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Trade-offs between fungal and bacterial respiration along gradients in temperature, nutrients and substrata: Experiments with stream derived microbial communities

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ABSTRACT

We examined the effects of temperature, nutrients and substrata on microbial respiration rates. Leaves of alder and oak were incubated in a natural stream. Leaf discs were incubated in antibiotics to manipulate the ratio of fungi to bacteria with three treatments: antifungal, antibacterial, and combined antifungal and antibacterial treatment in addition to controls. Discs were subsequently incubated in different nutrient set-ups and temperature regimes. Significant effects of temperature, nutrients, microbial treatment and leaf type on respiration rates were found. However, temperature did not significantly add to the effect of eutrophication on microbial respiration rates. A stronger effect of temperature on fungal mediated respiration than on bacterial mediated respiration was found. In streams where leaf litter constitutes the main energy source, fungi constitute the dominant microbial decomposer. Our results indicate that increased temperature due to global warming might have serious implications for ecosystem functioning when leaf litter constitutes the main energy source.

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Introduction

Human induced changes to the Earth's land surface have altered nutrient flows dramatically and caused eutrophication in freshwaters worldwide (e.g., Jeppesen *et al.* 2009). Furthermore, the Earth's climate is thought to be changing faster than previously experienced by human civilisation, with an average temperature rise of 3–5 °C over the next century (Pounds *et al.* 1999; Parmesan & Yohe 2003; Thomas *et al.* 2004). Temperature has a strong influence on biological processes (e.g., Woodward *et al.* 2010) and several studies have shown that increased temperature might exacerbate the negative impact of eutrophication on freshwater ecosystems (Blenckner *et al.* 2006; Jeppesen *et al.* 2009).

The availability of nutrients is increasing globally (Vitousek *et al.* 1997) causing eutrophication of aquatic resources (Giller & Malmqvist 1998). Increasing nutrient concentrations, due to anthropogenic influences, has been shown to significantly impact decomposition processes (Elwood *et al.* 1981; Pascoal *et al.* 2003; Dangles *et al.* 2004), acting mainly through the microbial pathway inducing increased microbial substrate processing rates and respiration (Fuss & Smock 1996). Predicted increases in stream and river temperatures with global warming (Webb 1996) are likely to profoundly impact cool water streams in northern Europe (Pedersen & Sand-Jensen 2007). The vast majority of running waters are heterotrophic with detritus constituting a primary basal resource on which the systems rely (Fisher & Likens 1973). Microbes play a key

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role in the energy transfer from dead organic matter to higher trophic levels as they increase the nutritional value of organic material such as leaf litter and increase the assimilation efficiency of invertebrate consumers (Cummins 1973; Arsuffi & Suberkropp 1989).

The microbial mediated decomposition of leaf litter is controlled by both internal and external factors such as the condition of the leaf as it falls into the water and the water temperature (Cummins 1974; Petersen & Cummins 1974). Also the quality of the leaf, mainly the amount of lignin and tannins, control the microbial decomposition process (Gessner & Chauvet 1994). Also the amount of nitrogen (N) and phosphorous (P) in the water column are important for the decomposition process (Suberkropp & Chauvet 1995; Graça *et al.* 2001). Other physico-chemical factors such as light, temperature, pH and hydrology also affect the microbial decomposition process (Gao *et al.* 2005; Fierer *et al.* 2007).

Aquatic hyphomycetes, are often considered the dominant microbial decomposer as fungal biomass and production generally exceed bacterial biomass and production on intact leaf litter (Findlay & Arsuffi 1989; Weyers & Suberkropp 1996). However, bacteria also constitute an important part of the microbial decomposer community (Hieber & Gessner 2002) as their ability to decompose leaf litter is almost as high as that of fungi (Findlay & Arsuffi 1989). Although fungi and bacteria live in close proximity to each other they interact with each other in different ways. For instance, bacteria can suppress fungi, but can also be suppressed, unaffected or even enhanced by the presence of fungi (Gulis & Suberkropp 2003a; Mille-Lindblom & Tranvik 2003). Studies on the effects of nutrients and temperature on respiration rates in aquatic environments have mainly focused on community respiration (Fuss & Smock 1996; Niyogi *et al.* 2001; Sand-Jensen & Pedersen 2005) or bacterial respiration (Lomas *et al.* 2002; Sand-Jensen *et al.* 2007) and only a few have addressed fungal respiration (Ely *et al.* 2010). Most studies on bacterial respiration have focused on biofilms (Hoellein *et al.* 2010) and sediment (Sand-Jensen *et al.* 2007), whereas most studies on leaf litter only focus on community respiration (Niyogi *et al.* 2001; Gulis & Suberkropp 2003b; Buesing & Gessner 2006). Consequently, there is a need to investigate whether changes in key environmental variables influence the relative importance of bacteria and fungi to overall community respiration in the case of leaf litter.

