C/N ratio, stable isotope (δ^{13}C, δ^{15}N), and *n*-alkane patterns of bryophytes 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 of wetlands. We present C/N ratio, δ^{13}C and δ^{15}N data of 400 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 taxa were investigated. The aim of the study is to see whether the inter- and intra-specific differences in biochemical and isotopic signatures are indicative of habitat with particular respect to water-level. Overall, we find high variability in all investigated parameters. The C/N ratios range between 15.4 and 70.4 (median: 42.9) and show large variations at intra-specific level. However, species preferring a dry habitat (xero-mesophilic mosses) show higher C/N 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

30 water, they do not need to invest in a sturdy stem-structure and accordingly have lower C contents in

31 their biomass. The δ^{13}C values range between -37.0 and -22.5‰ (median = -27.8‰). The δ^{15}N values

32 range between -6.59 and +1.69‰ (median = -2.17‰).We find differences in δ^{13}C and δ^{15}N signatures

33 between both habitat types and, for some species of the meso-hygrophilic group, a significant relation

34 between the individual habitat water-level and isotopic signature was inferred as a function of

35 microbial symbiosis. The *n*-alkane distribution also shows differences primarily between xero-

36 mesophilic and meso-hygrophilic mosses, i.e. having a dominance of *n*-alkanes with long (*n*-C_{29}, *n*-

37 C_{31}) and intermediate chain lengths (*n*-C_{25}), respectively. Overall, our results reveal that biochemical

38 and isotopic signals of certain moss taxa from polygonal wetlands are characteristic of their habitat

39 and can thus be used in (palaeo-)environmental studies.

1. Introduction

41 Specific physiological and morphological traits enable mosses to attain extensive surface coverage in

42 low-temperature ecosystems such as arctic tundra (Turetsky et al., 2012; Wasley et al., 2006). Mosses

43 are a major component of the biomass in arctic wetlands and contribute strongly to the biodiversity. In

44 particular, the vegetation of the widely distributed polygonal tundra is rich in moss taxa, which partly

45 originates from the strong compositional turnover along a small-scale hydrologic gradient (Zibulski et

46 al. 2016). As an intermediate layer between air and the permafrost soil, mosses control the water cycle,

47 greenhouse gas and energy exchange (Blok et al., 2011; McFadden et al., 2003), and the structure of

48 the habitats of vascular plant communities in arctic landscapes (Beringer et al., 2001; Gornall et al.,

49 2011; Malmer et al., 1994). Because of their low decomposition rates (Aerts et al., 1999; Turetsky,

50 2003), they contribute strongly to the peat and permafrost carbon pool (Tarnocai et al., 2009).

51 Despite the significance of mosses in high-latitude biodiversity and matter cycles only little is

52 known about their stable isotope and biochemical characteristics. Such information is not only

53 necessary to improve our understanding of the physiological adaptation or plasticity of mosses to

54 certain environmental characteristics, but can also be used when similar measurements of fossil plant

55 material are interpreted as proxies of former ecological or environmental conditions (e.g. Birks, 1982).

56   Carbon-to-nitrogen ratios (C/N), stable carbon and nitrogen isotope values ($\delta^{13}C$, $\delta^{15}N$) and the *n*-

57   alkane fingerprints of bulk organic matter are among the most commonly measured parameters of

58   plant matter (Chambers and Charman, 2004). The C/N ratios of mosses are generally in the range of

59   those of higher terrestrial plants (Prahl et al., 1980) but are known to depend on the available nitrogen,

60   which originates in pristine regions from decomposition of organic matter, microbial activity or

61   atmosphere deposits (e.g. Chanway et al., 2014; Lee et al., 2009). Furthermore, C/N ratios may be

62   related to growth form, i.e. higher ratios can be expected for mosses which compete with vascular

63   plants for light and thus need to invest in a high stem-stability (Sveinbjörnsson and Oechel, 1992).

64   The $\delta^{13}C$ signatures of an individual plant are a mixed signal of the physiological traits of the

65   species and the individual's direct environment. Mosses use the C_3 pathway for carbon assimilation

66   (O'Leary, 1988, Farquhar et al., 1989) and despite a lack of stomata in the photosynthetic active parts,

67   they have a similar range in their $\delta^{13}C$ values between -24 and -32 ‰ (Ménot and Burns, 2001; Rundel

68   et al., 1979; Smith and Epstein, 1971) as vascular C_3 plants. Differences in $\delta^{13}C$ values among several

69   species can be explained by individual plant physiology and biochemistry (Galimov, 2000).

70   Differences within a single species have been linked with environmental conditions such as

71   temperature (Skrzypek et al., 2007; Waite and Sack, 2011), the growing depth below water-level

72   (Raghoebarsing et al., 2005), the position within a cushion or hummock (Price et al., 1997), the lipid

73   content (Rundel et al., 1979) or the influence of microbial symbioses (Liebner et al., 2011; Vile et al.,

74   2014). Furthermore, even differences among branches and stems of single individuals are reported

75   (Loader et al., 2007). However, almost all of these studies were made on Sphagnaceae, which are not

76   representative of all mosses because of their specific morphology (i.e. the occurrence of a

77   photosynthetic active cell type and a dead cell type, which is responsible for water storage and often

78   an additional coating of the photosynthetic active cell) and their specific habitat preferences (i.e.

79   preferring acidic wetlands). Hence, this information cannot simply be transferred to brown mosses –

80   which form the major component in northern Siberian lowlands – due to their different morphology.

81   Most studies on $\delta^{15}N$ values of moss material have focused on the anthropogenic impact on the

82   nitrogen cycle (Harmens et al., 2011; Liu et al., 2008; Poikolainen et al., 2009), whereas reports on the

83    $\delta^{15}N$ signatures of mosses from relatively pristine ecosystems such as the Arctic are rare or have been

84   investigated in relation to the study of bird colonies (e.g. Lee et al., 2009). Potentially, such

85   information can indicate pathways and sources of the nutrient supply in these N-limited ecosystems

86   (Kielland, 1997; Michelsen et al., 1996, 1998).

