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REGULAR ARTICLE

# Phylogenetic or environmental control on the elemental and organo-chemical composition of *Sphagnum* mosses?

**Juul Limpens · Elisabet Bohlin · Mats B. Nilsson**

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**Abstract**
*Background and aims* Plant litter chemistry is a key driver of decomposition in peatlands. This study explored the relative contributions of phylogeny and environment to litter chemistry of peat mosses (*Sphagnum*), the key peat-forming plants on earth.
*Methods* Fifteen *Sphagnum* species, representing three taxonomic sections ACUTIFOLIA, CUSPIDATA and SPHAGNUM, were sampled across a wide range of hydro-geochemical conditions. For all species we characterised chemical composition within (i) inorganic elements, (ii) carbohydrate polymers (iii) non-carbohydrates.
*Results* The variation in carbohydrates was mostly explained by taxonomic section, suggesting phylogenetic conservation of carbohydrate composition. ACUTIFOLIA species invested relatively more in pectins, whereas CUSPIDATA and SPHAGNUM species invested more in hemicellulose. The composition of non-carbohydrates was mainly influenced by environment, except for some constituents for which the variation was more correlated to phylogeny. Finally, the variation in inorganic element concentrations mostly reflected hydro-geochemical conditions within and between peatlands.
*Conclusions* The separation into an environmentally independent, phylogenetically conserved group of compounds (structural carbohydrates) and an environmentally dependent, variable group of compounds (inorganic elements, non-carbohydrates) has important implications both for understanding patterns in and for upscaling of spatially variable ecosystem processes associated with peat decomposition such as carbon sequestration, nutrient cycling and greenhouse gas emissions.

**Keywords** Environment · Litter chemistry · Mires · Peatlands · Phylogenetic control · Chemical traits · *Sphagnum*

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J. Limpens (✉)
Plant Ecology and Nature Conservation group, Wageningen University, Droevendaalsesteeg 3a, 6708 PB, Wageningen, the Netherlands
e-mail: Juul.Limpens@WUR.nl

E. Bohlin · M. B. Nilsson (✉)
Soil Science, Biogeochemistry Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Skogsmarksgränd 1, S-901 83 Umeå, Sweden
e-mail: Mats.B.Nilsson@SLU.se

## Introduction

Production and decomposition of organic matter and the net return of carbon (C) to the atmosphere largely determine the strength of the soil-feedback to global warming. Organic matter decomposition is central to the development and functioning of the plant-soil system, controlling transfer rates of energy and carbon to

the microbial community, the speed of nutrient cycling and potential nutrient losses (Bradford et al. 2002; Wardle et al. 2004). Two of the key controls on decomposition and mineralisation are the elemental stoichiometry and organo-chemical composition of the plant litter entering the soil, particularly in organic soil layers and soils (Minderman 1968; Melillo et al. 1982; Ågren and Bosatta 1996; Aerts 1997). But what, in turn drives the chemical litter composition? Is it an emergent feature of the environment the plants grow in, or is it an evolutionary trait that can be tracked through the plant species' phylogeny? Separating the environmentally-variable and environmentally stable chemical components of the litter is essential to upscale and predict spatially variable processes controlled by litter quality, such as nutrient cycling, carbon sequestration, and greenhouse gas emissions.

We focussed our study on northern hemisphere peatlands, one of the world's biggest soil carbon reserves. These ecosystems store approximately 400 Pg of C as peat, (Loisel et al. 2014), amounting to about half of the C currently in the atmosphere as $CO_2$ (IPCC 2013). Besides being a sink for atmospheric $CO_2$, peatlands are also a major source of methane ($CH_4$), making them crucial players in the global C cycle (Olefeldt et al. 2013). Most of the high latitude peatlands are dominated by peat forming mosses from the genus *Sphagnum*. Here, up to 90 vol.% of the peat consists of *Sphagnum* litter, that may retain its macro-structure for decades after the plant has died (Turetsky 2003; Loisel et al. 2014). The slow litter decomposition in peatlands is generally attributed to the additive effects of environmental factors, such as acidic and nutrient-poor soil conditions above and anoxic conditions below the water table, and the chemical composition of the litter, particularly *Sphagnum* (Clymo 1965). In turn the acidic, nutrient poor and wet environment is a function of the chemical and structural properties of *Sphagnum* litter and peat (Clymo 1963; Van Breemen 1995), illustrating its role as ecosystem engineer. The direction and degree in which the physical and chemical properties at the peat surface are affected by *Sphagnum* strongly depends on *Sphagnum* species (Hayward and Clymo 1982), suggesting clustering of species and/or traits into strategies (Bengtsson et al. 2016).

The most commonly used distinction of "clusters" within the genus *Sphagnum* is that based on the micro-topographical position of the species above the water table, separating species occupying dry hummocks from those occupying moist lawns and wet hollows. The micro-topography itself is an emergent feature of the species themselves and is not related to the underlying mineral soil (Belyea and Baird 2006). Dry hummock species show a conservative resource strategy (cf. Coley et al. 1985; Grime et al. 1990) maximising nutrient and water retention by combining highly recalcitrant litter (Turetsky et al. 2008), high cation exchange capacity (Clymo 1963; Spearing 1972), and dense canopy structure (Hayward and Clymo 1982; Laing et al. 2014) at the cost of low maximum growth rates (Hájek 2009; Laing et al. 2014). Wet hollow species show a contrasting strategy, maximising growth rate instead by lowering litter recalcitrance, cat-ion exchange capacity and water retention. Lawn species generally take up an intermediate position. The distinct differences in growth strategies between hummock and hollow species coincide with differences in resource allocation to structural vs. metabolic carbohydrates (Turetsky et al. 2008), suggesting slow growing hummock species invest in poorly degradable carbohydrates, whereas faster-growing hollow species invest in easily degradable carbohydrates. The latter would indicate a causal relationships between species growth strategy and litter chemistry. To what extent this growth-decay trade-off is phylogenetically determined, or a consequence of the environment remains unresolved, however. The main taxonomic groups (sections) within the genus *Sphagnum* correlate partly with position along the hummock-hollow gradient (Vitt and Slack 1984; Gignac 1992; Bragazza 1997), and both taxonomic group and position along the hummock-hollow gradient are closely correlated to phylogenetic relatedness (Shaw 2000; Johnson et al. 2014). Consequently, it seems reasonable to assume that at least part of the carbon-based litter chemistry is related to phylogeny. Despite the latter, there is also evidence pointing towards an important environmental contribution to litter chemistry, as for example illustrated by the large intraspecific variation in innate decay rates, and thus presumably litter chemistry, reported in Bengtsson et al. (2016), the high correlation between major plant nutrients and the position of the same species along a nitrogen deposition gradient (Bragazza et al. 2005) and the correlation between inorganic element concentrations and acidity-alkalinity related gradients (Wheeler and Proctor 2000). The close interrelationship between environment, phylogeny and ecosystem functioning make peatlands in general and the genus *Sphagnum* in particular an ideal model ecosystems to separate effects of environment and phylogeny on litter chemistry.

In this study we set out to explore the relative contributions of environment (peatland type, eco-hydrological position within peatland) and phylogeny (taxonomic sections within the genus *Sphagnum*) in explaining the chemical composition of 15 *Sphagnum* species. In our analysis we distinguished between three chemistry types: (i) inorganic elements, (ii) carbohydrate polymers (polysacharides) and (iii) non-carbohydrates (aromatic and aliphatic constituents). We expected that the variation in inorganic element content between *Sphagnum* samples would mainly reflect growing conditions, i.e. the environment, whereas the variation in carbohydrate and non-carbohydrate contents would be explained mostly by phylogeny.

## Materials and methods

### Sites and sampling

Our study area was the province of Västerbotten, northern Sweden. The climate of the area is cold temperate humid (Dfc, Köppen classification system, McKnight and Darrel 2000) with the mean annual temperature ranging between +1 °C and +3 °C (reference period 1961–1990). The mean (1961–1990) January temperature ranges from −9 °C at the coast to −11 °C at the more inland sites. The mean July temperature is +15 °C in the entire region. Mean (1961–1990) annual precipitation is 600 at the coast and 700 mm further inland, with a January mean of 50 mm and a July mean between 50 and 70 mm (Alexandersson et al. 1991). Of the annual precipitation ~50% is lost through evapotranspiration (Laudon et al. 2013).

