Reply to reviewers’ comments concerning the manuscript:

“C/N ratio, stable isotope ($\delta^{13}C$, $\delta^{15}N$), and n-alkane patterns of bryophytes along hydrological gradients of low-centred polygons of the Siberian Arctic”
by R. Zibulski et al.

Referee #2

Received 19th September 2016

We thank reviewer #2 for the valuable comments.

comments:

The foremost issue is that the n-alkane data are inadequately presented and interpreted. As correctly noted by the authors, mosses typically have lower concentrations of these wax components than vascular land plants. Nonetheless, the absolute concentrations of all 400 samples should be reported in the supplemental material and summarized in either a figure or a table in the manuscript proper. Furthermore, the relative concentrations of the samples should be compared using some of the well established n-alkane ratios such as the Paq, the ACL, and the CPI. For the ACL, I recommend using an extended range (21-33), similar to the extended range used by Bush and McInerney (2015, Org Geochem 79, 65-73). Addition of these ratios will allow better comparison of these new results to results from existing and future studies of wetland biogeochemical records, and it will likely enable the authors to refine their interpretations.

Our response: In the original version of the manuscript we indicated that only 16 samples were selected for n-alkanes analyses because these samples were also used for other analyses. Thus, we consider this a preliminary study. We now include Table 2 with the absolute concentrations of all 16 n-alkanes samples and added the Paq of Ficken et al. (2000) and the ACL with the recommended range n-C21 to n-C33 (ACL21,33). During the carbon chain analyses of the 16 samples, there were selected 10 further samples for advanced analysis of even-chain homologues. Thus, we do not calculate the CPI.

This entailed changes in the Methods section for n-alkanes (added the formula), in the Results section (reference to Table 2), and in the Discussion section '4.4 n-alkane patterns'.

Methods: Additionally, we calculated the average chain length ($APL_{21,33}$), assumed to represent a proxy for moisture (Andersson et al, 2011) and temperature (Bush and McInerney, 2015), with a comprehensible extended range from n-C21 to n-C33 and the proxy ratio $P_{aq}$, which was developed as a proxy ratio to distinguish submerged or floating aquatic macrophytes from emergent and terrestrial plants (Ficken et al., 2000):

$$APL_n = \frac{\sum (n \times C_n)}{\sum C_n} , n = 21 - 33$$

$$P_{aq} = \frac{C_{23} + C_{25}}{C_{23} + C_{25} + C_{29} + C_{31}}$$
**Results:** Evaluations of the n-alkane biomarker proxies, ACL$_{21-33}$ and $P_{aq}$, also show a clear division between the xero-mesophilic and the meso-hygrophilic species groups (Table 2), whereas intraspecific variations are low (with the exception of Drepanocladus). The xero-mesophilic group is notable for high averages of the APL$_{21-33}$ (28.41) and $P_{aq}$ (-0.06) compared to low averages of APL$_{21-33}$ (25.61) and $P_{aq}$ (-0.7) for the meso-hygrophilic group.

**Discussion:** We added citations and reworded the Discussion section completely.

Another issue is that the authors do not make full use of their important documentation of the intraspecific variability in the geochemical properties of these plants. Other studies have found similar variability in both Sphagnum (Huang et al., 2012, Org Geochem 44, 1-7) and in vascular plants (Feakins et al, 2016, Org Geochem 100, 89-199), and they both discuss its possible significance and mention other reports of intraspecific variability. Better appreciation of this variability is important to better interpretation of the paleoenvironmental significance of these properties, and the authors’ data could make a better contribution to such understanding than it presently does.

Our response: We cite Huang et al. 2012 in the discussion of n-alkanes. The study of Feakins et al. (2016) concerns an analysis along a temperature gradient. This is not so relevant to our study as our 16 samples of n-alkanes come from one site, as explained in the Methods section 2.4.

Yet another issue is that aspects of this study seem to provide answers, at least partial, to some of the questions raised by Andersson et al. (2011, Org Geochem 42, 1065-C21075; 2012, J. Quat. Sci. 27, 545-552) from their study of the changes in C/N ratios, stable carbon and nitrogen isotope values, and n-alkane distributions recorded in the fen-bog transition of a peat sequence in the Russian Arctic. Consideration of these questions and how the new data may address them would enrich both the Introduction and the Discussion of this contribution.

Our response: We think this suggestion is justified with regard to meaningful palaeo-reconstructions in fens with a dominance of brown mosses. Both articles show interesting studies in a changing wetland with a dominant portion of brown mosses in the lower fen part. However, due to the different approach of Andersson et al. and especially the different experimental setup with measurements of bulk instead of species-specific material (e.g. only minor quantities of vascular plant material mask the signal of n-alkane$_{moss}$ with their higher amount of n-alkanes, and stable isotope properties are changed by physical fractionation within a soil column) cause problems for a meaningful comparison and discussion of contrary results. Furthermore, we agree with reviewer #1, who noticed that only recent material is measured and thus that interpretations and suggestions about fossil material could only be speculative. However, we added some information and comparisons.

Addition to Introduction: We provide C/N ratios by weight of arctic brown mosses, in the anticipation that they will be useful for comparative palaeo-environmental reconstructions (Andersson et al. 2011, ) and in the evaluation of organic matter sources in Russian permafrost soils with regard to species and habitat-specific patterns.
Addition to Discussion: Andersson et al. (2011) inferred $ACL_{27-31}$ values of 29 for brown-moss peat from western Russian during wet phases, which is however, poorly comparable to our results because they investigated total peat organic instead of pure moss material.

Finally, the authors need to specify in the text and figures whether the C/N ratios that they report are atomic or weight ratios.

