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Aquatic hyphomycetes and litter decomposition in tropical – subtropical low order streams

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A B S T R A C T

Leaf litter decomposition is an important ecosystem function carried out by a diverse array of consumers, including aquatic hyphomycetes. Aquatic hyphomycetes are found in streams worldwide, but their diversity and abundance varies across systems. In general, species diversity is lower across tropical and subtropical systems when compared with temperate biomes. The low diversity in tropical and subtropical areas may be related to: (a) lower seasonality; (b) our inability to detect fungi by traditional techniques; (c) low turbulence of rivers where many studies were carried out; (d) low nutrient content in many studied tropical systems; (e) leaves highly defended against consumers; and (f) competition from other decomposers. In terms of function, fungal biomass, sporulation rates and litter decomposition by aquatic hyphomycetes in the tropics was reported to be equivalent to or much lower than observed in temperate zones. The feeding ecology of shredder invertebrates is strongly related to the presence of microbial decomposers in the environment. The lack of shredders reported for some tropical rivers may be related to a low microbial biomass, well defended tropical leaves and frequent hydrological events which remove leaves before they can be used by shredders. Seasonal variations in rain fall in tropical and subtropical systems are likely to affect litter fall, the identity and quality of litter, the reproduction of aquatic hyphomycetes (due to turbulence effects) and therefore the community composition of aquatic hyphomycetes throughout the year. Future research on aquatic hyphomycetes and litter decomposition in the tropics and sub-tropics should address the diversity/identity gap, altitudinal gradient changes and the contribution of aquatic hyphomycetes to the trophic ecology of shredders.

Introduction: aquatic hyphomycetes in the tropics and sub-tropics

Aquatic systems are inhabited by a diverse array of decomposers which use dead plant tissues as an energy source. In this review we give an account of the aquatic hyphomycetes that grow on leaf litter, named “Ingoldian fungi” in honour of C.T. Ingold who discovered their typical substratum and habitat and described many new species (Shearer et al., 2006). These fungi have radiate and sigmoid asexually reproductive spores, adapted for life and dispersal in the flowing water. Their counterparts inhabiting lentic environments are aero-aquatic fungi, which are also hyphomycetes with typical spore morphology and life cycle. Aeroaquatic fungi will not be dealt with here. Other aquatic hyphomycetes also develop on woody litter. In studying aquatic litter fungi, the leaf litter and woody litter are generally examined in different ways and are treated as different fields. Yet there is an overlap in the fungi that decompose leaves and woody litter. The substrata are also studied in different ways –i.e. for woody litter, moist chambers are generally used (Tsui et al., 2000), while for leaf litter, studies use bubbles chambers (Chan et al., 2000a) or orbital shakers (Bärlocher, 2005). Thus different fungal assemblages are determined because of the methodology, but they overlap to a lesser or greater extent (Sridhar et al., 2010). In this paper we discuss only leaf litter inhabiting aquatic hyphomycetes, while the freshwater lignicolous fungi are reviewed in Hyde et al. (2016).

Earlier studies on aquatic hyphomycetes and their relationship with submerged leaves were those of Ingold (1942, 1943) in England with several new genera and species described. Soon aquatic hyphomycetes were studied in many other areas in Africa (Chergui and Pattee, 1991; Eicker and Baxter, 1999), the oceanic Islands (Ranzoni, 1979), Asia (Sridhar et al., 1992; Goh and Hyde, 1996; Goh, 1997; Chan et al., 2000a,b), Australia (Thomas et al., 1989), Caribbean islands (Marvanová and Marvan, 1969; Santos-Flores and Betancourt-López, 1997), Europe (e.g. Marvanová and Müller-Haeckel, 1980), North America (e.g. Woelkerling and Baxter, 1968; Suberkropp and Klug, 1976), and South America (Nilsson, 1962; Schoenlein-Crusius and Grandi, 2003; 90 species referred).

Aquatic hyphomycetes have a worldwide distribution, with more than 300 estimated species, most of them recorded from temperate regions and fewer from the tropics and sub-tropics (Goh and Hyde, 1996; Shearer et al., 2006). In temperate systems, aquatic hyphomycetes are the most important fungal group of litter decomposers in streams and rivers (Suberkropp and Klug, 1974).

