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# Interactive effects of temperature and soil moisture on fungal-mediated wood decomposition and extracellular enzyme activity

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ABSTRACT

Heterotrophic soil microbes regulate the rate-limiting step in soil organic matter decomposition via the production of hydrolytic and oxidative extracellular enzymes. The influence of climate change on heterotrophic microbial activity remains poorly understood, not least in terms of the differential sensitivity of microbial functional groups to warming and altered precipitation regimes. Cord-forming basidiomycete fungi dominate primary decomposition in temperate woodlands. We investigate the interactive influence of elevated temperature (3 °C), wetting and drying (6–9% increase and 5–6% decrease of soil moisture, respectively) on saprotrophic basidiomycete-mediated beech (*Fagus sylvatica*) wood decomposition, as well as on hydrolytic (β-glucosidase, cellobiohydrolase, β-xylosidase, *N*-acetyl-glucosaminidase, acid phosphatase and leucine aminopeptidase) and oxidative (peroxidase and phenoloxidase) enzyme potential activities, in woodland soil mesocosms. While drying decreased beech wood decomposition rate, warming resulted in an increased rate and compensated for the negative effect of drying. Moisture regulated the extracellular enzyme pool; all enzymes except leucine aminopeptidase had significantly greater potential activity under wetting than drying. Again, elevated temperature consistently compensated for the negative effect of drying, but did not increase extracellular enzyme potential activity, alone or in combination with wetting. This reflects microbial production (fungal biomass was not increased under these conditions) rather than *in situ* effects on enzyme kinetics. *N*-acetyl-glucosaminidase and acid phosphatase displayed differential responses to temperature and moisture in systems dominated by different fungi. Decomposer communities appear to be more functionally resilient to the combined effects of elevated temperature and altered moisture than is suggested based on the manipulation of single abiotic variables.



## 1. Introduction

Climate change has the potential to influence carbon exchange between the biosphere and the atmosphere. Soil respiration is thought to be more temperature-sensitive than primary production (Jenkinson et al., 1991); this implies that warming may lead to a net release of greenhouse gas from the terrestrial carbon pool (estimated at 2860 Pg C, more than three times the size of the atmospheric C pool; Lal, 2008). The influence of climate change on soil carbon storage, however, remains unclear (Bardgett et al., 2008; Singh et al., 2010), due mainly to poor resolution of the responses of different microbial groups to abiotic factors (Kandeler et al., 1998; Bardgett et al., 1999; A'Bear et al., 2013b). Elevated temperature and changing precipitation patterns (increasing incidence of prolonged precipitation or drought), through their direct physiological influences on soil organisms (Blankinship et al., 2011; A'Bear et al., 2013b), will be the most important determinants of soil biotic activity under climate change scenarios.

Heterotrophic microbes, in producing extracellular enzymes capable of breaking down the most recalcitrant components of plant material, such as lignin and cellulose, regulate the rate-limiting step of soil organic matter (SOM) decomposition (German et al., 2012). Slight temperature elevation increases physiological and metabolic processes rates in microbes, including enzyme production. The temperature sensitivity of soil extracellular enzymes (Koch et al., 2007; Sinsabaugh et al., 2008; German et al., 2012; Stone et al., 2012) implies that stimulation of respiratory $CO_2$ efflux from soil is likely to occur with warming, up to a maximum typically much higher than ambient conditions (Davidson and Janssens, 2006). Changing precipitation patterns (increasing frequency of prolonged periods of precipitation and

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drought) will alter soil moisture properties; as well as the enzyme producers themselves (A'Bear et al., 2013a), this will also affect substrate diffusion and metabolism by extracellular enzymes. Prolonged soil wetting or drying, therefore, has considerable potential to influence decomposition processes and modify the effect of elevated temperature.

Fungi exert a particularly strong influence on SOM dynamics, and on the sensitivity of decomposition to warming and altered patterns of precipitation (Yuste et al., 2011). While both temperature and soil moisture are known to influence microbial community composition, in general (Zhang et al., 2005; Castro et al., 2010), uncertainty remains regarding the differential responses of fungal functional groups. Saprotrophic basidiomycetes, as important producers of extracellular enzymes regulating the breakdown of complex lignocellulose substrata, are major agents of decomposition in temperate woodlands (Hättenschwiler et al., 2005). Decomposer fungi have rarely been partitioned from the general fungal, or even microbial, biomass in climate manipulation studies, making functional implications difficult to identify. An important ecological grouping of saprotrophic fungi, the cord-forming basidiomycetes, form dynamic networks of mycelium which ramify at the soil–litter interface, linking lignocellulose resources (e.g. wood) and releasing extracellular enzymes into the soil (Boddy, 1993, 1999). Mycelial growth and decomposition of colonised wood resources are stimulated by temperature elevation representing climate change predictions for temperate regions (A'Bear et al., 2012). Moisture also has the potential to influence the response of fungal growth and functioning to warming; mycelial development can be inhibited if soil is too wet or too dry (Donnelly and Boddy, 1997). Species-specific sensitivity of fungal growth and activity to temperature and soil moisture indicate that functional responses to abiotic factors could differ depending on the identity of the locally dominant decomposer basidiomycetes (A'Bear et al., 2013b). The fungal-mediated influence of abiotic conditions on the soil decomposer system represents a significant regulatory component of the balance of carbon uptake and release from temperate forest soil (Bardgett et al., 2008; Singh et al., 2010).