Our response: We thank you for this comment and have indicated the 'weight' information throughout (C/N_{wt}).
C/N ratio, stable isotope ($\delta^{13}C$, $\delta^{15}N$), and $n$-alkane patterns of brown mosses along hydrological gradients of low-centred polygons of the Siberian Arctic

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Abstract

Mosses are a major component of the arctic vegetation, particularly ofin wetlands. We present C/N ratio ratios (by weight), $\delta^{13}C$ and $\delta^{15}N$ data of 400 brown moss samples belonging to 10 species that were collected along hydrological gradients within polygonal mires located on the southern Taymyr Peninsula and the Lena River delta in northern Siberia. Additionally, $n$-alkane patterns of six of these species (n = 16) were investigated. The aim of the study is to see whether the inter- and intra-specific, intra-intraspecific differences in biochemical and C/N, isotopic signatures and $n$-alkanes are indicative of habitat with particular respect to water-level. Overall, we find high variability in all investigated parameters. The C/N$_{\text{ratio}}$ ratios range between 15.4 and 70.4 (median: 42.943) and show large variations at intra-intraspecific level. However, species preferring a dry habitat (xero-
mesophilic mosses) show higher C/N\((\text{wt})\) ratios than those preferring a wet habitat (meso-hygrophilic mosses). We assume that this mainly originates from the association of mosses from wet habitats with microorganisms which supply them with nitrogen. Furthermore, because of the stability provided by water, they do not need to invest in a sturdy stem-structure and accordingly have lower C contents in their biomass. The \(\delta^{13}\text{C}\) values range between -37.0 and -22.5\(^\circ\) (median = -27.8\(^\circ\)). The \(\delta^{15}\text{N}\) values range between -6.596 and +1.697\(^\circ\) (median = -2.172\(^\circ\)). We find differences in \(\delta^{13}\text{C}\) and \(\delta^{15}\text{N}\) signatures between both habitat types and, for some species of the meso-hygrophilic group, a significant relation was suggested as a function of microbial symbiosis. The \(n\)-alkane distribution also shows differences primarily between xero-mesophilic and meso-hygrophilic mosses, i.e. having a dominance of \(n\)-alkanes with long (\(n\)-C\(_{29}\), \(n\)-C\(_{31}\)) and intermediate (\(n\)-C\(_{25}\)) chain lengths (\(n\)-C\(_{25}\)), respectively. Overall, our results reveal that biochemical and C/N\((\text{wt})\) ratios, isotopic signals and \(n\)-alkanes of certain studied brown moss taxa from polygonal wetlands are characteristic of their habitat and can thus be used in (palaeo-)environmental studies.

1. Introduction

Specific physiological and morphological traits enable mosses to attain extensive surface coverage in low-temperature ecosystems such as arctic tundra (Turetsky et al., 2012; Wasley et al., 2006). Mosses are a major component of the biomass in arctic wetlands and contribute strongly to the biodiversity. In particular, the vegetation of the widely distributed polygonal tundra is rich in moss taxa, which partly originates from the strong compositional turnover along a small-scale hydrologic gradient (Zibulski et al. 2016). As an intermediate layer between air and the permafrost soil, mosses control the water cycle, greenhouse gas and energy exchange (Blok et al., 2011; McFadden et al., 2003), and the structure of the habitats of vascular plant communities in arctic landscapes (Beringer et al., 2001; Gornall et al., 2011; Malmer et al., 1994). Because of their low decomposition rates (Aerts et al., 1999; Turetsky, 2003), they contribute strongly to the peat and permafrost carbon pool (Tarnocai et al., 2009).
Despite the significance of mosses in high-latitude biodiversity and matter cycles only little is known about their C/N ratio, stable isotope and biochemical-alkane characteristics in comparison to vascular plants. Such information is not only necessary to improve our understanding of the physiological adaptation or plasticity of mosses to certain environmental characteristics, but can also be used when similar measurements of fossil plant material are interpreted as proxies of former ecological or environmental conditions (e.g. Birks, 1982).

Carbon-to-nitrogen ratios (C/N), stable carbon and nitrogen isotope values ($\delta^{13}C$, $\delta^{15}N$) and the n-alkane fingerprints of bulk organic matter are among the most commonly measured parameters of plant matter (Chambers and Charman, 2004). The C/N ratios of mosses are generally in the range of those of higher terrestrial plants (Prahl et al., 1980) but are known to depend on the available nitrogen, which originates in pristine regions from decomposition of organic matter, microbial activity or atmosphere deposits (e.g. Chanway et al., 2014; Lee et al., 2009). We provide C/N ratios by weight of arctic brown mosses, in anticipation that they will be useful for comparative palaeo-environmental reconstructions (Andersson et al., 2011, ) and in the evaluation of organic matter sources in Russian permafrost soils with regard to species and habitat-specific patterns. Furthermore, C/N ratios may be related to growth form, i.e. higher ratios can be expected for mosses which compete with vascular plants for light and thus need to invest in a high stem-stability (Sveinbjörnsson and Oechel, 1992).

As well as the C/N ratio, the $\delta^{13}C$ signature is barely altered by decomposition processes in the soil and also suitable for palaeo-environmental reconstructions. The $\delta^{13}C$ signatures of an individual plant are a mixed signal of the physiological traits of the species and the individual’s direct environment. Mosses use the C$_3$ pathway for carbon assimilation (O’Leary, 1988, Farquhar et al., 1989) and despite a lack of stomata in the photosynthetic active parts, they have a similar range in their $\delta^{13}C$ values of between -24 and -32 ‰ (Ménot and Burns, 2001; Rundel et al., 1979; Smith and Epstein, 1971) as vascular C$_3$ plants. Differences in $\delta^{13}C$ values among several species can be explained by individual plant physiology and biochemistry (Galimov, 2000). Differences within a single species have been linked with environmental conditions such as temperature (Skrzypek et al., 2007; Waite and Sack, 2011), the growing depth below water-level (Raghoebarsing et al., 2005), the
position within a cushion or hummock (Price et al., 1997), the lipid content (Rundel et al., 1979) or the influence of microbial symbioses (Liebner et al., 2011; Vile et al., 2014). Furthermore, even differences among branches and stems of single individuals have been reported (Loader et al., 2007). However, almost all of these studies were made on Sphagnaceae, which are not representative of all mosses because of their specific morphology (i.e. the occurrence of a photosynthetic active cell type and a dead cell type, which is responsible for water storage and often an additional coating of the photosynthetic active cell) and their specific habitat preferences (i.e. preferring acidic wetlands).

Hence, this information cannot simply be transferred to brown mosses – which form the major component in northern Siberian lowlands – due to their different morphology.

Most studies on δ15N values of moss material have focused on the anthropogenic impact on the nitrogen cycle (Harmens et al., 2011; Liu et al., 2008; Poikolainen et al., 2009), whereas reports on the δ15N signatures of mosses from relatively pristine ecosystems such as the Arctic are rare or have been investigated in relation to the study of bird colonies (e.g. Lee et al., 2009). Potentially, such information can indicate pathways and sources of the nutrient supply in these N-limited ecosystems (Kielland, 1997; Michelsen et al., 1996, 1998).

