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Insights into the Aquatic Hyphomycetes*

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ABSTRACT

The discipline 'aquatic hyphomycetology' with exciting historical background addresses the biology and ecology of a specific group of mycota adapted to stream ecosystems. The major attractions of these fungi are production of characteristic conidia (mainly staurosporous and scolecosporous) and wide geographic distribution. Their important ecological functions include breakdown and mineralization of plant lignocellulosic substrata and the transfer of energy to higher trophic levels in streams. The global proportion of life sustaining freshwater amounts to 2.75% with only 0.01% present as surface water in diverse habitats. Therefore, occurrence, distribution and role of aquatic hyphomycetes in freshwater food webs are of immense significance. In addition to field studies in streams, these fungi serve as model community for mesocosm and microcosm experiments to address many ecological issues. Many species of aquatic hyphomycetes remain unknown and are yet to be explored. There are many unsettled questions on their occurrence, distribution, adaptations and functions. In the current global scenario (climate change, global warming and pollution), the role of aquatic hyphomycetes in streams is highly valuable to understand their ecosystem services to enforce conservation strategies. This contribution is a general account of the inventory, approaches, boundaries, ecological services and future challenges concerning aquatic hyphomycetes.

Keywords: Distribution, diversity, ecology, food web, freshwater hyphomycetes, streams

INTRODUCTION

Studies on mycology in terrestrial ecosystems are significantly more common than in aquatic habitats (Bärlocher and Boddy, 2016). However, it is highly challenging to investigate fungi in aquatic ecosystems as they are biotically (flora, fauna and microbes) and abiotically (temperature, nutrients and hydrology) diverse. Decomposer fungal communities in freshwaters are represented by most of the major phyla (*Chytridiomycota*, *Zygomycota*, *Ascomytota*, *Basidiomycota* and Stramenopiles). Aquatic hyphomycetes (AQH) (also called 'freshwater hyphomycetes' or 'Ingoldian fungi') are polyphyletic mycota that produce morphologically distinct staurosporous (multiradiate) and scolecosporous (sigmoid) conidia with characteristic ontogeny (Ingold, 1942; Belliveau and Bärlocher, 2005; Gulis *et al*., 2005). Simple to highly diverse conidial shapes of these fungi are the product of convergent evolution and reflect functional significance such as impaction and sedimentation (Webster, 1959, 1987; Ingold 1975a). Due to environmental fluctuations, several adaptations might have taken place in AQH suitable to inhabit lotic habitats, semi-aquatic conditions and mutualistic interactions resulting in their unique lifestyles. The major substrata available for AQH are allochthonous leaf litter transferred from the riparian vegetation as well as adjacent stream boundaries (Bärlocher and Kendrick, 1974; Hynes, 1975). As important members of detritus food web in streams, AQH with their enzymatic capabilities breakdown plant lignocellulosic detritus to inorganic nutrients, to build up their biomass and serve as nutritional sources for stream fauna as consequences of energy flow (Suberkropp and Klug, 1981; Suberkropp, 1992, 2003; Bärlocher, 2005a).

Approximately 300 species of AQH have been reported from different geographic locations belonging to the five classes of subphylum *Pezizomycotina* (Shearer *et al*., 2007; Belliveau and Bärlocher, 2005; Baschien *et al*., 2013), which corresponds to 3.3% of described hyphomycetes (Kirk *et al*., 2008). For prediction of expected global number of fungal species, the criteria of plant-fungus ratio (Hawksworth, 2001) and molecular methods (Blackwell, 2011) have been considered. A recent global estimate projects the existence of 450,000 angiosperms (including 10-20% unknown) with up to two-thirds occurring in the tropics (Pimm and Joppa, 2015). With this notion, it might be presumed that plant detritus-dependent AQH are also more diverse in the tropics than other regions. Unfortunately explorations on AQH in the tropics are inadequate to evaluate such conclusions (Duarte *et al*., 2016).Several steps are necessary to explore and to understand the functions of AQH in streams (e.g. selection of location; criteria and methodology; field and mesocosm approaches; laboratory microcosm studies). The present contribution focuses on the basic aspects to investigate the AQH communities with experiences drawn from the Western Ghats of India.