Within Västerbotten we selected seven peatlands that cover much of the environmental variation that can be found in Scandinavian peatlands and represent differences in minerotrophy as well as nutrient richness (Table 1). Selection of peatlands was based on the mire-type classification of Eurola et al. (1984). This classification is based on a combination of physical characteristics and vegetation composition and correlates well with longer-term contrasts in water chemistry (Eurola et al. 1984). Six of the peatlands selected are located in the coastal area, below the highest shoreline (Renberg and Segerström 1981), one peatland (Björnmyran) is situated more inland (Table 1).

From the seven peatlands selected we collected material from 15 *Sphagnum* species (Table 2) of three common and wide-spread taxonomic sections (CUSPIDATA, SPHAGNUM, ACUTIFOLIA). Each *Sphagnum* species was collected in one to six peatlands in the second half of August in 1993.

The *Sphagnum* species were chosen from contrasting micro-topographical locations (referred to as microsites), differing in average water table level (Table 2). Sampled microsites comprised hollows with the average growing season water table close to the moss surface (0–10 cm below surface), moist lawns (10–20 cm below surface) and hummocks (>20–25 cm below surface). In addition, species were chosen both from peatland centres and peatland margins. For each species, on each peatland, a sampling area with a radius of about 5 m was defined. In each sampling area eight subsamples were collected and checked microscopically before merging them into one sample for chemical analyses. On each sampling area the occurrences of accompanying plant species were recorded in eight sub-plots of 20 × 20 cm (Table S1). Although the accompanying species differed between peatland and microsite, the variation was such that none of the species or sections had 100% identical accompanying species.

The samples were kept in cold storage (+4 °C) until preparation. The mosses were cleaned from litter, vascular plant roots and other plant material. After this each individual was cut with a pair of scissors at the transition between brown, senesced tissue and pigmented, photosynthetic active tissue. Only the pigmented photosynthetically active part (1 ~ 10 cm, short for hummock species, long for hollow species), comprising both capitulum, stem and branches, was used for the chemical analyses. The plant material was dried at 40 °C for 48 h until constant weight and stored until analysis. Time between sampling, preparation and drying was maximally three days. Prior to the chemical analyses, that were made within two years after sampling, the dried *Sphagnum* plant material was milled and sieved (0.25 mm mesh size).

### Chemical analysis

All our analyses are a result of chemical digestion or pyrolysis of the entire plant tissue. Consequently, our chemical characterisation mostly represents the structural rather than the metabolic components of the plant material.

**Table 1** Location and name of the seven peatlands sampled within this study

| Peatland | Code | Coordinates* | Elevation | Peatland type | |
|---|---|---|---|---|---|
| | | WGS84* | *m.a.s.l.* | *general* | *specific* |
| Björnmyran | B | 64°19′N 18°08′E | 398 | Medium rich fen | Mesotrophic tall sedge fen |
| Kroktjärnmyran | K | 64°21′N 20°14′E | 237 | Poor fen | *Sphagnum fuscum* true short sedge fen |
| Sjulsmyran | J | 64°01′N 20°38′E | 70 | Poor fen | Poor *Sphagnum papillosum* fen with small flarks |
| Stor-Åmyran | S | 63°44′N 20°05′E | 38 | Bog | *Calluna Sphagnum fuscum* bog |
| Stor-Vidmyran | I | 64°24′N 20°10′E | 276 | Fen | Pine fen with flarks |
| Torsmyran | T | 63°35′N19°36′E | 49 | Bog | *Calluna Sphagnum fuscum* bog |
| Våtömyran | V | 63°40′N20°11′E | 12 | Poor fen | Poor *Sphagnum papillosum* fen |

Code used as site abbreviation in Table 2. * World Geodetic System of 1984. Peatland types cf. Eurola et al. 1984

## Elements

We distinguished 10 elements in total: sodium (Na), potassium (K), magnesium (Mg), calcium (Ca), manganese (Mn), aluminum (Al), iron (Fe), phosphorus (P), nitrogen (N) and sulphur (S). All elements except N were determined with ICP-AES (Perkin Elmer, Plasma 2000) after digestion of 195–205 mg (DW) plant material in a mix of $HNO_3$ (65%) and $HClO_4$ (70%) at 110° - 130° C for 3 h. Detection limit was determined as 3SD for repetitions of reference mixture containing 5 ppm of each sample. Total nitrogen (N) was determined using elemental analyser (Perkin Elmer, CHN 2400).

## Carbohydrate polymers

Carbohydrates were assessed as neutral sugar constituents (alditol acetates) derived from polysaccharides

**Table 2** Overview of 15 *Sphagnum* species sampled with details on taxonomic section (ACUTIFOLIA, CUSPIDATA, SPHAGNUM), characteristic microsite (wet hollow, moist lawn and dry hummock) and peatlands where the species were collected

| *Sphagnum* species | Taxonomic section | Microsite | B | K | J | S | I | T | V | Total |
|---|---|---|---|---|---|---|---|---|---|---|
| *S. jensenii* | CUSPIDATA | hollow | BJE | | | | | | | 1 |
| *S. lindbergii* | CUSPIDATA | hollow | BLI | KLI | JLI | SLI | | TLI | VLI | 6 |
| *S. majus* | CUSPIDATA | hollow | | KMJ | JMJ | SMJ | | TMJ | VMJ | 5 |
| *S. pulchrum* | CUSPIDATA | hollow | | | JPU | | | TPU¤ | VPU | 3 |
| *S. tenellum* | CUSPIDATA | hollow | | | | STE | ITE | TTE | VTE | 4 |
| *S. balticum* | CUSPIDATA | lawn | | | | SBA | | | | 1 |
| *S. fallax* | CUSPIDATA | lawn | | KFA | JFA | SFA | | TFA | VFA | 5 |
| *S. magellanicum* | SPHAGNUM | lawn | BMA | KMA | JMA | SMA | | | VMA | 5 |
| *S. papillosum* | SPHAGNUM | lawn | BPA | KPA | JPA | SPA | | TPA¤ | VPA | 6 |
| *S. russowii* | ACUTIFOLIA | lawn | | KRU | | SRU | | TRU | VRU | 4 |
| *S. girgensohnii** | ACUTIFOLIA | lawn | | KGI* | JGI* | SGI* | | TGI* | | 4 |
| *S. subfulvum* | ACUTIFOLIA | lawn | BSU | | | | | | | 1 |
| *S. capillifolium* | ACUTIFOLIA | hummock | | KCA | | SCA | | TCA | VCA | 4 |
| *S. fuscum* | ACUTIFOLIA | hummock | BFU | KFU | JFU | SFU | | TFU | VFU | 6 |
| *S. warnsdorfii* | ACUTIFOLIA | hummock | BWA | | | | | | | 1 |
| Total | | | 7 | 9 | 8 | 11 | 1 | 10 | 10 | 56 |

Sample codes are used in Figs. 1, 2, 3 and 4 and are based on a combination of the first letter of the peatland (Table 1) and the first two letters of the species name

*- growing at peatland margins on shallow or no peat at all, i.e. not reflecting the nutrient conditions in the peatland centre

¤ - growing in a transitional fen between the bog and the upland forest

using sulphuric acid hydrolysis (72% $H_2SO_4$, 30 °C, 1 h; dilution to 2.5%, autoclaved at 125 °C, 1 h) followed by derivatization and gas capillary chromatography (Theander and Westerlund 1986). Quantification was made using myo-inositol as internal standard. The hydrolysis yielded seven analysable carbohydrate monomers: the two pentoses (arabinose and xylose) and five hexoses (fucose, galactose, glucose, mannose and rhamnose).

