease in litter quality can affect microbial litter decomposition in streams. *Oecologia* 167, 279-291.

Ferreira, V., Chauvet, E., 2011b. Synergistic effects of water temperature and dissolved nutrients on litter decomposition and associated fungi. *Global Change Biology* 17, 551-564.

Ferreira, V., Chauvet, E., 2012. Changes in dominance among species in aquatic hyphomycetes assemblages do not affect litter decomposition. *Aquatic Microbial Ecology* 66, 1-11.

Ferreira, V., Elosegi, A., Gulis, V., Pozo, J., Graça, M.A.S., 2006b. Eucalyptus plantations affect fungal communities associated with leaf-litter decomposition in Iberian streams. *Archiv für Hydrobiologie* 166, 467-490.

Ferreira V, Gonçalves, A.L., Canhoto, C., 2012. Aquatic hyphomycete strains from metal-contaminated and reference streams might repond differently to future increases in temperature. *Mycologia* 104, 613-622.

Ferreira, V., Graça, M.A.S., 2006. Do invertebrate activity and current velocity affect fungal assemblage structure in leaves. *International Review of Hydrobiology* 91, 1-14.

Ferreira, V., Gulis, V., Graça, M.A.S., 2006a. Whole-stream nitrate addition affects litter decomposition and associated fungi but not invertebrates. *Oecologia* 149, 718-729.

Ferreira, V., Gulis, V., Pascoal, C., Graça, M.A.S., 2014. Stream pollution and fungi, in: Jones, E.B.G., Hyde, K.D., Pang, K.L. (Eds) Freshwater fungi and fungal-like organisms. De Gruyter, Berlin, pp. 389-412.

Findlay, S.E.G., Dye, S., Kuehn, K.A., 2002a. Microbial growth and nitrogen retention in litter of *Phragmites australis* compared to *Typha angustifolia*. *Wetlands* 22, 616-625.

Findlay, S., Tank, J., Dye, S., Valett, H.M., Mulholland, P.J., McDowell, W.H., Johnson, S.L., Hamilton, S.K., Edmonds, J., Bowd, W.B., 2002b. A cross-system comparison of bacterial and fungal biomass in detritus pools of headwater streams. *Microbial Ecology* 43, 55-66.

Francoeur, S.N., Schaecher, M., Neely, R.K., Kuehn, K.A., 2006. Periphytic photosynthetic stimulation of extracellular enzyme activity in aquatic microbial communities associated with decaying *Typha* litter. *Microbial Ecology* 52, 662-669.

Geraldes, P., Pascoal, C. Cássio, F., 2012. Effects of increased temperature and aquatic fungal diversity on litter decomposition. *Fungal Ecology* 5, 734-740.

Gessner, M.O., 2001. Mass loss, fungal colonisation and nutrient dynamics of *Phragmites australis* leaves during senescence and early aerial decay. *Aquatic Botany* 69, 325-339.

Gessner, M.O., 2005. Ergosterol as a measure of fungal biomass, in: Graça, M.A.S., Bärlocher, F., Gessner, M.O. (Eds) Methods to study litter decomposition: a practical guide. Springer, Dordrecht, pp. 189-196.

Gessner, M.O., Chauvet, E., 1994. Importance of stream microfungi in controlling breakdown rates of leaf litter. *Ecology* 75, 1807-1817.

Gessner, M.O., Chauvet, E., 1997. Growth and production of aquatic hyphomycetes in decomposing leaf litter. *Limnology and Oceanography* 42, 496-595.

Gessner, M.O., Chauvet, E., Dobson, M., 1999. A perspective on leaf litter breakdown in streams. *Oikos* 85, 377-384.

Gessner, M.O., Gulis, V., Kuehn, K.A., Chauvet, E., Suberkropp, K., 2007. Fungal decomposers of plant litter in aquatic ecosystems, in: Kubicek, C.P., Druzhinina, I.S. (Eds), The Mycota, vol IV, Environmental and microbial relationship. Springer, Berlin, pp. 301-324.

Gessner, M.O., Swan, C.M., Dang, C.K., McKie, B.G., Bardgett, R.D., Wall, D.H., Hättenschwiler, S., 2010. Diversity meets decomposition. *Trends in Ecology and Evolution* 25, 372-380.

Gessner, M.O., Van Ryckegem, G., 2003. Water fungi as decomposers in freshwater ecosystems, in: Bitton, G. (Ed), Encyclopedia of environmental microbiology. Wiley, New York, DOI: 10.1002/0471263397.env314.

Gillies, J.E., Kuehn, K.A., Francoeur, S.N., Neely, R.K., 2006. Application of the ^{3}H-leucine incorporation technique for quantifying rates of bacterial secondary production associated with decaying wetland plant litter. *Applied and Environmental Microbiology* 72, 5948-5956.

Gonçalves, A.L., Chauvet, E., Bärlocher, F., Graça, M.A.S., Canhoto, C., 2014. Top-down and bottom-up control of litter decomposers in streams. *Freshwater Biology* 59, 2172-2182.

Grattan, R.M., Suberkropp, K., 2001. Effects of nutrient enrichment on yellow poplar leaf decomposition and fungal activity in streams. *Journal of the North American Benthological Society* 20, 33-43.

Grimmett, I.J., Shipp, K.N., MacNeil, A., Bärlocher, F., 2013. Does the growth rate hypothesis apply to aquatic hyphomycetes? *Fungal Ecology* 6, 493-500.

Guenet, B., Danger, M., Abbadie, L., Lacroix, G., 2010. Priming effect: bridging the gap between terrestrial and aquatic ecology. *Ecology* 91, 2850-2861.

Gulis, V., 2001. Are there any substrate preferences in aquatic hyphomycetes? *Mycological Research* 105, 1088-1093.

Gulis, V., Ferreira, V., Graça M.A.S., 2006a. Stimulation of leaf litter decomposition and associated fungi and invertebrates by moderate eutrophication: implications for stream assessment. *Freshwater Biology* 51, 1655-1669.

Gulis V., Kuehn, K.A., Suberkropp, K., 2006b. The role of fungi in carbon and nitrogen cycles in freshwater ecosystems, in: Gadd, G.M. (Ed), Fungi in Biogeochemical Cycles. Cambridge University Press, Oxford, pp. 404-435.

Gulis, V., Kuehn. K.A., Suberkropp, K., 2009. Fungi, in: Likens, G.E. (Ed) Encyclopedia of inland waters, Vol 3. Elsevier, Oxford, pp. 233-243.

Gulis, V., Rosemond, A.D., Suberkropp, K., Weyers, H.S., Benstead, J.P., 2004. Effects of nutrient enrichment on the decomposition of wood and associated microbial activity in streams. *Freshwater Biology* 49, 1437-1447.