Compared with vascular plants and *Sphagnum* species, relatively few investigations of *n*-alkane patterns of brown mosses are available. *Sphagnum* species, for example, show a dominance of *n*-C23 and *n*-Palaeoenvironmental reconstructions use the potential of *n*-alkanes to distinguish between different plant groups (Ficken et al., 1998, moisture conditions (Pancost et al., 2000, Nichols et al 2006, Zhou et al. 2010), whether organic material is to decomposed and changes in temperature (Feakins et al., 2016, Sachse et al., 2006) along distinct gradients. *Sphagnum* species, for example, show a dominance of *n*-C23 and *n*-C25 homologues (Baas et al., 2000) that are comparable to the pattern of vascular submerged plants (Ficken et al., 2000), and ratios are used as a proxy for wet moisture conditions. Other studies discuss the suitability of *n*-alkane patterns in moss species for chemotaxonomical studies on recent and fossil material (Bush and McInerney, 2013; Nott et al., 2000; Schellekens and Buurman, 2011). A greater protection potential of waxes with a higher content of long-chain *n*-alkanes against solar irradiation or alternatively an enhanced loss of short-chain *n*-alkanes by evaporation have been suggested as possible mechanisms to cause different *n*-alkane
patterns in leaf waxes of trees (Sachse et al., 2006). However, with respect to mosses the pattern and mechanisms are even less understood.

This study presents $\text{C/N}_{\text{wt}}$ isotopic ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) and biochemical ($\text{C/N}$, $n$-alkanes)alkane characteristics of mosses from low-centred polygons in northern Siberia. Low-centred polygons are geomorphological forms in arctic landscapes originating from frost-heave processes in the soil. They are characterized by elevated dry rims and a water-saturated or water-filled centre. This centimetre-scale hydrological gradient is well reflected by a strong turnover in the vascular plant and moss composition (Zibulski et al., 2016). We investigate the relationship between the $\text{C/N}_{\text{wt}}$ isotopic and biochemical-$n$-alkane signatures and the hydrological conditions within low-centred polygons. In particular, we aim to reveal whether fingerprints are habitat-specific or rather species-specific.

2. Material and methods

2.1 Sites

The plant material was collected from eight low-centred polygons located along a zonal vegetation gradient ranging from open forest via the forest-tundra intersection to subarctic tundra (Matveev, 1989) to obtain a representative sample set of northern Siberian lowlands (Fig. 1). Six of the polygons (06/P, 17/P, P3/I, P3/II, P3/III, 12/P), sampled in 2011, are located in the Khatanga River region (70–72° N, 97–102° E, southern Taymyr Peninsula) and a further two polygons (LP1 and LP2), sampled in 2012, are located on Samoylov Island in the Lena River Delta (72.4° N, 126.5° E). The climate is cold-humid (Khatanga climate station annual mean temperature and precipitation: -13.2°C and 272 mm, Rivas-Martinez and Rivas-Saenz, 2009; Samoylov climate station annual mean temperature and precipitation: -12.5°C and 232.7 mm, Boike et al., 2013).

2.2 Sampling and studied moss species

A representative continuous transect of adjacent one square-metre plots (from rim to rim) was selected for sampling in each polygon. The surface height in relation to water-level (collected measured at the centre of each plot) and vegetation (abundance information) were recorded. Individual characteristics of each low-centred polygon are presented in Table A1. Moss plants were hand-picked, dried in the field and transported to the Alfred Wegener Institute in Potsdam. Taxa identification is based on the
relevant literature (Frahm and Frey, 2004; Lobin et al., 1995; Smith, 1978) and the Bryophyte Flora of North America internet source (http://www.efloras.org).

In total, eight species that were observed to have different water-regime preferences were included in the analyses. The species were divided into xero-mesophilic and meso-hygro-philic habitat type groups. Generally the xero-mesophilic group represented by Hylocomium splendens (16 cm), Tomentypnum nitens (13 cm), Aulacomnium turgidum (13 cm) and Aulacomnium palustre (13 cm) can be separated from meso-hygro-philic taxa represented by Hamatocaulis lapponicus (3 cm), Warnstorfia exannulata (swimming mat), Meesia triquetra (-1 cm), Drepanocladus revolvens (-5 cm), Scorpidium scorpioides (-13 cm), and Calliergon giganteum (-30 cm). (Numbers in brackets denote the observed mean plant-position relative to the water-level.) To approximate water-regime preferences of each species, we calculated the mean plant-position in relation to water-level (h) from the recorded plot surface height. Warnstorfia exannulata was observed to grow as part of a swinging mat at water-level, it was assigned a preference for water-level. Using this information the species were classified as either as of xero-mesophilic mosses (mean plant-position between 13 and 16 cm in relation to water-level) or to the group of meso-hygro-philic mosses (mean plant-position between 3 and -30 cm in relation to water-level) to ease the presentation of results.

Table 1: Calculated mean plant-position relative to the water-level and the classification of the sampled brown moss species. (* Samples of Warnstorfia exannulata were growing on a swinging mat at water-level and mean plant position was thus set to zero.)

<table>
<thead>
<tr>
<th>species</th>
<th>abbreviation</th>
<th>h (mean plant-position in relation to water-level in cm)</th>
<th>classification</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hylocomium splendens</td>
<td>Hyl_spl</td>
<td>16</td>
<td>xero-mesophilic</td>
</tr>
<tr>
<td>Tomentypnum nitens</td>
<td>Tom_nit</td>
<td>13</td>
<td>xero-mesophilic</td>
</tr>
<tr>
<td>Aulacomnium turgidum</td>
<td>Aul_tur</td>
<td>13</td>
<td>xero-mesophilic</td>
</tr>
<tr>
<td>Aulacomnium palustre</td>
<td>Aul_pal</td>
<td>13</td>
<td>xero-mesophilic</td>
</tr>
<tr>
<td>Hamatocaulis lapponi</td>
<td>Ham_lap</td>
<td>3</td>
<td>meso-hygro-philic</td>
</tr>
<tr>
<td>Warnstorfia exannulata</td>
<td>War_ex</td>
<td>0 *</td>
<td>meso-hygro-philic</td>
</tr>
<tr>
<td>Meesia triquetra</td>
<td>Mee_tri</td>
<td>-1</td>
<td>meso-hygro-philic</td>
</tr>
<tr>
<td>Drepanocladus revolvens</td>
<td>Dre_rev</td>
<td>-5</td>
<td>meso-hygro-philic</td>
</tr>
<tr>
<td>Scorpidium scorpioides</td>
<td>Sco_sco</td>
<td>-13</td>
<td>meso-hygro-philic</td>
</tr>
<tr>
<td>Calliergon giganteum</td>
<td>Cal_gig</td>
<td>-30</td>
<td>meso-hygro-philic</td>
</tr>
</tbody>
</table>