87   Compared with vascular plants and *Sphagnum* species, relatively few investigations of *n*-alkane

88   patterns of brown mosses are available. *Sphagnum* species, for example, show a dominance of *n*-C_{23}

89   and *n*-C_{25} homologues (Baas et al., 2000) that are comparable to the pattern of vascular submerged

90   plants (Ficken et al., 2000). Other studies discuss the suitability of *n*-alkane patterns in moss species

91   for chemotaxonomical studies on recent and fossil material (Bush and McInerney, 2013; Nott et al.,

92   2000; Schellekens and Buurman, 2011). A higher protection potential of waxes with a higher content

93   of long-chain *n*-alkanes against solar irradiation or alternatively an enhanced loss of short-chain *n*-

94   alkanes by evaporation have been suggested as possible mechanisms to cause different *n*-alkane

95   patterns in leaf waxes of trees (Sachse et al., 2006). However, with respect to mosses the pattern and

96   mechanisms are even less understood.

97   This study presents isotopic ($\delta^{13}C$, $\delta^{15}N$) and biochemical (C/N, *n*-alkanes) characteristics of

98   mosses from low-centred polygons in northern Siberia. Low-centred polygons are geomorphological

99   forms in arctic landscapes originating from frost-heave processes in the soil. They are characterized by

100   elevated dry rims and a water-saturated or water-filled centre. This centimetre-scale hydrological

101   gradient is well reflected by a strong turnover in the vascular plant and moss composition (Zibulski et

102   al., 2016). We investigate the relationship between the isotopic and biochemical signatures and the

103   hydrological conditions within low-centred polygons. In particular, we aim to reveal whether

104   fingerprints are habitat-specific or rather species-specific.

2. Material and methods

2.1 Sites

107   The plant material was collected from eight low-centred polygons located along a zonal vegetation

108   gradient ranging from open forest via the forest-tundra intersection to subarctic tundra (Matveev,

109   1989) to obtain a representative sample set of northern Siberian lowlands (Fig. 1). Six of the polygons

110 (06/P, 17/P, P3/I, P3/II, P3/III, 12/P), sampled in 2011, are located in the Khatanga River region (70–

111 72° N, 97–102° E, southern Taymyr Peninsula) and a further two polygons (LP1 and LP2), sampled in

112 2012, are located on Samoylov Island in the Lena River Delta (72.4° N, 126.5° E). The climate is

113 cold-humid (Khatanga climate station annual mean temperature and precipitation: -13.2°C and

114 272 mm, Rivas-Martinez and Rivas-Saenz, 2009; Samoylov climate station annual mean temperature

115 and precipitation: -12.5°C and 232.7 mm, Boike et al., 2013)).

2.2 Sampling and studied moss species

117 A representative continuous transect of adjacent one square-metre plots (from rim to rim) was selected

118 for sampling in each polygon. The surface height in relation to water-level (collected at the centre of

119 each plot) and vegetation (abundance information) were recorded. Individual characteristics of each

120 low-centred polygon are presented in Table A1. Moss plants were hand-picked, dried in the field and

121 transported to the Alfred Wegener Institute in Potsdam. Taxa identification is based on the relevant

122 literature (Frahm and Frey, 2004; Lobin et al., 1995; Smith, 1978) and the Bryophyte Flora of North

123 America internet source (http://www.efloras.org).

124 In total, eight species that were observed to have different water-regime preferences were included in

125 the analyses. The species were divided into xero-mesophilic and meso-hygrophilic habitat type groups.

126 Generally the xero-mesophilic group represented by *Hylocomium splendens* (16 cm)*, Tomentypnum*

127 *nitens* (13 cm), *Aulacomnium turgidum* (13 cm) and *Aulacomnium palustre* (13 cm) can be separated

128 from meso-hygrophilic taxa represented by *Hamatocaulis lapponicus* (3 cm), *Warnstorfia exannulata*

129 (swimming mat), *Meesia triquetra* (-1 cm)*, Drepanocladus revolvens* (-5 cm)*, Scorpidium scorpioides*

130 (-13 cm)*,* and *Calliergon giganteum* (-30 cm). (Numbers in brackets denote the observed mean plant-

131 position relative to the water-level.)

2.4 Measurements of C/N ratios, stable carbon and nitrogen isotope values and *n*-alkane distributions

134 Selected plant material (i.e. apical parts of a specimen) were rinsed with de-ionised water and

135 mechanically cleaned from organic particulate material. The content of carbon and nitrogen (C_{total} and

136 N_{total}) and the ratio of stable isotopes ($\delta^{13}C$, $\delta^{15}N$) were measured with a DELTAplusXL isotope ratio

137 mass spectrometer (Thermo Fischer Scientific) coupled to an elemental analyser (NC2500 Carlo Erba)

138   via a CONFLOW III Interface. Due to the relatively wide range of C/N-ratios of mosses, we used

139   1.5 mg for each carbon stable isotope measurement and a replicate of 3.0 mg for each nitrogen stable

140   isotope measurement and the analysis of elemental composition. The calibration for carbon was

141   performed using a certified elemental standard (urea) and a δ^{13}C isotopic standard (IAEA CH-7). The

142   nitrogen contents were calibrated against an acetanilide standard and the nitrogen isotopic composition

143   with ammonium sulphate standard (IAEA N-1). The reliability of the method was checked with the

144   NIST plant standard SRM 1547. The isotopic ratios are given in delta notation relative to VPDB for

145   δ^{13}C values and relative to air for δ^{15}N values, respectively. The reproducibility for replicate analyses

146   is 0.2% for carbon and nitrogen and 0.2‰ for δ^{13}C and δ^{15}N values.

147   *n*-Alkane analyses were performed on a subset of samples. We took material from the polygon

148   complex P3 from the Khatanga region (72.149° N, 102.693° E), which comprises three successive

149   low-centred polygons (Table A1) to exclude effects of environmental conditions at different locations.