Gulis, V., Suberkropp, K., 2003a. Effect of inorganic nutrients on relative contributions of fungi and bacteria to carbon flow from submerged decomposing leaf litter. *Microbial Ecology* 45, 11-19.

Gulis, V., Suberkropp, K., 2003b. Interactions between stream fungi and bacteria associated with decomposing leaf litter at different levels of nutrient availability. *Aquatic Microbial Ecology* 30, 149-157.

Gulis, V., Suberkropp, K., 2003c. Leaf litter decomposition and microbial activity in nutrient-enriched and unaltered reaches of a headwater stream. *Freshwater Biology* 48, 123-134.

Gulis. V., Suberkropp, K., Rosemond, A.D., (2008) Comparison of fungal activities on wood and leaf litter in unaltered and nutrient-enriched headwater streams. *Applied Environmental Microbiology* 74, 1094-1101.

Harrison, S.J., Moss, S.T., Jones, E.B.G., 1988. Fungal adhesion in aquatic hyphomycetes. *International Biodeterioration* 24, 271-276.

Hieber, M., Gessner, M.O., 2002. Contribution of stream detritivores, fungi, and bacteria to leaf breakdown based on biomass estimates. *Ecology* 83, 1026-1038.

Hopkinson, C.S., 1992. A comparison of ecosystem dynamics in freshwater wetlands. *Estuaries* 15, 549-562.

Hotchkiss, E.R., Hall, R.O., Baker, E.J., Rosi-Marshall, E.J., Tank, J.L., 2014. Modeling priming effects on microbial consumption of dissolved organic carbon in rivers. *Journal of Geophysical Research G. Biosciences* 119, 982-995.

Ingold, C.T., 1971. Fungal spores: their liberation and dispersal. Clarendon Press, Oxford.

Jabiol, J.J., Bruder, A., Gessner, M.O., Makkonen, M., McKie, B.G., Peeters, E.T.H.M., Vos, V.C.A., Chauvet, E., 2013. Diversity patterns of leaf-associated aquatic hyphomycetes along a broad latitudinal gradient. *Fungal Ecology* 6, 439-448.

Jabiol, J.J., Chauvet, E., 2012. Fungi are involved in the effects of litter mixtures on consumption by shredders. *Freshwater Biology* 57, 1667-1677.

Jenkins, C.C., Suberkropp, K., 1995. The influence of water chemistry on the enzymatic degradation of leaves in streams. *Freshwater Biology* 33, 245-253.

Jennings, D.H., 1995. The physiology of fungal nutrition. Cambridge University Press, Cambridge.

Kayranli, B., Scholz, M., Mustafa, A., Hedmark, A., 2010. Carbon storage and fluxes within freshwater wetlands: A critical review. *Wetlands* 30, 111–124.

Kearns, S.G., Bärlocher, F., 2008. Leaf surface roughness influences colonization success of aquatic hyphomycete conidia. *Fungal Ecology* 1, 13-18.

Komínková, D., Kuehn, K.A., Busing, N., Steiner, D., Gessner, M.O., 2000. Microbial biomass, growth, and respiration associated with submerged litter of *Phragmites australis* decomposing in a littoral reed stand of a large lake. *Aquatic Microbial Ecology* 22, 271-282.

Krauss, G.J., Solé, M., Krauss, G., Schlosser, D., Wesenberg, D., Bärlocher, F., 2011. Fungi in freshwaters: ecology, physiology and biochemical potential. *FEMS Microbiology Reviews* 35:620-651.

Kuehn, K.A., 2008. The role of fungi in the decomposition of emergent wetland plants, in: Sridhar, S., Bärlocher, F., Hyde, K.D. (Eds), Novel techniques and ideas in mycology. Fungal Diversity Press, Hong Kong, pp. 19-41.

Kuehn, K.A., Churchill, P.F., Suberkropp, K., 1998. Osmoregulatory responses of fungi inhabiting standing litter of the freshwater emergent macrophyte *Juncus effusus*. *Applied Environmental Microbiology* 64, 607-612.

Kuehn, K.A., Francoeur, S.N., Findlay, R.H., Neely, R.K., 2014. Priming in the microbial landscape: periphytic algal stimulation of litter-associated microbial decomposers. *Ecology* 95, 749-762.

Kuehn, K.A., Gessner, M.O., Wetzel, R.G., Suberkropp, K., 1999. Decomposition and CO_2 evolution from standing litter of the emergent macrophyte *Erianthus giganteus*. *Microbial Ecology* 38, 50-57.

Kuehn, K.A., Lemke, M.J., Suberkropp, K., Wetzel, R.G., 2000. Microbial biomass and production associated with decaying leaf litter of the emergent macrophyte *Juncus effusus*. *Limnology and Oceanography* 45, 862-870.

Kuehn, K.A., Ohsowski, B.M., Francoeur, S.N., Neely R.K., 2011. Contributions of fungi to carbon flow and nutrient cycling from standing dead *Typha angustifolia* leaf litter in a temperate freshwater marsh. *Limnology and Oceanography* 56, 529-539.

Kuehn, K.A., Steiner, D., Gessner, M.O., 2004. Diel mineralization patterns of standing-dead plant litter: Implications for CO_2 flux from wetlands. *Ecology* 85, 2504-2518.

Kuehn, K.A., Suberkropp, K., 1998a. Decomposition of standing litter of the freshwater emergent macrophyte Juncus effusus. *Freshwater Biology* 40, 717-727.

Kuehn, K.A., Suberkropp, K., 1998b. Diel fluctuations in rates of CO_2 evolution from standing dead leaf litter of the emergent macrophyte Juncus effusus. *Aquatic Microbial Ecology* 14, 171-182.

Kuzyakov, Y., 2010. Priming effects: Interactions between living and dead organic matter. *Soil Biology and Biochemistry* 42, 1363-1371.

Langhans, S.D., Tiegs, S.D., Gessner, M.O., Tockner, K., 2008. Leaf-decomposition heterogeneity across a riverine floodplain mosaic. *Aquatic Sciences* 70, 337-346.

Langhans, S.D., Tockner, K., 2006. The role of timing, duration, and frequency of inundation in controlling leaf litter decomposition in a river-floodplain ecosystem (Tagliamento, northeastern Italy). *Oecologia* 147, 501-509.

Larned, S.T., Datry, T., Arscott, D.B., Tockner, K., 2010. Emerging concepts in temporary-river ecology. *Freshwater Biology* 55, 717-738.

Lozano, P., Combes, D., Iborra J.L., 1994. Effect of polyols on alpha-chymotrypsin thermostability: a mechanistic analysis of the enzyme stabilization. *Journal of Biotechnology* 35, 9-18.

Maharning, A.R., Bärlocher, F., 1996. Growth and reproduction in aquatic hyphomycetes. *Mycologia* 88, 80-88.

