Decomposition patterns, nutrient availability, species identities and vegetation changes in central-European summit bogs

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The global increase in atmospheric nitrogen deposition leads to changes in decomposition activity, which has been observed especially in nutrient-limited bog ecosystems relying on atmospheric inputs as the sole source of external nutrients. We conducted a reciprocal transplant decomposition experiment in two bogs in central Europe to test the effects of Sphagnum species (S. fallax, S. magellanicum, S. rubellum/russowii, cellulose strips as controls), material origin and the environment on Sphagnum decomposition and related nutrient release. Cellulose, but not Sphagnum biomass, decomposed more rapidly in the warmer and nitrogen-richer conditions of the suboceanic Jizera Mts. than in the subcontinental Jeseníky Mts. In the Sphagnum biomass transplants, interspecific differences in decomposition overruled the effects of both the origin of the material and the environment of the decomposition site, with S. magellanicum decomposing the slowest. Possible relationships between decomposition rates and recent changes in Sphagnum species composition in N-polluted bogs are discussed.

Introduction

Peatlands are one of the largest and most threatened global reservoirs of carbon (C). Due to their specific conditions, such as permanent waterlogging, cold climate, shortage of nutrients and slower plant tissue decomposability accompanied by low microbial activity, peatlands store dead organic matter. However, allogenic environmental changes disrupt the equilibrium between peat accumulation and peat decomposition (e.g., Franzén 2006, Gunnarsson et al. 2008).

Sphagnum mosses dominate the vegetation of ombrotrophic bogs, and their decay-resistant litter makes up the bulk of peat. Decomposition
rates of _Sphagnum_ biomass primarily depend on habitat conditions (Belyea 1996, Laiho 2006, Moore _et al._ 2007), litter quality (Johnson and Damman 1991, Turetsky _et al._ 2008, Hájek _et al._ 2011) and microbial activity (Thormann _et al._ 2004, Allison and Treseder 2011). Both the changing climate (drier summer periods, higher mean temperatures) and continuously high nitrogen deposition load in central Europe (Jiroušek _et al._ 2011, Granath _et al._ 2014, Hůnová _et al._ 2014) are supposed to enhance decomposition processes and thus carbon loss in bogs. These processes may become even more apparent when temperatures and N deposition increase synergistically (Berendse _et al._ 2001, Bragazza _et al._ 2006, Limpens _et al._ 2011). Hitherto, no consensus has been reached in the literature regarding the impacts of N on _Sphagnum_ decomposition. Fertilisation experiments (Aerts _et al._ 2001, Limpens and Berendse 2003, Bubier _et al._ 2007, Gerdol _et al._ 2007, Bragazza _et al._ 2012), a large-scale transplant experiment (Breeuwer _et al._ 2008) and a comparative study (Bragazza _et al._ 2006) found N to have a positive or no effect on _Sphagnum_ decomposition. Turetsky _et al._ (2008) even found a negative relationship between the concentration of N in _Sphagnum_ biomass and its decomposition rate. These discrepancies across studies focused on the effects of global change on _Sphagnum_ decomposition might be caused not only by different methodologies, but also by differences in the initial chemistry of _Sphagnum_ biomass, different background environmental conditions, duration of decomposition experiments or different species identity.

Recent studies focused on bog ecosystems in the context of ongoing global climate changes and alterations of nutrient cycles generally treat the entire genus _Sphagnum_ as a single functional group (Bragazza _et al._ 2005a, 2006, 2008, Bragazza and Freeman 2007, Gerdol _et al._ 2007, Straková _et al._ 2012). Decomposition rates of different _Sphagnum_ species have long been known to differ, however (Clymo 1965, Moore _et al._ 2007: table 6). Interspecific differences in _Sphagnum_ decomposition have so far been studied predominantly in the context of explaining bog microtopography (Johnson and Damman 1991, Hájek 2009), as hummock species are known to decay slower than lawn and hollow species (Belyea 1996, Limpons and Berendse 2003, Turetsky _et al._ 2008). Besides decomposition experiments using native _Sphagnum_ material, cellulose tests can be carried out to determine the decomposition rate of standard material not affected by the chemical properties of _Sphagnum_ material (Bartsch and Moore 1985, Braekke and Finér 1990, Hájek 2009). Although cellulose tests have limited relevance in bogs, because bog fungi specifically degrade particular compounds forming _Sphagnum_ tissues (Domsch _et al._ 1980, Thormann _et al._ 2001, 2002, Moore _et al._ 2007), cellulose is a useful standardized substrate for demonstrating the effects of environmental conditions on rates of decomposition.

We established a transplant experiment in two regions of the Sudetes Mts. in central Europe that differ in local climate, N deposition and nutrient availability, resulting in different nutrient concentrations and stoichiometry (N:P and N:K ratios) in _Sphagnum_ material (Jiroušek _et al._ 2011). We thus aimed to test the importance of the separate effects of (i) species identity, (ii) the origin of material, and (iii) the environment at decomposition sites on cellulose and _Sphagnum_ mass loss and related nutrient release.

**Material and methods**

**Study sites**

The experiment was carried out in two ombrotrophic mountain bogs in the Sudetes (border region between Czech Republic and Poland): Jizerka in the Jizera Mts. (50°49’38”N, 15°19’40”E, 870 m a.s.l.) and Vozka in the Jeseníky Mts. (50°09’32”N, 17°06’25”E, 1320 m a.s.l.). The distance between these sites is about 150 km. The two regions differ in their climate, nutrient conditions and N deposition load (Jiroušek _et al._ 2011). The westward located Jizerka Mts. are characterised by a suboceanic climate with higher temperatures, a more uniform course of precipitation during the year and a longer vegetation period. The subcontinental Jeseníky Mts. reach higher elevations and are about 2 °C colder than the Jizerka Mts. (Fig. 1a). The weather during the field experiment cor-
responded to long-term conditions without any exceptional fluctuations.