### Non-carbohydrates (aromatic and aliphatic compounds)

The dried and milled samples were suspended in 2 ml ultrapure-water and 200 μl ethanol and then treated for 15 min. in an ultrasonic bath. Pyrolysis was performed using a foil pulse pyrolyser; "Pyrola", Pyrol AB, Lund, Sweden (Tydén-Ericsson 1973); 3 μl of the suspension (approximately 50 μg sample) was placed in a cavity in a platinum foil. Pyrolysis conditions were as follows: chamber temperature 150 °C, pyrolysis temperature 550 °C, temperature rise time of 8 ms and total pyrolysis time 2 s. Pyrolysis temperature was chosen to maximise the amount of substituted aromatic fragments (data not shown). The pyrolyser was connected to a HP (Hewlett-Packard) 5890 Gas Chromatograph equipped with a split injector utilising a split ratio of 1:15. The injector temperature was 250 °C. A 15 m fused silica capillary column (coated with DB1301, id 0.26 mm, film thickness 0.25 μm) was used for separation of pyrolysis products. The oven temperature was increased from 50 °C to 270 °C with a rate of 5 °C per min. Helium was used as carrier gas at a velocity of about 1.4 ml / min. Eluting compounds were detected with a HP 5970 mass selective detector. The detector temperature was set to 180 °C. The electron impact ionisation energy was 70 eV and the measured mass range m/z = 35–300. Pyrolysis products were identified by comparison with the mass spectra present in the mass spectral data base belonging to the data system (HP 59973B Library software), or with mass spectra found in the literature (Boon et al. 1986; Van Smeerdijk and Boon 1987; Bracewell et al. 1980; Ralph and Hatfield 1991).

The original three-dimensional spectra (time, mass number and ion intensity) were transformed to two dimensions (time and total ion intensity). The baselines in these two-dimensional spectra (Total Ion Chromatograms, TICs or pyrolysis chromatograms, pyrograms) were adjusted. Based on the peaks in the pyrograms 34 regions were selected and integrated, yielding 34 fragments (Supporting information Table S2). The integration was made by summing the total ion intensity for each data point (scan) in the region. In order to eliminate most of the variations due to differences in amount of analysed sample, the integration sum for the 34 regions were normalised for each pyrogram. Of the 34 identified regions, 16 regions, known to represent carbohydrate polymers, were removed, focussing the data analysis of this study on the non-carbohydrates only.

### Data analysis

We used a combination of multivariate and univariate statistics to explore the chemical composition of our *Sphagnum* samples, focussing on three functional chemistry types: (i) inorganic elements, (ii) carbohydrates (iii) non-carbohydrates. Chemical data were transformed to meet statistical assumptions prior to analyses, if applicable. In the multivariate analysis all variables were auto scaled to unit variance and centred in order to allow all constituents to contribute equally to the total variance.

We used Principal Component Analysis (PCA) to examine how much of the total variance within each of the three types of chemical constituents was explained by latent variables by optimising the covariance (PC-components) and how this reflected known environmental or phylogenetic clustering of the *Sphagnum* species. Four separate PCAs were run with 10 inorganic elements, seven carbohydrates and 18 non-carbohydrates respectively, and one PCA where we combined all chemical constituents in one analysis. To further reveal the contribution of environment and phylogeny to the covariance structures in chemistry, we treated environment and phylogeny as supplementary variables, i.e. they were fitted into the chemical ordination space but did not contribute to the PC ordination itself. To characterize environment we used the variables "peatland" (six groups), and "microsite" (three groups) and to characterize "phylogeny" we used the taxonomic sections within the genus *Sphagnum* (three groups).

To specifically quantify how much of the total variance within each of the three types of chemical constituents was explained by environment and phylogeny respectively, we performed a variation-partitioning procedure (based on RDA) for each chemistry type (elements, carbohydrate polymers, non-carbohydrates). To test if the degree of explained variation

contributed by environment or phylogeny respectively differed between chemistry types we used a chi-square ($X^2$) analysis.

Based on the PCAs we also selected 5 constituents, contributing the most to PC1 and PC2 within each chemistry type to test the strength of the main effects of peatland, microsite and taxonomic group, using univariate techniques (Generalized Lineair Model). The constituents chosen were the ones that i) correlated strongly with one of the four PCA ordination axes and ii) correlated least with the other chemical constituents. For the analyses microsite and taxonomic group were nested within collection site.

The choice for linear ordination methods (PCA, RDA) was based on the degree of turnover in chemical data, as inferred from the length (0.3 SD units, irrespective of chemical constituents) of the first Detrended Correspondence Analysis axis (Lepš and Šmilauer 2003). All multivariate analyses were performed with CANOCO Engine Version 5.0 (Braak and Šmilauer 2012). Univariate analyses were performed with IBM SPSS statistics 20.

## Results

On average *Sphagnum* dry mass consisted of 2% (± 0.07% se) inorganic elements, 46% (± 0.54% se) carbohydrates and 60% (± 0.48% se) non-carbohydrates. The non-carbohydrate fragments included some unidentified fragments, which might explain the 8% surplus of mass. Based on these three types of chemical constituents together, *Sphagnum* samples were clustered according to taxonomic section and peatland, illustrating the combined influences of environment and phylogeny on *Sphagnum* chemistry (Fig.1). Along the first ordination axis (PC1) samples from the ACUTIFOLIA section (negative scores) were separated from the CUSPIDATA and SPHAGNUM sections (neutral-positive scores). Along the second ordination axis (PC2), samples from the medium rich fen Björnmyran (B**, positive scores) were separated from samples from the bogs and poor fen Kroktjärnmyran (K**, negative scores). The ordination was primarily driven by the inorganic element contents and the non-carbohydrates, and less by carbohydrates, as indicated by the lower loading values for the carbohydrates (short arrows in the PCA graph, Fig. 1b).

### Elements

Of the 10 inorganic elements analysed, nitrogen dominated with 42% (± 0.01% se) the total inorganic element content per *Sphagnum* sample. Based on content of all inorganic elements, *Sphagnum* samples from the same peatland were clustered more closely together than those from the same microsite or taxonomic section (Fig.2). The clearest separation along PC1 was between samples from the fen Björnmyran (B**) with positive scores and the two bogs Storåmyran (S**) and Torsmyran (T**) with negative scores. In line with the above, samples of *S. girgensohnii*, (*GI) a species from peatland margins, were clustered together with high scores on PC1. Along PC2, samples from the fen Björnmyran had highest positive scores closely followed by poor fen Sjulsmyran (J**). Most samples from the bogs Storåmyran and Torsmyran had scores close to zero and the lowest scores along PC2 were for samples from poor fen Kroktjärnmyran (K**). Repeating the ordination without *S. girgensohnii* maintained the positions of the peatland sites relative to each other.

The samples from fen Björnmyran were characterised by their high contents of elements Fe, Al, Ca, Mg and Mn (Fig. 2, Table 3), whereas samples from the bogs Storåmyran and Torsmyran where mainly characterised by their low Fe content. Contents of S and plant nutrients N, P and K were partly associated with specific peatland sites, sampling position within the peatland (centre vs margin) and microsite. Poor fen Kroktjärnmyran was characterised by high N, P, K and S contents. The peatland margin species *S. girgensohnii* reached the highest contents of N, P and K of all *Sphagnum* species. Within the peatland centre, species from lawn and hummocks were partly separated from those of hollows by their higher contents of N, P, and K and lower Na content.