Marano, A.V., Pires-Zottarelli, C.L.A., Barrera, M.D., Steciow, M.M., Gleason, F.H., 2011. Diversity, role in decomposition, and succession of zoosporic fungi and straminipiles on submerged decaying leaves in a woodland stream. *Hydrobiologia* 659, 93-109.

Mathuriau, C., Chauvet, E., 2002. Breakdown of leaf litter in a neotropical stream. *Journal of the North American Benthological Society* 21, 384-396.

Medeiros, A.O., Pascoal, C, Graça, M.A.S., 2009. Diversity and activity of aquatic fungi under low oxygen conditions. *Freshwater Biology* 54, 142-149.

Mehring, A.S., Kuehn, K.A., Thompson, A., Vellidis, G., Pringle, C.M., Rosemond, A.D., First, M.R., Lowrance, R.R., 2015. Leaf litter nutrient uptake in an intermittent blackwater river: Influence of tree species and associated biotic and abiotic drivers. *Functional Ecology* 29, 849-860.

Methvin, B.R., Suberkropp, K., 2003. Annual production of leaf-decaying fungi in two streams. *Journal of the North American Benthological Society* 22, 554-564.

Mille-Lindblom, C., Fischer, H., Tranvik, L.J., 2006. Antagonism between bacteria and fungi: substrate competition and a possible tradeoff between fungal growth and tolerance towards bacteria. *Oikos* 113, 233-242.

Mille-Lindblom, C., Tranvik, L.J., 2003. Antagonism between bacteria and fungi on decomposing aquatic plant litter. *Microbial Ecology* 45, 173-182.

Mitsch, W.J., Gosselink, J.G., 2007. Wetlands, 4th Edition. Wiley and Sons, New York

Money, N.P., 1994. Osmotic adjustment and the role of turgor in mycelial fungi, in: Wessels J.G.H., Meinhardt, F. (Ed.), The Mycota, I. Growth, Differentiation and Sexuality. Springer-Verlag, Berlin. pp. 67-88.

Money, N.P., 1995. Turgor pressure and the mechanics of fungal penetration. *Canadian Journal of Botany* 73(suppl), S96-102.

Mulholland, P.J., Palumbo, A.V., Elwood, J.W., Rosemond, A.D., 1987. Effects of acidification on leaf decompositionin streams. *Journal of the North American Benthological Society* 6, 147-158.

Neubert, K., Mendgen, K., Brinkmann, H., Wirsel, S.G.R., 2006. Only a few fungal species dominate highly diverse mycofloras associated with the common reed. *Applied and Environmental Microbiology* 72, 1118-1128.

Newell, S.Y., 2003. Fungal content and activities in standing-decaying leaf blades of plants of the Georgia Coastal Ecosystems research area. *Aquatic Microbial Ecology* 32, 95-103.

Newell, S.Y., Moran, M.A., Wicks, R., Hodson R.E., 1995. Productivities of microbial decomposers during early stages of decomposition of leaves of a freshwater sedge. *Freshwater Biology* 34, 135-148.

Nikolcheva, L.G., Bärlocher, F., 2004. Taxon-specific fungal primers reveal unexpectedly high diversity during leaf decomposition in a stream. *Mycological Progress* 3, 41-49.

Nikolcheva, L.G., Bärlocher, F., 2005. Seasonal and substrate preferences of fungi colonizing leaves in streams: traditional versus molecular evidence. *Environmental Microbiology* 7, 270-280.

Nikolcheva, L.G., Bourque, T., Bärlocher F., 2005. Fungal diversity during initial stages of leaf decomposition in a stream. *Mycological Research* 109, 246-253.

Niyogi, D.K., Lewis, W.M., McKnight, D.M., 2001. Litter breakdown in mountain streasm affected by mine drainage: biotic mediation of abiotic controls. *Ecological Applications* 11, 506-516.

Ohsowski, B.M., 2008. Annual secondary production of fungal and bacterial decomposers associated with standing and benthic litter of the freshwater emergent macrophyte, *Typha angustigolia*. MS thesis, Eastern Michigan University.

Pacioglu, O., Cornut, J., Gessner, M.O., Kasprzak, P., 2015. Prevalence of indirect toxicity effects of aluminium flakes on a shredder-fungal-leaf decomposition system. *Freshwater Biology* http://onlinelibrary.wiley.com/doi/10.1111/fwb.12529/epdf

Papendick, R.I., Mulla, D.J., 1986. Basic principles of cell and tissue water relations, in: Ayres, P.G., Boddy, L. (Ed.), Water, Plants and Fungi. Cambridge University Press, Cambridge. pp. 1-26.

Pascoal, C., Cássio, F., 2004. Contribution of fungi and bacteria to leaf litter decomposition in a polluted river. *Applied Environmental Microbiology* 70, 5266-5273.

Pascoal, C., Cássio, F., Marcotegui, A., Sanz, B., Gomes, P., 2005. Role of fungi, bacteria, and invertebrates in leaf litter breakdown in a polluted river. *Journal of the North American Benthological Society* 24, 784-797.

Pascoal, C., Cássio, F., Nikolocheva, L., Bärlocher, F., 2010. Realized fungal diversity increases functional stability of leaf litter decomposition under zinc stress. *Microbial Ecology* 59, 84-93.

Poon, M.O.K., Hyde K.D., 1998. Evidence for the vertical distribution of saprophytic fungi on senescent *Phragmites australis* culms at Mai Po marshes, Hong Kong. *Botanica Marina* 41, 285-292.

Pugh, G.J.F., Mulder, J.L., 1971. Mycoflora associated with *Typha latifolia*. *Transactions of the British Mycological Society* 57, 273-282.

Read, S.J., Moss, S.T., Jones, E.B.G., 1991. Attachment studies of aquatic hyphomycetes. *Philosophical Transactions of the Royal Society of London B* 334, 449-457.

Reddy, K.R., Delauune, R.D., 2008. Biogeochemistry of wetlands: science and applications. CRC Press, Boca Raton.

Rier, S.T., Kuehn, K.A., Francoeur, S.N., 2007. Algal regulation of extracellular enzyme activity in stream microbial communities associated with inert substrata and detritus. *Journal of the North American Benthological Society* 26, 439-449.

Rier, S.T., Shirvinski J.M., Kinek, K.C., 2014. In situ light and phosphorus manipulations reveal potential role of biofilm algae in enhancing enzyme-mediated decomposition of organic matter in streams. *Freshwater Biology* 59, 1039-1051.

Rosemond, A.D., Benstead, J.P., Bumpers, P.M., Gulis, V., Kominoski, J.S., Manning, D.W.P., Suberkropp, K., Wallace, J.B., 2015. Experimental nutrient additions accelerate terrestrial carbon loss from stream ecosystems. *Science* 347, 1142-1145.

Rothman, E., Bouchard, V., 2007. Regulation of carbon processes by macrophyte species in a Great Lakes coastal wetland. *Wetlands* 27, 1134-1143.