In the long-term, the mean water level in lawns is similar in both regions, about −12 cm in the Jizera Mts. and about −15 cm in the Jeseníky Mts. This small difference is caused by especially the more pronounced water level decrease in the subcontinental Jeseníky Mts. in drier periods, which did not occur during the experiment (Fig. 1b). The water regime in both regions has not been altered by human interventions.

Rates of N deposition in both study regions are high as compared with those in other areas of Europe, with higher long-term values (about 2–2.5 g m⁻² year⁻¹ over 3 years prior to the experiment) in the Jizera Mts. as compared with those (1.25 g m⁻² year⁻¹) in the Jeseníky Mts. (Bragazz et al. 2004, Jiroušek et al. 2011). Because of high precipitation, wet deposition predominates, and the proportion of nitrates and ammonium is approximately comparable (Hájková et al. 2011). In the Jizera Mts., the maximum peat depth of bogs is about 450 cm. The maximum peat depth of the study bog in the Jeseníky Mts. is 165 cm, and its age dates back 6000 years (Dudová et al. 2013).

The vegetation at the Jeseníky Mts. site is more homogeneous and relatively species-poor as compared with that at the Jizera Mts. site. Lawns and low hummocks at the Jeseníky Mts. site are formed by the peat mosses Sphagnum angustifolium, S. fallax, S. magellanicum and S. russowii, and are covered by Eriophorum vaginatum and the dwarf shrubs Andromeda polifolia, Calluna vulgaris, Empetrum hermaphroditum, Vaccinium oxyccocos and V. uliginosum. At the margins, the bogs gradually transition into peat spruce forests. The vegetation at the Jizera Mts. site is more heterogeneous because of the occurrence of Sphagnum papillosum, S. tenellum, Trichophorum cespitosum and other sub-oceanic plant species that are absent from the Jeseníky Mts. Lawns and low hummocks are formed predominantly by S. fallax, S. magellanicum, S. papillosum and S. rubellum, with the presence of Eriophorum vaginatum, Trichophorum cespitosum and dwarf ericoid shrubs. Higher hummocks are formed by Sphagnum fuscum and S. rubellum, and occur only at the eastern edge of the bog. The whole perimeter of the bog is covered by dwarf pine (Pinus mugo).

The nomenclature follows Danihelka et al. (2012) for vascular plants and Kučera et al. (2012) for bryophytes.

**Experimental setup**

In August 2008, individuals of dominant Sphagnum species (S. fallax, S. magellanicum and S. rubellum/russowii) were collected from low hummocks and lawns at both localities, always in mono-dominant patches with a low cover of vascular plants. These species were chosen because they differ taxonomically and ecologically, and are present in large amounts at both localities. Sphagnum rubellum and S. russowii are taxonomically allied species with transitional populations observed in the study area. In the suboceanic Jizera Mts., S. rubellum occurs in strictly ombrotrophic parts, while in the subcon-
tinental Jeseníky Mts, \textit{S. rubellum} is extremely rare and possibly does not occur in the study bog at all (Hájková \textit{et al.} 2010), \textit{S. russowii} being the dominant species. We therefore refer to \textit{S. rubellum/russowii} in this study, although when interpreting the results, we take into account the taxonomic difference between \textit{S. rubellum} and \textit{S. russowii}.

The material used in the experiments (i.e., live vs. dead, stem vs. capitulum) may affect the results considerably (Limpens and Berendse 2003). \textit{Sphagnum} mosses translocate nutrients from dying to living tissues, especially to the capitula, where metabolic activities are most concentrated (Malmer 1988, Rydin and Clymo 1989, Aldous 2002). The capitula (0–1 cm) were therefore cut off, and only young segments of stems below the capitula (approximately 1–3 cm from the top of the capitulum) were separated and used for the experiments (cf. Bragazza \textit{et al.} 2007, Breeuwer \textit{et al.} 2008, Hájek 2009).

Three grammes of oven-dried shoots were sealed inside nylon nets (50 ¥ 150 mm, mesh size 1 mm (Rychnovská and Fiala 1987). An additional part of the material was kept separate for subsequent analytical determination of nutrient concentrations. We prepared mesh bags for each of the three \textit{Sphagnum} species (30 repetitions ¥ 3 species ¥ 2 regions) and 60 mesh bags with cellulose (ash-free filter paper). In October 2008, all mesh bags were placed into the zone with senescent \textit{Sphagnum} stems (~1–6 cm). For each \textit{Sphagnum} species at each bog, we randomly selected five mono-dominant patches, in which we established decomposition experiment sites. Although we tried to avoid the influence of a fluctuating water table by placing mesh bags into drier microhabitats in the case of \textit{S. fallax}, two patches with this species in the suboceanic Jizera Mts. were submerged for part of the year. At each decomposition site, we placed both original and transplanted material from the other locality (three repetitions of both) and cellulose mesh bags as a standard (two repetitions). After one year (in September 2009), all mesh bags were collected and transported to the laboratory. In the laboratory, the biomass was separated from roots and other non-target material, oven-dried and weighed. Finally, the samples were analysed for nutrient and C concentrations.

### Nutrient concentration analyses

Dry \textit{Sphagnum} stems were oven-dried to constant weight (at 60 °C) and pulverized before analysis using Retsch planetary ball mill MM 400. Subsequently 10 g of homogenised dry matter was taken for the analytical determination of C, N, phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg) in 4–5 repetitions for each variant (material origin, \textit{Sphagnum} species). N was determined according to the Kjeldahl method with sulphuric acid and hydrogen peroxide; N concentration was detected by a distillation method with water vapour and sodium hydroxide addition. For determination of the other elements, material was digested in a sealed system with microwave heating. P was detected spectrophotometrically after colouration by a molybdenum agent whereas Ca$^{2+}$, Mg$^{2+}$ and K$^+$ concentrations were determined by flame atomic emission spectrometry and organic C gravimetrically after dry combustion.

