Dynamics of organic matter and mineral components in *Sphagnum*- and *Carex*-dominated organic soils

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SUMMARY

The aim of the study was to evaluate the dynamics of organic matter and mineral components on the basis of botanical composition, peat species, and physical, chemical and biochemical properties in the acrotelm (0–50 cm) and catotelm (50–100 cm) of 19 *Sphagnum*- and *Carex*-dominated organic soils. The botanical composition and structure of 19 Baltic-type raised bog and fen sites in Poland and Siberia (Russia) were investigated. Principal component analysis (PCA) was used for the classification of 18 physical, chemical, biological and biochemical factors in the acrotelm (0–50 cm) and catotelm (50–100 cm). These factors affect the dynamics of organic matter transformation in *Sphagnum*- and *Carex*-dominated peat soils. The relative physical, chemical, biological and biochemical properties indicate that oxidation and polymerisation processes, along with the formation of resistant compounds and a lower rate of decomposition, are more prevalent in *Sphagnum*- than in *Carex*-dominated organic soils.

KEY WORDS: acrotelm, biochemical properties, catotelm, chemical properties, physical properties, peat

INTRODUCTION

Mire soil has been described in the literature as a diplotelmic system, which comprises a hydrologically active lower-density upper layer (acrotelm) and a higher-density, hydrologically inactive lower layer (catotelm) (Ingram 1978). The acrotelm (predominantly oxic surface layer) is defined as the zone through which the water table fluctuates. The catotelm represents the water-saturated anaerobic zone with small pore spaces and hydraulic conductivity 3–5 orders of magnitude lower (Holden & Burt 2003, Daniels *et al.* 2008). The botanical composition of peat is mostly *Sphagnum* and *Carex* spp. plants remains. These plants create peat in different ways. *Sphagnum* grows from the apical bud and its lower layers die and form peat. In *Carex* peat the most important constituents are roots. A certain part of the roots dies and regenerates, so besides living roots, there are roots of different ages in the same peat volume. Finally, all roots die and form peat (Mäkilä 2011a). *Sphagnum* does not contain 'true' lignin but has a different polymeric phenolic network of lipids, fatty acids, cellulose or hemicellulose (van Breemen 1995, Inisheva & Dementieva 2000, Scheffer *et al.* 2001). *Carex* peat contains polysaccharides, soluble phenolics, stilbenes and fatty acids (Scheffer *et al.* 2001, Arraki *et al.* 2013).

The aim of the study was to evaluate the dynamics of organic matter and mineral components on the basis of botanical composition, peat species, and physical, chemical and biochemical properties in the acrotelm (0–50 cm), and catotelm (50–100 cm) of 19 *Sphagnum*- and *Carex*-dominated peat and peat-mursh soils.

METHODS

Study area

For the study 19 peatlands varying according to their state of peat soil decomposition and GPS localisations (determined by TRIMBLE GeoExplorer 3 with accuracy 1–3 m) have been chosen (Figure 1, Table 1).

Baltic-type raised bogs and fens

Kusowo Bog is located in the West Pomeranian Voivodship, Poland (Table 1). The area is over 326 ha. The maximum thickness of the peat deposit is 7.95 m (Gałka *et al.* 2014). The mean annual air temperature (MAAT) is 7.2 °C and mean annual precipitation (MAP) is 657 mm.

Stążka Mire is located in the Bory Tucholskie National Park (Table 1). This mire covers a total area of 478 ha. The maximum thickness of the peat

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Figure 1. Location map of study peatlands. A: General Dezydery Chłapowski Landscape Park; B: Kusowo; C: Stążka; D: Mukhrino; E: Vasyugan; F: Tagan.

deposit is 1.41 m (Lamentowicz *et al.* 2007). This region was characterised by a MAAT of 7.2 °C and a MAP of 589 mm.

Peat samples were also taken from four sites located on the 4.5 km long research transect within peatland (Table 1) in the General Dezydery Chłapowski Landscape Park in Turew. The thickness of the peat deposit ranged from 1.50 to 2.75 m. MAAT is 8.4 °C, MAP is 527 mm and the growing season is about 200 days.

Western Siberia peatlands

The Great Vasyugan Mire is situated within the four regions of Tyumen, Omsk, Tomsk and Novosibirsk (Table 1). The Great Vasyugan Mire spans over 5,269,437 ha. Peat deposit thickness ranges from 1.0 to 5.5 m. The MAAT is 1.6 °C and MAP around 469–506 mm (Inisheva *et al.* 2011).

The Tagan peatland is located 20 km from Tomsk (Table 1). The maximum thickness of peat deposit reaches 9.3 m (Inisheva *et al.* 2009). MAAT is 0.8 °C and MAP is 532 mm.

The Mukhrino peatland is situated on the eastern bank of the Irtysh River near the confluence with the Ob River, 26 km west of the town Khanty-Mansiysk. The growing season is relatively short, about 120 days. The peat deposit ranges in thickness from 1.0 to 4.0 m. MAAT is -1.1 °C and MAP around 531 mm.

Fieldwork and soil sampling

Soil samples were collected in triplicate from the study areas described above, from soil profiles (peat and peat-mursh soils) at depths of 0–50 cm (acrotelm) and 50–100 cm (catotelm) during the period 2014–2016.

Laboratory analysis

Degree of peat decomposition was estimated by von Post's method (von Post 1922). Peat type was determined based on plant macrofossil analysis (Gałka *et al.* 2014). Soil pH was measured potentiometrically in 1 M KCl (1:20 v/v). Peat bulk density was estimated from loss-on-ignition values (Blake & Hartge 1986). Total porosity was calculated from the bulk density ratio of the soil to the density of solids (Borren *et al.* 2004). Hot water extractable organic carbon (C_{HWE}) was analysed using TOC 5050A (Shimadzu, Japan). Soil samples were heated in deionised water at 100 °C for two hours under a reflux condenser. The supernatant was filtered

Table 1. Locations and general characteristics of the studied soils. ChLP = General Dezydery Chłapowski Landscape Park (sampling points 1–4).

