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Interactive plant functional group and water table effects on decomposition and extracellular enzyme activity in *Sphagnum* peatlands

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ABSTRACT

Peatland decomposition may be altered by hydrology and plant functional groups (PFGs), but exactly how the latter influences decomposition is unclear, as are potential interactions of these factors. We used a factorial mesocosm experiment with intact 1 m^3 peat monoliths to explore how PFGs (sedges vs Ericaceae) and water table level individually and interactively affect decomposition processes. Decomposition was measured using litter bags at three depths filled with cellulose strips to mimic decomposition of a simple plant-derived structure, and *Sphagnum* tissue to simulate decomposition of the most abundant recalcitrant material in peatlands. We also analyzed the potential activity of five hydrolytic extracellular enzymes at an intermediate depth. We found lowered water table reduced activity of several enzymes and increased cellulose and *Sphagnum* decomposition. Presence of Ericaceae reduced decomposition of the recalcitrant *Sphagnum* tissue, whereas higher activity of chitinase was found in the combined presence of sedges and Ericaceae. We found no relationship between any potential enzyme activity and *Sphagnum* decomposition rate. Overall our results showed a dominating role of water table controlling decomposition processes, as well as support for the hypothesis that the presence of mycorrhizal Ericaceae can slow decomposition processes of complex plant tissues in peatlands.

1. Introduction

Peatlands are the most important terrestrial ecosystems for long-term carbon sequestration (Clymo et al., 1998; Gorham, 1991) because the imbalance of biomass production and decay (e.g. Frolking et al., 2010; Kurnianto et al., 2015) leads to the accumulation of dead organic material often exceeding several meters in depth (Buffam et al., 2010). Peatlands have been net long-term carbon sinks under Holocene climatic conditions (Gorham, 1991; Nilsson et al., 2008), but climate change threatens these sinks (Waddington et al., 2015) both directly through altered water tables and temperature and indirectly through altered plant functional group (PFG) composition and biotic interactions (Weltzin et al., 2003). Whether peatlands will remain carbon sinks or become carbon sources (e.g. Charman et al., 2015; Moore et al., 1998; Wieder, 2001) will depend on the extent to which these hydrological and biological processes are altered as climate changes (Armstrong et al., 2015; Kardol et al., 2010; Trettin et al., 2006).

There are several different PFGs in peatlands. Ombrotrophic peatlands are dominated by *Sphagnum* mosses, which play a key role in peat formation (Turetsky et al., 2012; Vanbreemen, 1995). Vascular peatland plants mainly include two PFGs with divergent strategies for nutrient acquisition in a variably water saturated environment: sedges such as *Carex* and *Eriophorum* spp., and dwarf shrubs in the Ericaceae. Peatland sedge roots are typically non-mycorrhizal (Thormann et al., 1999; Miller et al., 1999), but possess aerenchyma (open air channels in stem and roots) providing oxygen for their roots that allows them to persist under permanently waterlogged and often anoxic soil/water conditions. Sedges thus have the potential to mine water and nutrients from deeper peat inaccessible to non-aerenchymous plants (Murphy et al., 2009). In contrast, Ericaceae roots are non-aerenchymous

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and hence can only withstand temporary waterlogged conditions. Their roots and associated ericoid mycorrhizal fungi (ErMF) require aerated peat for most of the growing season. Persistent low water table (WT) levels therefore favor the Ericaceae (Breeuwer et al., 2009; Weltzin et al., 2003).

ErMF may play a key role in determining decomposition processes in peatlands. These fungi (Bajwa et al., 1985; Read, 1996) produce a diverse assemblage of extracellular enzymes (Burke et al., 2014; Kohler et al., 2015), yet are believed to be inferior decomposers compared to the most competent free living saprotrophic microbes (Baldrian, 2009; Read et al., 2004) because they lack class II peroxidases, which are essential for oxidation of lignin (Kohler et al., 2015). Given that ErMF are supplied with labile carbon by host plants, it is believed that their main function is nutrient mining rather than carbon uptake (Hobbie et al., 2013; Lindahl and Tunlid, 2015; Treseder et al., 2006). This may lead to nutrient competition with free living saprotrophs (Michelsen et al., 1996; Orwin et al., 2011), which in turn may result in slowed decomposition (Averill et al., 2014; Clemmensen et al., 2013; Gadgil and Gadgil, 1971). Similarly, direct decomposer activity of mycorrhizal fungi (Talbot et al., 2008) targeting non-lignin polymers might exacerbate C limitation of free-living saprotrophs. Alternatively, the exudation of labile carbon by mycorrhizae and plant roots (Crow and Wieder, 2005) might result in a priming effect in which the additional labile substrates from the host plants enhance decomposition (Kuzyakov et al., 2000). Exactly which of these processes dominates remains to be elucidated.