150   The moss samples were washed, identified and air-dried. They were weighed (150–1000 mg dry

151   weight) and samples extracted with an accelerated solvent extractor (ASE) (Dionex, Sunnyvale; USA)

152   using Cl_2Me:MeOH (10:1) at 5 bar and 75°C. The extract was separated in to aliphatic hydrocarbon,

153   aromatic hydrocarbon and nitrogen, sulphur and oxygen compound fractions using medium pressure

154   liquid chromatography according to Radke et al. (1980). Considering the low *n*-alkane concentrations

155   of our samples, 5 µg of quantification standard (5α-androstane, 1-ethylpyrene, 5 α-androstan-17-one

156   and erucic acid) were added. Gas chromatography (GC) of aliphatic hydrocarbon fractions was

157   performed using a GC Agilent 6890 equipped with an Ultra-1 fused silica capillary column (Model

158   Agilent 19091A-105, length 50 m, inner diameter 200 µm, film thickness 0.33 µm). Helium was used

159   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

160   time) to 300 °C (65 min hold time) at a rate of 5 °C per minute. The samples were injected by means

161   of splitless injection. Quantitative evaluation of data was done with ChemStation software.

162   **2.5 Statistical Tests**

163   We calculated the range, .25, .5, and .75 quantiles of δ^{13}C and δ^{15}N values and the C/N ratios for all

164   species (Table A2). Significant differences in the C/N ratios and δ^{13}C and δ^{15}N values among different

165   groups were tested with a t-test. In addition, we performed linear regression between the obtained

166   values for each single species and surface height. All analyses were implemented in R version 3.2.0 (R

167   Core Team, 2015). Furthermore, we performed a PCA with the percentage of *n*-alkane homologues

168   (square-root transformed) in R with the vegan package version 2.0-10 (Oksanen et al., 2013).

3. Results

170   The overall ranges in C/N ratios of both groups have a broad overlap (xero-mesophilic: 22.5–67.9;

171   meso-hygrophilic: 15.4–70.4). However, the medians of the C/N values of the xero-mesophilic species

172   ranging from 47.6 to 52.9 (Fig. 2) are significantly higher than those of the meso-hygrophilic group,

173   which range from 37.1 to 46.5 (t = 8.17, $p \ll 0.001$). The C/N ratios among individual species are not

174   significantly correlated with the water-level (Fig. 3a), except for *Tomentypnum nitens* ($r^2 = 0.11$,

175    $p < 0.05$).

176   The δ^{13}C values of the meso-hygrophilic group (-34.9 to -22.5‰) cover the range of the xero-

177   mesophilic group (-32.1 to -24.2‰), which have a noticeably lower variance in δ^{13}C values (Fig. 2).

178   The medians of the single species in the xero-mesophilic group (range: -29.4 to -27.1‰) are not

179   significantly different (t = -1.69, $p = 0.09$) from those of the meso-hygrophilic group (range: -29.2 to

180   -24.8‰). δ^{13}C values of *Meesia triquetra, Drepanocladus revolvens,* and *Scorpidium scorpioides* (all

181   belonging to the meso-hydrophilic group) are significantly positively correlated with the position of

182   the water-level (Fig. 3b), while no member of the xero-mesophilic group revealed such relationship

183   (Fig. 3a).

184   The ranges of δ^{15}N values of both groups are rather similar (Fig. 2). However, individual species

185   medians of both groups are significantly different (t = -6.96, $p \ll 0.001$; xero-mesophilic group; -3.2

186   to -2.7‰, meso-hygrophilic group: -2.9 to -0.1). *Drepanocladus revolvens, Scorpidium scorpioides,*

187   and *Calliergon giganteum*, all belonging to the meso-hygrophilic group, exhibit a positive relation

188   between the δ^{15}N values and position relative to the water-level.

189   *n*-Alkane distributions show the expected odd-over-even predominance of the chain length. The

190   absolute *n*-alkane concentrations (n-C_{19} to n-C_{33}) range from 34 to 238 µg g^{-1} of dry weight. The

191   individual taxa show significant differences with respect to carbon number of the most abundant *n*-

192   alkane. It is n-C$_{31}$ for *Tomentypnum nitens*, which is also the only species containing n-C$_{33}$ in

193   detectable amounts, n-C$_{29}$ for *Aulacomnium turgidum*, n-C$_{27}$ for *Aulacomnium palustre*, n-C$_{27}$ and

194   n-C$_{25}$ for the *Drepanocladus* taxa, and n-C$_{25}$ for *Scorpidium scorpioides*. These differences in the

195   n-alkane composition largely correlate with the species-preferred position relative to water-level (Fig.

196   4).

197   The described general trends are also visible in the biplot of the first two PCA axes which

198   together explain only 16.9% of the variance in the dataset (Fig. 5). The first axis separates xero-

199   mesophilic from meso-hygrophilic taxa. *Aulacomnium* taxa are located in the upper range and

200   *Tomentypnum nitens* in the lower range of the second PCA axis, while no trend is observed within the

201   meso-hygrophilic group along the second axes.

4. Discussion

4.1 C/N ratios

204   The C/N ratios of mosses from polygonal tundra in Northern Siberia are relatively low when

205   compared with those obtained for mosses from Antarctic bogs that range between 80 and 100 (Björck

206   et al., 1991) or from western Canada that range between 55 and 76 (Kuhry and Vitt, 1996). However,

207   neither the taxa nor the habitats sampled were fully comparable to those of our analyses, i.e. many

208   more taxa typical of xeric and mesic growing conditions were sampled in Antarctica and Canada. Our

209   results reveal that C/N ratios for the xero-mesophilic moss group are higher than for the meso-

210   hygrophilic group, probably portraying the known difference between terrestrial and aquatic plants

211   (Meyers and Ishiwatari, 1993). Competition with vascular plants (1) and accessibility of nitrogen

212   pools (2) may be the main reasons for this finding. (1) If moss plants invest in a high stem-to-leaf

213   biomass ratio, which is reflected by a high C/N ratio, they will increase their height and stability,

214   resulting in better competition with vascular plants for light (Sveinbjörnsson and Oechel, 1992).