Due to their contrasting climatic and hydrological regimes, the tropics and sub-tropics encompass diverse environments ranging from dry desert zones, savannahs, and dry forests to swampy rain forests or peat swamps, and also covering a range of altitudes. Conditions in high-altitude tropical streams could be partially equivalent to those encountered in streams from temperate regions; we do not know if these similar conditions lead to convergence in species identity, diversity and function. The dynamics of litter input, litter decomposition and the environmental conditions imposed by the water chemistry and hydrology differ across the diverse

tropical biomes, potentially controlling the diversity, ecology and function of aquatic hyphomycetes (e.g. Graça et al., 2015).

Diversity

One of the most conspicuous observations is that species diversity tends to increase towards the equator (Scheiner and Willig, 2007), but this tendency seems to be less pronounced in the case of many freshwater organisms (Hillebrand, 2004). It has been proposed that species richness of aquatic hyphomycetes peaks at mid latitudes (Shearer et al., 2006). Indeed, in the only study on litter decomposition and aquatic hyphomycete richness across a latitudinal gradient, Jabiol et al. (2013) found that species richness was distributed as predicted by Shearer et al. (2006), with low species richness in a tropical stream (rain forest). However, tropical ecosystems are very different from each other as stated above and should be treated separately. Aquatic hyphomycetes in decomposing litter have been reported in all tropical and sub-tropical systems, but their diversity and abundance varies across systems as we will show next.

Al-Riyami et al. (2009) reported that in permanent desert streams, the biomass of aquatic hyphomycetes colonizing decomposing leaves was similar to that reported in temperate regions, but the number of species was lower, perhaps as the diversity in the riparian vegetation was also low. The same was reported for North African streams (Chergui, 1990; Chergui and Pattee, 1991). Intermittent streams in dry areas (North Africa, Brazilian Caatinga and Australia) were also reported to have lower numbers of aquatic hyphomycete species and low fungal biomass (Boulton, 1991; Maamri et al., 2001, 1998; Silvana et al., 2014).

Tropical and subtropical grasslands occupy vast areas in Africa, Australia and South America. Studies of aquatic hyphomycetes in these areas are scarce, but the few studies have revealed few aquatic hyphomycetes species associated with decomposing leaves from the trees in the riparian zones (Schoenlein-Crusius, 2002; Sales et al., 2014). As with savannahs, in tropical seasonal semi-deciduous forest aquatic hyphomycetes on leaves were also less diverse than in temperate zones (Abelho et al., 2005; Smits et al., 2007; Ardón and Pringle, 2008; Rincón and Santelloco, 2009).

The high productivity of tropical rain forests (here also included the Brazilian “Atlantic Forest”) is expected to result in large production of plant litter, a substratum for decomposers. Aquatic hyphomycetes have been reported from these systems (e.g. Schoenlein-Crusius et al., 1992) but, while Bärlocher et al. (2010) in Panama and Santos-Flores and Betancourt-Lopez (1997) in Puerto Rico reported a high number of species from submerged litter, other authors (e.g. Capps et al., 2011; Ferreira et al., 2012; Jabiol et al., 2013) found almost no conidia and/or very low fungal biomass from submerged litter.

Peat swamp forests are unique habitats found in the tropics. We are unaware of any studies targeting Ingoldian fungi in these habitats, but Pinnoi et al. (2006) and Pinruan et al. (2014) have studied the litter decomposing fungi in Sindhorn peat swamp forest, Thailand, and Yule and Gomez

(2009) looked at litter decomposition in Malaysian swamp forests. Litter decomposition was very slow in these systems and long-term accumulation of plant material under the acidic water-logged conditions mean peat swamps are one of the largest terrestrial organic sinks of carbon dioxide and thus extremely important. They are generally waterlogged and characterized by anaerobic soils and a thick layer of leaf litter, low nutrients and dissolved oxygen, dark coloured water due to tannins that leach from fallen leaves. Plant diversity is remarkably high and terrestrial fungal diversity is also high (Pinnoi et al., 2006; Pinruan et al., 2007, 2014). The diversity of fungi on submerged woody litter is, however, low (15 species – 11 sexual and 4 asexual; Fryar et al., 2004) compared to that of other subtropical and tropical freshwater habitats (35–80, Ho et al., 2001, 2002; Cai et al., 2003). If the same tendency applies to all decomposers, then a low diversity of aquatic hyphomycetes would be expected.