The interaction of PFGs and WT level influences decomposition in peatlands (Laiho, 2006; Robroek et al., 2015; Ward et al., 2015). Due to the specific adaptations described above, sedges and Ericaceae occupy different niches with respect to water tables. Thus, WT plays a key role in shaping plant communities and the associated microbial composition. In addition, WT level determines the availability of oxygen for decomposition. Whereas the acrotelm (shallow, lower bulk density, typically more oxic, variably flooded layer) supports saprotrophic bacteria and fungi as well as mycorrhizal fungi and ericaceous roots, the catotelm (deeper, higher bulk density, typically anoxic flooded layer) hosts sedge roots and chemoautotrophic prokaryotes, methanogens, and fermenting bacteria. Anaerobic breakdown of organic material yields less energy compared to aerobic decomposition and is therefore much less efficient, leading to the preservation of organic material in the catotelm (e.g. Beer et al., 2008). However, examining exactly how peat C storage is likely to change with changes in hydrology and PFG is difficult because of their interactive controls on peat redox conditions.

To disentangle these effects, we used a factorial mesocosm experiment to manipulate PFGs and hydrology. Specifically, we tested three main hypotheses examining how PFG composition and WT level influence extracellular enzyme activity (EEA) and decomposition processes at various depths, four years after the onset of the experimental manipulation of PFG type and water level. 1.) We anticipated a strong positive link between EEA and decomposition, as EEA plays a key role in organic matter breakdown (Sinsabaugh, 1994). 2) We expected the treatments to modify EEA due to a) WT effects, and b) effects by plant functional types and associated biotic communities. 3) We postulated lowered WT would increase decomposition, and Ericaceae would slow decomposition.

2. Methods

2.1. Experimental design

We used a mesocosm experiment initiated in summer 2011 at the USDA Forest Service, Northern Research Station in Houghton, Michigan. Briefly, intact monoliths (1 m^3) of peat were extracted from an extensive oligotrophic peatland in Meadowlands, MN (N47.07278°, W92.73167°) and transported to the mesocosm facility (Potvin et al., 2015). The experiment was a full factorial design replicated in four blocks. Treatments comprised two levels of WT (high and low; manipulated during the growing season, see Potvin et al. (2015), and supplementary material) and three PFG treatments: Ericaceae only (E), sedge only (S), untreated PFG controls (U) with both PFGs in mixture, which resulted in a total of 24 mesocosm bins. The sedge bins contained *Carex oligosperma* Michx., and *Eriophorum vaginatum* L., whereas the Ericaceae bins were dominated by *Chamaedaphne calyculata* L., Moench., *Kalmia polifolia* Wangenh., and *Vaccinium oxycoccos* L. For further details on the experimental setup and species composition see Potvin et al. (2015).

2.2. Decomposition assay

In late June 2014 three replicate cellulose assays were inserted into each bin. The assays were harvested in October 2014, after a four month incubation. Assay bags were constructed using Nytex mesh (size 80 μm) to minimize root ingrowth, and each bag contained three separate pockets, 9 cm long and 3 cm wide, containing a cellulose filter paper strip (Whatman 1001-929 Quantitative Filter Paper Sheet) with an initial dry (55 °C) mass of approximately 190 mg. The stacked pockets spanned the following depths A: 2–11 cm, B: 11.5–20.5 cm and C: 21–30 cm. In parallel to the cellulose assay we inserted an additional set of two replicates of *Sphagnum*-filled bags. We only had two replicates for the *Sphagnum* assay because we had pulled one set concurrently with the cellulose assay (after four months), but hardly any of the material had decomposed. Instead of the cellulose strips we used ca. 100 mg dried *Sphagnum rubellum* Wilson, tissue to fill the pockets. Prior to filling the pockets the green stem section of the mosses, spanning about 4 cm below the capitula, was collected and dried at 30 °C to stable mass. The *Sphagnum* assay was incubated for 12 months (June 2014–June 2015). We used different incubation times for the two decomposition assays to account for the fact that cellulose mass loss occurs at a much faster rate than *Sphagnum* tissue (c.f. Hajek, 2009). Upon harvest, assay bags were gently rinsed with DI water to remove adhering peat. The assay material was carefully extracted from the bags. Cellulose strips were dried and weighed at 55 °C, and *Sphagnum* was dried and weighed at 30 °C to determine mass loss over the period of incubation.

