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Short Communication

Aquatic hyphomycetes: a potential source of polyunsaturated fatty acids in detritus-based stream food webs

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ABSTRACT

To date, aquatic hyphomycetes have mainly been considered as a source of carbohydrates, mineral elements and proteins for detritivores in detritus-based headwater streams. Yet, consumers are highly dependent on other molecules, such as essential fatty acids, to complete their biological cycle. These molecules might be limiting in detritus-based ecosystems since they are primarily synthesized by autotrophic organisms. We investigated: (i) if aquatic hyphomycetes are able to synthesize polyunsaturated fatty acids (PUFAs); and (ii) if the abundance of phosphorus, often considered as a limiting factor in headwater streams, could affect the proportions of PUFAs in aquatic hyphomycetes. All hyphomycete species tested synthesized high amounts of PUFAs (C18 ω 3 and ω 6) and the proportions of these essential fatty acids varied with P availability. This study sheds new light on the importance of aquatic hyphomycetes in the detritus-based stream food web, but also on potential co-variations between mineral nutrient limitation and the availability of essential fatty acids for consumers.

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Introduction

The functioning of forested headwater streams mainly relies on the interactions between allochthonous detritus (e.g. leaf litter), fungal decomposers (mainly aquatic hyphomycetes), and detritivorous invertebrates (shredders) (Fisher and Likens, 1973; Gessner et al., 1999). In particular, aquatic

hyphomycetes improve the quality and palatability of plant detritus to detritivores, facilitating the flow of carbon from poor quality detritus to higher trophic levels (Bärlocher, 1985; Graça, 2001; Gulis and Suberkropp, 2003). Furthermore, as shown by Danger and Chauvet (2013), aquatic hyphomycetes are able to immobilize high amounts of nutrients from the water column, increasing in turn the detritus nitrogen and

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phosphorus (P) levels for consumers. However, the quality of the resource for aquatic invertebrates can also be strongly affected by polyunsaturated fatty acids (PUFAs) (Brett and Müller-Navarra, 1997). PUFAs, mainly synthesized by autotrophic organisms (Arts et al., 2009), are the product of the desaturation of saturated fatty acids (SAFAs) by specific enzymes, and contain two or more ethylic bonds. PUFAs are essential molecules conferring fluidity, flexibility and selective permeability to cell membranes (Wallis et al., 2002) and are involved in a wide range of physiological processes. For example, Stanley-Samuelson et al. (1988) stressed the role of PUFAs as precursors of prostaglandins and defensive secretions in terrestrial insects. Two studies on detritus-feeders have shown that lipids extracted from different fungi, particularly C18 and C20 fatty acids, were able to stimulate feeding of aquatic invertebrates according to their development stage (Cargill et al., 1985), and that leaf litter coated with fungal lipid extracts had the same effect as fungal conditioning and presumably drove the food preferences of some aquatic invertebrates (Rong et al., 1995). Several studies have also shown that growth and reproduction of planktonic invertebrates depend on the availability of alpha linolenic acid (18:3 ω 3), underlining the key role of this dietary ω 3 PUFA (Wacker and von Elert, 2001; Martin-Creuzburg et al., 2005; Masclaux et al., 2009). Yet, only a few species of metazoan consumers have the capacity to biosynthesize PUFAs *de novo* at sufficient rates to meet their physiological requirements, thus most consumers depend on PUFAs being supplied by their diets (Arts et al., 2009).

Despite the well known role of aquatic hyphomycetes as the main basal food sources in stream food webs, data on their lipid composition are extremely scarce. To date, lipid composition of fungi has been more extensively studied for taxa such as oomycetes, zygomycetes, ascomycetes, and basidiomycetes isolated from terrestrial ecosystems. In a study of 100 cultivated strains, Stahl and Klug (1996) showed that most of the investigated terrestrial fungi exhibited high amounts of PUFAs of the ω 6 series, such as linoleic acid (PUFA, 18:2 ω 6), but presumably lacked the essential fatty acids of the ω 3 series. Since aquatic hyphomycetes are mainly ascomycetes and some are basidiomycetes, it can be expected that at least some of them have the enzymatic capacities to synthesize PUFAs from the ω 6 series.