In this study, we investigated, using a full factorial design: (1) the effects of temperature, nutrients and substratum (i.e., leaf species) on microbial respiration rates; and (2) the influence of temperature, nutrients and leaf type on different ratios of fungi to bacteria. We used two different substrata, alder (*Alnus glutinosa*) and oak (*Quercus robur*). We experimentally manipulated nutrients and temperatures to the appropriate levels to mimic an eutrophication gradient and predicted global warming scenarios. Overall we expected temperature and nutrients to have a positive effect on respiration rates on both substrata. However, as decomposition rates of the distinct litter types are differentially influenced by temperature (Fierer *et al.* 2005), the strength of the response could vary between substrata. Alder has higher nutrient concentrations compared to oak and is also less recalcitrant to decomposition than oak (Jensen 1974), and respiration on oak leaves could thus be expected to respond

more strongly than alder leaves to increased temperature (Fierer *et al.* 2005). Nutrient enrichment also influences microbes differently depending on the nutrient content of the detritus, where substrata with higher C:N ratios have a more marked response to nutrient additions than substrata with lower C:N ratios (Stelzer *et al.* 2003; Gulis *et al.* 2004). Hence, we also expected that nutrient enrichment would stimulate microbial respiration rates of oak leaves to a greater extent than alder leaves. For our second objective we manipulated the ratio of fungi to bacteria by incubating naturally conditioned leaves in antibiotics with either fungicidal effects (Nystatin) or bactericidal effects (Penicillin–Streptomycin) as described in Abelho *et al.* (2005). Manipulating the ratios of fungi to bacteria was expected to change respiration rates and the response to nutrients and temperature. We expected that releasing fungi from bacterial antagonism would increase respiration rates, whereas removing fungi would decrease respiration rates.

Material and methods

Microbial colonisation of submerged leaves occurred *in situ* in the stream Pinnarpsbäcken, situated in the county of Östergötland, in southern Sweden (longitude: 57°58'06, 6", latitude: 15°30'51, 0"). Stream Pinnarpsbäcken (stream order 2; catchment area 55 km²; of which 39.4 km² is forested and 7.6 km² is arable land) is continuously monitored by the Swedish agricultural university, SLU (www.ma.slu.se, accessed 30.10.09), and water chemistry is measured four times a year according to Wilander *et al.* (2003). According to set Environmental Quality Standards (EQS) the stream is currently classified as having good chemical status and good nutrient status (www.viss.lst.se, accessed 15.09.10). A 3-year average (2007–2009) of monitoring data revealed a nitrate concentration of 337 µg NO₃ l⁻¹ and a phosphate concentration of 5 µg PO₄ l⁻¹, which were used to estimate background ambient conditions. During this period, temperature ranged from 0.4 °C to 21.1 °C and pH varied from 7.14 to 7.61.

Alder and oak leaves were collected during abscission in late Sep. early Oct. 2009. The leaves were air dried, weighed to 5.00 g, moistened in tap water and placed in mesh bags (1-mm mesh size). At the end of Oct. 2009 the leaf bags were placed in the stream for 28 d to be colonised by bacteria and fungi. Twenty-eight days of incubation were chosen to maximise microbial colonisation and minimise any potential fragmentation (Fisher *et al.* 2009). Visual estimates of the leaves indicated the leaves were intact upon retrieval; both alder and oak leaves were softer than initially, although alder much more so than oak, hence the leaves were not in an advanced stage of decomposition. After collection the leaves were kept for 6–24 hr in stream water at 4 °C in the dark until leaf discs (1 cm diameter) were cut from them. Care was taken not to include major leaf veins. At the time leaf bags were retrieved, temperature in stream Pinnarpsbäcken was 4 °C.

Artificial stream water was mixed according to Mille-Lindblom & Tranvik (2003); Milli-Q water, 15 mg anhydrous CaCl₂ l⁻¹, 15 mg MgSO₄·7H₂O l⁻¹ and 20 mg NaHCO₃ l⁻¹. Nutrients (KNO₃ and KH₂PO₄) were added to the artificial stream water to produce three different nutrient conditions in addition

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