2.3. Assay for measuring potential extracellular enzyme activity (EEA)

In late June 2015, four years after the onset of the experiment, a round steel core (diameter = 2 cm) was used to extract peat from one core in the center of each of the 24 bins. Homogenized, fresh peat material at 10–20 cm (overlapping in depth with the central pocket of the decomposition assay) was used in the enzyme assays. At sampling the low and high WT treatments averaged 40 cm and 20 cm below the peat surface, respectively. To quantify potential extracellular hydrolytic enzyme activity in the peat matrix we closely followed the protocol by Bell et al. (2013) using deep well incubations. Romanowicz et al. (2015) demonstrated that most enzyme activity in peat is associated with the peat matrix as compared to the pore water. To assay peat, a greater incubation volume (1000 μl instead of the commonly used 200 μl) and a subsequent centrifugation step to remove interfering peat tissue is particularly advantageous. To create a homogeneous peat suspension we used a 0.05 M sodium acetate buffer at pH 4.2 (ambient

pH), added 6 g wet peat and used a hand blender for 30 s. All of the following substrates were added well in excess at 200 μM: 4-Methylumbelliferyl β-D-cellobioside (Sigma M6018) to measure potential cellulase activity (CBH), 4-Methylumbelliferyl β-D-glucopyranoside (Sigma M3633) for potential glucosidase activity (BG), 4-Methylumbelliferyl N-acetyl-β-D-glucosaminide (Sigma M2133) for potential chitinase activity (NAG), 4-Methylumbelliferyl phosphate (Sigma M888) for potential phosphatase activity (PHOS) and 4-Methylumbelliferyl-sulfate (Sigma M7133) for potential sulfatase activity (SULF). We used eight technical replicates for each assay and incubated 1000 μl of the peat-substrate slurry in the 2 ml deep well trays at 25 °C in the dark. After a three hour incubation followed by centrifugation at 41 RCF for 3 min, 250 μl of the supernatant was transferred into corresponding opaque microplates then read for fluorescence on a Molecular Devices Spectramax M2 plate reader with excitation and emission wavelengths of 365 and 460 nm respectively. To convert the fluorescence readings into potential enzyme activity we followed the protocol by Bell et al. (2013), which utilizes a 4-Methylumbelliferone (Sigma M1381) standard curve for each peat sample.

2.4. Statistical analyses and data visualization

Mixed effects models following Bolker et al. (2009) were used to account for the nesting of multiple depths within each bin. For data visualization and statistical analysis we used R version 3.0.2 for linux-gnu (R Core Team, 2013) and the following packages "lme4" (Bates et al., 2015), "lmerTest" (Kuznetsova et al., 2015), "pbkrtest" (Halekoh and Højsgaard, 2014), "car" (Fox and Weisberg, 2011), "MASS" (Venables and Ripley, 2002), "multcomp" (Hothorn et al., 2008), and "ggplot2" (Wickham, 2009). PFG, WT, and depth were analyzed as fixed (categorical) factors. Bin and block were random terms. All models were tested with likelihood ratio tests for significant block contributions to the model; if not, block was removed from the model. For hypothesis testing analysis of variance type II with Kenward-Roger approximation for degrees of freedom were used for normally distributed data. Data from a single depth (10–20 cm) were analyzed with 2way-ANOVA (Type II). In case of significant PFG treatment effects multiple comparisons of means using Tukey contrasts (while accounting for the interaction structure of the model) were applied to assess the direction of the treatment response. Regression analyses were used to test for the explanatory power of the potential extracellular enzyme activity (EEA) on mass loss of both the cellulose assay and the *Sphagnum* tissue assay. For all statistical tests p-values <0.05 were considered to be statistically significant.