Forested headwater streams are often considered to be intrinsically limited by nutrients (e.g. P, Cross et al., 2007) while the role of PUFAs is rarely evoked (but see Torres-Ruiz et al., 2007). As recently shown by Danger et al. (2013) and González et al. (2014), P limitation can reduce the growth and survival of consumers in detritus-based ecosystems, yet one cannot exclude the possibility that the fatty acid composition of aquatic hyphomycetes could co-vary with P availability.

In this study, we hypothesized that at least some aquatic hyphomycete species are able to synthesize PUFAs and that the proportion of these PUFAs can be affected by P availability. To test our hypothesis we: (1) assessed the lipid composition of eight common and widely distributed aquatic hyphomycete species (Hesketh, 1978; Chauvet, 1991) to evaluate whether aquatic hyphomycetes could be a source of PUFAs in streams; and (2) evaluated if P availability in water could modify the fatty acid composition of aquatic hyphomycetes.

Materials and methods

Two distinct experiments were conducted. First, we investigated the fatty acid composition of eight common aquatic hyphomycete species from temperate headwater streams: *Alatospora acuminata*, *A. constricta*, *Anguillospora crassa*, *Arbusculina moniliformis*, *Clavariopsis aquatica*, *Heliscus lugdunensis*, *Tetrachaetum elegans* and *Tricladium chaetocladium*. These species were isolated from unpolluted forested headwater streams from south-western France and maintained in the laboratory in Malt extract (2 %). Selected species were then grown for 21 d in the dark at 15 °C on an orbital shaker in 250 ml-Erlenmeyer sterilized flasks containing 70 ml of a mineral salt solution modified from Gessner and Chauvet (1993) with glucose as the carbon source (for 1 l of demineralized water: MgSO₄, 7H₂O: 0.5 g; CaCl₂, 2H₂O: 0.15 g; FeCl₃, 6H₂O: 2 mg; MnSO₄, H₂O: 1 mg; ZnSO₄, 7H₂O: 1 mg; H₃BO₃: 1 mg; AlSO₄, 18H₂O: 0.1 mg; KI: 0.1 mg; Na₂MoO₄, 2H₂O: 0.1 mg; CoCl₂, H₂O: 25 µg; NiCl₂, 6H₂O: 25 µg; KNO₃: 1 g; 10 mg KH₂PO₄ and 10 mg Na₂HPO₄ corresponding to 4 400 µg P l⁻¹, Glucose 5 g l⁻¹). A similar volume of mycelium homogenate from the eight fungal species (150 µl) were inoculated, monospecifically and aseptically, in each Erlenmeyer flask, each culture being replicated three times. At the end of the experiment, the aquatic hyphomycetes were filtered on glass microfiber filters (GF/F, Whatman, Maidstone, England), freeze-dried and kept at -80 °C until the fatty acid extraction and analyses.

To determine if P availability could affect the PUFA composition of aquatic hyphomycetes, in a second experiment, four species were chosen that differed in their PUFAs synthesis performances according to the results of the first experiment: *H. lugdunensis*, *T. elegans*, and *T. chaetocladium*, in which PUFAs represented the highest proportions (>40 %) of the total fatty acids, and *A. constricta* in which PUFAs represented the lowest proportion (26 %). These fungi were grown along a P gradient according to the results obtained by Danger and Chauvet (2013). The lowest P level (40 µP l⁻¹), which was two orders of magnitude lower than the P level used in the first experiment, allowed testing of the effect of a P limitation without strong reductions in fungal biomass, and the second P level (400 µP l⁻¹) was intermediate between both extremes. To reach 400 µP l⁻¹, 0.9 mg KH₂PO₄ and 0.9 mg Na₂HPO₄ was added to 1 l of culture medium, and to reach 40 µP l⁻¹, 0.09 mg KH₂PO₄ and 0.09 mg Na₂HPO₄ was added. The experimental procedure used in this experiment was similar to the first one. The 24 Erlenmeyer flasks, i.e. four species × two P levels × three replicates, were incubated, freeze-dried and kept under the same conditions as for the first experiment.

For both experiments, fatty acid analyses were performed in triplicates. The method used for lipid analysis was fully described by Masclaux et al. (2011). Briefly, lipids were extracted using a chloroform/methanol solution according to the method proposed by Folch et al. (1957). Once extracted, fatty acids were converted into fatty acids methyl-esters (FAME) by acid catalyzed transesterification and analyzed on an Agilent technologies™ 6 850 gas chromatograph. FAME were identified by comparing retention times with those obtained from Supelco® and laboratory standards and quantified against

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