Place of sampling	Coordinates WGS 84 (N/E)	Depth (cm)	Peat type	Degree of decomposition (von Post)
***Sphagnum*-dominated peat soils**				
Kusowo	53° 48' 51.46" N 16° 35' 22.29" E	0–50 50–100	*Sphagnum*, cotton grass-*Sphagnum* *Sphagnum*, cotton grass-*Sphagnum*	H3 H4
Mukhrino 2	60° 89' 50.50" N 68° 69' 20.90" E	0–50 50–100	*Sphagnum* *Sphagnum*	H1 H2
Mukhrino 3	60° 53' 43.88" N 68° 40' 46.84" E	0–50 50–100	*Sphagnum* *Sphagnum*	H1 H2
Mukhrino 4	60° 53' 44.22" N 68° 40' 12.47" E	0–50 50–100	*Sphagnum* *Sphagnum*	H1 H1
Mukhrino 5	60° 53' 29.12" N 68° 41' 33.50" E	0–50 50–100	*Sphagnum* *Sphagnum*	H1 H2
Mukhrino 8	60° 52' 33.10" N 68° 36' 55.30" E	0–50	*Sphagnum*	H1
Mukhrino 9	60° 53' 43.50" N 68° 38' 20.40" E	0–50 50–100	*Sphagnum* *Sphagnum*	H1 H1
Vasyugan 1	56° 58' 13.85" N 82° 36' 02.78" E	0–50 50–100	Pine-cotton, grass-*Sphagnum* Wood-cotton grass, transitional mire	H4/H5 H6
Vasyugan 2	56° 58' 23.35" N 82° 36' 33.90" E	0–50 50–100	*Sphagnum fuscum* *Sphagnum fuscum*	H1 H1
***Carex*-dominated peat soils**				
Stążka	53° 36' 17.58" N 17° 57' 20.38" E	0–50 50–100	sedge-*Hypnum* sedge, fragments of wood	H3 H4/H5
ChLP 1	52° 00' 57.50" N 16° 53' 49.75" E	0–50 50–100	mursh, alder swamp wooden sedge, sedge-reed	H8 H8
ChLP 2	52° 01'12.61" N 16° 53' 23.38" E	0–50 50–100	mursh, sedge sedge-reed	H7 H8
ChLP 3	52° 01' 35.45" N 16° 52' 34.80" E	0–50 50–100	mursh, sedge with wooden sedge	H8 H7
ChLP 4	52° 02' 21.70" N 16° 51' 09.50" E	0–50 50–100	mursh, alder swamp sedge with wooden	H8 H8
Mukhrino 1	60° 53' 41.60" N 68° 41' 51.90" E	0–50 50–100	sedge woody woody-cotton grass	H2 H3/H4
Mukhrino 6	60° 53' 55.20" N 68° 44' 59.90" E	0–50 50–100	sedge woody sedge woody	H5 H6
Mukhrino 7	60° 52' 35.90" N 68° 36' 46.70" E	0–50 50–100	sedge-*Sphagnum* herbaceous (*Equisetum*)	H2 H2
Mukhrino 8	60° 52' 33.10" N 68° 36' 55.30" E	50–100	sedge-*Scheuchzeria*	H1
Tagan 1	56° 21' 00.00" N 84° 47' 00.00" E	0–50 50–100	grasses fens grasses fens	H4 H4
Tagan 2	56° 21' 00.00" N 84° 48' 00.00" E	0–50 50–100	wooden wooden-grasses	H3 H3

through a 0.45 µm Whatman GF/C filter (Smolander & Kitunen 2002). The total organic carbon (TOC) was measured using TOC 5050A analyser with Solid Sample Module (SSM-5000A, Shimadzu, Japan). The N_{total} was determined by the Kjeldahl method using Vapodest 10s analyser (Gerhardt, Germany). Ammonium and nitrate ions were determined chromatographically (Szajdak & Gaca 2010). Ferrous ions (Fe^{2+}) and ferric ions (Fe^{3+}) were evaluated colorimetrically (Szajdak *et al.* 2011). Urease [EC 3.5.1.5] activity was measured by Hoffmann and Teicher method (Szajdak *et al.* 2011). Nitrate reductase [EC 1.7.99.4] activity was assayed according to Kandeler (1996). Peroxidase [EC 1.11.1.7] activity was determined by Bartha & Bordeleau (1969) method. Xanthine oxidase [EC 1.17.3.2] activity was measured according to Krawczyński (1972). Phenol oxidase [EC 1.14.18.1] activity was detected by Perucci *et al.* (2000) method.

Statistical analysis

All chemical and biochemical analyses were done in triplicate and the results are given as mean values. The formula for confidence intervals is provided in the caption of Table 2. Linear correlations between the values were calculated. Normal distribution of the results and homogeneous variances were checked before statistical analysis. The PCA was performed with Statistica 9.1 and used to interpret the relationship between the studied variables and search the relationships between botanical composition, peat species, physical, chemical and biochemical properties in the acrotelm (0–50 cm), and catotelm (50–100 cm) of 9 *Sphagnum*- and 10 *Carex*-dominated peat soils. The number of factors extracted from the variables was determined by a scree test according to Kaiser's rule. With this criterion, the first two principal components with an eigenvalue greater than one were retained.

Table 2. Mean contents of chemical compounds, physical factors and enzyme activities in 0–50 cm and 50–100 cm layers of studied soils (n = 9 for *Sphagnum* layer 0–50 cm, n = 8 for *Sphagnum* layer 50–100 cm, n = 10 for *Carex* layer 0–50 cm, n = 11 for *Carex* layer 50–100 cm). C_{HWE} = hot water extractable organic carbon, N_{total} = total nitrogen, NRA = nitrate reductase activity, PA = peroxidase activity, POA = phenol oxidase activity, TOC = total organic carbon, UA = urease activity, XOA = xanthine oxidase activity, $\bar{x} \pm \Delta x$ = confidence interval of average at confidence level $\alpha = 0.05$ for n-1 degrees of freedom.

Factors	*Sphagnum*-dominated peat soils		*Carex*-dominated peat soils	
	0–50 cm	50–100 cm	0–50 cm	50–100 cm
pH	2.4–4.0	2.4–4.6	3.7–7.3	3.8–6.1
Moisture (%)	93.1±*1.0*	90.3±*3.5*	78.8±*3.4*	84.4±*2.7*
Bulk density (kg m^{-3})	81.2±*13.2*	99.9±*11.0*	221±*29.5*	144±*10.5*
Total porosity (%)	94.4±*0.9*	93.3±*0.8*	86.8±*1.51*	90.7±*0.6*
TOC (g kg^{-1})	450±*48.7*	488±*24.8*	462±*29.6*	491±*55.7*
C_{HWE} (g kg^{-1})	14.5±*1.4*	12.9±*1.6*	10.9±*1.2*	7.03±*0.8*
N-NH_4(mg kg^{-1})	32.5±*5.4*	26.1±*5.3*	23.6±*6.6*	23.6±*5.4*
N-NO_3(mg kg^{-1})	29.3±*10.1*	23.7±*13.0*	16.5±*3.5*	14.5±*2.2*
N_{total} (g kg^{-1})	12.6±*2.8*	11.5±*2.5*	23.1±*2.3*	23.3±*1.6*
C/N quotient	37.4±*9.4*	42.5±*10.3*	17.9±*3.4*	20.9±*2.5*
Fe^{2+} (mg kg^{-1})	30.2±*6.4*	32.6±*8.1*	27.7±*4.1*	25.6±*4.0*
Fe^{3+}(mg kg^{-1})	31.8±*2.9*	33.5±2.*3*	27.3±*1.6*	25.6±*3.7*
Fe_{total} (mg kg^{-1})	62.1±*9.8*	66.1±*4.2*	55.0±*7.5*	51.3±*7.5*
UA (µmol s^{-1} kg^{-1})	3.0±*0.5*	2.9±*0.5*	5.7±*1.1*	4.7±*1.0*
NRA (nmol s^{-1} kg^{-1})	0.1±*0.04*	0.1±*0.05*	0.4±*0.1*	0.3±*0.1*
PA (nmol s^{-1} kg^{-1})	2.2±*0.7*	2.2±*0.6*	1.3±*0.3*	1.4±*0.4*
XOA (µmol s^{-1} kg^{-1})	7.1±*1.4*	6.3±*1.5*	3.0±*1.0*	3.8±*1.0*
POA (µmol s^{-1} kg^{-1})	9.7±*1.7*	12.2±*3.1*	8.5±*2.3*	8.0±*1.7*