2.4 Measurements of C/N\textsubscript{(wt)} ratios, stable carbon and nitrogen isotope values and n-alkane distributions

Selected plant material (i.e. apical parts of a specimen) was rinsed with de-ionised water and mechanically cleaned from organic particulate material. The total content of carbon and nitrogen (C\textsubscript{total} and N\textsubscript{total})-and the ratio of stable isotopes (δ\textsubscript{13}C, δ\textsubscript{15}N) were measured with a DELTAplusXL isotope ratio mass spectrometer (Thermo Fischer Scientific) coupled to an elemental analyser (NC2500 Carlo
Erba) via a CONFLOW III Interface. Due to the relatively wide range of C/N-ratios of mosses, we used about 1.5 mg for each carbon stable isotope measurement and a replicate of 3.0 mg for each nitrogen stable isotope measurement and the analysis of elemental composition. The high weight needed for the nitrogen sample replicates prevented the measurement of δ¹⁵N and thus the C/N(wt) for some samples. The calibration for carbon was performed using a certified elemental an urea standard (urea) and a δ¹³C isotopic standard (IAEA CH-7). The nitrogen contents were calibrated against an acetanilide standard and the nitrogen isotopic composition with ammonium sulphate standard (IAEA N-1). The reliability of the method was checked with the NIST plant standard SRM 1547. The isotopic ratios are given in delta notation relative to VPDB for δ¹³C values and relative to air for δ¹⁵N values, respectively. The reproducibility for replicate analyses is 0.2% for carbon and nitrogen and 0.2‰ for δ¹³C and δ¹⁵N values.

n-Alkane analyses were performed on a subset of samples. We took material from the polygon complex P3 from the Khatanga region (72.149° N, 102.693° E), which comprises three successive low-centred polygons (Table A1) to exclude effects of environmental conditions at different locations. The moss samples were washed, identified and air-dried. They were weighed (150–1000 mg dry weight) and samples extracted with an accelerated solvent extractor (ASE) (Dionex, Sunnyvale; USA) using Cl₂Me:MeOH (10:1) at 5 bar and 75°C. The extract was separated into aliphatic hydrocarbon, aromatic hydrocarbon and nitrogen, sulphur and oxygen compound fractions using medium pressure liquid chromatography according to following Radke et al. (1980). Considering the low n-alkane concentrations of our samples, 5 µg of quantification standard (5α-androstan, 1-ethylpyrene, 5 α-androstan-17-one and erucic acid) were added. Gas chromatography (GC) of aliphatic hydrocarbon fractions was performed using a GC Agilent 6890 equipped with an Ultra-1 fused silica capillary column (Model Agilent 19091A-105, length 50 m, inner diameter 200 μm, film thickness 0.33 μm). Helium was used as a carrier gas at a constant flow rate of 1 ml min⁻¹. The GC oven was heated from 40 °C (2 min hold time) to 300 °C (65 min hold time) at a rate of 5°C per minute. The samples were injected by means of splitless injection. Quantitative evaluation of data was done with ChemStation software. Additionally, we calculate the average chain length (ACL₂₁-₃₃) assumed to represent a proxy for moisture (Andersson et al, 2011) and temperature (Bush and McInerney, 2015) with a
comprehensible extended range from \( n-C_{21} \) to \( n-C_{33} \) and the proxy ratio \( P_{aq} \), which was developed as a proxy ratio to distinguish submerged or floating aquatic macrophytes from emergent and terrestrial plants (Ficken et al., 2000):

\[
ACL_n = \frac{\sum(n \times C_n)}{\sum C_n}, n = 21 - 33
\]

\[
P_{aq} = \frac{(C_{23} + C_{25})}{(C_{23} + C_{25} + C_{29} + C_{31})}
\]

2.5 Statistical Tests

We calculated the range, .25, .5, and .75 quantiles of \( \delta^{13}C \) and \( \delta^{15}N \) values and the C/N\(_{\text{ext}}\) ratios for all species (Table A2). Significant differences in the C/N\(_{\text{ext}}\) ratios and \( \delta^{13}C \) and \( \delta^{15}N \) values among different groups were tested with a t-test. In addition, we performed linear regression between the obtained values for each individual species and surface height. All analyses were implemented in R version 3.2.0 (R Core Team, 2015). Furthermore, we performed a PCA with the percentage of \( n \) -alkane homologues (square-root transformed) in R using the vegan package version 2.0-10 (Oksanen et al., 2013).

3. Results

The overall ranges in C/N\(_{\text{ext}}\) ratios of both groups have a broad overlap (xero-mesophilic: 22.5–67.9; meso-hygrophilic: 15.4–70.4). However, the medians of the C/N\(_{\text{ext}}\) values of the xero-mesophilic species ranging from 47.6 to 52.9 (Fig. 2) are significantly higher than those of the meso-hygrophilic group, which range from 37.1 to 46.5 (\( t = 8.17, p << 0.001 \)). The C/N\(_{\text{ext}}\) ratios among individual species are not significantly correlated with the water-level (Fig. 3a), except for *Tomentypnum nitens* (\( r^2 = 0.11, p < 0.05 \)).

The \( \delta^{13}C \) values of the meso-hygrophilic group (-34.9 to -22.5\%) cover the range of the xero-mesophilic group (-32.1 to -24.2\%), which have a noticeably lower variance in \( \delta^{13}C \) values (Fig. 2).

The medians of the individual species in the xero-mesophilic group (range: -29.4 to -27.1\%) are not significantly different (\( t = -1.69, p = 0.09 \)) from those of the meso-hygrophilic group (range: -29.2...
to -24.8‰). δ¹³C values of *Meesia triqueta*, *Drepanoclados revolvens*, and *Scorpidium scorpioides* (all belonging to the meso-hydrophilic group) are significantly positively correlated with the position of the water-level (Fig. 3b), while no member of the xero-mesophilic group revealed such relationship (Fig. 3a).