### Ion-exchange resin analysis

Mineral N was trapped \textit{in situ} by ion exchange resins (IER) inserted into a special cover and IER stockings (Binkley and Matson 1983). These were prepared by placing a mixture of equal proportions of cation- and anion-exchange resin (50% of cation-exchange resin No. Purolite C100E and 50% of anion-exchange resin No. Purolite A520E) in cylindrical stockings (1.5 cm diameter by 10 cm length), made of a fine nylon mesh (grid size of 42 µm). Exchange sites of IER were saturated with Cl$^-$ and Na$^+$ ions before \textit{in situ} exposition. At each site, 30 IER stockings were installed; two in each microhabitat close to decomposition mesh bags. The ion-exchange resin stockings were deployed \textit{in situ} four times for six months (in May–September 2009, September 2009–May 2010, May–September 2010 and September 2010–May 2011). For the quantification of absorbed NH$_4^+$-N and NO$_3^-$-N trapped by the resin, the IER were eluted using a solution of 1.7 M NaCl and determined by distillation and titration (Peoples \textit{et al.} 1989). Results from the IER stockings were expressed as mg of NH$_4^+$-N per 10 ml IER and NO$_3^-$-N per 10 ml IER.
Data analyses

Differences in average mass loss and absorption of N ions by IER were tested using two-way ANOVA followed by Tukey’s HSD post-hoc test. For the analyses, the data on the mass loss and absorption of N ions by IER were shifted and transformed logarithmically \[\ln(x + 10)\] and \[\ln(x + 1)\] to achieve normality. In the decomposition experiment with cellulose, the following null hypotheses were tested: (1) There is no difference in mass loss between the two environmentally contrasting bogs in the Jizera Mts. and the Jeseníky Mts.; (2) There is no difference in cellulose mass loss among microhabitats characterised by mono-dominant *Sphagnum* species (*S. fallax*, *S. magellanicum* and *S. rubellum/russowii*); and (3) There is no significant interaction between the decomposition site and the microhabitat. Interactions are specified by a combination of particular levels of the two factors in the analysis. An interaction becomes significant when the impacts of the main factors are not simply additive, but the impact of one factor depends on the level of the other factor. Further tested hypotheses about the decomposition of cellulose were: (4) Within one bog, there is no difference in mass loss between the three types of microhabitats (separate analyses for the Jizera Mts. and for the Jeseníky Mts.); and (5) Within one type of microhabitat, there is no difference in mass loss between the two environmentally contrasting bogs (three analyses for the microhabitats characterised by *Sphagnum* species).

The analyses of *Sphagnum* decomposition were even more structured. Besides the factor “environment of the decomposition site”, two more factors were added: “species” and “origin of the material”. First, the data were divided according to the locality of the material’s origin, and the following null hypotheses were tested: (6) There is no difference in mass loss among the three *Sphagnum* species with respect to the environment of the decomposition site; (7) There is no difference in mass loss between the two decomposition sites with respect to the particular *Sphagnum* species; and (8) There is no significant interaction between the environment of the decomposition site and particular *Sphagnum* species. Second, the data on *Sphagnum* decomposition were divided according to the decomposition site, and the following null hypotheses were tested: (9) There is no difference in mass loss among the three *Sphagnum* species with respect to the origin of the material; (10) There is no difference in mass loss between the two origins of the material with respect to the particular *Sphagnum* species; and (11) There is no significant interaction between the origin of the material and particular *Sphagnum* species. Third, the data were divided according to the *Sphagnum* species, and each data set was used to test the following null hypotheses: (12) There is no difference in mass loss between the two origins of the material with respect to the decomposition site; (13) There is no difference in mass loss between the two decomposition sites with respect to the origin of the material; and (14) There is no significant interaction between the origin of the material and the decomposition site. Tukey’s HSD post-hoc test was performed to compare nutrient concentrations in *Sphagnum* tissues and N ions availability. Spearman’s correlations were calculated between initial nutrient concentrations and losses of biomass and nutrients during decomposition. Unfortunately, not all bags could be found in the field (5 bags of *S. rubellum/russowii*, 6 bags of *S. magellanicum* and 14 bags of *S. fallax*); some of those could have been pulled out or destroyed by deer. Moreover, biomass left in some bags after the year was insufficient to be analysed individually for nutrient contents after the decomposition experiment. For these reasons, we decided to present the results concerning nutrient losses as follows: nutrient loss (%) = \((C_0W_0 - C_1W_1)/C_0W_0 \times 100\), where \(C_0\) and \(C_1\) are mean nutrient concentrations, and \(W_0\) and \(W_1\) are mean weights of *Sphagnum* biomass in the bags before \((C_0, W_0)\) and after \((C_1, W_1)\) one year of decay. Positive values indicate net mineralisation; negative values indicate net immobilisation (Bragazza *et al.* 2007). Statistical analyses were performed using Statistica for Windows (Statsoft Inc. 2011) and R (R Development Core Team 2012).

Results

Cellulose mass loss

Decomposition of cellulose differed between the
two regions (Jizera and Jeseníky Mts.) with higher cellulose mass loss in the warmer and more N-polluted Jizera Mts. (two-way ANOVA: \( F_{1,35} = 10.7, p = 0.002 \)). Analogously, we found a higher mass loss of cellulose during decomposition in the Jizera Mts. when microhabitats of either \( S. \) magellanicum (\( F_{1,12} = 6.3, p = 0.027 \)) or \( S. \) rubellum/russowii (\( F_{1,11} = 5.1, p = 0.045 \)) were analysed separately. This difference was not significant for the microhabitat with \( S. \) fallax.