From the above studies, it seems that aquatic hyphomycete diversity and abundance are generally low in tropical and sub-tropical systems. There are several potential reasons for their lower diversity:

- (a) Seasonality. Shearer et al. (2006) proposed that the low seasonality of tropical and subtropical systems (in terms of temperature and litter input; but see below) results in lower environmental heterogeneity when compared with middle latitudes, which, in turn, results in low species diversity. The low seasonality of litter input leading to non-limiting resource to leaf decomposers has been reported from both lowland rivers and mountain streams (e.g. Mathuriau and Chauvet, 2002; Mathuriau et al., 2008).
- (b) Different life histories resulting in low investment in reproduction by aquatic hyphomycetes. In this case, aquatic hyphomycetes would be there, but we are unable to notice their presence because the conidial production is low and traditionally aquatic hyphomycetes have been identified by the conidial morphology. Here the new molecular techniques, including denaturing gradient gel electrophoresis (DGGE) and terminal-restriction fragment length polymorphism (T-RFLP; e.g. Nikolcheva and Bärlocher, 2005; Seena et al., 2008) as well as next generation sequencing will soon be of help.
- (c) Stream physical conditions. Some of the reports on litter decomposition and associated decomposers in tropical streams refer to work carried out in lowland streams or streams with low current and turbulence. Since conidial production by aquatic hyphomycetes is known to be stimulated by turbulence (e.g. Bärlocher et al., 2011) it is plausible that the low number of species reported could be the result of an unfavorable environment for sporulation.
- (d) Low nutrient content in stream waters. Nutrients may limit fungal growth and enzymatic litter decomposition (e.g. Jabiol et al., 2013; Sales et al., 2014), and many tropical streams where the studies were carried out are oligotrophic.
- (e) Low quality of substrata. It has been suggested that tropical tree species are better defended (chemically and physically; highly recalcitrant) against consumers than trees from other zones (Stout, 1989; Coley and Barone, 1996; Wantzen et al., 2002; Wright and Covich, 2005; but

see Campbell and Fuchshuber, 1995; Ardón et al., 2009). Consistently, litter defense traits (e.g. leaf toughness) within the same litter functional types were found to be higher at low latitude (Jabiol et al. 2013; supplementary data). Many of such defenses could be effective protecting leaves after senescence. A hard leaf is a common defense caused by water and temperature stress in many tropical areas, including the rain forests (Julião et al., 2014). Highly defended leaves can act as an environmental filter, selecting for specialist taxa and retard microbial growth and reproduction.

- (f) Competition from other decomposers. A large variety of aquatic fungi have been identified from submerged litter in the tropics (e.g. Wong et al., 1998; see below). It is plausible that in tropical systems these fungi may outcompete aquatic hyphomycetes in decomposing substrata. Bärlocher et al. (2012) reported that decomposing leaves of *Eucalyptus viminalis* in Australia released a large number of conidia, but the presence of zoospore fungi was also registered. The capability of such fungi to decompose leaves has been poorly investigated.

Function

Except some pioneer works (e.g. Padgett, 1976), research on the function of aquatic hyphomycetes, i.e., their role in litter decomposition, in tropical streams has lagged behind counterpart studies on diversity and distribution. This likely results from the more recent concerns about stream ecosystem functioning in the tropics together with the need for facilities and specialized equipment for quantitative assessments, which may be complicated overseas in contrast with traditional prospecting and taxonomic collection.

In a pioneer cross latitudinal study, Irons et al. (1994) hypothesized microbial decomposition to be higher in tropical than in temperate streams, unlike invertebrate shredders, which exhibited the opposite pattern. Results from the literature supporting this hypothesis are still inconclusive. In their global study, Boyero et al. (2011) found a drastic decrease in invertebrates' involvement in leaf decomposition towards the tropics. At the same time, leaf decomposition by microorganisms (presumably mainly aquatic hyphomycetes) was the highest in the tropics and showed a positive relationship with temperature, as reflected by the constant across-latitude decomposition rate when expressed on a degree-day basis. Other studies support the greater microbial functional importance in the tropics, where stream shredders seem to be scarce when compared to temperate regions (Gonçalves et al., 2006; Handa et al., 2014). Mathuriau and Chauvet (2002) reported for two leaf species in a Colombian neotropical stream, peak biomass of 9 % of detrital ash-free dry mass (AFDM) and 1 conidium produced per μg AFDM per day. These values were only slightly lower than those reported from temperate regions (Gessner, 1997). In a Venezuelan stream, Abelho et al. (2005) reported microbial biomass of up to 23 % of detrital mass (based on ATP determinations), which even if not entirely constituted of mycelial biomass could suggest a

prominent role of aquatic hyphomycetes in litter decomposition.