Using woodland soil mesocosms, the present study investigates the influence of temperature and soil moisture on basidiomycete-dominated microbial community functioning. Grazing by mycophagous collembola, when used as model grazers in two-species (fungus and grazing collembola) interactions in soil microcosms, can counteract the warming-induced stimulation of fungal colony expansion (A'Bear et al., 2012) and influence mycelial enzyme production (Crowther et al., 2011). Recent evidence from mesocosm experiments has, however, revealed that, in a realistic woodland decomposer community, competitive suppression of soil microfungi by cord-forming basidiomycetes limits the size of natural collembola populations (A'Bear et al., 2013a; Crowther et al., 2013). This reflects a reduction in the availability of fine microfungal hyphae, which are more palatable to collembola than thick cords (Crowther et al., 2013). This bottom-up limitation also restricted collembola population responses to experimental climate change, indicating they are unlikely to influence the biomass and function of cord-forming basidiomycetes in this system (A'Bear et al., 2013a). The direct and interactive influences of temperature and moisture are, therefore, expected to be the dominant factors regulating the functioning of microbial communities dominated by these decomposer macrofungi.

This study aims to determine the interactive impacts of elevated temperature and altered moisture (wetting or drying) on fungal biomass and potential enzyme activities (i.e. when substrate availability is not limiting) involved in decomposition of organic matter. Multifactorial experimental designs are rare in soil ecology; the time and cost involved often make them logistically unfeasible. To overcome this limitation and 'bridge the gap' between the simplicity of few-species microcosm experiments and natural conditions (Lawton, 1995, 1996), we used mesocosms made by extracting soil turves from temperate woodland, and subjected a realistic biotic community to controlled climatic conditions. Three specific hypotheses were tested: (1) warming will increase fungal biomass, enzyme activity and decomposition; (2) fungal biomass and enzyme activity will be increased by irrigation and reduced by drying; and (3) moisture limitation imposed by drying will prevent the warming-induced stimulation of fungal biomass, enzyme activity and decomposition. Fungal-mediated decomposition of colonised wood can be measured directly whereas, in soil, extracellular enzyme activity is an indicator of the microbial community function and the potential for decomposition in soil (Sinsabaugh et al., 2008; Henry, 2012). The activities of hydrolytic (β-glucosidase, cellobiohydrolase, β-xylosidase, *N*-acetyl-glucosaminidase, acid phosphatase and leucine aminopeptidase) and oxidative (peroxidase and phenoloxidase) enzymes were determined to provide an insight into the decay of organic substrates with differing rates of turnover. Hydrolytic enzymes regulate the decay of organic substrates with relatively rapid turnover times (e.g. carbohydrates, chitin) and oxidative enzymes break down substrates with relatively longer residence times in soil (e.g. lignin).

## 2. Materials and methods

### 2.1. Experimental design

The interactive influence of elevated temperature, wetting and drying on fungal biomass, extracellular enzyme activity and primary decomposition, in a saprotrophic basidiomycete-dominated microbial community, was investigated in woodland soil mesocosms. Three sets of mesocosms (two inoculated with a different saprotrophic basidiomycete species and one remaining uninoculated) were subjected to a fully-factorial combination of climate treatments: ambient moisture, wetting (ambient + 7.6 mm [10% above monthly UK late summer–autumn precipitation]; Alexander and Jones, 2001) or drying; and ambient or elevated (ambient + 3 °C) temperature. Ambient temperature was 15 °C, based on late summer–autumn temperatures beneath the litter layer in UK temperate woodland (Boddy, 1983). Six replicates were employed for all treatments.

### 2.2. Fungi

The cord-forming basidiomycete fungi *Resinicium bicolor* (Alb and Schwain.: Fr.) Parmasto and *Phanerochaete velutina* (DC.: Pers.) Parmasto were cultured on 2% malt agar (MA). Both species were originally isolated from, and are common in, UK temperate woodland. Freshly-felled beech (*Fagus sylvatica*) was cut into blocks (2 × 2 × 1 cm) and stored frozen (−18 °C), then defrosted in deionised water ($DH_2O$) for 12 h when required. Wood blocks were heat-sealed within two layers of autoclave plastic and autoclaved (121 °C) three times at 24 h intervals. Sterile wood blocks were placed in 14 cm diameter Petri dishes containing MA, pre-colonised with the experimental fungus, and incubated at 16 ± 1 °C for 3 months.

### 2.3. Mesocosm preparation and harvesting

Soil turves (30 × 30 cm, 5 cm deep) were extracted from mixed deciduous woodland (Tintern, Wye Valley, UK, NGR 352800, 201800) and immediately placed into lidded plastic boxes. The soil was silty loam, classified as a typical brown earth, and had a pH of 4.5 (measured in $H_2O$). Fresh litter was removed from the surface of