3. Results

3.1. Cellulose decomposition assay

There was an overall WT effect ($p < 0.0001$; Table 1) with higher decomposition in the low WT treatment (Fig. 1). When analyzing the 3 depths separately all 3 models show a significant WT effect and for A (2–11 cm) $p = 0.011$, B (11.5–20.5 cm) $p < 0.0001$, C (21–30 cm) $p < 0.0001$, with consistently higher decomposition in the low WT treatment (Fig. 1).

3.2. Sphagnum tissue decomposition assay

There was an overall WT × depth interaction ($p = 0.006$; Table 1) with higher decomposition in the low WT only at depth C (21–30 cm) (Fig. 1). When analyzing the 3 depths separately no treatment effect can be detected at A (2–11 cm). Depth B (11.5–20.5 cm) reveals a significant PFG effect ($p = 0.048$; Table 2), with highest decomposition in the sedge only treatment (U=S: $p = 0.039$; U = E: $p = 0.476$; S = E: $p = 0.318$; Fig. 1). At depth C (21–30 cm) we observed a significant WT effect ($p = 0.018$) with higher decomposition in the low WT treatment (Fig. 1).

Table 1
Estimates of fixed effects produced by mixed effects models of cellulose mass loss (in grams) as well as of the *Sphagnum rubellum* mass loss (in grams) with "bin" as random effect. Variables: veg comprises Ericaceae only (E), sedge only (S), untreated controls (U) with both vegetation types in mixture; depth = three levels (2–11 cm, 11.5–20.5 cm, 21–30 cm), WT = two levels of water table manipulation (high, low); n = 24 bins.

Variables	Full model for cellulose mass loss		Full model for *Sphagnum* mass loss	
	F test	p	F test	p
veg	$F_{(2,18)} = 0.041$	0.960	$F_{(2,18)} = 0.390$	0.682
depth	$F_{(2,40)} = 0.238$	0.790	$F_{(2,40)} = 0.333$	0.719
WT	$F_{(1,18)} = 65.281$	2.128e-07	$F_{(1,18)} = 0.823$	0.377
veg:depth	$F_{(4,40)} = 0.054$	0.994	$F_{(4,40)} = 1.074$	0.383
veg:WT	$F_{(2,18)} = 1.147$	0.340	$F_{(2,18)} = 1.167$	0.334
depth:WT	$F_{(2,40)} = 2.928$	0.065	$F_{(2,40)} = 5.798$	0.006

3.3. Potential extracellular enzyme activity (EEA)

The measured potential EEA revealed a strong WT effect, with higher enzyme activity at the high WT for four of five measured enzymes: BG, NAG, PHOS, and SULF (Table 2; Fig. 2). CBH did not show any significant responses to the treatments (Table 2). Only NAG showed a significant response to the PFG treatment (Table 2), with lower activity in the sedge and Ericaceae treatments compared to the untreated controls (U=S: $p = 0.011$; U = E: $p = 0.031$; S = E: $p = 0.884$; Fig. 2). However, we found a consistent trend toward significance ($p < 0.09$) across all five enzymes.

None of the assayed EEA showed any explanatory power for the *Sphagnum* decomposition patterns in regression analysis: CBH ($p = 0.741$), BG ($p = 0.499$), NAG ($p = 0.132$), PHOS ($p = 0.261$), SULF ($p = 0.868$). Regression analyses showed that cellulose mass loss could not be explained by CBH ($p = 0.612$) or NAG ($p = 0.343$). However, PHOS ($p = 0.0004$) was negatively correlated with cellulose mass loss (c.f. Figs. 1 and 2). BG ($p = 0.076$) and SULF ($p = 0.081$) showed marginally significant negative correlations with cellulose mass loss.

3.4. Water table level manipulation

Differences in water table level (WT) could only be maintained throughout the snow free period of the year from mid May to November (c.f. supplementary material). Monthly averages (daily measurements) in water table level for the high WT bins compared to the low WT bins were as followed: for 2014 (month: average high WT in cm/average low WT in cm): (June: 5.1/18.0), (July: 12.6/34.1), (August: 17.6/46.9), (September: 13.8/38.2), (October: 11.4/24.2), (November: 9.6/12.9), and for (June 2015: 19.3/30.2). During the winter month higher WT were observed in the low WT treatment due to enhanced subsidence (Potvin et al., 2015).