WHERE TO SEARCH?

Performing inventory is one of the basic steps to be followed to explore AQH in water bodies and substrata available in streams. Selection of appropriate locations, strategies of sampling and choosing suitable substrata are equally important. Small streams and streamlets passing through forests are convenient for sampling as they are not too deep and facilitate mesocosm experiments (Gulis and Suberkropp, 2003). Filtering representative water samples (through membrane filters) and fixing (in lactophenol cotton blue) helps to monitor drift conidia. Decaying plant detritus as coarse particulate organic matter (e.g. leaf/wood/bark litter and decaying roots) trapped in the crevices can be easily placed in sterile polythene bags and carried in cool packs for further assessment in the laboratory. Although there is no substrate specificity for AQH, their activity (e.g. conidium production and rate of decomposition) varies between substrates (e.g. leaf litter vs. woody litter) and leaf litter serves as an ideal material for easy assessment (Graça *et al*., 2005).

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Swirling water movement in some stretches of stream supports accumulation of foam/scum, its collection and assessment facilitates evaluation of the conidial consortium of streams. Sediment samples could be evaluated by indirect method to assess occurrence of AQH (Sridhar *et al*., 2008). Known quantity of sediment can be baited to sterile leaf disks (e.g. banyan or alder) on a shaker for about a week followed by bubble chamber incubation to convert fungal biomass into conidia for identification (Sridhar *et al*., 2008; Sudheep and Sridhar, 2012; Ghate and Sridhar, 2015b). Experiments may be designed to study spatial and temporal fluctuations in occurrence and activity of AQH in streams.

There is spatial disparity in inventories on AQH in temperate and tropical regions. For instance, studies are inadequate in the African continent as well as Southeast Asian regions (Duarte *et al*., 2016). Based on current literature, species richness/diversity is significantly higher in the mid-latitudes (temperate regions) than in low and high latitudes (tropical and polar regions) (Shearer *et al*., 2007; Jabiol *et al*., 2013; Duarte *et al*., 2016; Graça *et al*., 2016). However, the community similarity decreases with geographic distance. In contrast to leaf-dwelling AQH, wood-dwelling lignicolous freshwater fungal diversity is higher in the tropics/subtropics than in temperate locations (Hyde *et al*., 2016).Although studies on the impact of AQH on woody litter are scarce, the biomass of AQH in small woody litter was almost equivalent to those of leaf litter with 5-10 times lower growth rates (Findley *et al*., 2002; Gulis *et al*., 2008). Within a specific tropical biome, prevalence of high species richness/diversity due to congenial abiotic conditions cannot be ruled out. For example, community similarities are found amongst geographically distant biomes sharing similar climatic conditions (Wood-Eggenschwiler and Bärlocher, 1985; Duarte *et al*., 2016).

The Indian subcontinent spreads over tropical and subtropical geographic regions with a variety of biomes of ecological interest to evaluate AQH. The 10 biogeographic zones constitute: Trans-Himalayas, Himalayas, Thar Desert, semi-arid zones, Western Ghats, Deccan Peninsula, Gangetic Plain, North-Eastern zones, coasts and islands. Of these, four regions have been considered as the hotspots of biodiversity (Western Ghats, Western Himalayas, Eastern Himalayas and Nicobar Islands). The Western Ghats and Himalayas are of special interest as an array of freshwater bodies is flowing through variety of habitats at different altitudinal ranges, hydrologic conditions and climatic regimes. Mid-altitude streams in the Western Ghats of India (e.g. Sampaje) harbour nearly 25% of global estimate of AQH, which stands as an outlier or hotspot possibly due to the prevalence of suitable biotic and abiotic conditions. Comparison of distribution, richness and diversity of the AQH between Western Ghats and Himalayas may disclose several interesting facts especially latitudinal and altitudinal disparities. Inventory of AQH in the Indian Subcontinent may lead to the identification of ecologically sensitive and critically vulnerable regions to enforce conservation measures.

HOW TO PROCEED?