When we pooled the data from both regions, we found no difference in cellulose mass loss among microhabitats. On the other hand, we found differences among the microhabitats within the subcontinental Jeseníky Mts. (\( F_{2,18} = 4.5, p = 0.026 \)), where cellulose decomposed faster in the \( S. \) fallax microhabitat (average mass loss of 27.5%) than in the \( S. \) magellanicum microhabitat (average mass loss of 6.4%; Tukey’s HSD: \( p = 0.032 \); Fig. 2).

**Sphagnum mass loss**

We investigated *Sphagnum* mass loss with respect to locality of the material origin and decomposition site. We found significant differences in mass loss among species in both cases (Tables 1 and 2).

Tukey’s HSD post-hoc test revealed that the mass of \( S. \) magellanicum decomposed less than the mass of other species in all combinations of material origin and decomposition site (see Tables 1 and 2); differences between \( S. \) rubellum/russowii and \( S. \) fallax were not significant. The effect of decomposition site on *Sphagnum* mass decomposition was statistically insignificant (see Tables 1 and 2).

In subsequent analyses of the effects of material origin and decomposition site on individual *Sphagnum* species, the only significant difference was found for \( S. \) rubellum/russowii, where the material originating from the subcontinental Jeseníky Mts. decomposed more than the material originating from the suboceanic Jizera Mts. (Table 3). Within particular study sites, \( S. \) magellanicum decomposed significantly less than \( S. \) fallax or \( S. \) rubellum/russowii (\( S. \) russowii in this case) in the Jeseníky Mts. (Fig. 3).

**Table 1.** Effects of the *Sphagnum* species and decomposition site on mass loss evaluated by two-way ANOVA separately for material originating from the suboceanic Jizera and the subcontinental Jeseníky Mts. \( p \) values set in boldface indicate significant effects.

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<tbody>
<tr>
<td></td>
<td>( F(\text{df1,df2}) )</td>
<td>( p )</td>
</tr>
<tr>
<td>Species</td>
<td>6.04 (2,8274)</td>
<td>0.004</td>
</tr>
<tr>
<td>Tukey’s HSD</td>
<td>magellanicum vs. fallax</td>
<td>0.002</td>
</tr>
<tr>
<td>Decomposition site</td>
<td>0.97 (1,74)</td>
<td>0.327</td>
</tr>
<tr>
<td>Species × decomposition site</td>
<td>0.35 (2,74)</td>
<td>0.707</td>
</tr>
</tbody>
</table>

**Fig. 2.** Decomposition of cellulose (mass loss ± SD) in the suboceanic Jizera and the subcontinental Jeseníky Mts. separately for microhabitats characterised by mono-dominant *Sphagnum* species, \( S. \) rubellum/russowii (black), \( S. \) magellanicum (grey), \( S. \) fallax (white). Decomposition experiment took one year. Different letters above the bars indicate significant \( (p < 0.05, \) Tukey’s HSD) differences among *Sphagnum* species and between localities.
Nitrogen availability

In both study regions, the IER NH\textsubscript{4}\textsuperscript{+}-N values were significantly higher than the IER NO\textsubscript{3}\textsuperscript{−}-N values. This result was obtained for pooled data from all microhabitats (two-way ANOVA: \(F_{1,416} = 558.5, p < 0.001\)) as well as for particular microhabitats analysed separately (\(F_{1,146} = 220.2, p < 0.001\) for \(S.\) rubellum/russowii; \(F_{1,136} = 192.0, p < 0.001\) for \(S.\) magellanicum; \(F_{1,130} = 201.9, p < 0.001\) for \(S.\) fallax; Fig. 4). Comparing study sites, we unexpectedly found slightly higher concentrations of IER ammonium in the suboceanic Jizera Mts. (\(F_{1,203} = 0.1, p = 0.730\)) while the concentrations of IER nitrate (\(F_{1,203} = 4.5, p = 0.035\)) were higher in the subcontinental Jeseníky Mts, which does not correspond to higher N deposition in the suboceanic Jizera Mts. We found higher N availability during winter as compared with that during the vegetation period in the suboceanic Jizera Mts. (\(F_{1,108} = 18.8, p < 0.001\) for ammonium ions; \(F_{1,108} = 5.4, p = 0.022\) for nitrate ions). By contrast, in the subcontinental Jeseníky Mts, IER ammonium concentrations were relatively constant (\(F_{1,97} = 0.2, p = 0.625\)), and nitrate concentrations were not (\(F_{1,97} = 9.0, p = 0.003\)). Among the microhabitats formed by particular \(Sphagnum\) species, both more ammo-

![Fig. 3. Decomposition of \(Sphagnum\) species (mean \(±\ SE\) with respect to the origin of the material and decomposition site, the suboceanic Jizera Mts. (Jiz) and the subcontinental Jeseníky Mts. (Jes); the arrows indicate the direction of transplant from the site of the material origin to the decomposition site. \(S.\) rubellum/ russowii (black), \(S.\) magellanicum (grey) and \(S.\) fallax (white) are categorised according to the origin of the material and the decomposition site. The decomposition experiment took one year. Different letters above the bars denote significant differences among \(Sphagnum\) species in the relevant category.](image)

### Table 2. Effects of \(Sphagnum\) species and the origin of the material on mass loss evaluated by two-way ANOVA separately for decomposition site, the suboceanic Jizera and the subcontinental Jeseníky Mts. \(p\) values set in boldface indicate significant effects.

