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Temperature the dominant control on the enzyme-latch across a range of temperate peatland types

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ABSTRACT

The large accumulation of carbon in peatlands arises from slow organic matter decomposition where microorganisms and their enzyme activities play a critical role. However, there is a dearth of studies on the natural patterns of peatland microbial enzyme activity and inhibitory phenolic compounds over seasons, and across a range of depths and biogeochemically different peatland types. We report the spatiotemporal patterns for phenol oxidases, phenolics, and a suite of five key hydrolase enzymes at two depths in two ombrotrophic bogs, mineral poor and rich fens, and a forested basin swamp over the growing season. Results obtained using linear fixed and mixed effect models suggest that phenol oxidase activity varies significantly with temperature and, to a lesser extent pH, leading to a breakdown of inhibitory phenolics and increased hydrolase enzyme activity across all peatland types. Overall, enzyme activity decreased significantly with depth and showed significant variation over the course of the growing season with a minimum in the spring and a maximum in the summer and fall. Enzyme activities were generally greatest in the rich fen and lowest in the forested basin swamp with no significant difference between bogs and poor fens. Site-specific factors such as nutrient availability explain deviations from these patterns. Our results illustrate the widespread but conditional applicability of the enzyme-latch mechanism to peatlands and the vulnerability of the peatland soil organic carbon stock to climate warming.

1. Introduction

In peatlands, rates of plant-driven net primary production (NPP) exceed those of decomposition resulting in these ecosystems sequestering up to a third of the global soil organic carbon (SOC) stock despite covering only 3% of the Earth's surface (Yu et al., 2010). This imbalance between NPP and decomposition is thought to be due to cool temperatures, primarily anaerobic conditions, functionally limited decomposers, and the quality of organic matter substrates (Moore and Basiliko, 2006).

Extracellular enzymes are key to the peatland carbon cycle as they are used by microbes to access nutrients and energy present in complex organic substrates, making enzymes the proximate agents of decomposition (Sinsabaugh, 1994). Over the years, potential wetland extracellular enzyme activity (EEA) has received increasing attention in order to better understand and predict the fate of sequestered peatland carbon in response to anthropogenic climate change. Work by Freeman et al. (1996, 2001a, b, 2004) led to the hypothesis of an "enzyme-latch mechanism" (ELM) in peatlands whereby the activity of specialized carbon and nutrient acquiring extracellular enzymes, hydrolases, are inhibited by the ubiquitous phenolic compounds through their chemical binding with existing enzymes and inhibiting further enzyme production (Brouns et al., 2014 and references therein). The concentration of phenolics [PHEN], in turn, is influenced by the potential activity of phenol oxidases (POX), a group of extracellular enzymes capable of oxidizing phenolics from simple, inhibitory aromatics to complex, non-inhibitory polyphenols (Durán et al., 2002). Studies have suggested that POX activity is suppressed in peatlands due to low pH (Williams et al. 2000), low oxygen availability (Freeman et al., 2001a), and low temperature (Freeman et al., 2001b) - all common in peatlands. Should one or more of the proposed restraints on

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[1] Developed methodology, performed sample collection, processing, and data analysis, and wrote manuscript.

[2] Funded study, advised on methodology, sample processing, and data analysis, and reviewed manuscript.

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POX activity be eliminated, it could conceivably lead to a catastrophic mobilization of sequestered peatland carbon through enhanced hydrolase enzyme activity (HEA).

As the effects of anthropogenic climate change are predicted to be both spatially and temporally heterogeneous (Pachauri et al., 2014), it is crucial to establish the baseline spatiotemporal variation of EEA in biogeochemically different peatland types in order to better assess the sensitivity of peatland carbon stocks to change. In this study, we measured the potential activity of two key groups of extracellular enzymes – POX and hydrolases, total soluble phenolic concentration, and environmental variables at two depths over three seasons in an ombrotrophic bog, a fen-bog complex containing areas with rich and poor fen characteristics, and a forested basin swamp. A transect at each peatland permitted us to account for within-site variation and to assess different peatland types while measurements in the spring, summer, and fall allowed us to account for natural variations in pH, peat temperature, and water table depth (WTD) over the growing season. Our objectives were to (1) determine if the relationships inherent in the ELM are evident in the natural variation of EEA across a range of biogeochemically different peatland types, (2) establish the common dominant environmental regulators of POX activity across all sites, (3) determine how EEA varies with depth and season, and (4) determine how EEA compares between peatland types.

We hypothesized that: (1) EEA will decrease with depth across all peatland types owing to suboptimal temperature, oxygen availability, and pH; (2) EEA will be highest in the forested basin swamp owing to its higher pH and warm, well-aerated peat, and lowest in the poor fen due to its consistently high water table and lower pH; (3) [PHEN] will be negatively correlated with both POX activity and EEA across different peatland types despite the lack of artificial manipulation of any of the environmental variables thought to regulate POX activity; (4) temperature and WTD will correlate more strongly with POX activity than pH as they exhibit greater seasonal fluctuations; and (5) EEA maxima and minima will occur in the summer and spring respectively as they represent seasonal end-members in our data set with the former expected to exhibit the warmest peat temperatures and lowest WTD and the latter exhibiting the reverse.