The progress of any research field largely depends on the concepts, various approaches and methodology to be adapted. Application of different concepts and methods followed for terrestrial mycology and other fields have enriched our knowledge on the assemblage, diversity and ecological functions of AQH. Studies were initiated with simple methods and protocols for environmental samples (see Descals, 1997). Techniques of isolation and maintenance of pure cultures of AQH have also been described (Gessner *et al*., 2003; Descals, 2005; Marvanová, 2005).A variety of qualitative and quantitative methods are employed to study AQH and their activities in stream ecosystem (see Gessner *et al*., 2003). These methods can be subdivided into direct and indirect methods. Some of the direct methods include microscopic examination of leaf litter and foam samples to detect conidia (Webster, 1977; Descals, 2005), floatation-adhesion technique to capture conidia (Bandoni, 1972; Sridhar and Bärlocher, 1993), water filtration through membrane filters to trap drift conidia (Iqbal and Webster, 1973; Bärlocher, 2005b) and entrapment of drift conidia on suitable substrates (e.g. rosin-/latex-coated slides) (Bärlocher *et al*., 1977; Ghate and Sridhar, 2015a). Indirect methods include leaf litter incubation in bubble chambers in laboratory to induce conidia (Bärlocher, 2005), sediment baiting onto sterile leaf litter (Sridhar *et al*., 2008) and biochemical assays (e.g. ergosterol, chitin, ATP, glucosamine and enzymes) (Newell, 2000; Gessner, 2005; Gessner *et al*., 2003). Several methods of plant litter incubation to generate and enumerate conidia of AQH are described by Gessner *et al*. (2003).

Quantitative analysis is necessary to follow the extent of transformation of detritus by AQH into mycelial biomass as metabolically active mycelia (or conidia) could be directly linked to the quantities of ATP and ergosterol (Gessner *et al*., 2003). Besides, immunological and molecular approaches are also highly advantageous in assessing AQH in different substrata. However, to precisely follow their assemblage, distribution, diversity and functions, it is necessary to apply molecular techniques and some of those have already been applied (see Duarte *et al*. 2013). Despite molecular techniques being useful in deciphering species richness, diversity, phylogeny and ecological functions, it is still essential to follow basic microscopic examinations to observe conidial morphology although nearly10-20% of conidia are unidentifiable. Many valuable resources are available for identification based on conidial morphology (e.g. Ingold, 1975b; Carmichael *et al*., 1980; Webster and Descals, 1981; Nawawi, 1985; Marvanová, 1997; Santos-Flores and Betancourt-López, 1997; Gulis *et al*., 2005).

Several approaches are necessary to be followed in field (stream and mesocosms) and laboratory (microcosms) to evaluate AQH. Experiments can be broadly classified into three categories: i) in streams (long-term and short-term studies: e.g. diurnal, seasonal and annual); ii) in stream mesocosms (controlled *in situ* experiments: e.g. mesh bags and manipulation of stream stretches); iii) in microcosms (*ex situ* laboratory simulations with colonized substrata in streams or laboratory pure cultures). Breakdown of coarse particulate organic matter (CPOM) is one of the major ecosystem services of AQH, and protocols and methods to evaluate decomposition have been described by Graça *et al*.

(2005). Besides sampling various stream detritus for *in vitro* studies, establishing mesocosms in the streams is another important step. For instance, evaluation of leaf litter or other CPOM in the streams using coarse and fine (exclusion nets) mesh bags is one of the simple approaches to eliminate or to permit macroinvertebrates to process organic matter (e.g. Suberkropp, 2003). This approach allows understanding the extent of involvement of AQH and macroinvertebrates in detritus processing (as they are the main players in streams competing for the common substrata). Assessment of leaf mass loss under different environmental regimes (controlled and experimental variables) in mesocosms and microcosms helps elucidate the rates of detritus processing and turnover. One of the most interesting approaches to be followed in litter processing across the streams is transplant experiment (pristine vs. polluted; different altitudes; different latitudes). This helps to isolate the impact of biotic and abiotic factors controlling the substrate processing under altered stream regimes.

ARE THEY OUT OF BOUNDARY?