RESULTS

Peat physical and chemical properties

The *Sphagnum*-dominated peat soils revealed a lower degree of decomposition than *Carex*-dominated peat soils. The pH in *Sphagnum*- and in *Carex*-dominated peat soils ranged from 2.40 to 4.59 and from 3.72 to 7.26, respectively (Table 2). The moisture of *Sphagnum*-dominated peat soils in the acrotelm was 15.3 % higher than in *Carex* ones, but no significant differences were observed in the catotelm between studied soils (Table 2).

Sphagnum-dominated peat soils in both layers showed a significantly lower bulk density (81.2–99.9 kg m^{-3}) and higher porosity (93.2–94.4 %) in comparison with *Carex*-dominated soils (bulk density 143.8–221 kg m^{-3}, porosity 86.8–90.7 %) (Table 2).

The differentiation of N_{total} contents in *Sphagnum*- and in *Carex*-dominated peat soils are in line with significant differentiation of bulk density (Table 2). In contrast to the decrease of N_{total} in line with depth in *Carex*-dominated peat soils, an increase in TOC was observed. The contents of C_{HWE} and the C/N quotient were higher, but N_{total} was lower in both layers of *Sphagnum*- than in *Carex*-dominated peat soils (Table 2). In addition, Fe^{3+} and total iron (Fe_{total}) concentrations were significantly higher in the catotelm of *Sphagnum*- (Fe^{3+} 33.5 mg kg^{-1} and Fe_{total} 66.1 mg kg^{-1}) than in *Carex*-dominated peat soils (Fe^{3+} 25.6 mg kg^{-1} and Fe_{total} 51.3 mg kg^{-1}). There were no significant differences in the TOC, $N\text{-}NH_4^+$, $N\text{-}NO_3^-$ and Fe^{2+} concentrations in both layers in *Sphagnum*- and in *Carex*-dominated peat soils.

Biochemical properties

Urease activity was significantly lower in both layers in *Sphagnum*- (from 2.9 to 3.0 µmol s^{-1} kg^{-1}) versus *Carex*-dominated peat soils (from 4.7 to 5.7 µmol s^{-1} kg^{-1}) (Figure 2a, Table 2) and negatively correlated with bulk density (acrotelm r = -0.647, catotelm r = -0.685) in *Sphagnum*-dominated peat soils (Table 3). Nitrate reductase activity was also significantly lower in acrotelm and catotelm in *Sphagnum*- than in *Carex*-dominated peat soils and

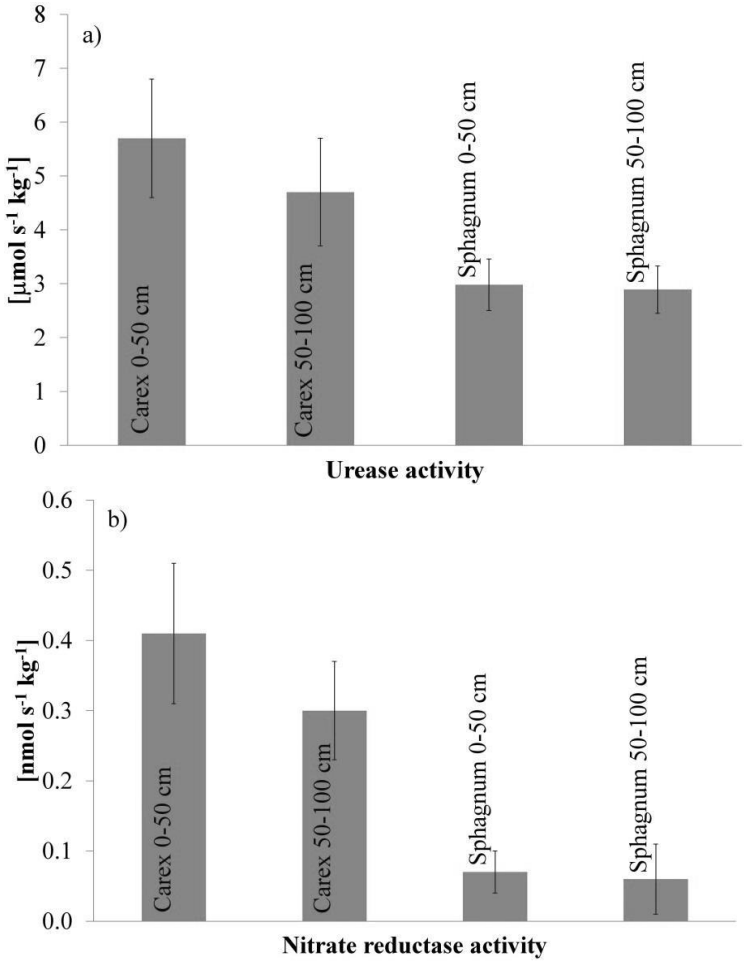

Figure 2. Enzymes participating in both hydrolytic and redox processes in studied soils: a) urease, b) nitrate reductase.

Table 3. Correlation coefficients in 0–50 cm and 50–100 cm soil layers. Significant correlation coefficients (significance level $p < 0.05$, see Table 2) are shown in **bold**.