215   Furthermore, a low N content of moss litter slows down the fungal and bacterial N mineralisation

216   which increases the thickness of moss litter mats (Gornall et al., 2007; Turetsky, 2003). This in turn

217   will increase the isolating function of moss mats, thus negatively affecting seed germination of

218   vascular plants (Gornall et al., 2007). (2) Higher amounts of dissolved nitrogen in water due to N_2-

219   fixation of algae, cyanobacteria, and other microorganisms may lead to a lower C/N ratio. Frahm

220   (2001) assumes that loose epi- and endophytic symbiotic relationships between mosses and

221   cyanobacteria are probably restricted to wetland taxa. Lindo et al. (2013) report such associations

222   between brown mosses and cyanobacteria. Thus, the N supply is better for mosses preferring wet than

223   dry habitats, and the respective taxa accordingly have lower C/N ratios. We expected to also find a

224   relationship between C/N ratios and water-level. However, the signal-to-noise ratio is probably too

225   low to give a meaningful result because only the average water level of each plot but not of each

226   individual plant was recorded.

227   4.2 δ^{13}C values

228   With respect to bryophytes, most isotopic studies have hitherto been performed on *Sphagnum* (Markel

229   et al., 2010) while our study focuses on brown mosses – a major component in Siberian wetlands. For

230   some meso-hygrophilic species (i.e. *Meesia triquetra, Drepanocladus revolvens, Scorpidium*

231   *scorpioides*) we find that the δ^{13}C signals are significantly related to the hydrological conditions at the

232   growing site of each individual, i.e. individuals growing at dry sites showed higher δ^{13}C values than

233   those growing at wet sites. No significant difference among the two habitat-groups is observed; rather

234   they partly contradict the intraspecific findings in that some of the xero-mesophilic species such as

235   *Hylocomium splendens* and *Tomentypnum nitens* known to prefer dry rims have particularly low δ^{13}C

236   medians.

237   Differences in moss δ^{13}C values either reflect a source signal depending on water level or a

238   physiological reaction of the plant related to water-level (Bramley-Alves et al., 2014; Proctor et al.,

239   1992). Mosses are typical C_3 plants (Farquhar et al., 1989, Rundel et al., 1979) characterized by a high

240   CO_2 compensation point (Bain and Proctor, 1980; Dilks and Proctor, 1975; Salvucci and Bowes,

241   1981). The high availability of atmospheric CO_2 and elevated diffusion rates of CO_2 in air compared to

242   water (O'Leary) result in typical terrestrial C_3 land plant δ^{13}C characteristics, because of a decreasing

243   cell water pressure in dry habitats which entails a strong discrimination rate against $^{13}CO_2$ induced by

244   RuBisCO (Rice and Giles, 1996). If plant tissue is coated by a water film, the cell water pressure

245   reaches an optimum, which results in a weaker discrimination rate against ^{13}C by RuBisCO (Rice and

246   Giles, 1996), because of a source restriction by the slower diffusion rate of CO_2 in water (Lloyd and

247   Farquhar, 1994). This basic signal may be masked by variations in $\delta^{13}C$ values of different carbon

248   sources, which are expected to be more influential in water-saturated habitats. As CO_2 uptake in

249   mosses occurs exclusively by the above-soil organs, the ^{13}C enriched sources of deeper soil sections,

250   originating from simple kinetic fraction by weight within the vertical soil profile, should not be

251   accessible.

252   The studies of Ruttner (1947) and Bain and Proctor (1980) show that, in general, moss taxa are

253   incapable of bicarbonate uptake. Hence, bicarbonate, known to be a carbon source for submerged

254   vascular plants and algae (Herzschuh et al., 2010; Merz, 1992), can most probably be excluded as a

255   carbon source for moss and thus as a factor influencing the $\delta^{13}C$ value. Moreover, the bicarbonate

256   content in pond waters in northern Siberian landscapes is very low (Wetterich et al., 2008). Mosses

257   potentially access ^{13}C-depleted CO_2 that originates from oxidation of typically strongly ^{13}C-depleted

258   biogenic methane by methanotrophic microorganisms (Kip et al., 2010; Liebner et al., 2011;

259   Raghoebarsing et al., 2005). Studies by Nichols et al. (2009) show that a higher water level at the peat

260   surface is crucial for an increasing methane-derived CO_2 release. Furthermore, symbiosis with

261   methanotrophs enhances the moisture-related effect on the $\delta^{13}C$ signal of bryophytes. Endophytic

262   microorganisms in hyalocytes of submerged *Sphagnum* (Raghoebarsing et al., 2005) or epiphytic

263   microorganisms on submerged brown mosses (Liebner et al., 2011) are presumed to provide directly

264   ^{13}C-depleted CO_2 to the lamina cells of mosses. Other sources of ^{13}C-depleted CO_2 are surface run-off

265   during spring flooding, rain events or decomposition processes in the pond (Leng and Marshall, 2004;

266   Maberly et al., 2013). Yet we cannot fully eliminate the possibility that the measured bulk material

267   was contaminated in parts with epi- or endo-phytic microorganisms. The overall signature would,

268   however, likely be unaffected, as Ménot and Burns (2001) could show that the $\delta^{13}C$ values of bulk

269   organic material and alpha-cellulose of *Sphagnum* are very similar.

4.3 $\delta^{15}N$ isotopes

271   Like $\delta^{13}C$, the interpretation of stable nitrogen isotope signatures of mosses is challenging because,

272   again, source signals need to be separated from those originating from physiological isotopic

273   discrimination processes. Our results yield relatively ^{15}N-depleted $\delta^{15}N$ values for xero-mesophilic

274   mosses growing preferentially on rims compared to meso-hygrophilic mosses.

275   The terrestrial arctic systems are generally thought to be nitrogen limited (Gordon et al., 2001;

276   Kielland, 1997). On the rim sites, atmospheric deposition can be considered to be the most important

277   source for nitrogen (Jonasson and Shaver, 1999) originating from fog, dew, precipitation and surface

278   run-off (Sveinbjörnsson and Oechel, 1992). However, most of the nitrogen available to rim mosses

279   originates from recycling of already ^{15}N-depleted higher plant and moss litter (Turetsky, 2003). The

280   ectohydric morphology enables an efficient nutrient uptake across the entire moss plant surface via

281   trapped water. In fact, the meso-hygrophilic group has a higher N content than the xero-mesophilic

282   group (see section on C/N ratio). Inorganic nitrogen, but especially the high amounts of organic

283   nitrogen provided by N-mineralization in tundra soils (Kielland, 1995) are important for mosses

284   growing on the rather dry sites such as the polygonal rims (Atkin, 1996).