4. Discussion

We found support for our hypothesis that the presence of Ericaceae may slow decomposition of complex tissues, leading to an accumulation of recalcitrant*Sphagnum*-derived material in the peat. The majority of the peat in*Sphagnum* dominated peatlands consists of *Sphagnum* remnants (Dorrepaal et al., 2005; Turetsky, 2003). Highest densities of ericaceous roots and mycorrhizae are found in the acrotelm (Murphy et al., 2009, and personal

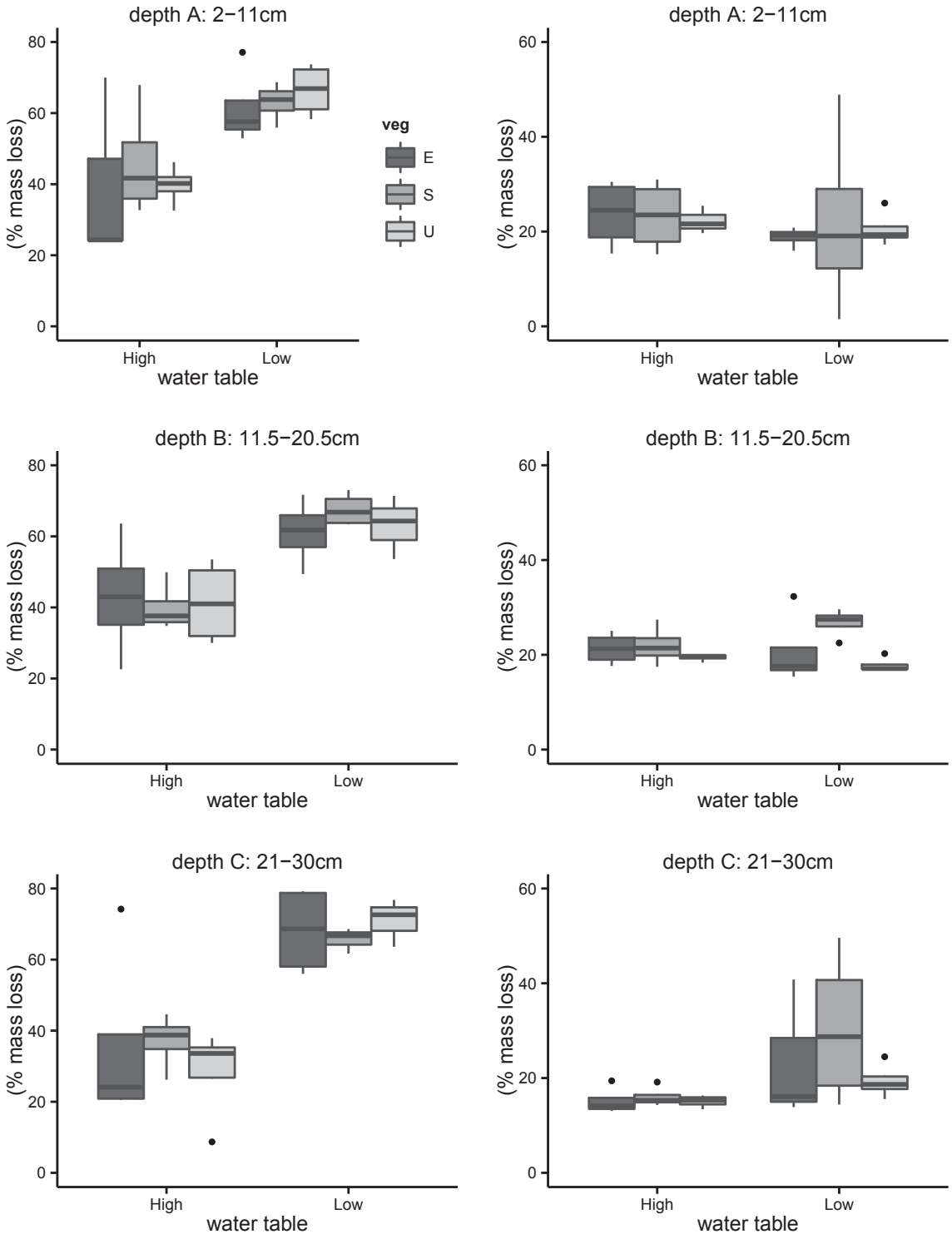

Fig. 1. Left panel; Average percent mass loss of cellulose assay after a four month (July–November) incubation period split by depth (2–11 cm, 11.5–20.5 cm, 21–30 cm; n = 24). The vegetation treatment (veg) comprises Ericaceae only (E), sedge only (S), untreated controls (U) with both vegetation types in mixture, water table: high and low. Right panel; Average percent mass loss of *Sphagnum rubellum* tissue assay after a twelve month (July–July) incubation period.