The ranges of δ¹⁵N values of both groups are rather similar (Fig. 2). However, individual species medians of both groups are significantly different (*t* = -6.96, *p* << 0.001; xero-mesophilic group; -3.2 to -2.7‰, meso-hygrophilic group: -2.9 to -0.1). *Drepanoclados revolvens*, *Scorpidium scorpioides*, and *Calliergon giganteum*, all belonging to the meso-hygrophilic group, exhibit a positive relationship between the δ¹⁵N values and position relative to the water-level. (Fig. 3b)

*n*-Alkane distributions show the expected odd over even predominance of the odd chain length (Table 2). The absolute *n*-alkane concentrations (*n*-C₁₉ to *n*-C₃₃) range from 34 to 238 µg g⁻¹ of dry weight. The individual taxa show significant differences with respect to carbon number of the most abundant *n*-alkane, *(n*-C₃₃) forming unimodal distribution patterns. It is *n*-C₃₁ for *Tomentypnum nitens*, which is also the only species containing *n*-C₃₃ in detectable amounts, *n*-C₂₉ for *Aulacomnium turgidum*, *n*-C₂₇ for *Aulacomnium palustre*, *n*-C₂₇ and *n*-C₂₅ for the *Drepanoclados* taxa, and *n*-C₂₅ for *Scorpidium scorpioides*. These differences in the *n*-alkane composition largely correlate with the species-preferred mean plant-position relative to water-level (Fig. 4).

The described Evaluations of the *n*-alkane biomarker proxies, ACL₂₁-₃₃ and Pₐq, also show a clear division between the xero-mesophilic and the meso-hygrophilic species groups (Table 2), whereas intraspecific variations are rather small (with the exception of *Drepanoclados*). The xero-mesophilic group is notable for high averages of ACL₂₁-₃₃ (28.41) and Pₐq (-0.06) compared to low averages of ACL₂₁-₃₃ (25.61) and Pₐq (-0.7) for the meso-hygrophilic group. There are no intersections, with the exception of *Drepanoclados*.

The general trends are also visible in the biplot of the first two PCA axes which together explain only 16.9% of the variance in the dataset (Fig. 5). The first axis separates xero-mesophilic from meso-hygrophilic taxa. *Aulacomnium* taxa are located in the upper range and *Tomentypnum nitens* in the
lower range of the second PCA axis, while no trend is observed within the meso-hygrophilic group along the second axes.

<table>
<thead>
<tr>
<th>Table 2: The concentration (µg/g dry weight) and ACL_{21-33} and P_{aq} (after Ficken et al., 2000) of n-alkanes in brown moss samples. (Numbers in brackets relates to the sample number.)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>species</strong></td>
</tr>
<tr>
<td><strong>Xero-mesophilic habitat group</strong></td>
</tr>
<tr>
<td>Tom nit (1)</td>
</tr>
<tr>
<td>Tom nit (2)</td>
</tr>
<tr>
<td>Tom nit (3)</td>
</tr>
<tr>
<td>Asul tar (1)</td>
</tr>
<tr>
<td>Asul tar (2)</td>
</tr>
<tr>
<td>Asul pal (1)</td>
</tr>
<tr>
<td>Asul pal (2)</td>
</tr>
<tr>
<td><strong>Meso-hygrophilic habitat group</strong></td>
</tr>
<tr>
<td>Dre rev (1)</td>
</tr>
<tr>
<td>Dre rev(2)</td>
</tr>
<tr>
<td>Dre sp</td>
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<tr>
<td>Sco Sco (1)</td>
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<tr>
<td>Sco Sco (2)</td>
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<td>Sco Sco (4)</td>
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<tr>
<td>Sco Sco (5)</td>
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<tr>
<td>Sco Sco (6)</td>
</tr>
</tbody>
</table>

### 4. Discussion

#### 4.1 C/N_{(wt)} ratios

The C/N ratios of mosses from polygonal tundra in Northern Siberia are relatively low when compared with those obtained for mosses from Antarctic bogs that range between 80 and 100 (Björck et al., 1991) or from western Canada that range between 55 and 76 (Kuhry and Vitt, 1996). However, neither the taxa nor the habitats sampled were fully comparable to those of our analyses, i.e. many more taxa typical of xeric and mesic growing conditions were sampled in Antarctica and Canada. All investigated species are considered as ectohydric mosses, which receive nitrogen mostly from precipitation deposits (Ayres et al., 2006). Our results reveal that C/N_{(wt)} ratios for the xero-mesophilic moss group are higher than for the meso-hygrophilic group, probably portraying reflecting the known difference between terrestrial and aquatic plants (Meyers and Ishiwatari, 1993). Competition with vascular plants (1) and accessibility of nitrogen pools (2) may be the main reasons for this finding. (1)
If moss plants invest in a high stem-to-leaf biomass ratio, which is reflected by results in a high C/N (wt) ratio, they will increase their height and stability, resulting in better competition with and thus their competitive ability against vascular plants for light (Sveinbjörnsson and Oechel, 1992). Furthermore, the low N input by precipitation and a low N content of moss litter slows down the fungal and bacterial N mineralisation which increases the thickness of moss litter mats (Gornall et al., 2007; Turetsky, 2003). This in turn will increase the isolating function of moss mats, thus negatively affecting seed germination of vascular plants (Gornall et al., 2007). (2) Higher C/N (wt) ratios of meso-hygrophilic mosses may originate from higher amounts of dissolved nitrogen in water due to polygon waters as a result of high net primary productivity, the presence of N₂-fixation of algae-fixers such as cyanobacteria, and other microorganisms may lead to a lower C/N ratio, the exudations of zooplankton. Frahm (2001) assumes that loose epi-epiphytic and endophytic symbiotic relationships between mosses and cyanobacteria are probably restricted to wetland taxa. Lindo et al. (2013) report such associations between brown mosses and cyanobacteria. Thus, the N supply is better for brown mosses preferring wet meso-hygrophilic than dry xero-mesophilic habitats, and the respective taxa accordingly have lower C/N (wt) ratios, indicating habitat-specific variation in C/N (wt) ratios. We expected to also find a relationship between C/N (wt) ratios and water-level. However, the signal-to-noise ratio is probably too low to give a meaningful result because only the average water level of each plot but not of each individual plant was recorded.