Factors	pH	Bulk density	TOC	C_{HWE}	$N\text{-}NH_4^+$	$N\text{-}NO_3^-$	N_{total}	Fe^{2+}	Fe^{3+}
***Sphagnum*-dominated peat soils**									
0–50 cm									
UA	0.309	**-0.647**	0.408	-0.381	-0.037	-0.235	0.261	**-0.757**	-0.211
NRA	0.108	**-0.640**	**0.867**	-0.180	0.293	0.048	0.195	-0.320	-0.004
PA	**0.849**	0.108	-0.040	-0.580	-0.080	-0.144	0.228	-0.345	-0.368
XOA	0.306	-0.616	**0.666**	-0.468	0.373	0.139	-0.021	0.079	0.191
POA	0.272	-0.488	0.240	**-0.695**	0.403	0.257	**0.713**	**-0.605**	-0.313
50–100 cm									
UA	-0.583	**-0.685**	-0.094	-0.115	-0.017	-0.495	-0.635	-0.114	-0.055
NRA	0.483	-0.179	**0.762**	-0.401	**0.701**	**0.923**	-0.075	-0.098	-0.199
PA	0.512	0.339	0.259	-0.332	0.164	0.154	0.561	0.365	0.352
XOA	0.576	-0.259	**0.631**	**-0.893**	**0.688**	0.470	0.290	0.409	0.327
POA	0.523	-0.153	**0.718**	**-0.695**	**0.755**	0.501	-0.003	-0.189	-0.275
***Carex*-dominated peat soils**									
0–50 cm									
UA	0.202	0.396	**-0.418**	-0.057	-0.394	-0.252	**0.564**	-0.085	-0.211
NRA	**0.566**	-0.299	0.364	-0.132	-0.297	-0.375	0.249	0.180	0.228
PA	**-0.495**	**-0.679**	**0.440**	**0.762**	0.209	0.136	-0.226	0.342	**0.424**
XOA	0.182	**-0.846**	**0.488**	-0.069	0.360	-0.105	-0.102	0.012	0.117
POA	0.348	**-0.695**	**0.567**	0.029	-0.128	0.012	**-0.462**	0.338	0.345
50–100 cm									
UA	**0.405**	**0.618**	-0.341	-0.071	-0.328	-0.060	0.321	**-0.488**	-0.412
NRA	**0.625**	0.131	**0.584**	**-0.480**	-0.359	**-0.475**	0.367	-0.201	-0.127
PA	**-0.576**	**-0.577**	0.070	**0.600**	0.056	-0.126	**-0.528**	0.349	0.358
XOA	-0.023	**-0.469**	0.143	-0.269	**0.607**	-0.353	0.278	-0.096	-0.116
POA	-0.127	**-0.594**	**0.413**	-0.034	-0.299	-0.116	-0.330	0.260	**0.396**

positively correlated with TOC (acrotelm r = 0.867, catotelm r = 0.762) in *Sphagnum*- and with pH (acrotelm r = 0.566, catotelm r = 0.625) in *Carex*-dominated peat soils.

The study showed a significant positive correlation between peroxidase activity and TOC (r = 0.440), C_{HWE} (r = 0.762) and Fe^{3+} (r = 0.424) in the acrotelm of *Carex*-dominated peat soils. Furthermore, this enzyme was negatively correlated with bulk density (acrotelm r = -0.679, catotelm r = -0.577) and with pH (acrotelm r = -0.495, catotelm r = -0.576) of *Carex*-dominated peat soils (Table 3).

Significant differences of xanthine oxidase activity were observed in both layers of sampling in *Sphagnum*- (from 6.3 to 7.1 µmol s^{-1} kg^{-1}) in comparison with *Carex*-dominated peat soils (from 3.0 to 3.8 µmol s^{-1} kg^{-1}) (Figure 3b, Table 2). Negative correlation coefficients for the activity of

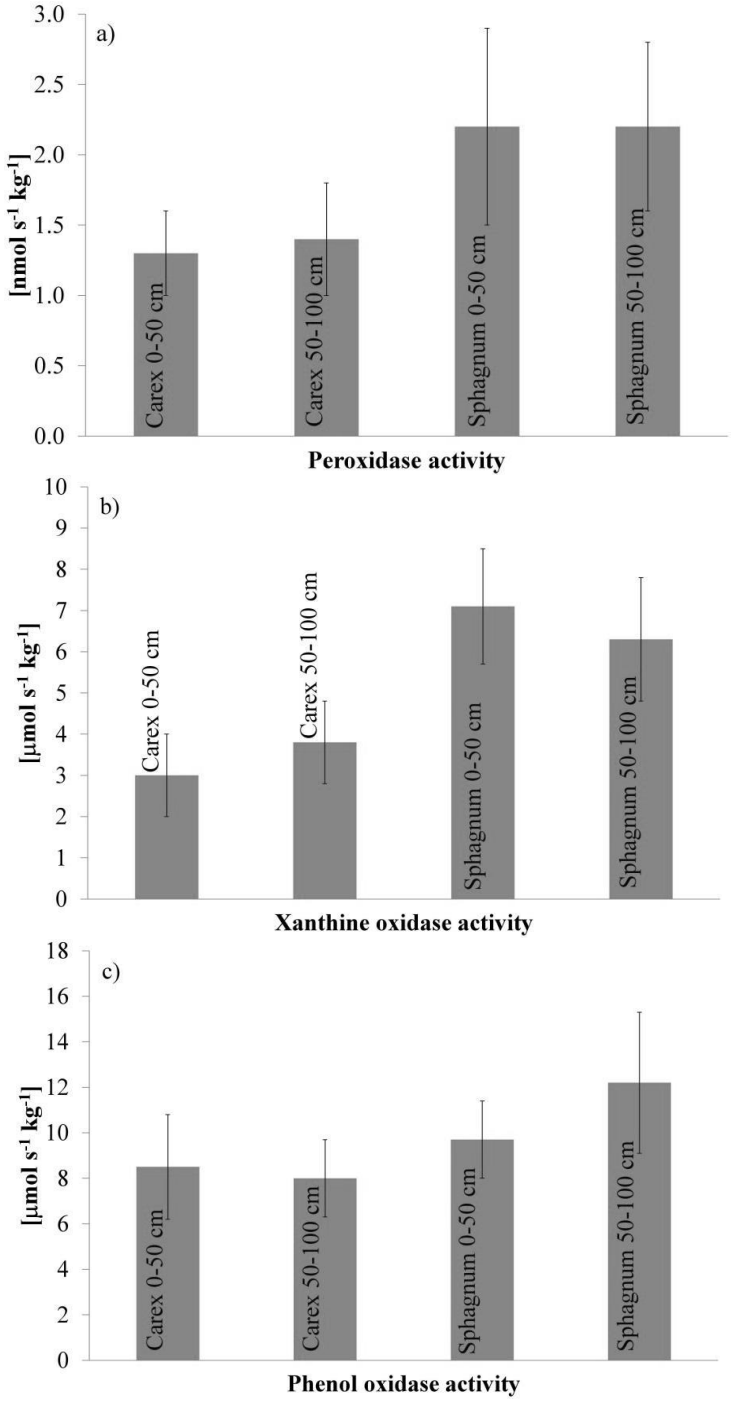

Figure 3. Enzymes participating in the oxidation processes in studied soils: a) peroxidase, b) xanthine oxidase, c) phenol oxidase.