communication for this experiment by Todd Ontl). Our results suggest that ErMF may have a strong influence on microbial communities and thus decomposition processes, but the exact mechanism behind the observed suppression of decomposition in the presence of ectomycorrhizal fungi has yet to be determined. In a recent review on studies addressing the 'Gadgil effect', Fernandez and Kennedy (2016) propose that the negative effects of competitive interaction between fungal guilds may be particularly pronounced when resources (nutrients, labile carbon and water) are in short supply. In support of the potential nutrient mobilization effects on decomposition, it is striking that the one significant PFG effect on enzymes was for NAG, a nitrogen-mobilizing enzyme.

Table 2
Statistical results of 2way-ANOVA (Type II) models on potential extracellular enzyme activity (in nmol activity/g dry peat/hr) and mass loss (in grams) of the cellulose as well as the *Sphagnum rubellum* tissue assay at a peat depth of 10–20 cm below the surface; variables: veg comprises Ericaceae only (E), sedge only (S), untreated controls (U) with both vegetation types in mixture, WT = two levels of water table manipulation (high, low); n = 24 bins.

Variables	Cellulase (CBH)		Glucosidase (BG)		Chitinase (NAG)		Phosphatase (PHOS)		Sulfatase (SULF)	
	F test	p	F test	p	F test	p	F test	p	F test	p
veg	$F_{(2,18)} = 3.221$	0.064	$F_{(2,18)} = 3.313$	0.060	$F_{(2,18)} = 6.223$	0.009	$F_{(2,18)} = 2.784$	0.088	$F_{(2,18)} = 2.797$	0.088
WT	$F_{(1,18)} = 1.033$	0.323	$F_{(1,18)} = 4.893$	0.040	$F_{(1,18)} = 4.761$	0.043	$F_{(1,18)} = 31.558$	2.489e-05	$F_{(1,18)} = 6.521$	0.020
veg:WT	$F_{(2,18)} = 0.799$	0.465	$F_{(2,18)} = 0.602$	0.559	$F_{(2,18)} = 2.770$	0.089	$F_{(2,18)} = 0.481$	0.626	$F_{(2,18)} = 2.153$	0.145

Variables	Mass loss cellulose		Mass loss Sphagnum	
	F test	p	F test	p
veg	$F_{(2,18)} = 0.030$	0.972	$F_{(2,18)} = 3.605$	0.048
WT	$F_{(1,18)} = 27.708$	5.264e-05	$F_{(1,18)} = 0.214$	0.650
veg:WT	$F_{(2,18)} = 0.259$	0.776	$F_{(2,18)} = 1.234$	0.315

We did not find any support for a priming effect on either the EEA or the decomposition processes. This agrees with previous studies concluding that priming effects were not evident for decomposition processes in peatlands (Basiliko et al., 2012; Linkosalmi et al., 2015). None of the EEAs were significantly reduced in the absence of ericaceous roots. Cellulose decomposition was solely influenced by WT level and the only PFG effect we found on the decomposition of the *Sphagnum* tissue pointed in the opposite direction, with higher decomposition in the absence of ErMF. Of course this does not preclude priming by sedge roots deeper in the peat, where oxygen transport could be more important, and where sedge roots are more plentiful.