Saccardo, P.A., 1898. Sylloge fungorum omnium hucusque cognitorum 13, Index universalis. Fratres Borntrager, Lipsiae

Schneider, T., Gerrits, B., Gassmann, R., Schmid, E., Gessner, M.O., Richter, A., Battin, T., Eberl, L., Riedel, K., 2010. Proteome analysis of fungal and bacterial involvement in leaf litter decomposition. *Proteomics* 10, 1819-1830.

Seena, S., Wynberg, N., Bärlocher, F., 2008. Fungal diversity during leaf decomposition in a stream assessed through clone libraries. *Fungal Diversity* 30, 1-14.

Shearer, C.A., 1993. The freshwater ascomycetes. *Nova Hedwigia* 56, 1-33.

Shearer, C.A., Descals E, Kohlmeyer, B., Kohlmeyer, J., Marvanová, L., Padgett, D., Porter, D., Raja, H.A., Schmit, J.P., Thorton, H.A., Voglymayr, H., 2007. *Fungal biodiversity in aquatic habitats. Biodiversity and Conservation* 16, 49-67.

Sinsabaugh, R.L., Belnap, J., Follstad Shah, J.J., Hill, B.H., Kuske, C., Litvak, M., Matinez, N., Moorhead, D.L., Findlay, S.G., Kuehn, K.A., Warnock, D., 2014. Extracellular enzyme kinetics scale with resource availability. *Biogeochemisty* 121, 287-304.

Sinsabaugh, R.L., Findlay, S., 1995. Microbial production, enzyme activity, and carbon turnover in surface sediments of the Hudson River estuary. *Microbial Ecology* 30, 127-141.

Sinsabaugh, R.L., Belnap, J., Follstad-Shah, J.J., Hill, B.H., Kuske, C., Litvak, M., Matinez, N., Moorhead, D.L., Findlay, S.G., Kuehn K.A., Warnock, D., 2014. Extracellular enzyme kinetics scale with resource availability. *Biogeochemisty* 121, 287-304.

Sinsabaugh, R.L., Follstad-Shah J.J., 2012. Ecoenzymatic stoichiometry and ecological theory. *Annual Review of Ecology, Evolution, and Systematics* 43, 313-343.

Sinsabaugh, R.L., Follstad-Shah, J.J., Findlay, S.G., Kuehn, K.A., Moorhead, D.L., 2015. Scaling microbial biomass, metabolism and resource supply. *Biogeochemistry* 122, 175-190.

Sridhar, K.R., Bärlocher, F., 1994. Viability of aquatic hyphomycete conidia in foam. *Canadian Journal of Botany* 72, 106-110.

Stelzer, R.S., Heffernan J., Likens, G.E., 2003. The influence of dissolved nutrients and particulate organic matter quality on microbial respiration and biomass in a forest stream. *Freshwater Biology* 48, 1925-1937.

Su, R., 2014. Fungal contribution to carbon and nutrient cycling in a subtropical freshwater marsh. Ph.D. dissertation, University of Southern Mississippi

Su, R., Kuehn, K.A., Phipps, S.W., 2015. Carbon and nutrient flow into decomposer fungi during standing-dead *Typha domingensis* decomposition in a subtropical freshwater marsh. *Freshwater Biology* http://onlinelibrary.wiley.com/doi/10.1111/fwb.12635/epdf

Su, R., Lohner, R.N., Kuehn, K.A., Sinsabaugh, R.L., Neely, R.K., 2007. Microbial dynamics associated with decomposing *Typha angustifolia* litter in two contrasting Lake Erie coastal wetlands. *Aquatic Microbial Ecology* 46, 295-307.

Suberkropp, K., 1984. Effect of temperature on seasonal occurrence of aquatic hyphomycetes. Tansactions of the British Mycological Society 82, 53-63.

Suberkropp, K., 1991. Relationships between growth and sporulation of aquatic hyphomycetes on decomposing leaf litter. *Mycological Research* 95, 843-850.

Suberkropp, K., 1992. Interactions with invertebrates, in: Bärlocher, F. (Ed), The ecology of aquatic hyphomycetes. Springer, Berlin, pp. 118-134.

Suberkropp, K., 1995. The influence of nutrients on fungal growth, productivity, and sporulation during leaf breakdown in streams. *Canadian Journal of Botany* 73(suppl.), S1361-S1369.

Suberkropp, K., 1997. Annual production of leaf-decaying fungi in a woodland stream. *Freshwater Biology* 38, 169-178.

Suberkropp, K., 1998. Effect of dissolved nutrients on two aquatic hyphomycetes growing on leaf litter. *Mycological Research* 102, 998-1002.

Suberkropp, K., 2001. Fungal growth, production and sporulation during leaf decomposition in two streams. *Applied and Environmental Microbiology* 67, 5063-5068.

Suberkropp, K., Arsuffi, T.L., Anderson, J.P., 1983. Comparison of degradative ability, enzymatic activity, and palatability of aquatic hyphomycetes grown on leaf litter. *Applied and Environmental Microbiology* 46, 237-244.

Suberkropp, K., Chauvet, E., 1995. Regulation of leaf breakdown by fungi in streams: influence of water chemistry. *Ecology* 76, 1433-1445.

Suberkropp, K., Gessner, M.O., 2005. Acetate incorporation into ergosterol to determine fungal growth rates and production, in: Graça, M.A.S., Bärlocher, F., Gessner, M.O. (Eds) Methods to study litter decomposition: a practical guide. Springer, Berlin, pp. 197-202.

Suberkropp, K., Gessner, M.O., Chauvet, E., 1993. Comparison of ATP and ergosterol as indicators of fungal biomass associated with decomposing leaves in streams. *Applied Environmental Microbiology* 59, 3367-3372.

Suberkropp, K., Gulis, V., Rosemond, A.D., Benstead, J.P., 2010. Ecosystem and physiological scales of microbial responses to nutrients in a detritus-based stream: results of a 5-year continuous enrichment. *Limnology and Oceanography* 55, 149-160.

Suberkropp, K., Klug, M.J., 1980. The maceration of deciduous leaf litter by aquatic hyphomycetes. *Canadian Journal of Botany* 58, 1025-1031.

Suberkropp, K., Weyers, H.S., 1996. Application of fungal and bacterial production methodologies to decomposing leaves in streams. *Applied Environmental Microbiology* 62, 1610-1615.

Tank, J.L., Rosi-Marshall E.J., Griffiths, N.A., Entrekin, S.A., Stephen, M.A., 2010. A review of allochthonous organic matter dynamics and metabolism in streams. *Journal of the North American Benthological Society* 29, 118-146.

Tant, C.J., Rosemond A.D., First, M.R., 2013. Stream nutrient enrichment has a greater effect on coarse than on fine benthic organic matter. *Freshwater Science* 32, 1111-1121.