285   Three of the investigated submerged or floating moss species show a significant positive

286   relationship between water-level and δ^{15}N values. These results are similar to those of Asada et al.

287   (2005) who tested a relationship between δ^{15}N values of different *Sphagnum* species and their position

288   relative to the groundwater level, which they assumed to originate from different nitrogen sources and

289   different internal fractionating processes. We assume that the often heavier nitrogen isotope signature

290   of meso-hygrophilic brown moss individuals originates from the high degree of symbiotic associations

291   with aquatic atmospheric nitrogen-fixing autotrophic microorganisms such as *Nostoc* or *Anabena*

292   (Lindo et al., 2013) or methanotrophs (Vile et al., 2014). The high spatial degree with endo- or

293   ectosymbiotic N_2-fixing microorganisms enables the direct uptake of their nitrogen products, which is

294   similar to that of N_2 in air.

295   4.4 *n*-alkane patterns

296   Compared to vascular plants that are characterized by a thick leaf-wax layer, mosses produce only a

297   small amount of *n*-alkanes (Baas et al., 2000; Ficken et al., 1998). Like previous studies on vascular

298   plants (Aichner et al., 2010; Ficken et al., 2000; Meyers and Ishiwatari, 1993), our results generally

299   reveal a differentiation between terrestrial taxa (i.e. xero-mesophilic group) characterized mainly by *n*-

300   alkanes maximizing at *n*-C_{29} and *n*-C_{31} and submerged living taxa (i.e. the meso-hygrophilic group)

301   maximizing at *n*-C_{25} and *n*-C_{27}. Our results thus confirm earlier investigations of Nott et al. (2000) and

302 Bingham et al. (2010), who compared the *n*-alkane fingerprints of *Sphagnum* taxa growing along a

303 hydrological gradient.

304   We furthermore found that individual specimens of a single xero-mesophilic moss species show

305 high variability in their *n*-alkane patterns, potentially originating from significant small-scale

306 environmental variability on polygon rims. In contrast, the *n*-alkane patterns of wet-habitat taxa cover

307 a small range only, potentially reflecting the buffering function of water, and thus these patterns are

308 promising for chemotaxonomic identification of their remains in peat sequences (Bush and

309 McInerney, 2013; Nott et al., 2000). However, these initial results of our study need to be corroborated

310 with a larger data set.

311 **5. Conclusions**

312 The habitat and intraspecific isotopic and chemical patterns of 10 brown-moss species detected along

313 small-scale hydrological gradients in Siberian polygonal tundra was studied.

314   The observed higher C/N ratios of xero-mesophilic mosses compared to those of the meso-

315 hygrophilic mosses originate from the different trait requirements when living emergent (i.e.

316 investment in a higher stability resulting in high C/N ratios) as opposed to submerged. Furthermore,

317 the latter group may also gain a better nitrogen supply through microbial symbioses.

318   With respect to the isotopic source pools, the meso-hygrophilic species have greater access than

319 xero-mesophilic species, probably through symbioses with microorganisms. The approximate habitat-

320 specific division of $\delta^{13}C$ values resulting from discrimination by RuBisCO under different

321 hydrological regimes, is overturned by the influence of microbial symbioses and makes a clear

322 distinction between both habitat types impossible.

323   Our analyses reveal that, compared with xero-mesophilic mosses, meso-hygrophilic mosses are

324 characterized by enriched $\delta^{15}N$ values probably originating from microbial symbioses. Both carbon

325 and nitrogen isotopic ratios seem to be valuable proxies to differentiate between taxa preferring the

326 polygon rim or pond. Moreover, with respect to meso-hygrophilic mosses, the detected positive

327   relations between intraspecific variations and the individuals' relative growing position could allow

328   even more semi-quantitative information about water-level changes to be inferred.

329   We also find that *n*-alkane patterns of brown mosses are characteristic for single species as well

330   as for the individuals' specific hydrological growing conditions. However, the potential

331   chemotaxonomic and proxy value of *n*-alkane analyses needs to be further explored in a more

332   extensive study.

333   Overall, our study indicates that isotopic and biochemical analyses of recent or fossil moss

334   material has a high environmental indicator potential, if species-specific material, because of the

335   physiological characteristics of mosses, instead of bulk material is analysed.

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563 **Figures**

564

565 *Fig. 1: The Khatanga study sites are located in the south-east of the Taymyr Peninsula and both the sites on*
566 *Samoylov Island are in the southern Lena River delta (Map by Th. Böhmer).*