Vegetation impacted enzyme activity. Although only NAG showed a significant effect of vegetation at $P < 0.05$, the other 4 enzymes all showed a trend of having a vegetation effect ($P = 0.06–0.09$). The likelihood of this happening by chance for 5 out of 5 enzymes tested is exceedingly low (McDonald, 2014), suggesting a consistent vegetation effect which is at the limit of our power to detect. The consistent theme in all of these marginal effects was that, especially under high water tables, the treatments with both types of vegetation (U) tended to be higher in activity than in the Ericaceae only treatments (E). NAG shows a similar pattern with significantly higher EEA in the untreated (U) bins compared to both the sedge and Ericaceae treatments alone. One possible interpretation is that in the untreated bins we observed synergistic effects of both enhanced ErMF abundance providing greater chitinase potential and sedges (S) providing enhanced rhizosphere oxygen; these two factors could have stimulated overall aerobic activity, leading to higher EEA. Chitinases are enzymes that catalyze the depolymerization of chitin and peptidoglycan. They are hence associated with the decomposition of fungal and arthropod tissue, both important N sources, and have been found in ErMF (Kerley and Read, 1995). These results contrast with earlier results from the same experiment, which found no significant PFG effects on extracellular hydrolytic enzymes (Romanowicz et al., 2015). This is possibly because we ran our tests two years later in the experiment, and treatment effects had become more pronounced.

Analyses of individual EEA seemed to support the hypothesis that low WT levels in peatlands can lead to transient drought stress for decomposers (Christiansen et al., 2017; Toberman et al., 2008). Four of the five measured EEAs showed higher activity in the high WT treatment. The strongest WT effect was shown by PHOS. Phosphatases are secreted by both roots and microorganisms to extract phosphorus from organically bound forms. Both the fungal community as well as the Ericaceae with their mostly shallow roots might respond to drought conditions with decreased enzyme production. PHOS and BG are often used as general indicators of microbial activity (Sinsabaugh, 1994) and a reduction in activity supports the possibility of a drought related response. This leads to another key finding of this study, that long term decomposition processes were not captured with point measurements of EEA. The mass loss of the *Sphagnum* tissue could not be explained by any of the potential enzyme activities. The mass loss of the cellulose tissue showed opposite responses to the WT treatment compared to the EEA. In particular for PHOS we observed high potential activity in the high WT treatment, whereas highest mass loss of the cellulose tissue occurred at the low WT treatment. This strong opposite response might be responsible for the strong negative correlation observed between the cellulose mass loss and PHOS and highlights that temporal drought stress might influence EEA, but is not necessarily reflected in overall decomposition processes. Extracellular enzyme measurements have become a standard tool in decomposition studies because of the key role of extracellular enzymes for decomposition (Sinsabaugh, 1994). The activity of soil enzymes depends not only on substrate availability but also on nutrient availability, especially nitrogen and phosphorus, and sufficient energy to synthesize and excrete the enzymes (Allison and Vitousek, 2005). Accordingly, the breakdown of complex materials such as *Sphagnum* often requires a multiplex of concerted processes and hence specific enzymes do not necessarily result in higher mass loss (c.f. Thormann, 2006). Thus, snapshot measurements might not reflect long term decomposition processes because of the many temporally fluctuating biotic and abiotic factors modifying enzyme production and function (c.f. Kivlin and Treseder, 2014).

Climate change will alter temperature and precipitation patterns, particularly at high latitudes (IPCC, 2014). Accordingly, it is likely that specific local conditions will determine whether a peatland will remain a net carbon sink or will turn into a net carbon source due to enhanced decomposition. Drier conditions are generally believed to promote decomposition (Trettin et al., 2006), yet drier conditions are also anticipated to favor Ericaceae and other mycorrhizal woody shrubs and trees (Breeuwer et al., 2009; Weltzin et al., 2003) over *Sphagnum* and sedges. Dominance of Ericaceae consequently might slow decomposition due to competitive suppression of the saprotrophic decomposers (e.g. Averill et al., 2014) and higher inputs of recalcitrant litter (Cornelissen et al., 2007; Strakova et al., 2012). Under lower WT levels a shift in PFG composition toward dominance of Ericaceae (Potvin et al., 2015) might limit the anticipated positive effect of increased oxygen on decomposition. However, this must be considered in the context of the other factors that regulate peatland carbon balance, such as the effects of drought on moss production and deep peat fires (Kettridge et al., 2015; Turetsky et al., 2011, 2015). Thus to determine the net effect on C cycling, it is essential