### Carbohydrates

Of the seven carbohydrate monomers analysed, glucose dominated with 56% (± 0.01% se) of the total carbohydrate content per *Sphagnum* sample. The PCA of the carbohydrate composition (Fig. 3) showed an entirely different pattern from that of element composition: samples of all three taxonomic sections were clearly separated by PC1 and PC2. The clearest distinction along PC1 was between samples from the ACUTIFOLIA section (negative scores) and the CUSPIDATA section

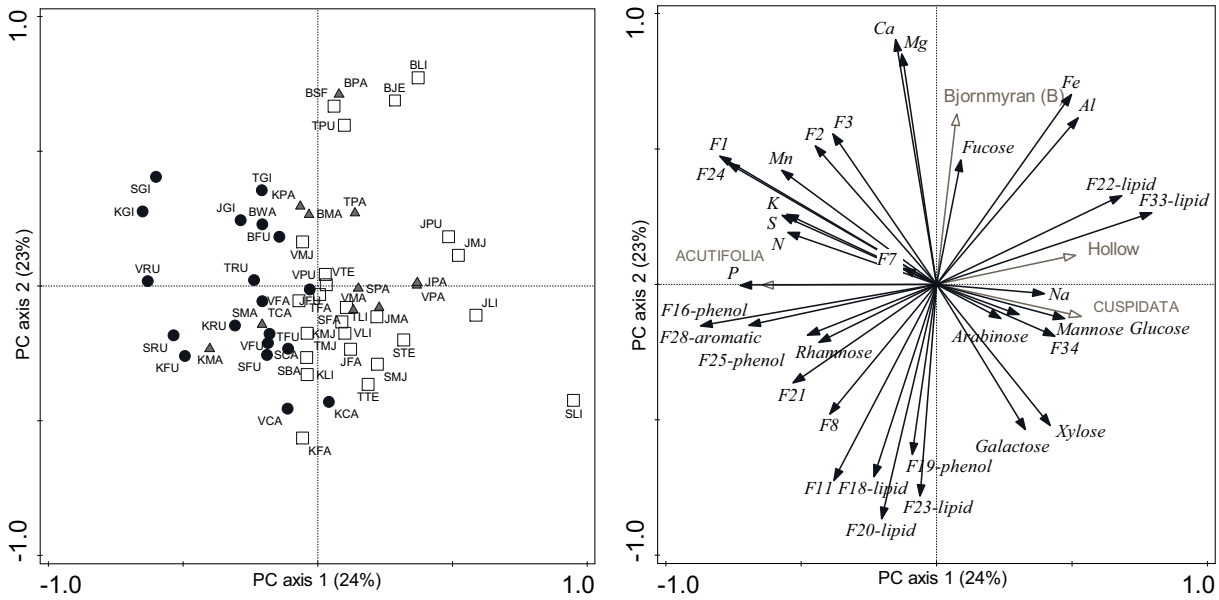


**Fig. 1** PC ordination based on the contents of 10 inorganic elements, seven carbohydrate monomers and 18 non-carbohydrate fragments (F) from pyrolysis of 56 *Sphagnum* samples. Together, the four ordination axes of the PCA explained 69% of the total variation in elements among samples, with 47% being explained by the first two axes (PC1, PC2). ***Left panel*****:** position of all *Sphagnum* samples in ordination space. Samples positioned closely to each other have similar chemical compositions. Open squares = samples from the taxonomic CUSPIDATA section, solid grey triangles = section SPHAGNUM and solid black circles = section ACUTIFOLIA. Sample codes consist of three letters: first letter indicates peatland identity whereas the second two letters are the first two of the scientific *Sphagnum* species name (see Table 2 for abbreviations). ***Right panel*** shows the correlation between the PC axes and the chemical contents (*black arrows*) and those supplementary variables (*grey arrows*) with a correlation coefficient ≤ −0.4 or ≥ +0.4 with PC1 and/or PC2. F6, F19 are characteristic of phenolic compounds, F20 of lipids, F2 and F33 are pyrolysis fragments of unknown origin (Table S2)

(positive scores). The samples from the CUSPIDATA section were characterised by high contents of monomers such as fucose, galactose, glucose, arabinose and xylose, whereas ACUTIFOLIA samples had low contents of these same carbohydrates but were particularly high in rhamnose (Fig. 3, Table 4). Similar to the ACUTIFOLIA, samples from the SPHAGNUM section had lower scores on PC1. SPHAGNUM samples were characterised by high contents of mannose but also low content of rhamnose, separating the SPHAGNUM section from the other sections along PC2.

## Non-carbohydrates

Of the 18 non-carbohydrate fragments analysed, fragment of unidentified origin F1 dominated with 47% (± 0.002% se) the total non-carbohydrate content per *Sphagnum* sample. In comparison, fragments of known phenolic and aromatic origin (F16, F19, F25 and F28) made up 12%. Based on non-carbohydrate composition the *Sphagnum* samples were separated according to peatland and taxonomic section (Fig. 4). Separation of samples along PC1 was mainly related to taxonomic section, whereas separation along PC2 was more related to peatland and *Sphagnum* species within the ACUTIFOLIA section. ACUTIFOLIA samples were characterized by mostly negative PC1 scores (more aromatic fragments), however substantially overlapping with both CUSPIDATA and SPHAGNUM samples (Fig. 4, Table 5). PC1 was mainly characterised by high contents of lipid fragment F22 and fragment of unknown origin F33 (positive scores) and low contents of aromatic fragments (F16, F25, F28; negative scores). PC2 was characterized by positive correlation to lipid fragments (F11, F20, F23) and one phenolic fragment (F19) and negative correlation to two unknown fragments (F2, F3). The most obvious separation along PC2 was between samples of different species from the ACUTIFOLIA section. Here hummock species such as *S. fuscum* (*FU) and *S. capillifolium* (*CA) had high content of lipid fragments (F11, F20, F23) and one phenolic fragment (F19), i.e. high positive PC2 scores.

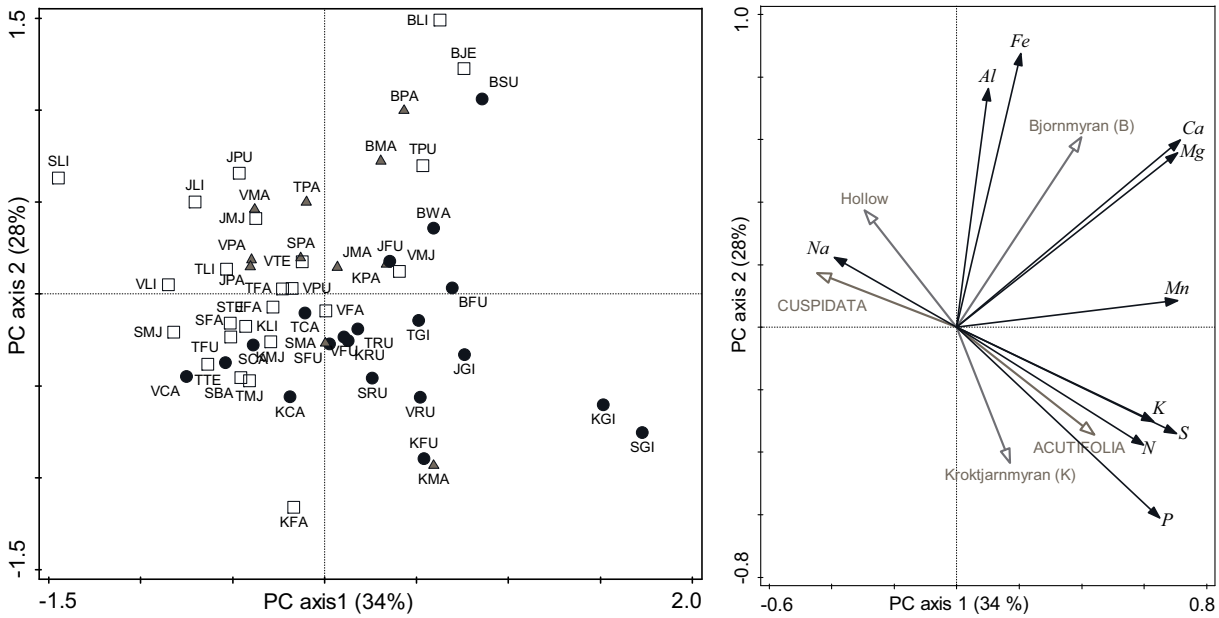


**Fig. 2** PC ordination based on the contents of 10 inorganic elements of 55* of the 56 *Sphagnum* samples. Together, the four ordination axes explained 84% of the total variation in elements among samples, with 62% being explained by the first two axes (PC1, PC2). ***Left panel*****:** position of all *Sphagnum* samples in ordination space. Samples positioned closely to each other have similar chemical compositions. Open squares = samples from the taxonomic CUSPIDATA section, solid grey triangles = section SPHAGNUM and solid black circles = section ACUTIFOLIA. For information about sampling codes see legend Fig. 1. ***Right panel*** shows the correlation between the PC axes and the element contents (*black arrows*) and those supplementary variables (*grey arrows*) with a correlation coefficient ≤ −0.4 or ≥ +0.4 with PC1 and/or PC2. * Sample ITE was omitted due to extremely high (> 2*SE) Mn concentration

Samples of peatland margin species *S. girgensohnii* (*GI) were low in the same fragments (negative scores) but had high contents of unknown fragments (F2, F3). Samples of the other peatland margin species *S. russowii* (*RU) scored around zero between *S. fuscum* and *S. capillifolium* and *S. girgensohnii* respectively along PC2. The second axis also to some extent separated samples from the poor fen Sjulsmyran (S**) from those of the medium rich fen Björnmyran (B**).