<table>
<thead>
<tr>
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<tbody>
<tr>
<td></td>
<td>(F(df_1,df_2))</td>
<td>(p)</td>
</tr>
<tr>
<td>Species</td>
<td>4.29 (2,7482)</td>
<td>0.017</td>
</tr>
<tr>
<td>Tukey’s HSD</td>
<td></td>
<td></td>
</tr>
<tr>
<td>magellanicum vs. rubellum/russowii</td>
<td>0.028</td>
<td></td>
</tr>
<tr>
<td>magellanicum vs. fallax</td>
<td>0.047</td>
<td></td>
</tr>
<tr>
<td>Material origin</td>
<td>0.91 (1,82)</td>
<td>0.343</td>
</tr>
<tr>
<td>Species (\times) material origin</td>
<td>0.38 (2,82)</td>
<td>0.686</td>
</tr>
</tbody>
</table>

### Table 3. Effects of the origin of the material and the decomposition site separately for \(S.\) rubellum/russowii, \(S.\) magellanicum and \(S.\) fallax evaluated by two-way ANOVA. \(p\) value set in boldface indicate significant effect.

<table>
<thead>
<tr>
<th>Effect</th>
<th>(S.) rubellum/russowii</th>
<th>(S.) magellanicum</th>
<th>(S.) fallax</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(F(df_1,df_2))</td>
<td>(p)</td>
<td>(F(df_1,df_2))</td>
</tr>
<tr>
<td>Material origin</td>
<td>6.44 (1,51)</td>
<td>0.014</td>
<td>0.39 (1,50)</td>
</tr>
<tr>
<td>Decomposition site</td>
<td>0.06 (1,51)</td>
<td>0.808</td>
<td>1.54 (1,50)</td>
</tr>
<tr>
<td>Material origin (\times)</td>
<td>0 (1,51)</td>
<td>0.956</td>
<td>0.03 (1,50)</td>
</tr>
<tr>
<td>decomposition site</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
nium ($F_{2,203} = 8.3, p < 0.001$) and more nitrate ions ($F_{2,203} = 1.8, p = 0.163$) were captured in the S. magellanicum microhabitats than in the S. fallax (post-hoc test for ammonium ions, $p = 0.014$) and S. rubellum/russowii microhabitats (post-hoc test for ammonium ions: $p < 0.001$).

**Initial nutrient concentrations in Sphagnum biomass and nutrient loss during decomposition**

We found higher tissue nutrient concentrations in the subcontinental Jeseníky Mts. (significantly P, K and Mg; regardless of the species) than in the suboceanic Jizera Mts, and generally for S. fallax (significantly K; without respect to the origin of the material). By contrast, C, Ca and N concentrations in Sphagnum biomass did not vary significantly across all species and localities (Table 4). In addition, concentrations of P, K, Ca and Mg correlated significantly.

K was most quickly released during the decomposition experiment, followed by P, and then by N, Ca and Mg (Fig. 5). In the case of Ca and Mg, we frequently observed higher concentrations in Sphagnum material after the decomposition experiment than the initial concentration. There were only minor differences in C loss, but the lowest C loss in S. magellanicum was related to the lowest mass loss of this species as compared with the others (Fig. 3). K, P and Ca concentrations determined before the decomposition experiment correlated significantly positively with N loss during the decomposition experiment. In addition, C loss correlated significantly positively with Ca concentrations, and Mg loss with Mg concentrations. Among all the tested nutrients (N, P, K, Ca and Mg), Sphagnum mass loss correlated significantly only with initial Ca concentrations (Table 5).

**Discussion**

**Decomposition of cellulose and Sphagnum biomass in warmer and nitrogen-richer conditions**

We found faster decay of cellulose in the suboceanic Jizera Mts., where higher temperatures and higher atmospheric N deposition occur as compared with the subcontinental Jeseníky Mts. Our results on cellulose decomposition indicate that, although the separate effects of temperature and N deposition could not be disentangled in our study, the environment of the decomposition sites influenced decomposition rates. Furthermore, we found the highest cellulose decay rates in the S. fallax microhabitat, which is characterised by higher nutrient availability (N, P, K, Ca and Mg). The high nutrient availability may have caused C:N, C:P and other C ratios to decrease, enhancing microbial decomposition (Kuhry and

Contrary to the cellulose test, we did not find significant differences between original and transplanted Sphagnum material as well as

![Fig. 5](image-url) Mean nutrient loss (%) from Sphagnum biomass after one year of decomposition. Negative values of nutrient loss indicate immobilisation in biomass during decomposition experiment. Jiz = suboceanic Jizera Mts., Jes = subcontinental Jeseníky Mts.; the arrows indicate the direction of transplant from the site of the material origin to the decomposition site.