Contemporary research on AQH revealed broader multiple niches within and outside their preferred water columns. Although AQH are perfectly adapted to running waters, they have been repeatedly documented from different niches *in situ* (e.g. hyporheos, sediments, live plant tissues, intestine of aquatic fauna), intermediary (e.g. substrate in aero-aquatic phase), other aquatic (e.g. lentic and brackish waters) and terrestrial (e.g. forest floor, below ground and canopy) habitats (see Chauvet *et al*., 2016). Some evidence is available on the occurrence and functions of AQH on forest floors/soils, below ground, intermittent and above ground habitats. The AQH are common in hyporheic habitats/aquifers, sediments and groundwater, however, low dissolved oxygen in underground streams is responsible for their low biomass (Chauvet *et al*., 2016; Sudheep and Sridhar, 2012).

The AQH have been reported from leaf litter on forest floor, soils and leaf litter accumulated at considerable distances from temperate/tropical streams (see Chauvet *et al*., 2016). Those geographical locations receive heavy rains and have wet forest floor for considerable duration (2-3 months), which facilitates AQH survival over long periods (e.g. Western Ghats). Similarly, snow cover of forest flour for several months may preserve these fungi (Sridhar and Bärlocher, 1993). Besides, there is evidence that the AQH colonized in leaf litter survive for long periods when subsequently exposed to dry conditions (see Chauvet *et al*., 2016). Some AQH survive as endophytes in terrestrial roots. They are also inhabitants of organic matter/sediments of intermittent streams (Bruder *et al*., 2011; Ghate and Sridhar, 2015b). In sediments of the nine intermittent streams of Southwest India, the species similarity of AQH showed a decreasing trend from sediments characterized as loam > sandy clay loam > sandy loam and the conidial output was positively correlated with sediment organic carbon only during the wet season (Ghate and Sridhar, 2015b).

Foam samples in streams being major repository of conidia of AQH, their accumulation and transport by air especially via escarpments of high altitude streams (e.g. Western Ghats) directly to the tree canopies cannot be ruled out (Selosse *et al*., 2008). Reports are available on the occurrence of AQH in substrates of canopies (e.g. trapped leaf litter, twigs, inflorescences and crown humus) (Chauvet *et al*., 2016). Canopies of more than 60 plant species are known to harbor AQH in stemflow, throughfall, trapped leaf litter, crown sediment and tree holes. In addition, honey dew and floral honey in canopy also possess typical conidia of AQH and conidia-like propagules (Magyar *et al*., 2005). There are reports on their occurrence in live tissues of fern (*Drynaria quercifolia*), live roots (orchids), live twigs and live gymnosperm needles (*Picea marina*) (see Chauvet *et al*., 2016). Even though conidia derived from canopies show morphological features similar to those of AQH, nearly 15-20% of them are unidentified.

Attempts to isolate pure cultures of AQH from surface sterilized riparian root segments of 10 tree species collected from the two Western Ghat streams failed even though the characteristics of many isolates resemble typical cultural features of AQH (e.g. *Flagellospora curvula, Lunulospora curvula, Phalangispora constricta* and *Synnematophora constricta*) (Ghate, S.D. and Sridhar, K.R., unpublished observations). Moreover, incubation of agar pieces of such pure cultures in bubble chambers failed to release conidia. But the surface sterilized segments released conidia of freshwater hyphomycetes on bubble chamber incubation, which indicates the possibility of impaired reproductive ability (Ghate and Sridhar, 2017). Such uncertainties need to be addressed by appropriate molecular techniques (see Bärlocher, 2016).

Several of AQH are also inhabitants of lentic (Wurzbacher *et al*., 2010; Pietryczu *et al*., 2014; Kuehn, 2016) and estuarine habitats (Sridhar and Kaveriappa, 1988). If AQH occur outside their preferred habitats, their functions in those habitats also gain importance (e.g. saprophytism, mutualism and role in food web). It is challenging to address boundaries between fungi and their niches in the interest of their ecosystem services.