### Variance partitioning

To further quantify the contributions of environment and phylogeny respectively, we performed a variation-partitioning procedure for inorganic elements, carbohydrates and non-carbohydrates respectively (Fig. 5, Table S3). Variation in inorganic element composition of *Sphagnum* was explained mainly by peatland (25%), whereas microsite (7%) and taxonomic section (10%) were of considerable less importance (Fig. 5). In contrast to the element composition, only 5% of the variation in carbohydrate composition was explained by peatland site. Instead, taxonomic section explained 43% of the variation in carbohydrate composition between the *Sphagnum* samples of which 19% was shared with microsite, i.e. 24% was uniquely explained by taxonomic section. Microsite alone was not important in explaining the variation in carbohydrates (3%). For the non-carbohydrates none of the variables could be identified as the main driver, although the contribution of environment seemed stronger than that of phylogeny: peatland and microsite explained 16% and 12% respectively, whereas taxonomic section explained 8%, with half of the variation shared between microsite and taxonomic section.

## Discussion

### *Environment* vs *phylogeny*

We show a large variation in both elemental and organochemical composition among the 15 *Sphagnum* species sampled. We also show that the elemental and non-

**Table 3** Sample sizes (n), untransformed mean contents (% dw) and standard errors (se) of 5 inorganic elements aggregated per taxonomic section, microsite and peatland. Only those elements with a strong correlation with one of the four PCA ordination axes (Fig. 2) and low correlation with other elemental constituents were shown. Taken together the inorganic elements shown represent between 11% and 54% of the total inorganic element content per *Sphagnum* sample

| | n | **Fe** mean | se | **Ca** mean | se | **Mn** mean | se | **P** mean | se | **Na** mean | se |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Tax. section** | | | | | | | | | | | |
| ACUTIFOLIA | 20 | .062c | .025 | .227a | .032 | .020a | .003 | .064a | .008 | .035a | .003 |
| CUSPIDATA | 25 | .142b | .056 | .190b | .038 | .006b | .001 | .038b | .004 | .062a | .008 |
| SPHAGNUM | 11 | .124c | .043 | .251a | .042 | .013c | .003 | .047b | .008 | .037a | .004 |
| **Microsite** | | | | | | | | | | | |
| Hollow | 15 | .216a | .090 | .227a | .060 | .006a | .002 | .034a | .003 | .065a | .012 |
| Hummock | 11 | .051b | .019 | .165b | .027 | .016b | .005 | .048b | .006 | .034a | .005 |
| Lawn | 30 | .078b | .023 | .228a | .026 | .014a | .002 | .057a | .007 | .044a | .004 |
| **Peatland** | | | | | | | | | | | |
| Björnmyran | 7 | .508 | .156 | .521 | .073 | .029 | .006 | .040 | .004 | .041 | .008 |
| Kroktjärnmyran | 9 | .051 | .020 | .172 | .041 | .012 | .004 | .083 | .011 | .029 | .003 |
| Sjulsmyran | 8 | .115 | .021 | .137 | .014 | .005 | .001 | .042 | .007 | .039 | .006 |
| Stor-Åmyran | 11 | .032 | .007 | .137 | .024 | .012 | .003 | .050 | .013 | .065 | .014 |
| Stor-Vidmyran | 1 | .039 | - | .199 | - | - | - | .027 | - | .096 | - |
| Torsmyran | 10 | .036 | .014 | .236 | .051 | .006 | .001 | .035 | .003 | .056 | .012 |
| Våtömyran | 10 | .046 | .007 | .170 | .016 | .013 | .003 | .046 | .008 | .045 | .006 |
| **Statistics*** | **df** | **W-X2** | ***P*** | **W-X2** | ***P*** | **W-X2** | ***P*** | **W-X2** | ***P*** | **W-X2** | ***P*** |
| Tax. section | 2 | 7 | .026 | 15 | <.001 | 40 | <.001 | 18 | <.001 | 1 | .735 |
| Microsite | 2 | 17 | <.001 | 16 | <.001 | 9 | .011 | 15 | .001 | 4 | .121 |
| Peatland | 5–6 | 126 | <.001 | 59 | <.001 | 49 | <.001 | 36 | <.001 | 21 | .002 |
| **Transformation** | | ln | | ln | | ln | | ln(ln) | | ln | |

Full data are available in the Dryad data-repository. Statistics refer to individual Generalised Linear Models with main effects only for each inorganic element. Df = degree of freedom, W-X2 = Wald-Chi square. Different letters (a, b, c) indicate statistically significant differences between microsites or between taxonomic sections. Transformation indicates how data were transformed to achieve normal distribution and homogeneity of variances prior to statistical analyses

carbohydrate compositions were mainly determined by environmental factors and micro-topographic variation within the peatland. In contrast, the dominant control on carbohydrate composition was *Sphagnum* phylogeny, i.e. the taxonomic sections within the genus *Sphagnum*. The above implies that *Sphagnum* chemistry can be separated into an environmentally dependent, variable group of compounds and an environmentally independent, phylogenetically conserved group of compounds.

That environment affects inorganic elements and non-carbohydrates more than carbohydrates seems in line with evidence from fertilisation and water-table experiments, although experimental support for peatlands remains scarce. Nitrogen deposition has been shown to alter *Sphagnum* nutrient stoichiometry (Bragazza et al. 2004; Limpens et al. 2011) and phenolic constituents (Bragazza and Freeman 2007). Likewise, drier surface conditions associated with water table drawdown enhanced both N and P concentrations in *Sphagnum* (Straková et al. 2010). Finally, comparisons of plant litters across latitudinal climate gradients suggest significant differences in N, P and phenolic constituents for a wide number of litter types (Aerts 1997, Bragazza and Gerdol 2002), including *Sphagnum* (Dorrepaal et al. 2005). In contrast to nutrient concentrations and phenolic constituents, evidence for direct environmental effects on carbohydrate polymers in *Sphagnum* remains incidental: changes in carbohydrate monomers, such as glucose, have been observed in response to drought (Straková et al. 2010) and $CO_2$ enhancement (Van der Heijden et al. 2000). On account of the above it seems reasonable to assume that environmental factors control inorganic elements and

