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Depth rather than microrelief controls microbial biomass and kinetics of C-, N-, P- and S-cycle enzymes in peatland

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ABSTRACT

The formation of microrelief forms in peatlands - elevated and dry hummocks, depressed wet hollows and intermediate lawns - is controlled by the interaction of water table, nutrient availability and dominant plant communities. This affects the composition and activity of various functional groups of microorganisms. With depth, the change in peat quality from less to more highly processed organic material additionally regulates microbial activity. We hypothesized that microbial biomass and enzyme activities are driven by aeration and by peat quality and therefore (i) they increase from hollows (water saturated/anaerobic) through lawns (intermediate) to hummocks (aerobic) in the top peat and ii) they decrease with depth due to increasing distance from fresh plant-derived inputs and lower oxygen availability. These hypotheses were tested for enzymes catalysing the decomposition of C-, N-, P- and S-containing organic compounds in peat of the three microform types at three depths (15, 50 and 200 cm). Microbial biomass and peat chemical characteristics were compared with enzyme kinetic parameters, i.e. maximal potential activity (V_{max}) and the Michaelis constant (K_m).

Microbial biomass carbon (MBC) and V_{max} of β-glucosidase and *N*-acetyl glucosaminidase increased by 30–70% from hummocks and lawns to hollows in the top 15 cm, contradicting the hypothesis. Similarly, K_m and the catalytic efficiency of enzymes ($K_a = V_{max}/K_m$) were best related to MBC distribution and not to the aeration gradient. With depth, V_{max} of β-glucosidase, xylosidase and leucine aminopeptidase followed the hypothesized pattern in hollows. In contrast, MBC was 1.3–4 times higher at 50 cm, followed by successively lower contents at 15 and 200 cm in all microforms. The same depth pattern characterized the V_{max} distribution of 6 out of 8 enzymes. Phosphatase activity decreased from drier hummock to wetter hollows and the higher activity throughout the peat profile suggested a high microbial demand for P. Enzyme activities and catalytic efficiency in peat were closely linked to the distribution of microbial biomass with depth, which in turn was best explained by P content. From the ecological perspective, these results clearly show that peat decomposition will be accelerated when microbial activity is stimulated e.g. by increased P availability.

1. Introduction

Peatlands are an important source of greenhouse gases (GHG) and play a key role in the global carbon (C) budget (Lai, 2009). Boreal peatlands (> 45°N) cover only 3% of the terrestrial surface but contribute a significant portion of CH_4 (46 Tg CH_4-C yr^{-1}) to the atmosphere and are a steady sink for CO_2 (Limpens et al., 2008; Nilsson et al., 2008). Due to low annual mean temperatures and dominant anoxic belowground conditions, the rate of litter decomposition in peatlands is slow, leading to a net C accumulation (Moore and Basiliko, 2006). Nonetheless, C pools and storages here may become vulnerable due to continuous temperature increase and change of precipitation (IPCC, 2013) as well as eutrophication. According to IPCC (2013), the annual CO_2 emissions from anthropogenic greenhouse gas sources including changes in forestry and other land use systems are predicted to increase by 27 Gt in the upcoming decade. This makes it critically important to understand mechanisms regulating the C balance in peatlands.

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Table 1
Selected hydrolytic enzymes and their function for the degradation of organic matter. For more detailed information, respective references are provided.

Enzymes	Acronyms	Degradation of macromolecules	Potential role	References
β-1, 4-glucosidase	β-GLU	Cellulose	C-cycle	Gong and Tsao, 1979
Cellobiohydrolase	CEL	Cellulose	C-cycle	Gong and Tsao, 1979
Xylosidase	XYL	Hemicellulose	C-cycle	Gong and Tsao, 1979
N-acetyl-β-D-glucosaminidase	NAG	Chitin and bacterial polypeptidoglycan	N-cycle	Allison and Jastrow, 2006
Leucine aminopeptidase	LEU	Protein and peptides	N-cycle	Sinsabaugh et al., 1993
Tyrosine aminopeptidase	TYR	Protein and peptides	N-cycle	Sinsabaugh et al., 1993
Phosphatase	PHO	Nucleic acids, phospholipids and other ester phosphates	P-cycle	Turner et al., 2002; Toor et al., 2003
Sulphatase	SUL	Organic ester sulphates and C-bounded S	S-cycle	Sinsabaugh et al., 1991

The water table level and plant communities shape the surface of peatlands into three main microform types (microrelief sub-units): 1) elevated and relatively dry hummocks, 2) wet depressed hollows and 3) intermediate lawns (Saarnio et al., 1997; Nungesser, 2003; Shen et al., 2006). The specific conditions in each microform affect numerous biochemical processes and microbial parameters (Dorodnikov et al., 2011). Microorganisms use either secreted or membrane-bound digestive enzymes to decompose soil organic matter (SOM). The enzymes differ based on the principal reaction type by which microorganisms catalyse SOM decomposition or the synthesis of new biochemical compounds (Allison and Vitousek, 2005). Hydrolytic enzymes, functioning under aerobic and anaerobic conditions, play an important ecological role: they are mainly responsible for degrading polymeric compounds of plant- and microbial residues (e.g. cellulose, hemicellulose, chitin, peptidoglycan and lignin-prevalent components of SOM, see Table 1). The degradation products are utilized by microorganisms for their metabolism and growth (German et al., 2011).