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this enzyme with bulk density (acrotelm r = -0.846, catotelm r = -0.469) in *Carex*-dominated peat soils were observed.

Phenol oxidase activity in the acrotelm and catotelm of *Sphagnum*- was significantly higher than in *Carex*-dominated peat soils, but did not differ as a function of depth in these peat soils (Table 2).

Phenol oxidase activity was negatively correlated with bulk density (acrotelm r = -0.695, catotelm r = -0.594) of *Carex*- and with C_{HWE} (acrotelm and catotelm r = -0.695) of *Sphagnum*-dominated peat soils (Table 3). The positive correlation for phenol oxidase with TOC (acrotelm r = 0.567, catotelm r = 0.413) in *Carex*- dominated peat soils was measured. A projection of the variables on the factor-plane clearly demonstrated a correlation between the data in the acrotelm and catotelm of *Sphagnum*- and *Carex*-dominated peat soils. The three first principal components (PC1, PC2 and PC3) explained from 69.9 to 84.8 % of the total variance in the acrotelm and catotelm of *Sphagnum*- and *Carex*-dominated peat soils (Tables 4 and 5). The correlations of variables with two of the most important principal components are presented in Figures 4a–d.

In the acrotelm of *Carex*-dominated peat soils, three major principal components of the PCA explained 69.9 % of the dataset variability, with PC1, PC2 and PC3 accounting for 37.3 %, 19.0 % and 13.6 %, respectively (Table 4). The PC1 in the acrotelm of *Carex*-dominated peat soils was closely positively associated with moisture, TOC, porosity, xanthine oxidase, peroxidase and phenol oxidase activity; while bulk density and urease activity showed negative coordinates on this axis. These variables suggest that the first principal component describes the dependence of enzyme activity on the moisture and organic matter.

An increase in oxido-reductive enzyme activity with increasing TOC content and decreasing activity of hydrolytic enzymes and bulk density was found. The PC2 was positively correlated with nitrate reductase activity and pH and negatively with N-NO_3^- (Figure 4a). The relationship with pH is evidenced by the high correlation of variable nitrate reductase activity (r = 0.566). The PC3 was closely positively associated with N_{total} and negatively with C/N quotient. In the catotelm of *Carex*-dominated peat soils three major principal components of the PCA explained 73.3 % of the dataset variability, with PC1, PC2 and PC3 accounting for 36.0 %, 20.4 % and 16.9 %, respectively (Table 4). The PC1 in the catotelm of *Carex*-dominated peat soils was positively correlated with Fe^{2+}, Fe^{3+}, C/N quotient, porosity and peroxidase activity and negatively with

Table 4. Results of the principal component analysis.

Principal components	Eigenvalues	% of total variance	Cumulative eigenvalues	Cumulative % of variance
Carex-dominated peat soils 0–50 cm				
PC1	6.35	37.33	6.35	37.33
PC2	3.23	19.01	9.58	56.33
PC3	2.31	13.58	11.89	69.92
Carex-dominated peat soils 50–100 cm				
PC1	6.12	36.04	6.13	36.04
PC2	3.46	20.35	9.59	56.39
PC3	2.87	16.86	12.45	73.25
Sphagnum-dominated peat soils 0–50 cm				
PC1	5.59	32.90	5.59	32.90
PC2	3.84	22.59	9.43	55.50
PC3	2.71	15.96	12.15	71.45
Sphagnum-dominated peat soils 50–100 cm				
PC1	6.03	35.49	6.03	35.49
PC2	4.66	27.40	10.69	62.89
PC3	3.73	21.94	14.42	84.83

N_{total}, bulk density, urease activity and pH. The PC2 was closely associated with xanthine oxidase activity and moisture with both positive effects of peat soils in the 50–100 cm soil layer. The PC3 was positively correlated with N-NH_4^+ and negatively with TOC. Considering these results, it appears that the first principal component suggests that the decrease of nitrogen content, pH and urease activity may indicate the accumulation of organic matter. The water content changes, TOC and xanthine oxidase activity may affect the anabolic processes in this layer.

In the acrotelm of *Sphagnum*-dominated peat soils the first three principal components explained 71.5 % of the variance of original data, with PC1, PC2 and PC3 accounting for 32.9 %, 22.6 % and 15.9 %, respectively (Table 4). The PC1 in the acrotelm of *Sphagnum*-dominated peat soils showed positive weightings with C_{HWE}, bulk density, Fe^{2+} and negative with porosity, TOC, phenol oxidase, urease and nitrate reductase activity. The PC2 was closely positively associated with N_{total} and bulk density but TOC, C/N quotient and porosity showed negative coordinates on this axis. Moisture, N-NO_3^-, Fe^{2+} and Fe^{3+} had high loadings in relation to PC3. The data suggest that increase of Fe^{2+} content and decrease of phenol oxidase, urease and nitrate reductase, whose activity significantly depends on oxygen conditions, is indicative of accumulation processes rather than ones of decomposition.

In the catotelm of *Sphagnum*-dominated peat soils three major principal components of the PCA explained 84.8 % of the dataset variability, with PC1, PC2 and PC3 accounting for 35.5 %, 27.4 % and 21.9 %, respectively (Table 4). The PC1 was positively correlated with the variable C_{HWE} content and negatively with soil moisture, TOC, N-NH_4^+, N-NO_3^-, xanthine oxidase, phenol oxidase and nitrate reductase activity. The PC2 was positively correlated with C/N quotient, porosity, urease activity and proved negative with pH, bulk density, N_{total} and

Table 5. Factor loadings and explained variance of three principal components in PCA. Significant correlation coefficients (significance level $p < 0.05$) are shown in **bold**. For acronyms, see Table 2.