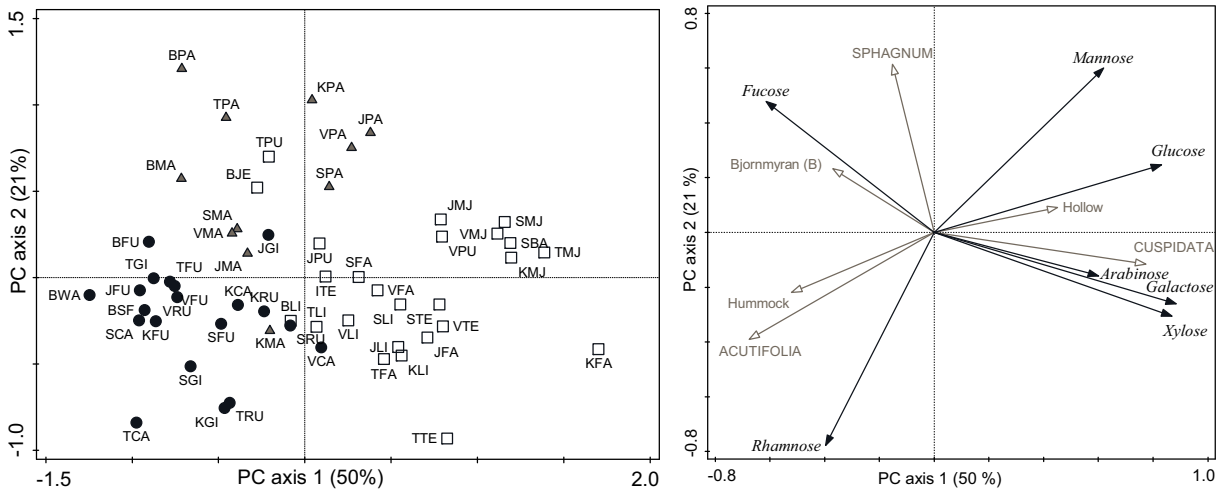


**Fig. 3** PC ordination based on the contents of seven carbohydrate monomers of 56 *Sphagnum* samples. Together, the four ordination axes explained 90% of the total variation in carbohydrates among samples, with 71% being explained by the first two axes. ***Left panel*** shows the position of all *Sphagnum* samples in ordination space. *Open squares* = samples from the taxonomic CUSPIDATA section, *solid grey triangles* = section SPHAGNUM and *solid black circles* = section ACUTIFOLIA. See Fig. 2 and Table 2 for explanation of sample codes. ***Right panel*** shows the correlation between the PC axes and the carbohydrate monomers (*black arrows*) and those supplementary variables (*grey arrows*) with a correlation coefficient ≤ −0.4 or ≥ +0.4 with PC1 and/or PC2

secondary metabolites (phenolics or metabolic carbohydrates) rather than the primary ones, especially the cell-wall carbohydrate polymers as they form the majority of plant biomass and thus cannot be replaced, only produced. However, the little evidence there is, is not in agreement with this assumption: Straková et al. (2010) reported changes in glucose concentrations associated with cell-wall carbohydrate polymers, whereas Van der Heijden et al. (2000) reported changes in glucose concentrations associated with metabolic carbohydrates. Disentangling the contribution of environment from that of phylogeny would require a more extensive experimental approach, coupled with chemical characterisation.

The effect of environment on *Sphagnum* chemistry can be either a direct result of abiotic drivers, or an indirect result mediated by biotic interactions with accompanying plant species (Table S1) or microorganisms showing the same preference for peatland type or microsite. Part of the variation in microsite was shared with phylogeny (Fig. 5), as only species of ACUTIFOLIA occurred on hummocks and CUSPIDATA occurred in hollows (Table 2). Nevertheless, since representatives of all three taxonomic sections shared the intermediate lawn microhabitat, it seems unlikely that the variance partitioning procedure overestimated the pure phylogenetic signal by more than a few % (Fig. 5).

## Elements

The patterns we found in base cations (Mg, Ca) and metals (Mn, Al, Fe) were mostly correlated to general peatland type (Table 1), varying mostly along the fen-bog gradient and direct mineral soil contribution within the peatland margin. This pattern is similar to what is found along hydro-geochemical acidity-alkalinity gradients for a wide range of peatlands (Vitt et al. 1990; Bragazza and Gerdol 2002) and illustrates the strong association with geo-hydrological variables such as catchment mineralogy, catchment to peatland areal ratio, the hydrological isolation from mineral sources and distance to the sea (Mullen et al. 2000). Base cations and metal ions as Mn serve important functions in peatlands, strongly determining bryophyte distributions and vascular plant diversity (Bridgham et al. 1996; Bragazza and Gerdol 2002).

The patterns in major plant nutrients (N, P, K) but also S and Na in the *Sphagnum* mosses partly covaried with the acidity-alkalinity gradient, with values being generally higher in fens than in bogs, as also observed by other authors (Wheeler and Proctor 2000). The patterns seemed to be explained by a combination of peatland type, specific species or species-combinations and/or position (margin, centre, hollow) within the peatland. The low nutrient

**Table 4** Sample sizes (n), untransformed mean contents (% dw) and standard errors (se) of 5 carbohydrate monomers aggregated per taxonomic section, microsite and peatland. Only those carbohydrates with a strong correlation with one of the four PCA ordination axes (Fig. 3) and low correlation with other constituents were shown. Taken together these five carbohydrate monomers represent between 87% and 89% of the total carbohydrate content per *Sphagnum* sample

| | n | **Rham** mean | se | **Fuc** mean | se | **Man** mean | se | **Gluc** mean | se | **Gal** mean | se |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Tax. section** | | | | | | | | | | | |
| ACUTIFOLIA | 20 | 3.84a | .07 | .45a | .01 | 3.12a | .05 | 23.22a | .33 | 6.31a | .13 |
| CUSPIDATA | 25 | 3.26b | .08 | .52b | .02 | 3.59b | .09 | 27.21b | .38 | 8.15b | .22 |
| SPHAGNUM | 11 | 3.17c | .07 | .41a | .02 | 3.90b | .20 | 25.76b | .40 | 6.37a | .17 |
| **Microsite** | | | | | | | | | | | |
| Hollow | 15 | 3.10a | .10 | .51a | .02 | 3.49a | .12 | 27.54a | .58 | 7.77a | .28 |
| Hummock | 11 | 3.81b | .08 | .44a | .01 | 3.14a | .09 | 22.43b | .34 | 6.16b | .21 |
| Lawn | 30 | 3.50b | .08 | .47a | .02 | 3.61a | .11 | 25.61c | .29 | 7.18a | .23 |
| **Peatland** | | | | | | | | | | | |
| Björnmyran | 7 | 3.31 | .22 | .42 | .02 | 3.22 | .17 | 24.28 | .68 | 5.65 | .19 |
| Kroktjärnmyran | 9 | 3.56 | .16 | .53 | .04 | 3.60 | .20 | 25.39 | .93 | 7.22 | .34 |
| Sjulsmyran | 8 | 3.27 | .11 | .46 | .03 | 3.61 | .22 | 25.53 | .77 | 7.19 | .29 |
| Stor-Åmyran | 11 | 3.48 | .12 | .48 | .02 | 3.54 | .17 | 26.15 | .83 | 7.63 | .40 |
| Stor-Vidmyran | 1 | 3.44 | . | .44 | | 3.30 | | 26.88 | | 8.62 | |
| Torsmyran | 10 | 3.57 | .20 | .48 | .03 | 3.32 | .13 | 24.83 | .69 | 7.24 | .51 |
| Våtömyran | 10 | 3.45 | .11 | .47 | .02 | 3.60 | .16 | 26.24 | .83 | 7.29 | .31 |
| **Statistics** | **df** | **W-X2** | ***P*** | **W-X2** | ***P*** | **W-X2** | ***P*** | **W-X2** | ***P*** | **W-X2** | ***P*** |
| Tax. section | 2 | 24 | <.001 | 35 | <.001 | 23 | <.001 | 13 | .002 | 69 | <.001 |
| Microsite | 2 | 9 | .010 | 3 | .242 | 3 | .211 | 12 | .003 | 7 | .026 |
| Peatland | 5–6 | 3 | .796 | 21 | .002 | 7 | .292 | 11 | .097 | 44 | <.001 |
| **Transformations** | | none | | ln | | ln(ln) | | none | | ln(ln) | |

Full data are available in the Dryad data-repository. Rham = rhamnose, Fuc = fucose, Man = mannose, Gluc = glucose, Gal = galactose. Statistics refer to individual Generalised Linear Models with main effects only for each carbohydrate. Df = degree of freedom, W-X2 = Wald-Chi square. Different letters (a, b, c) indicate statistically significant differences between microsites or between taxonomic sections. Transformation indicates how data were transformed to achieve normal distribution and homogeneity of variances prior to statistical analyses

concentrations in hollow species from the peatland centre potentially reflects the lower nutrient retention capacity of hollows (Bragazza et al. 2004), the prevailing direction of water flow and dissolved nutrients from hollows to lawns and hummocks in more continental climates (Eppinga et al. 2010) or, alternatively, extra nutrient relocation from deeper depths by co-occurring vascular plant species in lawns and hummocks (Malmer et al. 1992; Malmer et al. 2003). As nutrient concentrations in *Sphagnum* plant material co-determine its degradability and speed of mineralisation (Damman 1988; Limpens and Berendse 2003; Straková et al. 2012), differences in nutrient concentrations in *Sphagnum* may have direct implications for mineralisation rates and nutrient cycling in peatlands.