2. Materials and methods

2.1. Site descriptions

Sample collection was conducted at the Mer Bleue Bog, the Lanoraie Peatland Complex, and Hemlock Swamp (Table 1). Mer Bleue, an ombrotrophic bog located 10 km east of Ottawa, Ontario, is ~28 km^2 in area with peat depths approximately 0.3 m at the margins, with a narrow band of beaver ponds surrounding the bog, and increasing to 5–6 m near the center (Roulet et al., 2007). The mean annual temperature (MAT) at Mer Bleue is 6.6 ± 0.9 °C and the mean annual precipitation (MAP) is 920 mm (Environment Canada, 2015a). The bog surface has a hummock-lawn-hollow microtopography dominated by both ericaceous shrubs and *Sphagnum* mosses.

The Lanoraie peatland complex, located 40 km northeast of Montreal, Quebec, is approximately 76 km^2 in area with 4.7 km^2 of it classified as an ecological reserve (Réserve Écologique des Tourbières-de-Lanoraie). The MAT at Lanoraie is 6.3 ± 1.9 °C and the MAP is 1000 mm (Environment Canada, 2015a). This complex is mainly composed of minerotrophic peatlands covered with *Alnus* spp. (alder) and *Acer rubrum* (red maple) trees as well as scattered areas of ombrotrophic peatland characterized by a hummock-hollow microtopography dominated by ericaceous shrubs and *Sphagnum* mosses (Rosa and Larocque, 2008; Rosa et al., 2009). Average peat depth within the reserve is 1.8 m but it reaches 7 m in places (Rosa and Larocque, 2008).

Hemlock Swamp is a 0.06 km^2 basin swamp located 35 km east of Montreal, Quebec in the Gault Nature Reserve at Mont St. Hilaire, a Monteregian hill. The MAT at Hemlock Swamp is 6.2 ± 3.2 °C and the MAP is 1011 mm (Environment Canada, 2015a). The swamp, containing 0.75–2 m of peat underlain by a bedrock of limestone, was formerly a small lake and drains a 0.62 km^2 watershed (Richard and Occhietti, 2005). The surrounding catchment is covered with undisturbed mixed northern hardwood forest (Phillips, 1972) while vegetation in the swamp itself is primarily *Betula alleghaniensis M.* (yellow birch), *Tsuga canadensis* L. (eastern hemlock), *A. rubrum*, *Thuja occidentalis* (eastern white cedar), and *Fraxinus nigra M.* (black ash) with an understory dominated by ferns and mosses (Dalva and Moore, 1991).

2.2. Sample collection

1 m^2 experimental plots spaced at least 50 m apart were established along transects at each of the three peatlands. At Hemlock Swamp, 4 plots were established along a 413 m long transect following a hydrological gradient with spring 2013 water table depths of 1 cm, 3 cm, 29 cm, and 21 cm for plots 1, 2, 3, and 4 respectively. At Lanoraie, 7 plots were established along a 1.2 km long transect following a peatland type/pH gradient with plots 5, 6, and 7 located in the rich fen, plots 8 and 9 located in the poor fen, and plots 10 and 11 located in the ombrotrophic bog. At Mer Bleue, 4 plots were established along a 328 m long transect following a microtopographical/hydrological gradient with plots 12 and 15 located on hollow/lawn microtopography and plots 13 and 14 located on hummock microtopography. Triplicate peat samples were collected at 10 cm and 30 cm depth from each plot between May 14th and May 17th, 2013 (spring), August 1st and August 5th, 2013 (summer), and October 28th and October 31st, 2013 (fall). MAT and MAP in 2013 for each site followed 1981–2010 climate normals with MATs of 6.7 °C, 6.9 °C, and 7.1 °C for Mer Bleue, Lanoraie, and Hemlock Swamp respectively and MAP of 881 mm,

Table 1
Peatland type characteristics.

	Hemlock Swamp	Lanoraie	Lanoraie	Lanoraie	Mer Bleue
Peatland Type	Forested Basin Swamp	Rich Fen	Poor Fen	Ombrotrophic Bog	Ombrotrophic Bog
Coordinates	45.10°N, 73.10°W	46.00°N, 73.33°W	46.00°N, 73.33°W	46.00°N, 73.33°W	45.41°N, 75.48°W
Plot No.	1–4	5–7	8–9	10–11	12–15
Mean Growing Season pH	6.2 ± 0.2	6.1 ± 0.2	4.4 ± 0.1	4.0 ± 0.3	4.0 ± 0.2
Mean Growing Season WTD (cm)	39 ± 27	11 ± 7	10 ± 5	15 ± 5	26 ± 11
Mean Growing Season Peat Temperature, (°C)	11.8 ± 3.3	12.7 ± 1.9	11.7 ± 1.4	10.5 ± 2.2	8.8 ± 2.9
Mean Pore Water DOC:TDN	13.4 ± 5.0	25.7 ± 5.1	30.7 ± 6.0	38.8 ± 8.4	31.3 ± 8.2
Mean Corrected Conductivity (μS cm^{-1})	100 ± 41	95.0 ± 13.9	50.0 ± 3.8	38.0 ± 5.0	34.9 ± 8.4
Mean % Soil Organic Matter	91.9 ± 2.2	92.6 ± 2.1	94.2 ± 0.7	96.4 ± 0.7	93.9 ± 4.6