	Carex-dominated peat soils 0–50 cm			*Carex*-dominated peat soils 50–100 cm			*Sphagnum*-dominated peat soils 0–50 cm			*Sphagnum*-dominated peat soils 50–100 cm		
Variable	**PC1**	**PC2**	**PC3**	**PC1**	**PC2**	**PC3**	**PC1**	**PC2**	**PC3**	**PC1**	**PC2**	**PC3**
Moisture	**0.90**	0.07	0.02	0.14	**0.85**	0.22	-0.26	0.15	**0.63**	**-0.67**	-0.07	-0.55
TOC	**0.74**	0.28	-0.10	0.22	0.43	**-0.76**	**-0.60**	**-0.72**	0.14	**-0.84**	0.19	0.30
C_{HWE}	0.43	-0.60	-0.43	0.59	-0.54	0.17	**0.77**	-0.38	-0.14	**0.76**	-0.03	0.58
NH_4^+	0.25	-0.48	0.13	0.12	0.24	**0.83**	-0.47	0.27	0.51	**-0.85**	0.11	0.35
NO_3^-	0.15	**-0.70**	0.17	0.18	-0.48	0.32	-0.15	0.42	**0.64**	**-0.66**	-0.13	0.59
N_{total}	-0.40	0.14	**-0.69**	**-0.81**	0.35	0.13	-0.59	**0.66**	0.07	0.04	**-0.93**	-0.26
Fe^{2+}	0.45	-0.37	-0.55	**0.79**	-0.22	-0.23	**0.60**	-0.06	**0.77**	-0.09	-0.26	**-0.91**
Fe^{3+}	0.53	-0.31	-0.55	**0.76**	-0.14	-0.39	0.27	-0.47	**0.62**	-0.02	-0.18	**-0.95**
C/N	0.57	-0.07	**0.60**	**0.83**	-0.13	-0.46	0.46	**-0.79**	0.15	-0.50	**0.76**	0.16
Bulk density	**-0.88**	-0.28	0.18	**-0.78**	-0.47	-0.27	**0.70**	**0.67**	0.04	0.37	**-0.81**	0.39
Porosity	**0.92**	0.23	0.01	**0.81**	0.42	0.22	**-0.71**	**-0.67**	-0.03	-0.33	**0.80**	-0.44
XOA	**0.76**	0.36	0.14	0.09	**0.81**	0.41	-0.54	-0.38	0.56	**-0.92**	-0.24	-0.29
POA	**0.74**	0.40	0.04	0.50	0.41	-0.38	**-0.84**	0.23	-0.14	**-0.83**	-0.06	0.19
PA	**0.76**	-0.33	-0.16	**0.70**	0.04	-0.01	-0.44	0.42	-0.03	-0.46	**-0.66**	-0.24
UA	**-0.63**	0.19	-0.54	**-0.62**	-0.37	-0.14	**-0.75**	-0.16	-0.42	0.12	**0.82**	-0.24
NRA	0.17	**0.66**	-0.51	-0.29	0.57	-0.60	**-0.64**	-0.44	0.03	**-0.82**	-0.09	0.34
pH	-0.13	**0.92**	0.08	**-0.81**	0.29	-0.43	-0.43	0.37	0.32	-0.45	**-0.77**	0.18

peroxidase activity. The PC3 was closely associated with Fe^{2+} and Fe^{3+} contents but the ions showed negative correlations on this axis. These variables suggest that the principal components describe the accumulation processes in this layer of *Sphagnum*-dominated peat soils. In the catotelm of *Sphagnum*-dominated peat soils *Sphagnum* species decompose more slowly, which has a long-term impact on the C/N quotient. The data showed that slow degradation of organic matter in acidic *Sphagnum*-dominated peat soils implies a limited activity of oxido-reductive enzymes.

DISCUSSION

Peat soil physical properties

During periods of low water level in summer, aerobic conditions and observed high pH values of about 7.26 in *Carex*-dominated peat soils are likely to enhance: (i) the breakdown of the organic matter; (ii) conversions and biochemical pathways; and (iii) the stability of organic material susceptible to decomposition (Table 2). This more pronounced high pH value in *Carex*-dominated peat soils is probably caused by a high oxidation level presented in these