SOM degradation and the release of C, nitrogen (N), phosphorus (P) and other macro- and microelements (e.g. sulphur (S)) is controlled by SOM quality and environmental factors. Peatlands are nutrient-poor environments, and microbial C mineralization and assimilation is strongly limited by the availability of key nutrients, particularly P and N (Lin et al., 2014b). Nutrient limitation was proven to influence both microbial community composition and enzyme activities (Amador and Jones, 1993; Lin et al., 2014a). Seasonal and weather-related changes of the water table, together with different vegetation communities, are responsible for the surface-specific conditions in the three microforms (Dorodnikov et al., 2011). With peat depth, the abrupt oxygen decrease and the increasing distance from fresh plant-derived deposits promote the development of anaerobic microbial communities (Kotiaho et al., 2013; Deng et al., 2014; Loeppmann et al., 2016). However, little is known about the relationships between peat quality (nutrient contents), microbial biomass and activity as affected by microrelief position and peat depth.

To fill the knowledge gaps, we determined Michaelis-Menten kinetics parameters of several common hydrolytic enzymes contributing to the peat C cycle (β-glucosidase, cellubiohydrolase, xylosidase), N (*N*-acetylglucosaminidase, leucine aminopeptidase, tyrosine aminopeptidase), P and S cycles (phosphatase, sulphatase). We then linked them to microbial biomass carbon in peat of three microrelief forms (hummocks, lawns, hollows) at three depths of a boreal peatland. The substrate-dependent enzyme activity approximated with Michaelis-Menten kinetics provides information about two key parameters: (1) the maximal velocity (V_{max}), i.e. the maximal rate, of an enzyme-mediated reaction at saturating substrate concentrations and (2) the Michaelis constant (K_m), i.e. the substrate concentration at half of the maximal velocity, which represents enzyme affinity to a substrate (German et al., 2011). We hypothesized that microbial biomass C and enzyme activities (i) increase from hollows (water saturated/anaerobic) through lawns (intermediate) to hummocks (dry/aerobic conditions) and (ii) decrease with depth due to increasing distance from fresh plant-derived inputs.

2. Materials and methods

2.1. Site description

Peat samples were collected from the Salmisuo mire complex in eastern Finland (62°47′ N, 30°56′ E). The peatland is an oligotrophic low-sedge *Sphagnum* pine fen (Saarnio et al., 1997; Becker et al., 2008; Dorodnikov et al., 2013). Three microform types were selected based on water table depth and dominant plant species (Becker et al., 2008): elevated hummocks, depressed hollows and intermediate lawns between the two. The most common plant species in hummocks were *Sphagnum fuscum* (Schimp.) Klinggr and *Eriophorum vaginatum*. Lawns were characterized by *S. angustifolium*, *S. balticum* (Russow) C. Jens. and *E. vaginatum*. The dominant plant types in wet hollows were *Sphagnum* species, *Scheuchzeria palustris* and *E. vaginatum* (Saarnio et al., 1997). The average depth of the water table below the studied microforms during the sampling period was -23 ± 5 cm, -5 ± 2 cm and 0 ± 2 cm from the surface of hummocks, lawns and hollows, respectively (Lozanovska et al., 2016).

2.2. Peat sampling

A stainless-steel peat corer (Eijkelkamp Agrisearch Equipment, Giesbeek, Netherlands) was used to collect peat samples. Three replicate sampling plots in three different locations of each microform were randomly selected for collecting peat cores (total nine experimental units). From each plot, peat was collected at three depths: 15, 50, and 200 cm from the surface of microforms for a total samples size of 27 altogether. At each sampling plot, collection was repeated at least 3 times to obtain the necessary amount of peat for each depth. The sample was *Sphagnum* type peat of weakly, partially and highly decomposed state in the top, middle and bottom layers, respectively. Samples were immediately placed in air-tight Whirl-pack plastic bags and after transportation to the laboratory in a cooled thermobox were stored at 4 °C temperature for one week in a dark room. To minimize the oxygen contamination of the samples collected beneath the water tables, samples were kept closed under field-moist (saturated) condition after sampling.

2.3. Peat chemical analyses

The chemical composition of peat samples was determined after drying (60 °C, 2–3 days) and grinding to fine powder by a Fritsch Pulverisette (type 00.502, Oberstein, Germany) equipped with an agate pocket and ball mill. Total C and N contents were measured with an automated CN analyser (Elementar Vario EL Cube, Elementar Analysensysteme GmbH, Hanau, Germany). Total P and S contents were determined with an ICP spectrophotometer (iCAP 6000 series, ASX-520 AutoSampler, Thermo Scientific, USA) after sample digestion in a mixture of nitric and hydrochloric acid (2:1 v:v) by a Digestore Milestone MLS 1200 (Microwave Laboratory System, Sorisole BG, Italy). The elemental composition is given in mg g^{-1}-of peat dry