### Non-carbohydrates: aromatic and aliphatic compounds

Peatland explained the largest part of the variation in both aromatic and aliphatic compounds in *Sphagnum*, again with most variation connected to the fen-bog gradient. Nevertheless, some aromatics (phenolics) and aliphatic compounds (lipids) seemed to be restricted to some species or taxonomic sections. Many aromatic and aliphatic compounds are among those compounds most resistant to decay (Minderman 1968). This is also reflected in *Sphagnum* peat as the relative contributions of the aromatic and aliphatic fractions increase with increased peat decomposition (Bohlin et al. 1989; Nordén et al. 1992). In highly decomposed *Sphagnum* peat the aromatic and aliphatic carbon make up a major portion of the finest particle size fraction (Nordén et al.

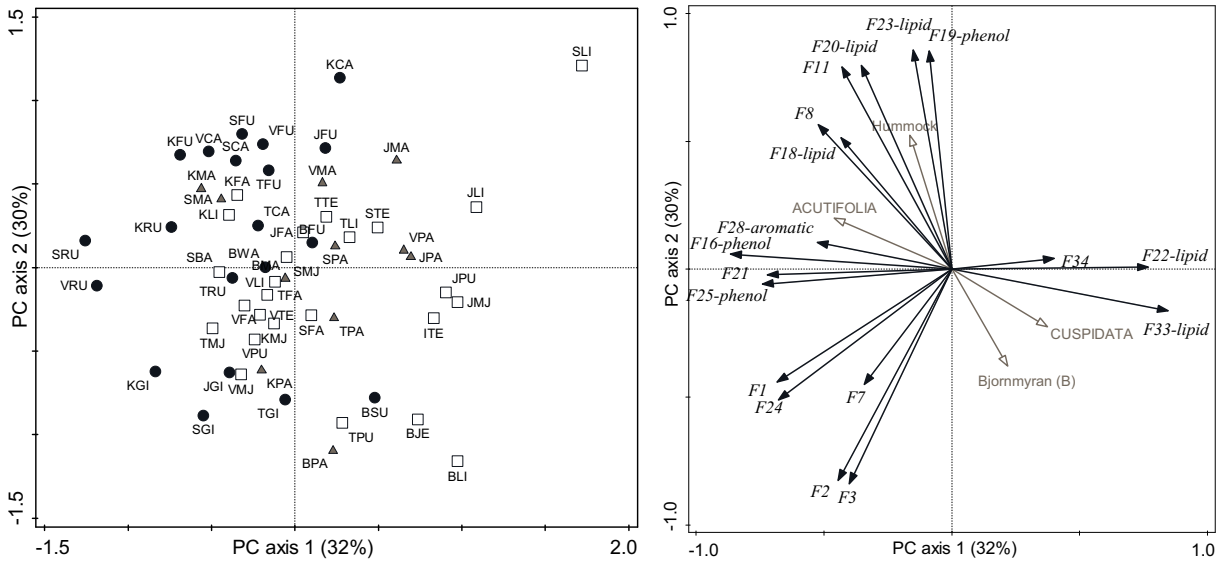


**Fig. 4** PC ordination based on the contents of 18 non-carbohydrate fragments (F) from pyrolysis of 56 *Sphagnum* samples. Together, the four ordination axes explained 81% of the total variation in non-carbohydrates among samples, with 62% being explained by the first two axes. ***Left panel*** shows the position of all *Sphagnum* samples in ordination space. Open squares = samples from the taxonomic CUSPIDATA section, *solid grey triangles* = section SPHAGNUM and *solid black circles* = section ACUTIFOLIA. See Fig. 2 and Table 2 for explanation of sample codes. ***Right panel*** shows the correlation between the PC axes and the non-carbohydrates (*black arrows*) and those supplementary variables (*grey arrows*) with a correlation coefficient ≤ −0.4 or ≥ +0.4 with PC1 and/or PC2

1992), i.e. the most decomposed material. The results from this study suggest that the differences in the concentrations of many of these compounds between peat profiles might be more related to environmental controls (peatland type and micro topography) than phylogeny.

Most phenolics in *Sphagnum* are associated with polyphenols coating the cell wall surface offering both structural support and physical protection against decomposition, similar to lignin in many other plant genera (Tsuneda et al. 2001). These lignin-like phenolic networks may decompose into soluble monomers such as sphagnum acid (Rudolph and Samland 1985; Williams et al. 1998) that inhibit the activity of extracellular enzymes under anaerobic conditions (Verhoeven and Liefveld 1997; Freeman et al. 2001) together with other low-molecular weight soluble phenolics excreted by living cells (Rasmussen et al. 1995). Consequently, environmentally induced variation in the amount and concentration of these phenolics may have consequences for both carbon accumulation and mineralisation rates.

Most lipids in *Sphagnum*, as in other bryophytes, are either an insoluble component of cell-wall membranes or are part of cell solutes where they serve an energy storage function (Longton 1988). In living *Sphagnum*, the largest concentrations of total lipids are soluble (Karunen and Ekman 1982; Karunen and Salin 1982) and vary seasonally, with highest concentrations generally reached just before winter. In contrast, the insoluble, polymerised cell-wall lipids that are preserved in peat profiles have low concentrations in living tissue (Karunen and Salin 1982). As we sampled living tissue, most of the variation in lipid content between *Sphagnum* samples is likely associated with the soluble storage lipids, rather than the cell-wall lipids.

## Carbohydrates

In contrast to both inorganic elements and non-carbohydrates, most variation in carbohydrates was explained by *Sphagnum* taxonomy, implying that carbohydrate composition is phylogenetically conserved. In addition, taxonomic group shared considerable variation with microsite, illustrative of the correlation between *Sphagnum* phylogeny and position along the hummock-hollow gradient (Shaw 2000; Johnson et al. 2014). The central role of *Sphagnum* species in maintaining micro-topography is illustrated by Hájek (2009). He showed that species occupying elevated hummocks combined slow decomposition rates with sufficient

**Table 5** Sample sizes (n), relative integration sums multiplied by 1000) and standard errors (se) of 5 non-carbohydrate polymer fragments (F) from pyrolysis aggregated per taxonomic section, microsite unit and peatland. Only those non-carbohydrates with a strong correlation with one of the four PCA ordination axes (Fig. 4) and low correlation with other constituents were shown. Taken together these five non-carbohydrates represent between 21 and 26% of the total non-carbohydrate content per *Sphagnum* sample

| | n | **F2** mean | se | **F16** mean | se | **F20** mean | se | **F19** mean | se | **F33** mean | se |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Tax. section** | | | | | | | | | | | |
| ACUTIFOLIA | 20 | 95.3a | 3.8 | 25.2a | .6 | 8.9ab | .2 | 12.0a | .2 | 8.8a | .4 |
| CUSPIDATA | 25 | 97.8b | 3.0 | 21.2b | .6 | 8.5b | .2 | 11.1a | .2 | 10.9b | .4 |
| SPHAGNUM | 11 | 87.4c | 3.2 | 22.9b | .7 | 8.2a | .3 | 11.2a | .2 | 10.3b | .4 |
| **Microsite** | | | | | | | | | | | |
| Hollow | 15 | 97.0a | 4.9 | 20.9a | .9 | 8.3a | .3 | 11.1a | .3 | 11.1a | .4 |
| Hummock | 11 | 81.7b | 1.8 | 24.4a | .7 | 9.4b | .2 | 9.2b | .2 | 9.2a | .4 |
| Lawn | 30 | 94.9a | 2.4 | 23.0a | .5 | 8.5a | .2 | 9.8a | .1 | 9.9a | .4 |
| **Peatland** | | | | | | | | | | | |
| Björnmyran | 7 | 100.7 | 5.0 | 21.4 | 1.0 | 7.4 | .4 | 10.8 | .4 | 11.4 | .6 |
| Kroktjärnmyran | 9 | 98.2 | 5.0 | 25.3 | 1.0 | 9.4 | .3 | 11.9 | .4 | 8.8 | .5 |
| Sjulsmyran | 8 | 86.9 | 5.2 | 20.2 | .9 | 8.4 | .3 | 11.5 | .3 | 10.4 | .5 |
| Stor-Åmyran | 11 | 89.7 | 5.4 | 23.2 | .9 | 9.1 | .3 | 11.5 | .3 | 9.6 | .8 |
| Stor-Vidmyran | 1 | 97.3 | | 20.5 | | 7.9 | | 10.7 | | 15.3 | |
| Torsmyran | 10 | 97.5 | 3.6 | 23.3 | .8 | 8.3 | .3 | 11.3 | .3 | 10.2 | .4 |
| Våtömyran | 10 | 97.0 | 5.4 | 24.1 | 1.0 | 8.8 | .2 | 11.4 | .3 | 9.7 | .5 |
| **Statistics** | **df** | **W-X2** | ***P*** | **W-X2** | ***P*** | **W-X2** | ***P*** | **W-X2** | ***P*** | **W-X2** | ***P*** |
| Tax. section | 2 | 30 | <.001 | 25 | <.001 | 5 | .078 | 1 | .584 | 14 | .001 |
| Microsite | 2 | 48 | <.001 | 4 | .136 | 18 | <.001 | 46 | <.001 | 4 | .156 |
| Peatland | 6 | 17 | .011 | 34 | <.001 | 39 | <.001 | 6 | .013 | 32 | <.001 |
| **Transformations** | | none | | ln | | ln(ln) | | none | | ln(ln) | |