In contrast to the above reports, [Ferreira et al. \(2012\)](#) found a mycelial biomass and fungal reproductive activity 64 and 99 %, respectively, lower in the Amazonian than in a Portuguese stream. Consistently, both lower mycelial biomass and rate of conidial production have been observed in tropical streams along latitudinal gradients examined by [Handa et al. \(2014\)](#) and [Jabiol et al. \(2013\)](#); A. Bruder and J. Jabiol, pers. com.). Interestingly, [Gonçalves et al. \(2007\)](#) pointed out that leaves decomposing in a Cerrado stream had lower mycelial biomass (as determined by ergosterol), but much higher ATP content (as an indicator of total microbial biomass) than leaves of the same plant species decomposing in a temperate stream (Portugal). Altogether this would mean that other microorganisms, presumably bacteria and/or protists, occur in high abundance on tropical leaves, but are perhaps only marginally involved in leaf decomposition.

The divergence among studies in terms of biomass and litter decomposition rates mediated by aquatic hyphomycetes may be partially due to the differences in methodologies used for detecting abundance and activities of these fungi. In addition, and probably more important, regional climatic variations can be responsible for between-study discrepancies, with tropical streams and rivers likely being much more variable than their temperate counterparts ([Boyero et al., 2015](#)).

Interactions with invertebrates

In temperate systems shredder invertebrates play a pivotal role in litter decomposition ([Benfield and Webster, 1985](#); [Graça, 2001](#)). In the tropics and sub-tropics, the importance of shredders in litter decomposition seems to be less important than in temperate systems as judged by litter experiments excluding invertebrates (e.g. [Boulton, 1991](#); [Ardón and Pringle, 2008](#); [Al-Riyami et al., 2009](#); [Rincón and Santeloco, 2009](#); [Boyero et al., 2011](#)). Common shredders in temperate regions (e.g. trichoptera, amphipoda) are lacking in some tropical systems and their role as leaf consumers seems to be occupied by other invertebrates including scrapers ([Boulton, 1991](#); [Chergui and Pattee, 1991](#); [Tanaka et al., 2006](#)) or decapod omnivores ([Crowl et al., 2006](#); [Cogo and Santos, 2013](#); [Tenkiano and Chauvet, 2015](#)).

Feeding by shredders is strongly influenced by the presence of aquatic hyphomycetes in litter, which increases its nutrient (N) content and makes it less tough and more assimilable ([Bärlocher, 1992](#); [Graça, 2001](#); [Canhoto and Graça, 2008](#)). Moreover, aquatic hyphomycetes can be directly consumed by shredders (reviewed by [Canhoto and Graça, 2008](#)) and increase shredder fitness, as measured by growth ([Lawson et al., 1984](#)) and reproductive output ([Graça et al., 1993](#)). Comparable information is uncommon for tropical areas. If aquatic hyphomycetes are less common in decomposing leaves in the tropics, what would be the role of aquatic hyphomycetes in the trophic ecology of litter consumers?

In places where aquatic hyphomycetes attain a large biomass in leaf litter, the lack or scarcity of shredders cannot be due to insufficient mycelial production and/or enzymatic

maceration of leaf litter by aquatic fungi. An alternative explanation may lie in the quality of leaves, suspected to be lower in the tropics due to a higher content in chemical defense compounds ([Stout, 1989](#); see also above), which may be more detrimental to invertebrate decomposers than to aquatic hyphomycetes. However, while some studies support this pattern (e.g. [Dobson et al., 2002](#); [Wantzen et al., 2002](#)), others show similar concentrations of condensed tannins in tropical and temperate leaf litter ([Campbell and Fuchshuber, 1995](#); [Ardón et al., 2009](#)).

Although litter production can be high as expected from high primary production in many tropical areas, less litter may be available for consumers in zones where frequent spates transport leaves to the banks, downstream areas or bury the leaves with inorganic sediments. Tropical fungi also grow more quickly than temperate species ([Yuen et al., 1998](#)), and therefore may degrade leaves more quickly which would be available to shredders for less time (see also [Graça et al., 2015](#)). Whether the relatively high importance of aquatic hyphomycetes in the tropics is related to the poor colonization of leaves by shredders, and the limited competition with other fungi, remains undetermined.