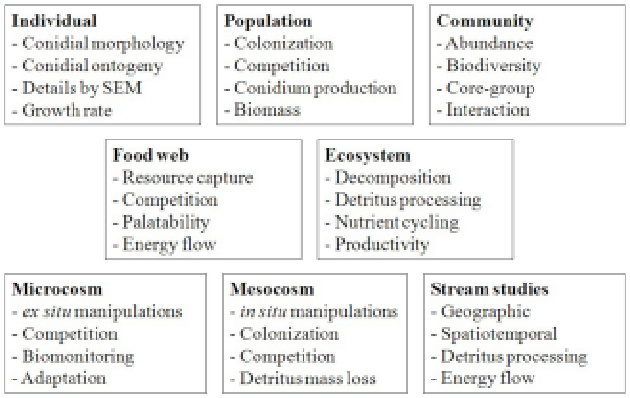
DO THEY SERVE AS MODEL MYCOTA?

The success of AQH community in streams depends on their ability to degrade recalcitrant polysaccharides (lignin, cellulose and xylan). As they are major colonizers of coarse particulate organic matter (FPOM) in streams, they mineralize carbon and nutrients through production of fine particulate organic matter (FPOM) followed by dissolved organic matter (DOM). The AQH community constitutes a hub with interaction in their surroundings (aquatic, semi-aquatic and terrestrial), providing ample opportunities to assess their adaptability to understand several concepts of community ecology and interactions. Breakdown and mineralization of plant lignocellulosic materials in freshwaters and transfer of energy to higher trophic levels are the primary ecosystem services of AQH, which are under the control of complex biotic and abiotic factors. They serve as highly suitable model community to address many fundamental issues of developmental biology, ecology, population dynamics, energy transfer and other ecological complexities.

Generally, fungi and their activities (species richness, diversity, growth, biomass, respiration and conidium production) in stream detritus (leaf and woody litter) have been positively correlated with rates of decomposition (Bärlocher and Corkum, 2003; Duarte *et al*., 2006; Gessner *et al*., 2007).However, in the current global climatic scenario (increased temperature, drought, floods, and eutrophication), response of fungal variables may be considerably altered (Dang *et al*., 2009; Canhoto *et al*., 2016). In addition to breakdown of plant detritus, AQH have intricate or mutualistic association with host plant species (endophytic in live plant tissues) to deter herbivores and some are known to produce bioactive compounds, which may be powerful plant protectants (Sati and Arya, 2010).

There is ample scope to design experiments to address the influence of biotic and abiotic factors on AQH and their functions (**Fig. 1**). Several variables could be used to measure activity of AQH include: estimation of biomass, concentration of ATP, ergosterol content, rate of conidium release, conidial impaction on surface, formation of appressoria by conidia on surface and extent of conidial germination. The AQH have the capacity to generate enormous numbers of conidia from various substrata (e.g. 1 g of leaf litter releases up to 8 conidia), fungal biomass is equivalent to ATP concentration and ergosterol content (5.5 mg ergosterol = 1 g fungal biomass) (Bärlocher, 1992; Gessner and Chauvet, 1993; Suberkropp *et al*., 1993; Abelho, 2009).

Fig. 1. Schematic outlook on studies which could be performed in stream and laboratory.



To produce conidial crop from leaf litter or mycelial agar pieces, aeration with a jet of filtered air in bubble chambers (conical flask with sterile distilled water) through Pasteur pipette to create turbulence up to 48 hr is usually sufficient (Iqbal and Webster, 1973). A modified bubble chamber (mini-glass receptacle) has been designed by Suberkropp (1991) to release conidia from the substrata or cultured agar pieces serve as a perfect laboratory microcosm. Similar to continuous flow aquarium, continuous flow systems could also be designed in a laboratory setup. Such attempts (similar to chemostat approach) help to address the impact of single species or consortium of species (core-group) on litter breakdown and role of invertebrates in aquatic bodies, so also the impact of single or multiple factors.

The biomass of AQH in substrata in stream ecosystem depends on the litter quality (e.g. lignin and nitrogen), stream physicochemical features (e.g. pH and oxygen) and is also influenced by other organisms (e.g. bacteria, other fungi and invertebrates). The biomass in substrata serves several core functions (mass loss and biomass production for energy flow), key functions (detoxification and trapping heavy metals) and ecological functions (succession and interactions) (Krauss *et al*., 2011).important methods to study the role of AQH have been dealt by Graça *et al*. (2005).