Tant, C.J., Rosemond, A.D., Mehring, A.S., Kuehn, K.A., Davis, J.M., 2015. The role of aquatic fungi in transformations of organic matter mediated by nutrients. *Freshwater Biology* 60, 1354-1363.

Thomas, K., Chilvers, G.A., Norris, R.H., 1992. Aquatic hyphomycetes from different substrates: substrate preference and seasonal occurrence. *Australian Journal of Marine and Freshwater Research* 43, 491-509.

Tiner, R.W., 1991. The concept of a hydrophyte for wetland identification. *BioScience* 41, 236-247.

Townsend, C.R., Hildrew, A.G., 1994. Species traits in relation to a habitat templet for river systems. *Freshwater Biology* 31, 265-275.

Tsui, C.K.M., Hyde, K.D., 2003. Freshwater Mycology. Fungal Diversity Press, Hong Kong.

Van Ryckegem, G., Gessner, M.O., Verbeken, A., 2007. Fungi on leaf blades of *Phragmites australis* in a brackish tidal marsh: diversity, succession, and leaf decomposition. *Microbial Ecology* 53, 600-611.

Van Ryckegem, G., Van Driessche, G., Van Beeumen J.J., Verbeken A., 2006. The estimated impact of fungi on nutrient dynamics during decomposition of *Phragmites australis* leaf sheaths and stems. *Microbial Ecology* 52, 564-574.

Van Ryckegem, G., Verbeken, A., 2005a. Fungal diversity and community structure on *Phragmites australis* (Poaceae) along a salinity gradient in the Scheldt estuary (Belgium). *Nova Hedwigia* 80, 173-197.

Van Ryckegem, G., Verbeken, A., 2005b. Fungal ecology and succession on *Phragmites australis* in a brackish tidal marsh. I. Leaf sheaths. *Fungal Diversity* 19, 157-187.

Van Ryckegem, G., Verbeken, A., 2005c. Fungal ecology and succession on *Phragmites australis* in a brackish tidal marsh. II. Stems. *Fungal Diversity* 20, 209-233.

Verma, B., Robarts, R.D., Headley, J.V., 2003. Sesonal changes in fungal production and biomass on standing dead *Scirpus lacustris* litter in a northern prairie wetland. *Applied Environmental Microbiology* 69, 1043-1050.

Wallace, J.B., Eggert, S.L., Meyer, J.L., Webster, J.R., 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science* 277, 102-104.

Wallace, J.B., Eggert, S.L., Meyer, J.L., Webster, J.R., 1999. Effects of resource limitation on a detrital-based ecosystem. *Ecological Monographs* 69, 409-442.

Wallace, J.B., Webster, J.R., 1996. The role of macroinvertebrates in stream ecosystem function. *Annual Review of Entomology* 41, 115-139.

Walther, D.A., Whiles, M.R., 2011. Secondary production in a southern Illinois headwater stream: relationship between organic matter standing stocks and macroinvertebrate productivity. *Journal of the North American Benthological Society* 30, 357-373.

Webster, J., 1987. Convergent evolution and the functional significance of spore shape in aquatic and semi-aquatic fungi, in: Raynor, A.D.M., Brasier, C.M., Moore, D. (eds), Evolutionary biology of the fungi. Cambridge University Press, Cambridge, United Kingdom. pp. 191-201.

Webster, J., Descals, E., 1981. Morphology, distribution, and ecology of conidial fungi in freshwater habitats, in: Cole, G.T., Kendrick, B. (Eds) Biology of conidial fungi, vol 1. Academic Press, New York, pp. 295-355.

Webster, J., Moran, S.T., Davey, R.A., 1976. Growth and sporulation of *Tricladium chaetocladium* and *Lunulosporula curvula* in relation to temperature. *Transactions of the British Mycological Society* 67, 491-495.

Webster, J.R., Benfield, E.F., 1986. Vascular plant breakdown in freshwater ecosystems. *Annual Review of Ecology and Systematics* 17, 567-594.

Webster, J.R., Meyer, J.L., 1997. Stream organic matter budgets. *Journal of the North American Benthological Society* 16, 3-4.

Welsch, M., Yavitt, J.B., 2003. Early stages of decay of *Lythrum salicaria* L. and *Typha latifolia* L. in a standing-dead position. *Aquatic Botany* 75, 45-57.

Wetzel, R.G., 2006. Wetland ecosystem processes, in: Batzer, D.P., Sharitz, R.R. (Eds), Ecology of freshwater and estuarine wetlands. University of California Press, Berkley, California, USA. pp. 285-312.

Weyers, H.S., Suberkropp, K., 1996. Fungal and bacterial production during the breakdown of yellow poplar leaves in two streams. *Journal of the North American Benthological Society* 15, 408-420.

Wood-Eggenschwiler, S., Bärlocher, F., 1983. Aquatic hyphomycetes in sixteen streams in France, Germany and Switzerland. *Transactions of the British Mycological Society* 81, 371-379.

Wood-Eggenschwiler S., Bärlocher F., 1985. Geographical distribution of Ingoldian fungi. *Verhandlungen des Internationalen Verein Limnologie* 22, 2780-2785.

Woodward G., Gessner, M.O., Giller, P.S., Gulis, V., Hladyz, S., Lecerf, A., Malmqvist, B., McKie, B.G., Tiegs, S.D., Cariss, H., Dobson, M., Elosegi, A., Ferreira, V., Graça, M.A.S., Fleituch, T., Lacoursière, J.O., Nistorescu, M., Pozo, J., Risnoveanu, G., Schindler, M., Vadineanu, A., Vought, L.B., Chauvet, E., 2012. Continental-scale effects of nutrient pollution on stream ecosystem functioning. *Science* 336, 1438–1440.

Wurzbacher, C., Bärlocher, F., Grossart, H.P., 2010. Fungi in lake ecosystems. *Aquatic Microbial Ecology* 59, 125-149.

Wurzbacher, C., Janice, K., Grossart H.P., 2011. Aquatic Fungi, in: Grillo, O., Venora, G. (Eds) The dynamic processes of biodiversity – case studies of evolution and saptial distribution. InTech Press, Rijeka, pp. 227-258.

Wurzbacher, C., Rösel, S. Rychla, A. Grossart H.P., 2014. Importance of saprotrophic freshwater fungi for pollen degradation. *PLOS one* 9, e94643.

Yu, J., Liu, J., Meixner, F.X., Wang, J., Gao, Y., Wang, Y., Qi, X., Chen, X., 2010. Estimated net primary productivity and nutrient stock in plant in freshwater marsh, Northeastern China. *Clean-Soil, Air and Water* 38, 1080-1086.

Zare-Maivan, H., Shearer, C.A., 1988. Extracellular enzyme production and cell wall degradation by freshwater lignicolous fungi. *Mycologia* 80, 365-375.