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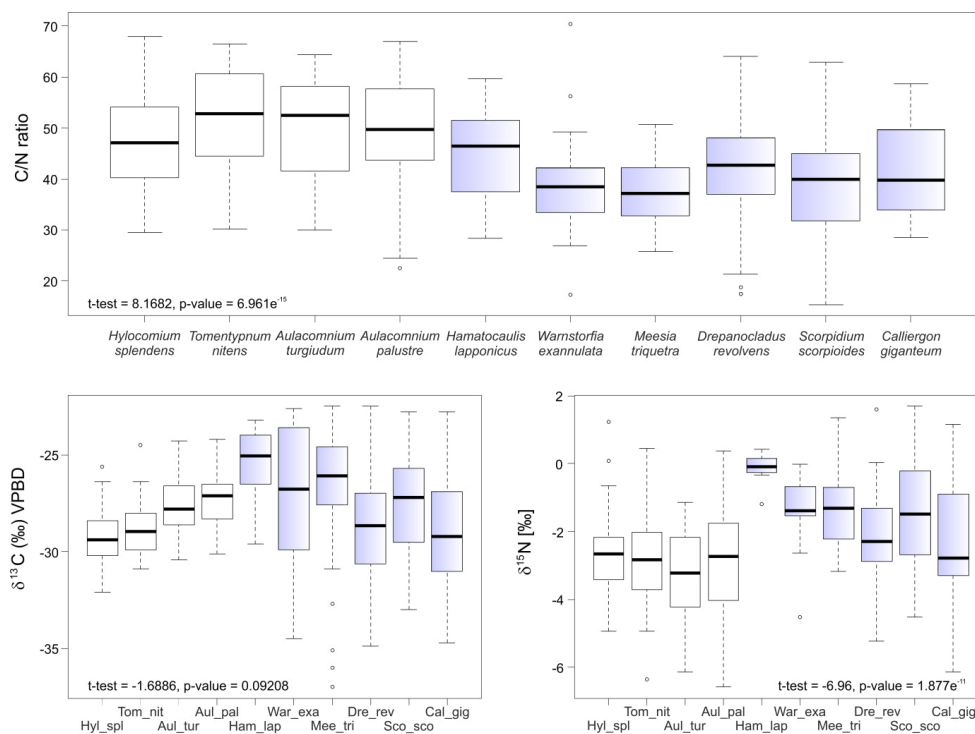
Fig. 2: *C/N ratios, $\delta^{13}C$ and $\delta^{15}N$ values of the 10 moss taxa studied. White boxplots are the xero-mesophilic group and boxplots shaded in blue are the meso-hygrophilic group which prefers mesic to wet moisture conditions. A t-test was done to distinguish between both habitat groups.*

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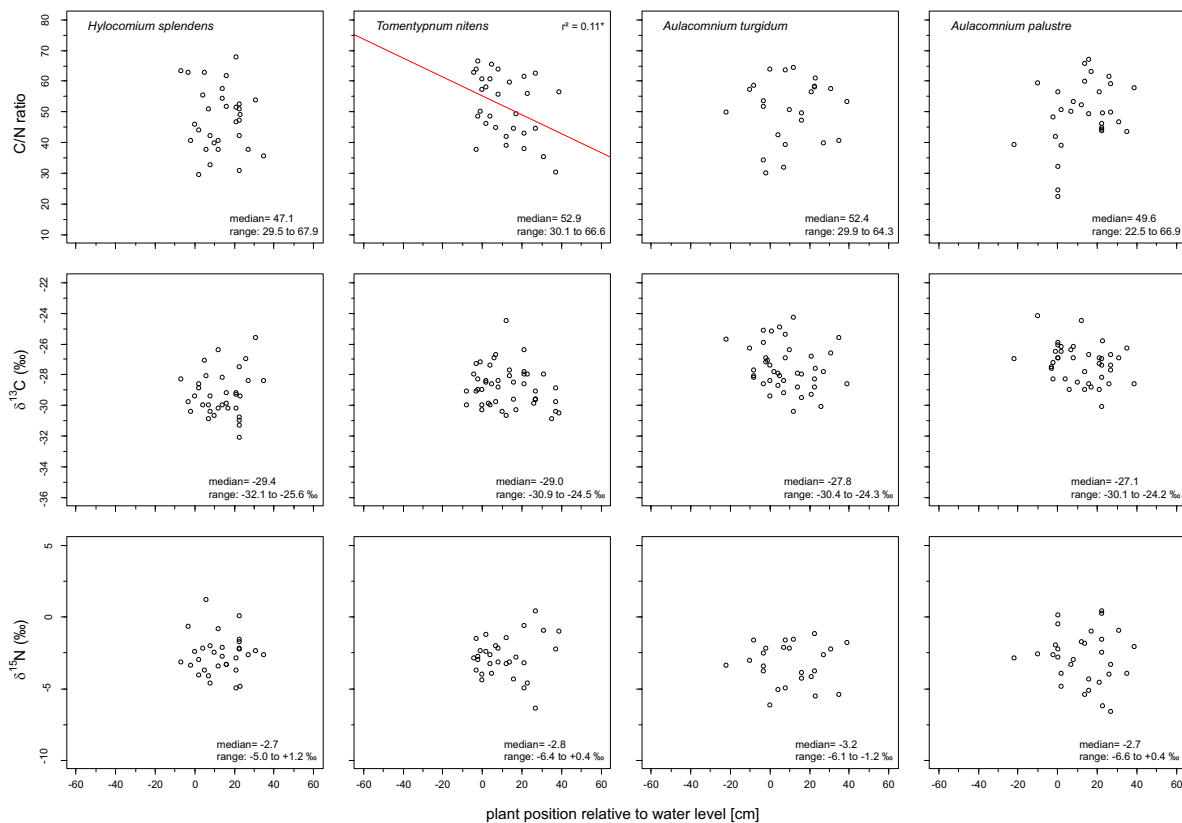
Fig. 3a: *Intraspecific relations of the C/N ratio and the stable isotope values of carbon and nitrogen related to the water-level of the xero-mesophilic moss group. Regression lines (red) are only plotted for significant data sets.*
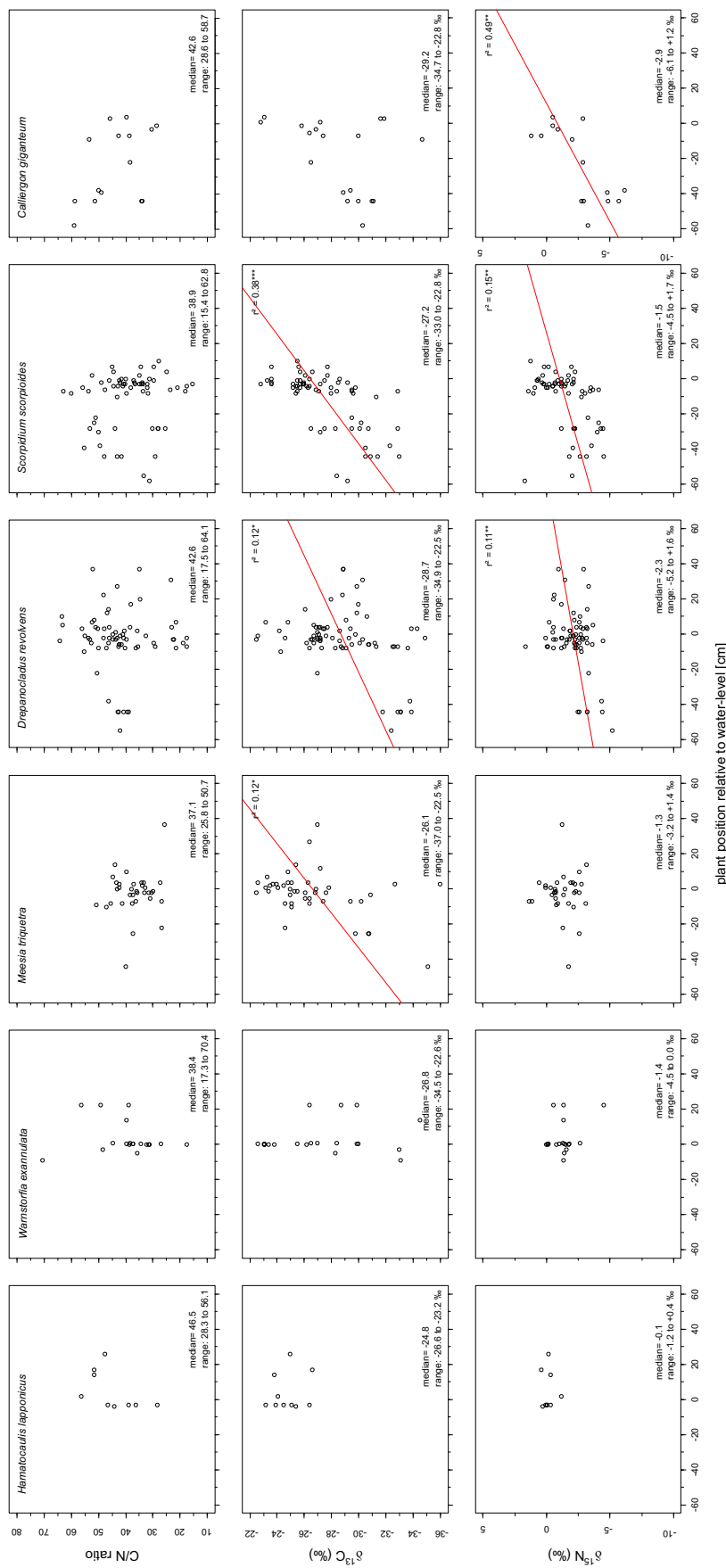
Fig 3b: *Intraspecific relations of the C/N ratio and the stable isotope values of carbon and nitrogen related to the water-level of the meso-hygrophilic moss group. Regression lines (red) are only plotted for significant data sets.*