Bärlocher (2009) has proposed a phenomenon called 'boom-bust cycle' ('Bärlocher's effect') related to conidial arrival, release of conidia and biomass retention, which operates sequentially in a stream or mesocosm with time lapse. Three variables in 'Bärlocher's effect' include conidial recruitment (settling from water on to a fresh substratum), conidial output (release from fungal mycelia in a substratum) and the fungal biomass (mycelial retention in a substratum). This effect serves as an exponential time-dependent decay function until the substrata becomes scarce or inhospitable for colonization. Depending on the geographic location, biotic and abiotic influences/stresses either expand or compress the curves denoting the impacts on fundamental ecosystem services. Likewise, impacts of abrupt and gradual changes in abiotic factors may also be studied using AQH as model fungi.

CONCLUSIONS AND OUTLOOK

Most of our basic knowledge on AQH is the result of conventional studies and techniques that have been applied for the past several decades. More advancement is required on stream-based, technique-based and microcosm-based studies to circumvent gaps in our knowledge. Several unsettled broad concepts and questions include pattern of distribution, adaptability to climate change, effect of pollution and impact of habitat loss. The evolutionary significance and developmental biology of freshwater hyphomycetes are still challenging.

Organic matter input from riparian vegetation constitutes about 99% of the energy in streams (Webster and Meyer, 1997). As AQH have connection with common terrestrial ancestors (*Ascomycota* and *Basidiomycota*) (Taylor *et al*., 2014), they might have gradually invaded the freshwaters and those terrestrial fungi colonized plant parts on entering freshwaters continued detritus processing in new or altered environment (Bärlocher, 2008). Despite being largely cosmopolitan with occurrence in polar, temperate and tropical locations, species-specific traits as well as adaptability may differ. Results and generalizations derived from the temperate habitats on AQH are not entirely transferable to polar and tropical regions. Such geographic bias has to be addressed by additional studies from low and high latitudes. molecular approaches initiated over a decade throw light on several fundamental concepts of phylogeny, expansion of niches, involvement in decomposition and ecological services (Duarte *et al*., 2013). Molecular evidence suggests a close evolutionary proximity of freshwater and endophytic AQH from distant geographic ecosystems providing evidence of their wide geographic distribution (Seena and Monroy, 2016).

What are the physiological and ecological adaptations of AQH in response to changed temperature and hydrological regimes? The impacts of global warming on freshwater habitats influence fungal growth, metabolism, enzymes and reproduction (Canhoto *et al*., 2016). The climate change assessments on freshwaters are mainly monitored on individual species rather than at community, food web and ecosystem levels (Woodward *et al*., 2010). A modest rise in temperature stimulates more fungal colonization of substrata, but there is a possibility of imbalance between fungal growth and reproduction which may influence fungal composition ultimately influencing their functions in streams (Canhoto *et al*., 2016). Are such influences dependent on the type of substrata (e.g. leaf litter and woody litter)? If the substrata are long-lasting woody litter, will it influence fungal biomass at least selectively and induce a switch to the formation of perfect states as survival or defence mechanism? Unfortunately, studies on woody litter pertain to colonization of AQH are relatively scarce (Sridhar *et al*., 2010).

Among the 10 worst perturbations of the planet earth, freshwaters are affected by as many as seven (Rockström *et al*., 2009) which demands enforcing conservation measures. Habitat loss and pollution (deforestation, land use pattern, input of heavy metals, contamination of xenoorganics and transfer of nanoparticles) are the major factors influencing the diversity and functions of AQH. There is a danger that some fungi might vanish before they have described and soon future studies may have to apply IUCN Red List criteria (e.g. vulnerable, threatened, endangered and critically endangered).Fulfillment of the agenda proposed by CBD, deeper understanding of biogeographic distribution, convergent evolution and ecological services of AQH mainly depends on the development of new techniques and strategies. To move towards broadening the scope of the discipline (to get a global blueprint of biodiversity and to understand ecological functions), collaborative efforts, massive networking and coordinated movements are inevitable through metagenomic approaches.

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