<table>
<thead>
<tr>
<th>Sphagnum species and their origin</th>
<th>N</th>
<th>P</th>
<th>K</th>
<th>Ca</th>
<th>Mg</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td>S. rubellum/russowii</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Jizera</td>
<td>8.6 ± 0.6&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.38 ± 0.02&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.5 ± 0.1&lt;sup&gt;b&lt;/sup&gt;</td>
<td>2.4 ± 0.1&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.6 ± 0.1&lt;sup&gt;bc&lt;/sup&gt;</td>
<td>489.9 ± 0.1&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Jeseniky</td>
<td>8.7 ± 0.8&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.54 ± 0.05&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>4.2 ± 0.4&lt;sup&gt;a&lt;/sup&gt;</td>
<td>3.1 ± 0.2&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.9 ± 0.1&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>487.2 ± 0.2&lt;sup&gt;a&lt;/sup&gt;</td>
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<tr>
<td>S. magellanicum</td>
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<tr>
<td>Jizera</td>
<td>10.6 ± 0.3&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.48 ± 0.04&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>1.6 ± 0.3&lt;sup&gt;a&lt;/sup&gt;</td>
<td>2.7 ± 0.2&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.6 ± 0.1&lt;sup&gt;c&lt;/sup&gt;</td>
<td>486.1 ± 0.1&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Jeseniky</td>
<td>10.1 ± 0.4&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.52 ± 0.04&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>4.2 ± 0.2&lt;sup&gt;a&lt;/sup&gt;</td>
<td>2.9 ± 0.2&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.1 ± 0.0&lt;sup&gt;a&lt;/sup&gt;</td>
<td>487.6 ± 0.0&lt;sup&gt;a&lt;/sup&gt;</td>
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<tr>
<td>S. fallax</td>
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<tr>
<td>Jizera</td>
<td>10.3 ± 0.4&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.48 ± 0.06&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>4.1 ± 0.6&lt;sup&gt;a&lt;/sup&gt;</td>
<td>3.1 ± 0.4&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.8 ± 0.1&lt;sup&gt;abc&lt;/sup&gt;</td>
<td>489.1 ± 0.1&lt;sup&gt;a&lt;/sup&gt;</td>
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<tr>
<td>Jeseniky</td>
<td>9.7 ± 0.1&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.63 ± 0.05&lt;sup&gt;a&lt;/sup&gt;</td>
<td>6.3 ± 1.2&lt;sup&gt;a&lt;/sup&gt;</td>
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<td>1.1 ± 0.1&lt;sup&gt;a&lt;/sup&gt;</td>
<td>486.1 ± 0.7&lt;sup&gt;a&lt;/sup&gt;</td>
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between the contrasting environmental conditions at the decomposition sites during the experiment. In accordance with earlier studies (Johnson and Damman 1991, Belyea 1996, Limpens and Berendse 2003, Straková et al. 2011), our study showed that differences in the intrinsic properties of the biomass of each Sphagnum species override the effects of material origin as well as decomposition site. In the case of S. rubellum/russowii only, material collected from the subcontinental Jeseníky Mts. decomposed significantly faster than material from the suboceanic Jizera Mts. However, these results have to be treated with caution, as the material from the two origins also differs taxonomically. Sphagnum rubellum occurs in the Jizera Mts. whereas S. russowii occurs in the Jeseníky Mts.

The discrepancy between cellulose and Sphagnum mass loss confirms that higher temperatures and N deposition seem to be insufficient at altering the abundance of microorganisms decomposing polyphenols in sphagna to an extent that influences decomposition rates, at least during the one-year study period. Previous studies (Moore et al. 2007, 2008) demonstrated that short-term assessments of decomposition rates may not be necessarily related to longer-term patterns. Results concerning initial mass loss can be biased towards species-identity controls, while longer-term experiments capture more of environmental variation. Nevertheless, local environmental conditions seem to be more important when comparing contrasting wetland environments such as birch forests with mires (Lang et al. 2009), minerotrophic versus ombrotrophic mires (Bragazza et al. 2007) or drained versus natural mires (Lieffers 1988).

Nitrogen uptake in conditions of high N deposition

Our data from the ion-exchange resin analysis demonstrate differences in peat N availability between the two study regions (generally slightly higher IER ammonium in the Jizera Mts.) and partly also among the Sphagnum species (Fig. 4). Higher ammonium availability in the Jizera Mts. is very likely a consequence of higher atmospheric N deposition in combination with a more positive balance between production and consumption of ammonium ions (between ammonization and immobilization) due to warmer suboceanic climate conditions there. Concerning nitrate availability, Francez et al. (2011) evaluated the impact of increasing N inputs on denitrification rates beneath the S. magellanicum layer. As a consequence of increasing levels of N deposition, higher amounts of mineral N reach the underlying peat layer, modifying its N sink capacity via denitrification (Francez et al. 2011). By analogy, the lower IER nitrate levels in the suboceanic Jizera Mts. probably reflect a lower N sink capacity caused by elevated denitrification activity. The higher microbial activity (ammonization and denitrification) under the warmer suboceanic climate conditions of the Jizera Mts. follow the same pattern as the higher cellulose decomposition (see Fig. 2).

The critical N load for Sphagnum growth, previously recommended by Bobbink et al. (1996) (0.5–1.0 g m⁻² yr⁻¹), was latter described as reliable (Bobbink et al. 2003). Additionally Vitt et al. (2003) found out for net primary production of Sphagnum species a critical N-deposition value of between 1.48 and 1.57 g m⁻² yr⁻¹, and Xing

Table 5. Correlation matrix (Spearman’s correlation coefficients) between initial nutrient concentrations and their losses in Sphagnum biomass during the decomposition experiment. *** = p < 0.001; ** = p < 0.01; * = p < 0.05; n.s. = not significant.