Table 1. Range of fungal and bacterial biomass and production rate estimates reported from decaying plant litter in streams and freshwater marsh ecosystems.

Plant species	Stream/Marsh Site	Microbial Biomass (mg C/g C)		Microbial Production (mg C/g C/d)		Source
		Fungi	Bacteria	Fungi	Bacteria	
Freshwater Streams						
Liriodendron tulipifera	Schultz (AL, USA)	20-207 [a,d]	--	0.65-18.52 [d]	--	Suberkropp (1995a)
	Cottingham (AL, USA)	19-165 [a,d]	--	0.87-9.88 [d]	--	
	Sandy (AL, USA)	11-52 [b,d]	--	0.96-7.26 [d]	--	
Mixed deciduous [e]	Walker Branch (TN, USA)	51-102 [a,d]	--	0.81-3.51 [d]	--	Suberkropp (1995b)
L. tulipifera	Schultz (AL, USA)	4-161 [a,d]	0.04-0.44 [d]	0.07-7.24 [d]	0.04-0.30 [d]	Weyers and Suberkropp (1996)
	Payne Creek (AL, USA)	3-44 [b,d]	0.04-0.80 [d]	0.01-0.59 [d]	0.01-0.04 [d]	
Alnus glutinosa	Himmelreichbach (Germany)	1-15	0.08-0.43	0.11-1.00	0.05-1.25	Baldy and Gessner (1997)
L. tulipifera	Hugh White (NC, USA)	19-149 [a,d]	--	0.34-0.94 [d]	--	Suberkropp (2001)
	Walker Branch (TN, USA)	41-113 [a,d]	--	0.06-6.77 [d]	--	
Quercus alba	Hugh White (NC, USA)	17-92 [a,d]	--	0.09-1.01 [d]	--	
	Walker Branch (TN, USA)	40-123 [a,d]	--	0.29-3.58 [d]	--	

Table 1. continued.

Populus gr. nigra	Garonne River (France)	1-80	0.03-0.52	0.09-1.40	0.01-0.41	Baldy et al. (2002)
Mixed deciduous [e]	Basin Creek (AL, USA)	47-90 [d]	--	1.13-6.94 [d]	--	Methvin and Suberkropp (2003)
	Hendrick Mill (AL, USA)	53-115 [d]	--	1.57-7.62 [d]	--	
Mixed deciduous [e]	Payne Creek (AL, USA)	29-87 [d]	--	0.72-11.35 [d]	--	Carter and Suberkropp (2003)
	Hendrick Mill (AL, USA)	37-108 [d]	--	0.53-9.29 [d]	--	
Alnus glutinosa	Ave River (Portugal)	2-120	--	1.40-7.60	0.03-0.28	Pascoal and Cássio (2004)
Alnus glutinosa	Ave River (Portugal)	2-73	--	1.70-9.10	0.06-0.62	Pascoal et al. (2005)
Mixed deciduous [e]	Coweeta (NC, USA)					Gulis et al. (2008)
	Catchment 53 (Ref.)	24-74	--	0.24-2.17	--	
	Catchment 54 (Treat.)	25-86	--	1.88-6.34	--	
Mixed wood [e]	Catchment 53 (Ref.)	19-21	--	0.08-0.21	--	Gulis et al. (2008)
(<40mm dia)	Catchment 54 (Treat.)	22-28	--	0.18-0.34	--	
Mixed deciduous [e]	Coweeta (NC, USA)					Suberkropp et al. (2010)
	Catchment 53 (Ref.)	24-74 [d]	0.38-1.66 [d]	0.24-2.82 [d]	0.02-0.30 [d]	
	Catchment 54 (Treat.)	17-104 [d]	0.32-1.82 [d]	0.96-6.72 [d]	0.03-0.37 [d]	
Freshwater Marshes						
Mixed macrophytes [e, f]	Hudson River (NY, USA)					
	Sediment plant litter	1-63 [d]	0.25-0.95 [d]	0.07-5.01 [d]	0.01-0.07 [d]	Sinsabaugh and Findlay (1995)
Carex walteriana	Okefenokee (GA, USA)					Newell et al. (1995)
	Standing-dead leaf litter	20-34 [d]	0.26-0.40 [d]	0.23-0.92 [d]	<0.01-0.01 [d]	
	Sediment leaf litter	18-62 [d]	0.54-1.72 [d]	0.23-0.81 [d]	<0.01-0.04 [d]	

Table 1. continued.

Phragmites australis	Lake Neuchatel (Switzerland)					Kominkova et al. (2000)
	Submerged leaf litter	50-84	0.46-5.66	0.37-1.23	--	
	Submerged culm litter	12-14	0.14-0.88	0.08-0.21	--	
Juncus effuses	TWE Wetland (AL, USA)					Kuehn et al. (2000)
	Submerged leaf litter	8-50 [d]	0.12-0.45 [d]	0.15-5.67 [d]	0.01-0.06 [d]	
Typha angustifolia	Hudson River (NY, USA)					Findlay et al. (2002)
	Standing-dead leaf litter	11-16 [c, d]	--	0.137 [d]	<0.01 [c]	
	Sediment leaf litter	18-53 [c, d]	<0.01-0.06 [d]	0.09-1.59 [d]	<0.01 [c]	
P. australis	Standing-dead culm litter	6-29 [c, d]	<0.01 [d]	0.11-1.28 [d]	<0.01 [c]	
	Sediment culm litter	16-77 [c, d]	--	0.06-0.47 [d]	<0.01 [c]	
Scirpus lacustris	Pond 50 (Canada)					Verma et al. (2003)
	Submerged leaf litter	<1-12 [d]	--	<0.01-0.74 [d]	--	
	Standing leaf litter	<1-3 [d]	--	0.02-0.75 [d]	--	
P. australis	Lake Hallwill (Switzerland)					Buesing and Gessner (2006)
	Submerged leaf litter	16-44	1.10-2.70	0.20-2.4	2.60-18.60	
T. angustifolia	Lake Erie (MI, USA)					Su et al. (2007)
	Sediment leaf litter	46-125	0.02-1.92	0.93-4.91	<0.01	
	Winous Point (MI, USA)					
	Submerged leaf litter	20-57	0.21-2.13	0.62-2.91	<0.01	
T. angustifolia	Paint Creek (MI, USA)					Ohsowski (2008)
	Standing leaf litter	56-103	0.01-0.11	0.13-1.93	<0.01-0.50	

Table 1. continued.