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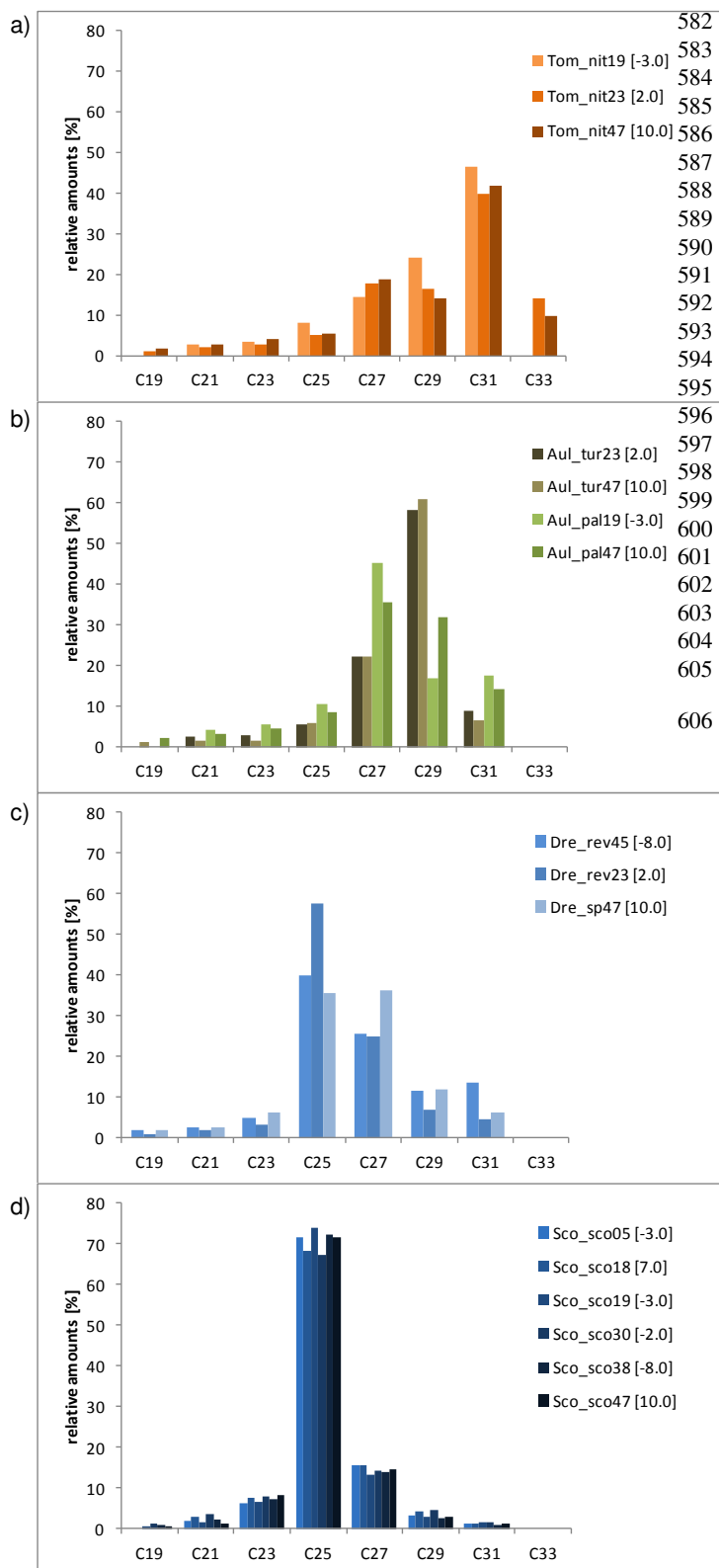
Fig. 4: *The relative amounts [%] of* n-*alkanes with an odd number of carbon atoms in selected moss species along the P3 polygon complex (species code plus position in metres at P3) grouped by species and ordered by their preferences with respect to water-level from dry (a) to wet (d). Additionally, the sample-specific water level in cm is given after the species code in square brackets. Tom-nit: Tomentypnum nitens; Aul_tur: Aulacomnium turgidum; Aul_pal: Aulacomnium palustre; Dre_rev: Drepanocladus revolvens; Dre_sp: Drepanocladus sp.; Sco_sco: Scorpidium scorpioides*