<table>
<thead>
<tr>
<th></th>
<th>N loss (n = 12)</th>
<th>P loss (n = 12)</th>
<th>K loss (n = 12)</th>
<th>Ca loss (n = 12)</th>
<th>Mg loss (n = 12)</th>
<th>C loss (n = 12)</th>
<th>Mass loss (n = 51)</th>
</tr>
</thead>
<tbody>
<tr>
<td>N conc.</td>
<td>-0.07**n.s.</td>
<td>-0.30**n.s.</td>
<td>0.16**n.s.</td>
<td>0.21**n.s.</td>
<td>0.03 n.s.</td>
<td>-0.47 n.s.</td>
<td>-0.07**n.s.</td>
</tr>
<tr>
<td>P conc.</td>
<td>0.74**</td>
<td>0.22**n.s.</td>
<td>0.35**n.s.</td>
<td>0.27**n.s.</td>
<td>0.32 n.s.</td>
<td>0.57 n.s.</td>
<td>0.24**n.s.</td>
</tr>
<tr>
<td>K conc.</td>
<td>0.75**</td>
<td>0.29**n.s.</td>
<td>0.50**n.s.</td>
<td>0.32**n.s.</td>
<td>0.52 n.s.</td>
<td>0.57**n.s.</td>
<td>0.23**n.s.</td>
</tr>
<tr>
<td>Ca conc.</td>
<td>0.89***</td>
<td>0.52**n.s.</td>
<td>0.55**n.s.</td>
<td>0.40**n.s.</td>
<td>0.45 n.s.</td>
<td>0.78**</td>
<td>0.43**</td>
</tr>
<tr>
<td>Mg conc.</td>
<td>0.52**n.s.</td>
<td>0.24**n.s.</td>
<td>0.47**n.s.</td>
<td>0.20**n.s.</td>
<td>0.68*</td>
<td>0.38**n.s.</td>
<td>0.21**n.s.</td>
</tr>
</tbody>
</table>
et al. (2011) specified a similar threshold for N retention capacity in northern peatlands (1.6 g m\(^{-2}\) yr\(^{-1}\)). The rate of N deposition in the experimental study region in the Jizera Mts. exceeded the above-mentioned threshold values (about 2–2.5 g m\(^{-2}\) yr\(^{-1}\)). In the Jeseníky Mts, the rate of N deposition was very close to these thresholds (about 1.25 g m\(^{-2}\) yr\(^{-1}\)). However, there is growing awareness that unacceptable habitat changes may not only be caused by exceedance of the critical load, but that they can also be derived from short-term exposure to high N concentrations (Pearce and van der Wal 2008). Nevertheless, current critical loads for peatlands are likely to hold under the future climate even though the predicted impacts of likely changes in N deposition (Pearce and van der Wal 2008). Neverthe-
less, current critical loads for peatlands are likely to hold under the future climate even though the predicted impacts of likely changes in N deposition on Sphagnum appear to be less severe than those of the climate (Granath et al. 2014).

The low uptake rate of N by S. magellanicum revealed by our IER analysis is consistent with the finding of Jauhiainen et al. (1998), who compared intracellular uptake of NH\(_4^+\) and NO\(_3^-\) in seven Sphagnum species. The low ability of S. magellanicum to compete for N probably leads to its competitive exclusion by other fast-growing Sphagnum species like S. fallax (Twenhöven 1992, Hájek and Adamec 2009). Limpens et al. (2003) hypothesised that S. fallax can dominate if the N concentration in the Sphagnum capitula reaches at least 7 mg g\(^{-1}\) and the P concentration reaches at least 0.7 mg g\(^{-1}\), which are values corresponding to N-polluted central-European subcontinental summit bogs. In the previous study, Jiroušek et al. (2011) found that the growth of S. fallax in the suboceanic Jizera Mts. still seems to be P-limited. In the subcontinental bogs of the Jeseníky Mts., by contrast, higher P availability may allow its expansion. Similarly, Granath et al. (2012) found that the future expansion of fast-growing species like S. fallax under elevated N conditions may depend on P availability.

**Nutrient stoichiometry and losses**

Nitrogen concentration in Sphagnum biomass did not correlate with atmospheric N deposition, which corresponds with larger data set collected by Jiroušek et al. (2011). Under high N deposition, mosses become saturated by nitrogen unless availability of other nutrients increases and no longer uptake superfluous nitrogen (Bragazza et al. 2004), but this is probably not our case (see below). Besides N uptake, biomass N concentration can be affected by species-specific physiological processes (Harmens et al. 2011). Other possible factors are the dilution effect, which possibly takes place in the more biomass producing S. fallax and S. rubellum/russowii (Fritz et al. 2012), and the ability of Sphagnum mosses to detoxify excess N (Fritz et al. 2014).

Unlike Breeuwer et al. (2008), we did not find any relationship between N concentration in Sphagnum biomass and N loss during field decomposition experiment (Table 5), which could be caused by microbial immobilisation. Alternatively, Breeuwer et al. (2008) used different species (S. fuscum and S. balticum) and also found much lower N concentrations in Sphagnum stems and capitula, ranging from 3 to 8 mg g\(^{-1}\), in contrast to our study where N concentrations of Sphagnum stems were higher and ranged from 8 to 11 mg g\(^{-1}\). In both regions under study, atmospheric N deposition was probably too high to be absorbed by Sphagnum tissues (Bragazza et al. 2004). In such cases, the bog environment tends to become N-oversupplied, so its productivity becomes limited by other nutrients, especially P (Wang and Moore 2014). Hogg et al. (1994) found that the decomposition of S. magellanicum biomass is influenced more by P than by N. We found the N:P ratio in the Sphagnum biomass to be about 17 in the subcontinental bog in the Jeseníky Mts, which corresponds to the previous study of Jiroušek et al. (2011). The N:P ratio of about 22 found in the suboceanic Jizera Mts. is lower as compared with that reported in the previous study of Jiroušek et al. (2011); the N:P ratio for the same locality measured in 2006 was 28.57, which may be explained by decreased N deposition between 2006 and 2008. Based on the threshold N:P ratio of about 30 for continuing Sphagnum growth under increasing N deposition (Bragazza et al. 2004), we could argue that N seems to be still the limiting nutrient even in the case of the Jeseníky Mts. (Jiroušek et al. 2011) despite high atmospheric N deposition.

In our study, we hypothesized that higher initial nutrient concentrations in the biomass would
cause higher mass loss. Initial P, K, Ca and Mg concentration, but only Ca concentration significantly, were positively correlated with the total mass loss (Table 5). The similar result for K, but not for Ca, was already reported by Lang et al. (2009). On the other hand, Ivarson (1977) found higher decomposition of Sphagnum peat after CaCO$_3$ and MgCO$_3$ addition. We further found K to show the highest release during the decomposition, corroborating the results of Bragazza et al. (2007, 2008). Because K leaching occurs easily, it is rather difficult to distinguish between the effects of physical leaching and microbial activity; however, they are probably connected (Limpens and Berendse 2003). It is also important to note that both high initial K concentration and high K loss were specific for the most rapidly decomposing S. fallax, making it impossible to generalise the patterns found for K.