	Standing stem litter	11-25	0.01-0.11	0.02-0.51	<0.01-0.09	
	Sediment litter	44-78	1.20-2.11	0.95-2.70	1.85-3.93	
T. angustifolia	Independence Lake (MI, USA)					Kuehn et al. (2011)
	Standing leaf litter	6-106	--	0.18-3.34	--	
T. domingensis	Weeks Bay (AL, USA)					Su et al. (2015)
	Standing leaf litter	3-37	--	0.02-0.42	--	
Cladium jamaicense	Weeks Bay (AL, USA)					Su (2014)
	Standing leaf litter	25-31	--	0.02-1.91	--	
T. angustifolia	Paint Creek (MI, USA)					Kuehn et al. (2014)
	Submerged leaf litter	21-39	1.30-1.90	0.55-3.60	1.61-6.98	
Schoenoplectus acutus	Paint Creek (MI, USA)					Kuehn et al. (2014)
	Submerged leaf litter	37-49	1.00-1.20	0.72-1.92	7.25-9.94	

[a] Fungal biomass determined from reported litter ergosterol concetrations using a conversion factor of 5.5 µg ergosterol / mg fungal biomass.

[b] Fungal biomass determined from reported litter ergosterol concetrations using a conversion factor of 10.9 µg ergosterol / mg fungal biomass.

[c] Fungal biomass determined from reported litter ergosterol concetrations using a conversion factor of 5.0 µg ergosterol / mg fungal biomass.

[d] Biomass and/or production values reported in the study converted to mgC/gC and mgC/gC/d, respectively, assuming 43% C in fungal dry mass, 50% C in litter ash-free dry mass or 45% C in litter dry mass.

[e] Studies determined biomass and production rates associated with naturally occurring plant litter (unknown age). All other cited studies determined biomass and production rates associated with decaying plant matter as part of a timed litter mass loss decomposition experiment.

[f] Only includes estimates from plant litter that was >1.0mm in size.

Figure Legends

Figure 1. Spores of the aquatic hyphomycetes, *Flabellospora* sp. (A), *Alatospora acuminata* (B), *Anguillospora* sp. (C), Unidentified conidium (D), and *Condylospora* sp. (E). All spores were collected, filtered, and microscopically examined from a single sample from a stream in Alabama, USA. Micrographs taken and provided by Vladislav Gulis. Ascoma (F), ascospore (G), asci (H) and ascus (I) of *Phaeosphaeria typharum* (Desm.) L. Holm colonizing dead submerged *Typha latifolia* stems in Wisconsin, USA. Micrographs taken and provided by Carol Shearer. Basidiomata (J) of *Panellus copelandii* (Pat.) Burds. & Mill. colonizing standing-dead *J. effuses* leaves in west-central Alabama, USA. Micrograph taken by the author. This illustration is a modified version previously published in Gulis et al. (2009).

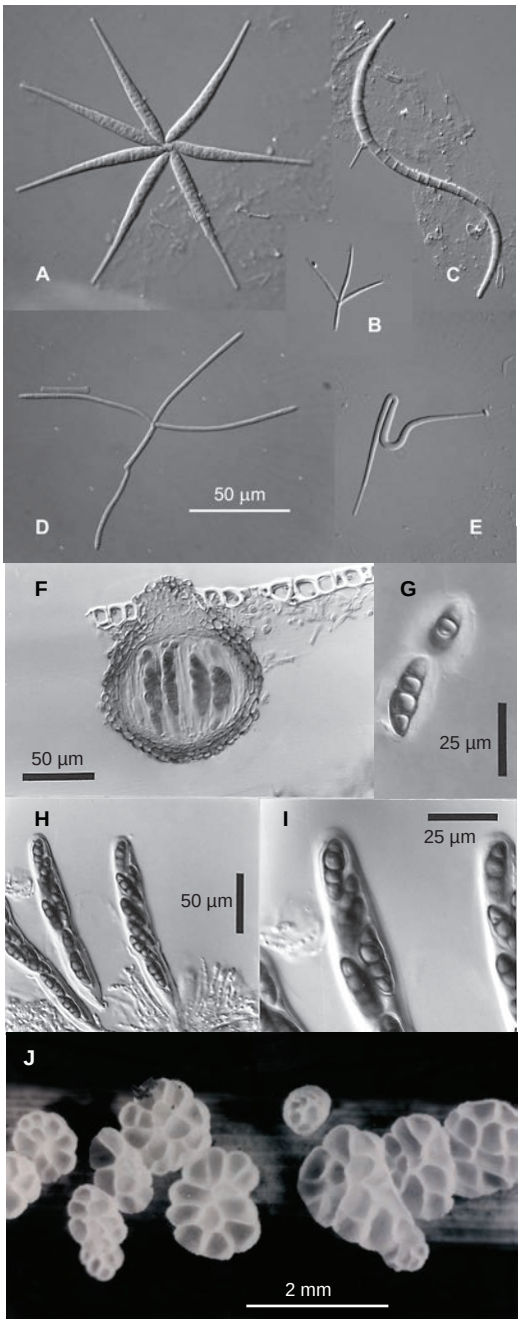
Figure 2. Mass loss (A) of yellow poplar (*Liriodendron tulipifera* L.) leaf litter during natural leaf decomposition in a second order stream (Schultz) in west-central Alabama, USA. Corresponding dynamics of fungal biomass (B), aquatic hyphomycete sporulation rate (C), and production rate (D) of fungi during litter decomposition are also illustrated (data from Suberkropp 1995). Symbols indicate means ± 1 SE (n=3). Mass loss (E) of ash leaf discs (*Fraxinus excelsior* L.) in experimental stream microcosms inoculated with the aquatic hyphomycete, *Articulospora tetracladia*. Corresponding dynamics of biomass (F), sporulation rate (G), and production rate (H) of *A. tetracladia* during leaf-disc decomposition are also illustrated (data from Gessner and Chauvet 1997). Symbols indicate means ± 1 SE (n=3).

Figure 3. Fungal biomass (A) associated with *T. angustifolia* (Michigan) and *T. domingensis* (Alabama) leaves during plant senescence and early standing litter decomposition (data from