4.2 δ¹³C values

With respect to bryophytes, most isotopic studies have hitherto been performed on Sphagnum (Markel et al., 2010, Ménot and Burns, 2001) while our study focuses on brown mosses – a major component in Siberian wetlands. For the intraspecific variability for some meso-hygrophilic species (i.e. Meesia triquetra, Drepanocladius revolvens, Scorpidium scorpioides) we find show that the δ¹³C signals are significantly related to the hydrological conditions at the growing site of each individual, i.e. individuals growing at dry sites showed higher δ¹³C values than those growing at wet sites. No significant difference among the two habitat-groups is observed; rather they partly contradict the intraspecific findings in that some of the xero-mesophilic species known to prefer dry rims such as
Hylocomium splendens and Tomentypnum nitens, known to prefer dry rims, have particularly low δ¹³C medians.

Differences in moss δ¹³C values either reflect a source signal depending on water level or a physiological reaction of the plant related to water-level (Bramley-Alves et al., 2014; Proctor et al., 1992). Mosses are typical C₃ plants (Farquhar et al., 1989, Rundel et al., 1979) characterized by a high CO₂ compensation point (Bain and Proctor, 1980; Dilks and Proctor, 1975; Salvucci and Bowes, 1981). The high availability of atmospheric CO₂ and elevated diffusion rates of CO₂ in air compared to water (O’Leary) result in typical terrestrial C₃ land plant δ¹³C characteristics, because of a decreasing cell water pressure in dry habitats which entails a strong discrimination rate against ¹³CO₂ induced by RuBisCO (Rice and Giles, 1996). With respect to the xero-mesophilic group, we observe an increase in discrimination against ¹³C from taxa preferring a low position relative to the water-level (e.g., Aulacomnium taxa) than those preferring high positions (e.g., Hylocomium splendens). In contrast, if plant tissue is coated by a water film, the cell water pressure should reach an optimum, which is expected to results in a weaker discrimination rate against ¹³C by RuBisCO (Rice and Giles, 1996), because of a source restriction by the slower diffusion rate of CO₂ in water (Lloyd and Farquhar, 1994). A lower carbon isotope discrimination related to water saturation is observed for only three species out of six meso-hygrophilic mosses. However, this basic signal may be masked by variations in δ¹³C values of different carbon sources, which are expected to be more influential in water-saturated habitats. As CO₂ uptake in mosses occurs exclusively by the above soil organs, the ¹²C enriched sources of deeper soil sections, originating from simple kinetic fraction by weight within the vertical soil profile, should not be accessible.

For meso-hygrophilic mosses in water-saturated conditions, Ménot and Burns (2001) studied intraspecific variations for three Sphagnum species, which prefer three different habitat types (dry, meso, wet) along an elevational gradient, which was positively correlated with precipitation. They find a decline in discrimination against ¹³C with increasing wetness, and similar to our results no relationship for species with a strong wet–preference. This is attributed to the variation in δ¹³C from highly varying dissolved inorganic carbon (Proctor et al., 1992).
Bain and Proctor (1980) show that, in general, moss taxa are incapable of bicarbonate uptake. Hence, bicarbonate, known to be a carbon source for submerged vascular plants and algae (Herzschuh et al., 2010; Merz, 1992), can most probably be excluded as a carbon source for moss and thus as a factor influencing the $\delta^{13}$C value. Moreover, the bicarbonate content in pond waters in northern Siberian landscapes is very low (Wetterich et al., 2008). Mosses potentially access $^{13}$C-depleted CO$_2$ that originates from oxidation of typically strongly $^{13}$C-depleted biogenic methane by methanotrophic microorganisms (Kip et al., 2010; Liebner et al., 2011; Raghoebarsing et al., 2005). Studies by Nichols et al. (2009) show that a higher water level at the peat surface is crucial for an increasing high methane-derived CO$_2$ release. Furthermore, symbiosis with methanotrophs enhances the moisture-related effect on the $\delta^{13}$C signal of bryophytes. Endophytic microorganisms in hyalocytes of submerged Sphagnum (Raghoebarsing et al., 2005) or epiphytic microorganisms on submerged brown mosses (Liebner et al., 2011) are presumed to provide directly $^{13}$C-depleted CO$_2$ directly to the lamina cells of mosses. The studies of Ruttner (1947) and Bain and Proctor (1980) show that, in general, moss taxa are incapable of bicarbonate uptake. Hence, bicarbonate, known to be a carbon source for submerged vascular plants and algae (Herzschuh et al., 2010; Merz, 1992), can most probably be excluded as a carbon source for moss and thus as a factor influencing the $\delta^{13}$C value. Moreover, the bicarbonate content in pond waters in northern Siberian landscapes is very low (Wetterich et al., 2008). Other sources of $^{13}$C-depleted CO$_2$ are surface run-off during spring flooding, rain events and decomposition processes in the pond (Leng and Marshall, 2004; Maberly et al., 2013). Yet we cannot fully eliminate the possibility that the measured bulk material was contaminated in parts with epiphytic or endophytic microorganisms. The overall signature would, however, likely be unaffected, as Ménot and Burns (2001) could have shown that the $\delta^{13}$C values of bulk organic material and alpha-cellulose of Sphagnum are very similar. Finally, considering the relationship of selected brown mosses to mean plant position, the complex origin of plant-available carbon makes it difficult to interpret the $\delta^{13}$C record, especially for meso-hygrophilic brown mosses as well as Sphagnum (Prince et al., 1997, Ménot and Burns, 2001).

4.3 $\delta^{15}$N isotopes
Like $\delta^{13}C$, the interpretation of stable nitrogen isotope signatures of mosses is challenging because, again, source signals need to be separated from those originating from physiological isotopic discrimination processes. Our results yield relatively $^{15}N$-depleted $\delta^{15}N$ values for xero-mesophilic mosses growing preferentially on rims compared to meso-hygrophilic mosses.

The terrestrial arctic systems are generally thought to be nitrogen limited (Gordon et al., 2001; Kielland, 1997). On the rim sites, atmospheric deposition can be considered to be the most important source for nitrogen (Jonasson and Shaver, 1999) originating from fog, dew, precipitation and surface run-off (Sveinbjörnsson and Oechel, 1992). However, most of the nitrogen available to rim mosses originates from recycling of already $^{15}N$-depleted higher plant and moss litter (Turetsky, 2003). The ectohydric morphology enables an efficient nutrient uptake across the entire moss plant surface via trapped water. In fact, the meso-hygrophilic group has a higher N content than the xero-mesophilic group (see section on C/N ratio). Inorganic nitrogen, but especially the high amounts of organic nitrogen provided by N-mineralization in tundra soils (Kielland, 1995) are important for mosses growing on the rather dry sites such as the polygonal rims (Atkin, 1996).