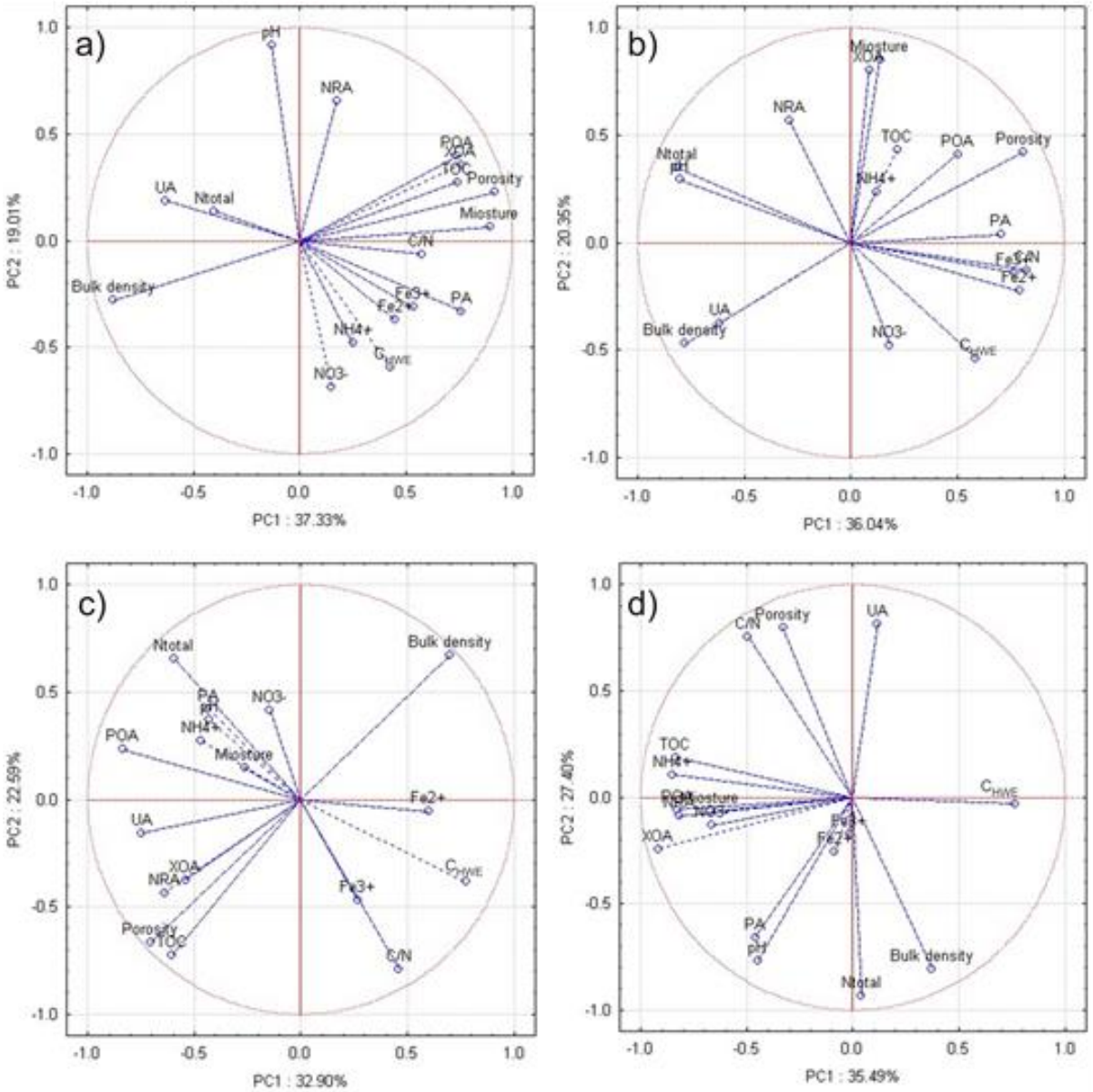

Figure 4. Eigenvectors of soil chemical variables in a) *Carex*-dominated peat soils 0–50 cm, b) *Carex*-dominated peat soils 50–100 cm, c) *Sphagnum*-dominated peat soils 0–50 cm, d) *Sphagnum*-dominated peat soils 50–100 cm, where: Ntotal - total nitrogen, TOC - total organic carbon, C_{HWE} - hot water extractable organic carbon, UA - urease activity, NRA - nitrate reductase activity, PA - peroxidase activity, XOA - xanthine oxidase activity, POA - phenol oxidase activity.

peat soils. This is notwithstanding that all our samples were taken in summer and early autumn, when the aerobic conditions of peat appear to be affected by the decrease of the water level. Golovchenko *et al.* (2007) demonstrated the pH of the saline extract varied between 2 and 4 in ombrotrophic peatlands (shrubby-sedge-sphagnum) and Błońska (2010), Palozzi & Lindo (2017) indicated lower pH in *Sphagnum*- than *Carex*-dominated peat soils.

A significantly lower bulk density in both layers of *Sphagnum*- in comparison with *Carex*-dominated peat soils (Table 2) is in line with the study by Verry *et al.* (2011), who showed a positive linear relationship between bulk density and the von Post humification index, suggesting that moss peats are characterised by lower bulk density than fen peats in large part due to a lower degree of decomposition. In addition, Robinson (2006) and Borren *et al.* (2004) observed that bulk density and cumulative carbon increased in line with depth in studied soils. We observed subsequently an impact of respective kinds of peat on the significant differences of porosity (Table 2). Hayward & Clymo (1982), Kremer *et al.* (2004) and Rezanezhad *et al.* (2016) pointed out that the total porosity of peat includes the relatively large, inter-particle pores that can actively transmit water as well as relatively small, closed, and dead-end pores formed by the remains of plant cells. The structure of peat soil consists of pores that are open and connected, dead-ended or isolated. The resulting dual-porosity nature of peat soils affects water flow and solute migration (enzymes, salts, hydrophilic organic bioactive compounds), which influences reactive transport processes and biogeochemical functions. A higher total porosity in *Sphagnum*- than in *Carex*-dominated peat soils does not prevent the flow and migration of dissolved compounds (Hayward & Clymo 1982, Kremer *et al.* 2004, Rezanezhad *et al.* 2016).

Chemical properties

No significant differences were found between TOC content in both layers of *Sphagnum*- and *Carex*-dominated peat soils (Table 2), which are in line with the results achieved by Bejger *et al.* (2011). However, Beilman *et al.* (2009), Inisheva *et al.* (2011) and Mäkilä (2011b) reported a lower content (but not significant) of TOC in *Sphagnum*- than in *Carex*-dominated peat soils. In addition, Koerselman *et al.* (1993) observed a higher content (but not significant) of TOC in *Sphagnum*- than in *Carex*-dominated peat soils.

A statistically lower in both layers of *Carex*- than *Sphagnum*-dominated peat soils C_{HWE} drops by about 18 % between the layers and in accord with bulk density. Peatlands are particularly interesting because they form the highest amounts of surface-water C_{HWE} and may contribute to the cycling of soil nutrients (McDowell & Likens 1988). Our research on *Carex*-dominated peat soils agrees with the data of Cole *et al.* (2002) and suggests that the concentration of C_{HWE} was higher in the upper 10 cm of peat than at 50 cm depth.

Significantly higher C/N quotients in both layers of *Sphagnum*-dominated peat soils are in accord with levels of soil moisture, porosity and C_{HWE} (Table 2). Our results are in line with Scheffer *et al.* (2001), who proved that *Sphagnum* litter decomposed more slowly than that of *Carex*. However, Glenn *et al.* (2006) pointed out a lower than half content of N_{total} in *Sphagnum* spp. of the poor fen site, whereas the C/N quotient was twice as great as *Carex lasiocarpa* at the extremely rich fen.

In both layers of *Carex*-dominated peat soils there was a significantly lower Fe^{3+}/Fe^{2+} redox couple, lower moisture content and higher pH than in *Sphagnum*-dominated peat soils (Table 2), which have clearly documented oxido-redox potential changes upon oxidation caused by anaerobic conditions. Our results are in line with Steinmann & Shotyk (1997), who demonstrated the increase of Fe^{2+} and Fe^{3+} content with the depth in *Sphagnum*-dominated peat soils.

Biochemical properties

The higher urease activity in both layers of *Carex*- than *Sphagnum*-dominated peat soils is related to a high rate of urea degradation in *Carex*-dominated peat soils. Significant differentiation of urease activity in the studied peat types and higher activity of this enzyme in *Carex*- than in *Sphagnum*-dominated peat soils can be associated with significantly higher concentrations of N_{total} and lower C/N quotient in *Carex*-dominated peat soils. Higher urease activity, nitrogen content, acidic and lower moisture conditions indicate a faster decomposition of humic and fulvic acids in *Carex*- than in *Sphagnum*-dominated peat soils (Bohlin *el al.* 1989, Kolka *et al.* 2016) (Table 2).

In addition, lower pH in *Sphagnum*- than in *Carex*-dominated peat soils enhances phenolic accumulation, which inhibits urease activity in *Sphagnum*-dominated peat soils. No significant difference in ammonium content between *Sphagnum*- and *Carex*-dominated peat soils indicates that the current content of these ions is a result of not only hydrolysis of the urea and should take into account other processes such as the balance between decomposition/formation of organic matter,

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volatilisation losses, nitrate reduction, oxidation of ammonium, and absorption of ammonium by the plants. Enzyme activities declining with soil depth are therefore likely to be a consequence of reduced resource availability and thus less microbial activity in deeper soil horizons (Fierer *et al.* 2003, Herold *et al.* 2014), which is also observed in our study in case of C_{HWE} content. Soil moisture, temperature, pH and microbial activity are the major drivers in change of urease activity (Xiang *et al.* 2013).