Seasonality

Contrary to conventional belief, tropical systems are, in some way, also seasonal in terms of litterfall, with different plants shedding leaves at different periods of the year ([Sales et al., 2014](#)), but generally with higher incidence in the dry season or at the beginning of the rainy season ([Gonçalves et al., 2014](#)). Moreover, green leaves enter the streams much more frequently in tropical systems than in the temperate regions; green leaves mechanically removed from trees by rain, wind or herbivores could be more nutritious to decomposers than senescent leaves (because reabsorption of nutrients has not occurred) and their decomposition could be carried out by a different array of decomposers. Furthermore, in temperate regions aquatic hyphomycete sporulation peaks in the autumn ([Iqbal and Webster, 1973](#)), which is the time of high rain and therefore higher turbulence. Consistently, in the Cerrado (South American Woody savannah), the peak of sporulation occurred during the rainy season ([Sales et al., 2014](#)). These observations on seasonal changes in litter input and turbulence may result in some seasonality in the abundance and dominance of aquatic hyphomycete conidia, and thus litter decomposition.

Decay of woody litter by aquatic hyphomycetes

Another group of aquatic fungi grow on woody litter ([Wong et al., 1998](#)) and these organisms decompose lignocelluloses, and are important in nutrient release from submerged wood ([Yuen et al., 1998](#); [Bucher et al., 2004](#)). In contrast to the decreased diversity of freshwater leaf-inhabiting hyphomycetes, the freshwater lignicolous hyphomycete diversity is higher in tropical regions ranging from 25 species in a UK stream and 28 in a Japanese stream to 52–80 species in tropical streams ([Cai et al., 2003](#); [Hu et al., 2010](#); [Kurniawati et al.,](#)

2010; Hyde et al., 2016). Unlike the leaf inhabiting aquatic fungi which predominantly produce asexual spores, the freshwater lignicolous fungi produce both asexual (aquatic hyphomycetes) and sexual morphs (aquatic ascomycetes) on submerged wood (or in moist chambers when wood is removed from streams) and should not be studied separately. The lignicolous freshwater fungi also occur on woody litter in lakes and ponds (Hyde and Goh, 1998; Luo et al., 2004; Sridhar et al., 2010), but the diversity is generally lower than in streams. The diversity, distribution and role of this group of fungi is reviewed by Hyde et al. (2016).

Investigation of fungi on woody litter using bubble chambers as well as moist chamber incubation is less common (Sridhar et al., 2010). The fungi revealed from bubble chamber incubation differed widely from those revealed in moist chamber incubation (Gönczöl and Révay, 1993; Sridhar et al., 2010). Aeration of bark and cambium from sites in the Western Ghats of India yielded 30 taxa of Ingoldian fungi, which is generally lower than that revealed from leaves. This is an under considered aspect of aquatic hyphomycete ecology.

Conclusions and future works

In this review we have discussed the aquatic hyphomycetes that grow on leaf litter in streams and condition the litter for consumption by shredders. The evidence suggests that the diversity of aquatic hyphomycetes is lower in tropical and subtropical areas than in temperate systems. Future research on aquatic hyphomycetes in the tropics should address some poorly investigated questions. To start with, is diversity really lower in the tropics than in temperate areas, or are we missing species because of the use of inadequate methodology? As pointed out above, new molecular biology techniques may soon address this question.

If aquatic hyphomycetes are really poorly represented in the tropics, what is the relative importance of aquatic hyphomycetes as compared with other fungi in tropical vs. temperate zones in litter decomposition?

Are altitudinal gradients in the tropics comparable to the latitudinal gradients? Since temperatures decrease by about 6.4 °C for each 1000 m decrease in elevation, the question is whether high-altitude streams in the tropics resemble those in temperate regions in terms of litter decomposition and diversity and activity of aquatic hyphomycetes. This question is being investigated in the Ecuadorian Andes and Colorado Rocky mountains (Encalada et al., 2014) and in Borneo (Jinggut and Yule, 2015). As expected by the altitudinal – latitudinal equivalence, some montane Venezuelan tropical streams are rich in aquatic hyphomycetes (Cressa and Smits, 2007), and decomposition rates together with fungal biomass were high in Colombian montane streams where aquatic hyphomycetes were very important decomposers (Mathuriau and Chauvet, 2002).

Finally, what is the importance of aquatic hyphomycetes in the trophic ecology of shredders and other generalist detritivores? With some exceptions, the interactions between shredders and aquatic hyphomycetes have been poorly investigated. If shredders need litter conditioning by aquatic hyphomycetes or derive a large proportion of their energy or

nutrient requirements from aquatic fungi, then aquatic hyphomycetes may be limiting the abundance of shredder invertebrates.

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