Three of the investigated submerged or floating moss species show a significant positive relationship between water-level and $\delta^{15}N$ values. These results are similar to those of Asada et al. (2005) who tested a relationship between $\delta^{15}N$ values of different Sphagnum species and their position relative to the groundwater level, which they assumed to originate from different nitrogen sources and different internal fractionating processes. We assume that the often heavier nitrogen isotope signature of meso-hygrophilic brown moss individuals originates from the high degree of symbiotic associations with aquatic atmospheric nitrogen-fixing autotrophic microorganisms such as Nostoc or Anabena (Lindo et al., 2013) or methanotrophs (Vile et al., 2014). The high spatial degree with endo- or ectosymbiotic N$_2$-fixing microorganisms enables the direct uptake of their nitrogen products, which is similar to that of N$_2$ in air.

### 4.4 $n$-alkane patterns

Compared to vascular plants that are characterized by a thick leaf-wax layer, mosses produce only a small amount of $n$-alkanes (Baas et al., 2000; Ficken et al., 1998). Like previous studies on vascular
plants (Aichner et al., 2010; Ficken et al., 2000; Meyers and Ishiwatari, 1993), our results generally reveal a differentiation between terrestrial taxa (i.e. xero-mesophilic group) characterized mainly by \(n\)-alkanes maximizing at \(n\)-C_{29} and \(n\)-C_{31} and submerged living taxa (i.e. the meso-hygrophilic group) maximizing at \(n\)-C_{25} and \(n\)-C_{27}. Our results thus confirm earlier investigations of Nott et al. (2000), Baas et al. (2000) and Bingham et al. (2010), who compared the \(n\)-alkane fingerprints of *Sphagnum* taxa growing along a hydrological gradient—agree with our results.

We furthermore found that individual specimens of a single xero-mesophilic moss species show high variability in their \(n\)-alkane patterns, potentially originating from significant small-scale environmental variability on polygon rims. In contrast, the \(n\)-alkane patterns of wet habitat taxa cover a small range only, potentially reflecting the buffering function of water, and thus these patterns are promising for chemotaxonomic identification of their remains in peat sequences (Bush and McInerney, 2013; Nott et al., 2000). However, these initial results of our study need to be corroborated with a larger data set.

Huang et al. (2012a) and Ficken et al. (1998) used proxy ratios (ACL, P_{aq}) to divide moss taxa roughly by their moisture preferences. They calculate the ACL_{23-33} for samples of lichens and *Racomitrum lanuginosum*, which have similar hydrological requirements to our xero-mesophilic mosses. Despite the slightly narrower ACL_{23-33} range, their results show similarities to our xero-mesophilic group. A comparison between ACL_{21-33} ratios of *Sphagnum* (plant position nearly at water-level) of Huang et al. (2012b) and our brown mosses shows that the ACL_{21-33} ratios of *Sphagnum* species are rather lower. The intraspecific conclusion of Huang et al. (2012b) (wetter moisture conditions entail lower ACL_{21-33} for *Sphagnum*) is reflected by our measurements for *Drépanoclados* and *Scorpidium*, i.e. they show a dependence with water level. As we observed a clear difference in the ACL_{21-33} between the xero-mesophilic and the meso-hygrophilic group, we suggest that the inclusion of mid-chain \(n\)-alkanes (\(n\)-C_{21} to \(n\)-C_{25}) in the equation of ACL improves its value as a proxy for moisture conditions. Andersson et al. (2011) inferred ACL_{27-33} values of 29 for brown-moss peat from western Russian during wet phases, which is however, poorly comparable to our results because they investigated total peat organic matter instead of pure moss material.
Ficken et al. (2000) proposed $P_{aq}$ as a semi-quantitative proxy ratio for the differentiation of terrestrial and aquatic plants (<0.1 terrestrial plants, 0.1–0.4 emergent macrophytes, 0.4-1 submerged/ floating macrophytes). Our inferred $P_{aq}$ results for the individual species fit well with these assumptions. For example, submerged/ floating Scorpidium ($P_{aq}$ median: 0.56) has a higher median $P_{aq}$ value than floating/ mesic Drepanocladus ($P_{aq}$ median: 0.34), which is again higher than that of the xero- mesophilic mosses Tomentypnum ($P_{aq}$ median: 0.13) and Aulacomnium ($P_{aq}$ median: 0.13). Ficken et al. (2000) also measured a Drepanocladus sample ($P_{aq}$ = 0.30). Overall, our results do not support the inference of Nichols et al. (2006) that a hydrological classification is possible between Sphagnum and non-Sphagnum formed peat as the latter show wide variations between different habitats. The inferred broad $P_{aq}$ range of Drepanocladus and Aulacomnium probably indicates that intraspecific variation is related to the individual’s growing condition, which could provide the basis to develop $P_{aq}$ as a proxy for water-level when measured on taxonomically identified fossil plant material.

As with $P_{aq}$, n-alkanes seem to be species-specific given stable environmental parameters and are related to the species-specific moisture requirements, which are adapted to changing environmental conditions. Thus, our results confirm the conclusions of Bingham et al. (2010), Bush and McInerney (2015) and Nott et al. (2000) that the pattern of n-alkanes has the potential to become a valuable proxy for chemotaxonomic identification and moisture conditions. Scorpidium scorpioides, a species with a rather narrow preference range (i.e. it is limited to open water conditions), shows low intraspecific variations. This matches the results for Sphagnum compiled by Bingham et al. (2010), which also show minor intraspecific variations. Aulacomnium in contrast, which grows in a rather wide range of moisture conditions, shows strong variations in its n-alkane spectra: whether this is a function of the individual’s growing conditions, however, needs to be investigated in a more extensive study.

5. Conclusions

The habitat and intraspecific isotopic and chemical patterns of 10 brown-moss species detected along small-scale hydrological gradients in Siberian polygonal tundra were studied.
The observed higher C/N ratios of xero-mesophilic mosses compared to those of the meso-hygrophilic mosses originate from the different environmental requirements when living emergent (i.e. investment in a higher stability resulting in high C/N ratios) as opposed to submerged. Furthermore, the latter group may also gain a better nitrogen supply through microbial symbioses.

With respect to the isotopic source pools, the meso-hygrophilic species have greater access than xero-mesophilic species, probably through symbioses with microorganisms and dissolved carbon. The approximate habitat-specific division of δ¹³C values resulting from discrimination by RuBisCO under different hydrological regimes, is overturned by the influence of microbial symbioses and makes a clear distinction between both habitat types impossible. For species, growing near the water level, no intraspecific relationship with water level was observed probably as a result of the parallel impact of processes causing opposing δ¹³C trends.