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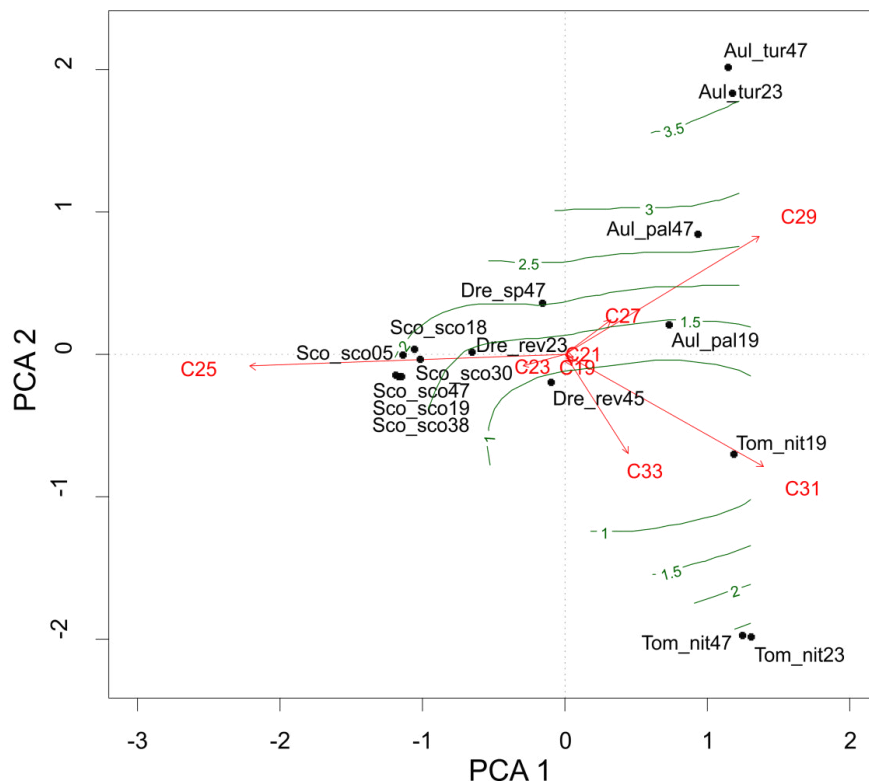
Fig 5: *PCA of* n-*alkanes separates the meso-hygrophilic group on the left side of axis 1 from the xero-mesophilic group on the right side. Along the second axis the* Aulacomniaceae *are distinguished from* Tomentypnum nitens *according to the distribution of long-chain* n-*alkanes with more or less than 30 carbon atoms.*

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612 **Appendix**

613 *Table A1: Brief description of studied polygons. (For further information see Zibulski et al., 2016)*

polygon cross section, (length of transect = polygon size)	coordinates	short description vegetation type; additional information
06/P	70.666° N, 97.708° E	open forest; swinging bog (mat of mosses)
17/P	72.243° N, 102.233° E	forest-tundra intersection; shallow and sparsely vegetated
P3/I		forest-tundra intersection; a complex of three individual polygons:
P3/II	72.149° N, 102.693° E	P3/I - deep, open water body P3/II - shallow, open water body
P3/III		P3/III - shallow completely vegetated
12/P	72.431° N, 102.373° E	tundra; shallow and vegetated
LP1	72.375° N, 126.483° E	tundra; deep polygon without thaw depth below the water body
LP2	72.370° N, 126.481° E	tundra; shallow and vegetated

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615 *Table A2: C/N ratio, $\delta^{13}C$ and $\delta^{15}N$ data of individual mosses depending on their position relative to the water-level (cm).*

Species	C/N			$\delta^{13}C$ [‰]			$\delta^{15}N$ [‰]		
	median	range	n	median	range	n	median	range
H. splendens (Hyl_spl)	47.1	29.5 to 67.9	34	-29.4	-32.1 to -25.6	31	-2.7	-5.0 to +1.2
T. nitens (Tom_nit)	52.9	30.1 to 66.6*	46	-29.0	-30.9 to -24.5	30	-2.8	-6.4 to +0.4
A. turgidum (Aul_tur)	52.4	29.9 to 64.3	41	-27.8	-30.4 to 24.3	24	-3.2	-6.1 to -1.2
A. palustre (Aul_pal)	49.6	22.5 to 66.9	40	-27.1	-30.1 to -24.2	30	-2.7	-6.6 to +0.4
H. lapponicus (Ham_lap)	46.5	28.3 to 56.1	10	-24.8	-26.6 to -23.2	9	-0.1	-1.2 to +0.4
W. exannulata (War_exa)	38.4	17.3 to 70.4	20	-26.8	-34.5 to -22.6	19	-1.4	-4.5 to 0.0
M. triquetra (Mee_tri)	37.1	25.8 to 50.7	45	-26.1	-37.0 to -22.5*	34	-1.3	-3.2 to +1.4
D. revolvens (Dre_rev)	42.6	17.5 to 64.1	72	-28.7	-34.9 to -22.5*	67	-2.3	-5.2 to +1.6**
S. scorpioides (Sco_sco)	38.9	15.4 to 62.8	69	-27.2	-33.0 to -22.8***	65	-1.5	-4.5 to +1.7**
C. giganteum (Cal_gig)	42.6	28.6 to 58.7	21	-29.2	-34.7 to -22.8	17	-2.9	-6.1 to +1.2**

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