



Temperature sensitivity of extracellular enzymes differs with peat depth but not with season in an ombrotrophic bog

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ABSTRACT

Peatlands contain a large portion of Earth's terrestrial soil organic matter in part due to a reduction in decomposition rates. Organic matter decomposition is initially mediated by extracellular enzyme activity, which is in turn controlled by temperature, moisture, and substrate availability; and all are subject to seasonal variation. As depth increases in peatlands, temperature variability and labile carbon inputs decrease. We hypothesized that the more stable recalcitrant subsurface would contain a smaller less diverse enzyme pool, that is better adapted to a narrow temperature range. Thus temperature dependence would be diminished at depth compared to superficial peat. Potential enzyme activity rates were determined across seasons and with depth in peat samples collected from the Marcell Experimental Forest in northern Minnesota, USA. The temperature dependence, assessed by activation energy, was quantified for three hydrolytic enzymes involved in nutrient cycling at up to 15 temperature points ranging from 2 °C to 65 °C. Potential enzyme activity decreased with peat depth as expected and corresponded with changes in peat composition and microbial biomass from the acrotelm to the catotelm. In an environmentally relevant temperature range (2–23 °C), activation energy decreased with depth for β -glucosidase as predicted and leucine amino peptidase activation energy was the lowest of all enzymes. Stable temperatures at depth appear to result in a microbial community containing enzymes that have lower sensitivity to temperature increases. Surprisingly, there was no significant seasonal effect on enzyme temperature dependence observed in our study. Based on these results, and without shifts in microbial community composition, warming of peat could result in increased carbon and phosphorus cycling at the surface but little change at depth. Additionally differences in enzyme temperature sensitivity suggest nitrogen cycling could remain constant with warming, potentially resulting in proteolytic nitrogen cycling being decoupled from carbon and phosphorus cycling.

1. Introduction

Northern peatlands store an estimated 436 to 547 Gt carbon due to low rates of decomposition relative to net primary productivity (Clymo et al., 1998). Limitations imposed by temperature (Jassey et al., 2012; White et al., 2008), nutrient availability (Turetsky et al., 2008), water table depth/oxygen availability (Churchill et al., 2015; Deppe et al., 2010a; Fenner et al., 2005a), and pH (Criquet et al., 2000) all contribute to reduced net primary productivity and decomposition in peatlands (Andersen et al., 2013; Freeman et al., 1996). These conditions alter the type of organic matter present (Clymo et al., 1998; Tffail

et al., 2014; Yavitt et al., 2005) and which microorganisms are actively decomposing organic matter (Andersen et al., 2013; Galand et al., 2002; Lin et al., 2014). Concurrent changes in temperature, redox potential, organic matter composition, and microbial community, both seasonally and with depth, indicate a possible shift in the mode and tempo of decomposition reactions and how microorganisms may allocate their resources (Deppe et al., 2010b; Schimel et al., 2007; Sinsabaugh and Moorhead, 1994).

Microorganisms allocate their resources to four main areas: biomass/growth, maintenance, respiration, and enzyme production (Sinsabaugh et al., 2009; Xu et al., 2014). Of these four areas,

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production of extracellular enzymes is responsible for the initial breakdown of organic matter prior to assimilation and consumption by the microorganism, and is of high relevance for understanding microbial interactions with their environment. Production of specific enzymes can be based on microbial demand for a limiting nutrient (Allison et al., 2011) and/or high availability of a nutrient (Allison and Vitousek, 2005). Enzymatic activity, like all biochemical reactions, is directly and indirectly responsive to changes in, temperature, moisture, and substrate inputs, all of which change with seasons and a soils depth below the surface (Jassey et al., 2011, 2012; Romanowicz et al., 2015; Steinweg et al., 2012, 2013a; Trasar-Cepeda et al., 2007; Wallenstein et al., 2010). Enzymatic reactions proceed more rapidly as temperatures increase, to an extent, increasing the depolymerization efficiency per enzyme (Koch et al., 2007; Wallenstein et al., 2010). The sensitivity of enzyme activity to temperature can be measured through activation energy, the difference in energy between reactants, transitional species, and products. However, not all enzymes respond equally to changes in temperature making determination of activation energy enzyme specific (Steinweg et al., 2013b). Some nitrogen acquiring enzymes, such as proteases, have different activation energies compared to carbon and phosphorus acquiring enzymes, which may lead to a decoupling of nitrogen acquisition efficiency from carbon and phosphorus acquisition efficiencies with rising temperatures (Brzostek and Finzi, 2012; Wallenstein et al., 2009; Weedon et al., 2012).

Shifts in temperature can be attributed to climate change, but also occur as seasonal fluctuations at time scales relevant for microbial ecology, and can be quite extreme depending on site location and soil depth. Northern peatlands are characterized by cooler temperatures, especially in the winter where peat surface temperatures can be well below freezing while summer temperatures are about 20 °C. Changes in average seasonal temperatures can affect enzyme activity due to the sensitivity of enzymatic kinetics to temperature (Koch et al., 2007; Trasar-Cepeda et al., 2007; Weedon et al., 2014). In addition, shifts in thermal optima of enzyme activity have been measured, with the optima shifting up or down based on the seasonal ambient temperatures (Fenner et al., 2005; Wallenstein et al., 2009). In general, enzymes found in warm soils tend to have a lower temperature sensitivity than enzymes found in cold soils (Brzostek and Finzi, 2012; Fenner et al., 2005; Koch et al., 2007).