Differences in decomposition among Sphagnum species

We hypothesized that S. fallax (sect. Cuspidata) would decompose faster than S. magellanicum (sect. Sphagnum) and that S. rubellum/russowii (sect. Acutifolia) would decompose the slowest. However, this hypothesis turned out to be true only in the case of S. fallax, which decomposed the fastest in all treatments, except for material originating from the subcontinental Jeseníky Mts. that was incubated in the suboceanic Jizera Mts. Surprisingly, we found a lower mass loss of S. magellanicum as compared with that of S. rubellum/russowii. These interspecific differences can generally be explained by C allocation strategies of these species (Turetsky et al. 2008, Hájek et al. 2011). Species avoiding water stress (typically S. magellanicum or S. rubellum rather than S. russowii) invest relatively more C into structural, water holding tissues consisting of dead cells than their competitors (species from the sect. Cuspidata or S. russowii rather than S. rubellum) that allocate more C to photosynthesis and growth (i.e., metabolically active tissue that is rich in mineral nutrients and less recalcitrant C). Competitors are therefore more efficient in nutrient uptake and utilization, and become competitively successful under reduced stress.

Interspecific differences may also explain the sole statistically significant effect of material origin (Table 3). Although Sphagnum rubellum and S. russowii are taxonomically allied species (S. rubellum is probably a parent of S. russowii; Shaw et al. 2005), belonging to the same section and even forming morphologically transitional populations, Sphagnum rubellum (collected in the suboceanic Jizera Mts.) decomposed more slowly than S. russowii collected in the subcontinental Jeseníky Mts. Note that for the other two species there was no difference in decomposition between material originating at different localities. This result suggests that interspecific differences, independent of environmental effects, may hold also for closely related and sympatically occurring species. It, moreover, suggests that it may not be appropriate to consider Sphagnum species from the same section as a single homogeneous entity in studies of ecosystem functioning and the effects of global changes. Although S. russowii is one of the dominant Sphagnum species in subcontinental European summit bogs (Bragazza et al. 2005b, Hájková et al. 2006, 2010), it is not included in analogous studies from Scandinavia or North America, where this species occurs in more minerotrophic environments (Gignac and Vitt 1990, Laine et al. 2009).

Interconnection between ecosystem functioning and vegetation change

Our finding that in highly polluted summit bogs, interspecific differences govern Sphagnum decomposition patterns, inherently affecting C and nutrient cycling, may have crucial consequences for ecosystem change predictions. Many species have recently changed their frequencies in bogs (Gunarsson et al. 2002, Hájková et al. 2011, Kapfer et al. 2011), and this change has an ecophysiological background. Previously, Press et al. (1986) pointed out that some Sphagnum species are more sensitive to atmospheric pollution than others. In a more recent study, Wiedermann et al. (2009) suggested that S. balticum is more sensitive than S. fuscum to high N supply. Analogously, our data from the ion-exchange resin analysis demonstrate that S. magellanicum is unable to take advantage of higher mineral
N availability as effectively as S. fallax and S. rubellum/russowii under high N deposition load.

Considering the causality of relationships concerning N deposition, species-specific responses to it, ongoing vegetation change and decomposition patterns, we can integrate the results of this study with those already available from the same bogs (Jiroušek et al. 2011, Hájková et al. 2011, Dudová et al. 2013). This can further our understanding of ecosystem functioning and improve predictions of future development. The gradual replacement of S. magellanicum by the other Sphagnum species has been confirmed by a permanent-plot study from the same regions, the Jizera Mts. and the Jeseníky Mts. (Hájková et al. 2011). In the subcontinental Jeseníky Mts., the frequency of S. magellanicum in permanent plots in hummocks and lawns decreased from 40% in 1991 to 7% in 2008. On the other hand, Sphagnum species from sect. Cupidata slightly increased in both study regions (Hájková et al. 2011) despite the slightly decreasing water table. At the Holocene scale, Dudová et al. (2013) found that S. russowii rather recently replaced S. magellanicum in the peat sediment, but exact dating of this event was impossible because of a hiatus in the palaeoecological record separating S. magellanicum and S. russowii phases. Nevertheless, this hiatus is probably caused either by increasing human intervention in the bog or a drier climate (Dudová et al. 2013). This change of species composition could therefore lead to a change in decomposition rates and hence C cycling, but more focused long-term research is needed.

Conclusions

We found faster decay of cellulose in summit bogs in the warmer and highly N-polluted suboceanic Jizera Mts. as compared with that in the subcontinental Jeseníky Mts. However, because of the specificity of decomposers, it is impossible to generalise this result to Sphagnum decomposition. In the case of Sphagnum decomposition, interspecific differences outweighed the effects of both the origin of the material and the environment of the decomposition site. S. magellanicum decomposed more slowly than both S. russowii and S. fallax, the species which gradually replace it in summit bogs of the Czech Republic. We conclude that (i) taxonomic identity should be carefully taken into account in large-scale studies and meta-analyses focused on Sphagnum decomposition patterns, and that (ii) the relationships between nutrients in the environment and the competitive force of more nutrient-demanding Sphagnum species may lead to vegetation changes in moss layers, and with respect to species-specific mass loss, indirectly to shifts in decomposition rates in N-polluted areas. Any changes in Sphagnum species composition should therefore be considered when predicting future nutrient cycling in bogs.

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References