Our analyses reveal that, compared with xero-mesophilic mosses, meso-hygrophilic mosses are characterized by enriched δ¹⁵N values probably originating from microbial symbioses. Both carbon and nitrogen isotopic ratios seem to be valuable proxies to differentiate between taxa preferring the polygon rim or pond. Moreover, with respect to meso-hygrophilic mosses, the detected positive relations between intraspecific variations and the individuals’ relative growing position could allow even more semi-quantitative information about water-level changes to be inferred. The n-alkane patterns of brown mosses (limited 16 individuals belonging to five species) indicate that they are species-specific and have thus the potential to be developed as a chemotaxonomic proxy.

We also find that n-alkane patterns of brown mosses are characteristic for single species as well as for the individuals’ specific hydrological growing conditions. However, the potential chemotaxonomic and proxy value of n-alkane analyses needs to be further explored in a more extensive study.

Overall, our study indicates that C/N isotopic and biochemical n-alkane analyses of recent or fossil brown moss material has a high environmental indicator potential, particularly if species-specific material, because of the physiological characteristics of mosses, instead of bulk material is analysed.
References


Fig. 1: The Khatanga study sites are located in the south-east of the Taymyr Peninsula and both the sites on Samoylov Island are in the southern Lena River delta (Map by Th. Böhmer).
Fig. 2: C/N ratios by weight, $\delta^{13}C$ and $\delta^{15}N$ values of the 10 moss taxa studied. White boxplots are the xeromesophilic group and boxplots shaded in blue are the meso-hygrophilic group which prefers mesic to wet moisture conditions. A t-test was done to distinguish the signals between the two habitat groups.
Fig. 3a: Intraspecific relationships of the C/N ratio and the stable isotope values of carbon and nitrogen related to the water-level of the xero-mesophilic moss group. Regression lines (red) are only plotted for significant data sets.
Fig 3b: Intraspecific relationships of the C/N ratio and the stable isotope values of carbon and nitrogen related to the water-level of the meso-hygrophilic moss group. Regression lines (red) are only plotted for significant data sets.
**Fig. 4:** The relative amounts [%] of n-alkanes with an odd number of carbon atoms in selected moss species along the P3 polygon complex (species code plus position in metres at P3) brown mosses grouped by species and ordered by their preferences with respect to their mean plant-position relative to water-level from dry (for xeromesophilic (a) to wet (b) and meso-hygrophilic (c, d). Additionally, the sample-specific water level in cm is given after the species code in square brackets: mosses. Tom-nit: Tomentypnum nitens; Aul_tur: Aulacomnium turgidum; Aul_pal: Aulacomnium palustre; Dre_rev: Drepanocladus revolvens; Dre_sp: Drepanocladus sp.; Sco_sco: Scorpidium scorpioides.
Fig 5: PCA of n-alkanes separates the meso-hygrophilic group on the left side of axis 1 from the xero-mesophilic group on the right side. Along the second axis the Aulacomniaceae are distinguished from Tomentypnum nitens according to the distribution of long-chain n-alkanes with more or less than 30 carbon atoms.
Table A1: Brief description of studied polygons. (For further information see Zibulski et al., 2016)

<table>
<thead>
<tr>
<th>polygon cross section, (length of transect = polygon size)</th>
<th>coordinates</th>
<th>short description</th>
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<tbody>
<tr>
<td></td>
<td>06/P 70.666° N, 97.708° E</td>
<td>open forest; swinging bog (mat of mosses)</td>
</tr>
<tr>
<td></td>
<td>17/P 72.243° N, 102.233° E</td>
<td>forest-tundra intersection; shallow and sparsely vegetated</td>
</tr>
<tr>
<td></td>
<td>P3/II 72.431° N, 102.373° E</td>
<td>tundra; shallow and vegetated</td>
</tr>
<tr>
<td></td>
<td>LP1 72.375° N, 126.483° E</td>
<td>tundra; deep polygon without thaw depth below the water body</td>
</tr>
<tr>
<td></td>
<td>LP2 72.370° N, 126.481° E</td>
<td>tundra; shallow and vegetated</td>
</tr>
</tbody>
</table>
Table A2: C/N ratio by weight, $\delta^{13}$C and $\delta^{15}$N data of individual mosses depending on their position relative to the water-level (cm).

<table>
<thead>
<tr>
<th>Species</th>
<th>C/N ratio</th>
<th>$\delta^{13}$C [‰]</th>
<th>$\delta^{15}$N [‰]</th>
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<tbody>
<tr>
<td></td>
<td>median</td>
<td>range</td>
<td>median</td>
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<td><em>H. splendidens</em> (Hyl_spl)</td>
<td>47.1</td>
<td>29.5 to 67.9</td>
<td>34</td>
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<tr>
<td><em>T. nitens</em> (Tom_nit)</td>
<td>52.9</td>
<td>30.1 to 66.6*</td>
<td>46</td>
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<tr>
<td><em>A. turgidum</em> (Aul_tur)</td>
<td>52.4</td>
<td>29.9 to 64.3</td>
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<td><em>A. palustre</em> (Aul_pal)</td>
<td>49.6</td>
<td>22.5 to 66.9</td>
<td>40</td>
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<tr>
<td><em>H. lapponicus</em> (Ham_lap)</td>
<td>46.5</td>
<td>28.3 to 56.1</td>
<td>10</td>
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<tr>
<td><em>W. exannulata</em> (War_exa)</td>
<td>38.4</td>
<td>17.3 to 70.4</td>
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<td><em>M. triqueta</em> (Mee_tri)</td>
<td>37.1</td>
<td>25.8 to 50.7</td>
<td>45</td>
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<tr>
<td><em>D. revolvens</em> (Dre_rev)</td>
<td>42.6</td>
<td>17.5 to 64.1</td>
<td>72</td>
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<td><em>S. scorpioides</em> (Sco_sco)</td>
<td>38.9</td>
<td>15.4 to 62.8</td>
<td>69</td>
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<td><em>C. giganteum</em> (Cal_gig)</td>
<td>42.6</td>
<td>28.6 to 58.7</td>
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</table>

Stars designate significant linear regressions between parameter and the plant position relative to water-level (* p≤0.01, ** p≤0.05, *** p≤0.001).