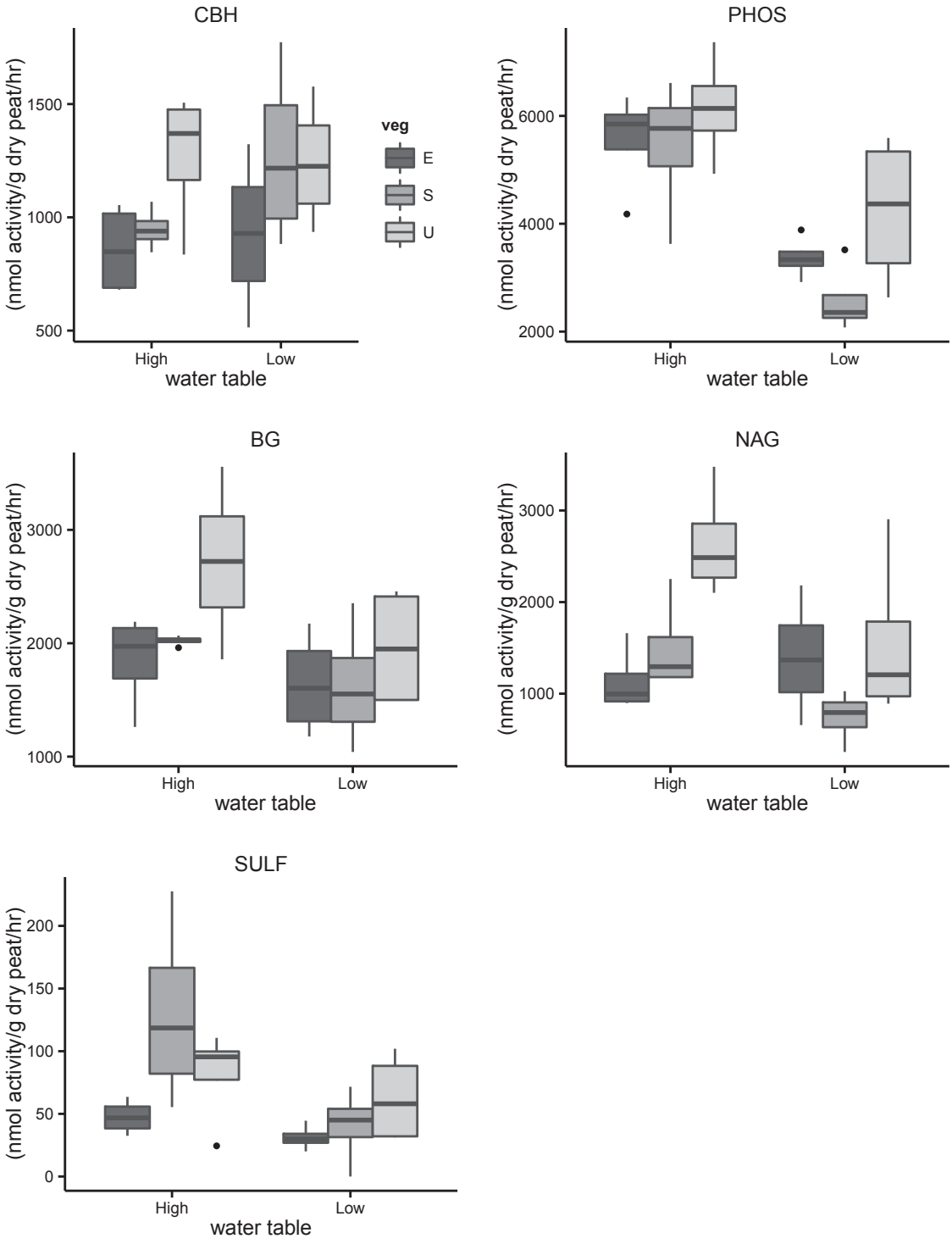

Fig. 2. Potential enzyme activity at 10–20 cm below the peat surface of Cellobiohydrolase (CBH), Phosphatase (PHOS), β-Glucosidase (BG), N-acetyl-Glucosaminidase (NAG), Sulfatase (SULF) in nmol/g dry peat/hr averaged over treatment. Treatments: water table: high (−20 cm at sampling date) and low (−40 cm at sampling date), vegetation treatment (veg): comprises Ericaceae only (E), sedge only (S), untreated controls (U) with both vegetation types in mixture; n = 24.

that we incorporate the potential negative feedbacks that we observed into whole ecosystem carbon cycling models.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2017.01.008.

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