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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 paper 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

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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