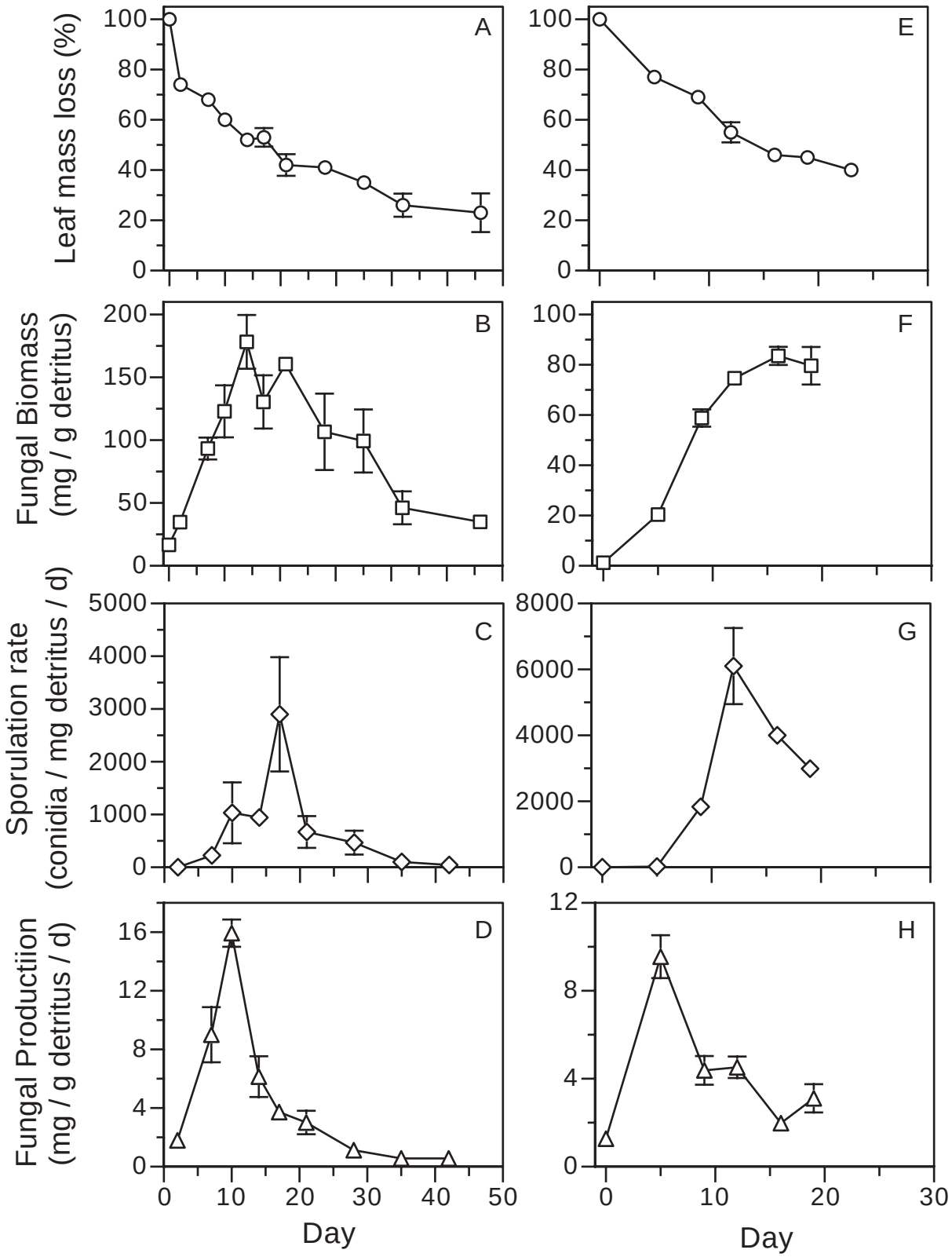
Kuehn et al. 2011 and Su 2014). Symbols indicate means ± 1 SE (n=6). Dynamics of fungal biomass (B) associated with leaf and culm litter of *Erianthus giganteus* (Alabama) during plant senescence and early standing litter decomposition (data from Kuehn et al. 1999). Symbols indicate means ± 1 SE (n=3).

Figure 4. Diel changes in rates of microbial CO_2 evolution (A) from standing *Juncus effusus* leaf litter during field studies conducted on September 7-8, 1994 in Alabama. Corresponding diel changes in (B) plant litter water potentials, (C) total polyol and trehalose concentrations extracted from *J. effuses* litter, and (D) air temperatures (°C) and relative humidity (%) above the *J. effusus* plant stand are also illustrated (data from Kuehn et al. 1998). Symbols indicate means ± 1 SE (n=3) except for relative humidity, which are from a single measurement.

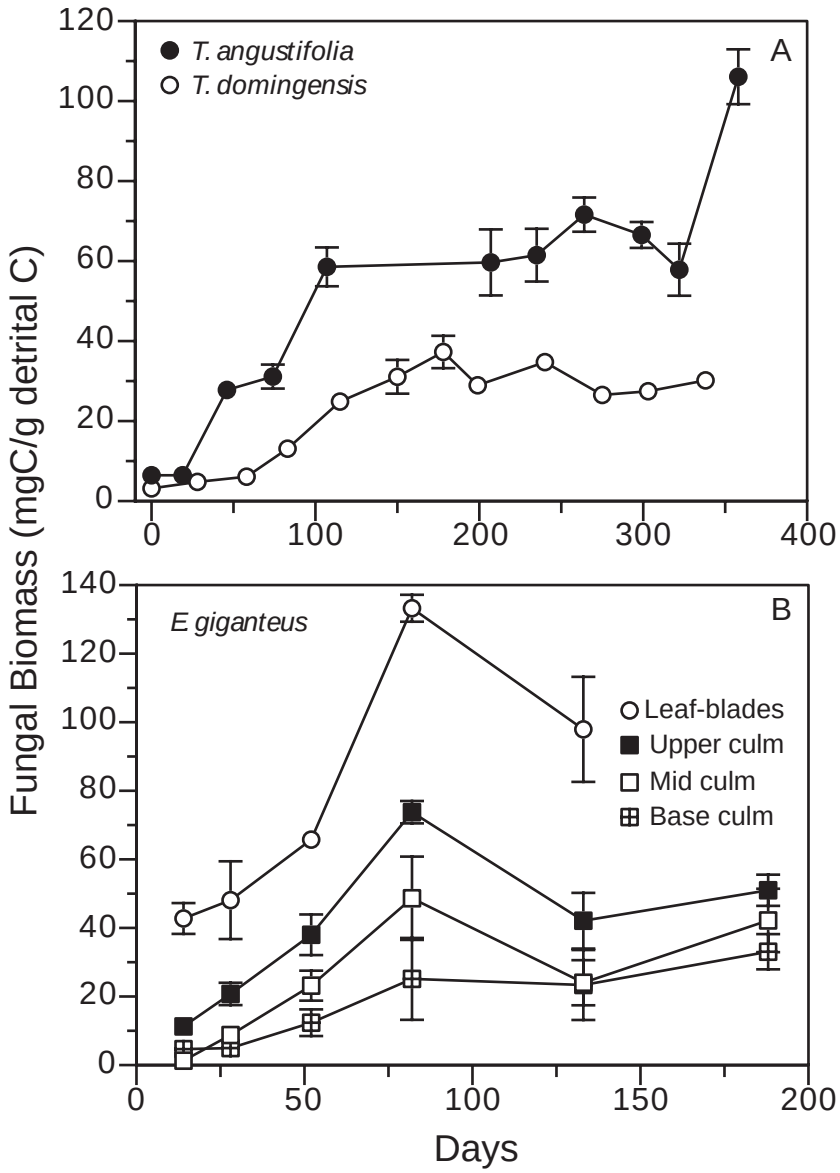
Kuehn - Figure 1



Kuehn - Figure 2



Kuehn - Figure 3



Kuehn - Figure 4