Lower nitrate reductase activity in both layers of *Sphagnum*- than in *Carex*-dominated peat soils is indicative of lower denitrification and nitrification in *Sphagnum*- peat soils (Figure 2b, Table 2). A significantly positive correlation between the nitrate reductase activity and TOC in both layers of *Sphagnum*- and with pH in *Carex*-dominated peat soils (Table 3) suggests that nitrification and denitrification are closely related to organic matter and soil pH. Acidification in *Sphagnum*-dominated peat soils appears to lead to a decrease in the rate of organic matter decomposition and at the same time reduces the enzyme activity. The PCA analysis confirmed a strong negative relationship of this enzyme activity with $N\text{-}NO_3^-$ contents in acrotelm of *Carex*-dominated peat soils (Szajdak *et al.* 2018).

There was no significant difference in peroxidase activity between the layers of *Sphagnum*- and *Carex*-dominated peat soils (Table 2); and in the acrotelm of *Carex*-dominated peat soils, peroxidase positively correlated with TOC, C_{HWE} and Fe^{3+} (Table 3). Peroxidase catalyses the oxidation of phenols and aromatic amines and may lead to carbon dioxide production in soil (Choinowski *et al.* 1999, Dec *et al.* 2003).

The higher xanthine oxidase activity in *Sphagnum*- than *Carex*-dominated peat soils expresses the higher rate of purine derivative degradation in *Sphagnum*- than in *Carex*-dominated peat soils, which indicates an advantage of catabolism over anabolism in *Sphagnum*- compared to *Carex*-dominated peat soils (Battelli *et al.* 2018, Monika *et al.* 2019). This enzyme is closely related to soil organic matter transformations (Vaughan & Ord 1982, Dick 1997, Szajdak *et al.* 2016). However, it is interesting to note that the differentiation of xanthine oxidase activity in the studied peat soils was found and can be associated with significant differences in the C/N quotient. Xanthine oxidase oxidises the purines (hypoxanthine and xanthine) to uric acid in the purine catabolic pathway and aromatic heterocycles and aldehydes to their hydroxyl derivatives, participating in the cycle of nitrogen in soils (Hille & Massey 1985). The increase in the breakdown of purine derivatives in *Sphagnum*- and in *Carex*-dominated peat soils leads to the formation of organic nitrogen compounds of low molecular weight, such as amino acids, amines, amides, and amino sugars. These simpler organic compounds are responsible for a higher concentration of C_{HWE} in *Sphagnum*- than in *Carex*-dominated peat soils. Thus, the mechanism changes in xanthine oxidase activity drive the transformation in C_{HWE} release from peat soils (Mastnýa *et al.* 2018).

The phenol oxidase activity was negatively correlated with C_{HWE} in *Sphagnum*- and with bulk density in *Carex*-dominated peat soils (Table 3). This enzyme participates in the formation of humic acids and expresses microflora's capacity to degrade recalcitrant organic substances (Freeman *et al.* 2004). Peat soils are normally devoid of molecular oxygen in all but the uppermost layer, and thus phenol oxidase, which requires molecular oxygen for its activity, is rarely active. Interestingly, even the activities of hydrolases (urease) that have no oxygen requirement are also extremely limited in peatlands. We propose that the lower urease activity in *Sphagnum*- than in *Carex*-dominated peat soils can be indirectly attributed to oxygen constraints on phenol oxidase. Thus, oxygen constraints upon phenol oxidase activity promote a condition that inhibits decomposition.

Collectively, our studies have established that enzyme activity in *Sphagnum*- and in *Carex*-dominated peat soils will differ from one enzyme class to another. The activity of xanthine oxidase, phenol oxidase and peroxidase mediating the oxidation processes was lower in *Carex*- than in *Sphagnum*-dominated peat soils (Figure 3, Table 2). The function of these enzymes is related to a variety of purposes including ontogeny, defense and the acquisition of carbon, and nitrogen.

The opposite was shown for enzymes involved in hydrolysis (urease) and reduction (nitrate reductase) processes. These enzyme activities in *Carex*- were more significantly enhanced than in *Sphagnum*-dominated peat soils (Figure 2, Table 2).

The PCA analysis showed that the activity of enzymes is closely related to organic matter quantity. The decrease in organic matter content and pH in *Sphagnum*-dominated peat soils affects the microbial community composition and decreases enzyme activity (Table 5). In *Carex*-dominated peat soils carbohydrates were decomposed faster than lignin, thus leading to the increase of carbon.

A negative correlation between oxidative enzymes activity and bulk density in both layers of *Carex*-dominated peat soils (Table 3) agrees with Li *et al.* (2002). In general, *Sphagnum*- in comparison with *Carex*-dominated peat soils is characterised by a greater contribution of biological pores made by

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soil fauna and plant roots that increase the movement of enzymes and water (Nimmo 2005). Therefore, significant high porosity of *Sphagnum*-dominated peat soils promotes high moisture content, C/N quotient and high content of C_{HWE}, but contrary evidence was shown for *Carex*-dominated peat soils (Table 2).

PCA showed that the activities of enzymes were also associated with the physical properties of peat soils (moisture, bulk density and porosity). The effect of bulk density on enzyme activities can be related to physical properties, including total porosity, oxygen content and thereby on microbial activity. The increase of soil bulk density and decrease of porosity may limit microbial activities and biochemical processes, which lead to poor aeration and reduced nutrient availability through inhibition of organic matter and nitrogen mineralisation.

The relative physical, chemical and biochemical properties indicate that oxidation and polymerisation processes along with the formation of resistant compounds and lower rate of peat decomposition are more prevalent in *Sphagnum*- than in *Carex*-dominated peat soils. We believe that the simultaneous measurements of physical, chemical, biological and biochemical studies are a potentially important component. Arguably, the best hope for better peatland-scale dynamics of organic matter is an improved mechanistic understanding of the factors controlling peat accumulation and the development of knowledge to allow processes and mechanisms to be predicted. However, more studies are needed to correlate the data with the mechanism of conversions. Thus, our understanding can be further improved by applying broad chemical and biochemical methods in tandem.

All the results suggest that combining physical, chemical, biological and biochemical analyses reveals significantly more potential than has previously been recognised as a probe of the processes and organic matter transformation. The results indicate that a functional theory on acrotelm-catotelm for biochemical and chemical conversions is tenable.

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AUTHOR CONTRIBUTIONS

LWS, MS, LII, EL, TM and WG performed the field measurements and laboratory analysis. MS and WG made the statistical data calculations. LWS, MS and WG drafted the manuscript and designed the Figures. LWS wrote the manuscript with input from all authors. All authors discussed the results and commented on the manuscript.

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