In addition to the direct influence of temperature on the kinetics of enzyme activity, there can also be indirect influences on activity through changes in both substrate availability and substrate accessibility. Substrate availability is defined here as the presence of a substrate regardless of quality, while accessibility refers to the likelihood for microbes and their extracellular enzymes to encounter a substrate (Dungait et al., 2012). Changes in temperature along with substrate (plant) inputs can also occur concurrent with seasonal shifts (Kshattriya et al., 1992). Even if substrate availability remains unchanged, moisture and temperature can affect microbial community physiology by altering substrate accessibility. For example, at low moisture levels enzyme activity in upland soils is controlled primarily by lack of diffusion rather than temperature, whereas when moisture is non-limiting temperature becomes the dominant controlling variable (Steinweg et al., 2012). Additionally, since carbon and nitrogen mineralization are coupled, enzyme activity related to both of these nutrients changes over the course of the year with substrate inputs (Weintraub and Schimel, 2005).

Availability and accessibility of nutrients can also be influenced by soil depth depending on depth of root inputs, organic matter quality and other limiting factors. Peatlands especially are vertically stratified into at least three distinct zones based on redox potential and organic matter transformation: acrotelm, mesotelm, and catotelm. The acrotelm (~0–30 cm) contains fresh litter with a high C:N ratio dominated by carbohydrates (Tfaily et al., 2014), and has the greatest bacterial and fungal abundance (Lin et al., 2014; Williams and Crawford, 1983) resulting in high decomposition activity, both aerobic and anaerobic. The mesotelm (~30–75 cm) has water table fluctuations leading to an oxic-

anoxic boundaries and intense decomposition by archaea, bacteria, and fungi resulting in a lower C:N and a shift towards increasing aromatics (Lin et al., 2014; Tfaily et al., 2014). The deepest layer, catotelm (75 cm–200 cm) is dominated by bacteria and archaea, greater aliphatic and aromatic abundance compared to carbohydrates, and reduced decomposition (Galand et al., 2002; Lin et al., 2014; Tfaily et al., 2014).

Soil depth can also influence microbial communities by naturally dampening the extreme seasonal temperature changes, potentially resulting in enzyme concentrations with different temperature responses at different depths. Peat temperatures change throughout the year due to temperature dependent energy inputs, but how much they change and how rapidly depends on the season and depth within the peat layer. The varying microbial communities that have established at these different depths over the thousands of years since the bog's development (McFarlane et al., 2018) may produce similar enzyme types, but the temperature regime experienced by these groups over time may have resulted in different thermal optima and sensitivities for the enzyme pool at each depth.

Given the above we designed our study to investigate the temperature dependence of enzyme activity across season, peat depth and enzyme type. Three enzymes were assayed: beta-glucosidase, leucine amino peptidase, and acid phosphomonoesterase as representatives of carbon, nitrogen and phosphorus cycling, respectively to assess native temperature sensitivity, prior to initiation of ongoing whole ecosystem warming treatments. We hypothesized that enzymes at the surface of the bog would have a greater sensitivity to temperature as compared to enzymes found deep below the peat surface due to differences in the current and historic temperature ranges experienced at these depths. In addition, it was hypothesized that a larger pool of each enzyme, as indicated by greater activity, would be present at the peat surface due to the availability of fresh carbon inputs from plants, higher microbial biomass, and oxygen availability. Finally, at the surface we hypothesized that activity would be greatest during the summer because of the availability of labile carbon from plants, while temperature sensitivity would be lower in summer compared to winter due to high and variable temperatures.

2. Methods

2.1. Site characteristics

Peat samples were collected during pretreatment periods from the SPRUCE experiment site (Hanson et al., 2017; <http://mnspruce.ornl.gov>) in the S1 bog at the Marcell Experimental Forest (MEF) located in northern Minnesota, USA (47° 30.476'; W 93° 27.162'). The mean annual temperature is 3.3 °C and the mean annual precipitation is 768 mm with the majority of precipitation occurring mid-April to early November (Verry et al., 1988). The S1 bog is an 8.1 ha ombrotrophic bog dominated by Sphagnum moss, ericaceous shrubs, black spruce, and eastern tamarack that was previously harvested in strip cuts in 1969 and 1974 (Verry, 1986). The surface of the bog has a hummock/hollow microtopography with a ~10–30 cm relief between hummock tops and hollow bottoms (Nichols, 1998). The average peat depth is 2.5 m and the peat pH is ~3–4.5 with primary water inputs from precipitation. Surface peat temperatures change an average of 3 °C daily and ranged from ~0 to 20 °C throughout the year in 2012 (Supplemental Fig. S1) whereas peat temperatures at 2 m depth are relatively stable, changing less than 0.2 °C daily and remain within the range of ~6–8 °C throughout the year (Supplemental Fig. S1). More detailed hydrologic and vegetation information is given in Sebestyen et al. (2011) and Griffiths et al. (2017).

2.2. Sample collection

Peat samples were collected from peat hollow surfaces at three coring locations on separate boardwalks/transects (near current plots 4,

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