Full data are available in the Dryad data-repository. F16, 19 are characteristic of phenolic compounds, F20 of lipids, F2 and F33 are pyrolysis fragments of unknown origin (Table S2). Statistics refer to individual Generalised Linear Models with main effects only for each non-carbohydrate fragment. Df = degree of freedom, W-X2 = Wald-Chi square. Different letters (a, b, c) indicate statistically significant differences between microsites or between taxonomic sections. Transformation indicates how data were transformed to achieve normal distribution and homogeneity of variances prior to statistical analyses

production to offset the faster production and faster decomposition of hollow dwelling species, thus maintaining the relative difference in elevation between these microsites. The apparent trade-off between poor degradability and high production between hummock and hollow species has been attributed to differences in resource partitioning over metabolic and structural carbohydrates (Turetsky et al. 2008). In our work we cannot make a similar distinction, as our focus on carbohydrate monomers rather than pyrolysis fragments means our patterns are dominated by the composition of the carbohydrates making up most of the plant mass: the structural carbohydrates rather than the metabolic ones. Nevertheless in our work species from the ACUTIFOLIA section, known for their position at the higher end of the hummock-hollow gradient (Anderson et al. 1995) were distinguishable from the CUSPIDATA section, known for their position at the lower end of the hummock-hollow gradient (Anderson et al. 1995) by the their C allocation to main structural carbohydrate polymers, hemicellulose and pectin in particular. In our study CUSPIDATA were characterised by high contents of monomers that make up hemicellulose, notably xylose, whereas ACUTIFOLIA had higher contents of rhamnose, component of rhamnogalacturonan, a type of highly branched pectin. Species from SPHAGNUM were mainly characterised by their low concentrations of rhamnose and high concentrations of mannose, also a monomer from hemicellulose. Consequently, our results point towards a phylogenetic signal in the composition

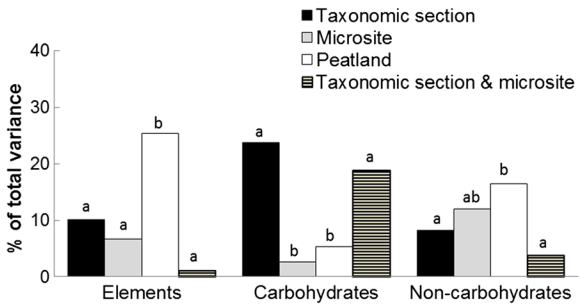


**Fig. 5** Percentage of total variation within three functional chemistry types in *Sphagnum* uniquely explained by taxonomic section, microsite and peatland as well as the variation shared by taxonomic section and microsite (the only combination that explained more than 5% of the variation within one of the chemistry types). For other shared variation see Table S3). Variance partitioning was based on separate RDAs, one for each functional chemistry type (Table S3). Statistical differences in explained variation between chemical types were assessed for each driver separately using $X^2$-tests. Different letters above each column show statistical significant differences between the columns $P < 0.05$, based on Bonferroni corrected pairwise comparisons

of cell-wall carbohydrates that coincides with the position of the species and sections along the hummock-hollow gradient.

Taken together, the correlations between: I) *Sphagnum* taxonomy and the position of the sections and species along the hummock-hollow gradient (Shaw 2000; Johnson et al. 2014); II) the position along the hummock-hollow gradient and litter degradability (Johnson and Damman 1991, Bengtsson et al. 2016) and III) *Sphagnum* taxonomy and structural carbohydrate composition (this study), implies that the differences in degradability between *Sphagnum* species are at least in part a function of their carbohydrate chemistry. Cell-wall carbohydrates have been shown to play a role in the low-degradability of *Sphagnum* as a genus (Bohlin et al. 1989; Turetsky et al. 2008; Hájek et al. 2011). For example, Bohlin et al. (1989) compared concentrations of structural carbohydrate monomers after acid digestion of fresh litter, lightly decomposed peat and highly decomposed peat of both *Sphagnum* and sedges (*Carex*). They showed that glucose concentrations in highly decomposed *Sphagnum* peat remained near that to fresh *Sphagnum* plant litter, whereas glucose concentrations in sedge material significantly decreased. Using in vitro incubations of *Sphagnum* material chemically stripped from all non-carbohydrates, Hájek et al. (2011) also argued for a carbohydrate-determined recalcitrance of *Sphagnum* litter. They suggest that *Sphagnum* carbohydrate polymers have a similar role in litter decomposition recalcitrance as lignin in many vascular plants. To what extent the same agents responsible for low degradability of *Sphagnum* as a genus are indeed responsible for the differences in degradability observed between species and sections (Bengtsson et al. 2016) remains to be determined. However, the close associations between *Sphagnum* phylogeny, microtopography and carbohydrate chemistry suggest that differences in carbohydrate chemistry may have driven speciation in *Sphagnum*, contributing to the emergence of micro-habitats, and thus micro-topography, in peatlands.

### Implications for peatland processes

The high variation of inorganic elements and non-carbohydrates along environmental gradients suggest that the amount and concentration of these compounds will be the first to respond when the environment changes. Likewise, the low variation of carbohydrate composition along environmental gradients suggests low responsiveness to changes in environment, as long as species-replacement occurs within the same taxonomic section. For example, as availability of nutrients change, low-productive species, such as *S. balticum*, may become replaced by more productive species, such as *S. fallax* (section CUSPIDATA, Gunnarsson 2005). But, as long as species replacement occurs within taxonomic section, the consequences for peat accumulation may be limited as microtopography, and thereby overall hydrologic functioning, will be maintained (Bohlin et al. 1989; Belyea and Clymo 2001). Assuming our inferences above are correct, the phylogenetically conserved carbohydrate chemistry thus likely reinforces the strong control exerted by *Sphagnum* species on their environment, contributing to the resilience of peatlands to environmental change (Belyea 2009; Turetsky et al. 2012; Heijmans et al. 2013).

## Conclusions

Our study shows that the elemental and non-carbohydrate compositions of *Sphagnum* are mainly determined by environmental factors and microtopographic variation within the peatland. The dominant control on carbohydrate composition is *Sphagnum* phylogeny, i.e. the taxonomic sections within the genus *Sphagnum*. The separation into an environmentally

dependent, variable group of compounds and an environmentally independent, phylogenetically conserved group of compounds has important implications both for understanding patterns in and for upscaling of spatially variable ecosystem processes such as carbon sequestration, nutrient cycling and greenhouse gas emissions. Our study is a first step towards understanding the interactions between chemical traits, phylogeny and environment. Further separating these interactions and the consequences for nutrient and carbon cycling, however, requires a combination of targeted experiments and modelling.

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