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Habitat and species controls on *Sphagnum* production and decomposition in a mountain raised bog

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I evaluated production and decomposition characteristics of six dominant *Sphagnum* species in their natural microhabitats distributed along the gradient of water table in an open ombrotrophic bog. The growth in length was much higher in pools and hollows than in hummocks but the resulting annual production was roughly similar in the microhabitats due to a greater shoot density and consequently higher bulk density in hummocks. Although hummocks provided much higher potential for decomposition than hollows, the *Sphagnum* litter decomposed more slowly in hummocks due to much lower litter quality of the hummock sphagna. Thus the hummock *Sphagnum* species possess both principal mechanisms participating in maintaining hummocks above hollows — a sufficient production rate and limited decomposition rate. These mechanisms emphasize the role of *Sphagnum* mosses as autogenic ecosystem engineers controlling also the microhabitat diversification in patterned mires.

Introduction

Sphagnum-dominated peatlands cover large areas in the boreal zone. They developed due to long-term accumulation of extremely slowly decomposing plant litter (Clymo 1984). Decay-resistant *Sphagnum* mosses (Coulson and Butterfield 1978) and tissues of vascular plants or animals impregnated with *Sphagnum* leach (Verhoeven and Toth 1995, Painter 1991) undergo only partial decomposition during peat formation. Moreover, the accumulated peat provides environmental conditions that are unfavourable for communities of aerobic microbial decomposers, since peat is waterlogged and anoxic, cold, acid, poor in available nutrients and rich in antimicrobial compounds (Johnson and Damman 1993).

The surface of peatlands is generally differentiated into a mosaic of contrasting microhabitats such as elevated hummocks, flat lawns, wet carpets and hollows and water-filled pools. The long-term persistence of the hummock-hollow pattern (Backéus 1972, Svensson 1988, Belyea and Clymo 2001, Rydin and Barber 2001) is a consequence of the same rate of vertical peat accumulation below the hummocks and hollows. Position of the water table is the main factor constraining species' morphological and physiological adaptations and, consequently, species composition in this hummock–hollow gradient (e.g. Rydin 1993, Nordbakken 1996). Generally, hum-

mocks are formed by *Sphagnum* species from the section Acutifolia. Their tiny shoots form densely growing cushions with efficient conduction and retention of water but they are characterized by slow growth and smaller production. On the contrary, robust and rapidly growing shoots of hollow sphagna, belonging mostly to the section Cuspidata, form relatively productive sparse carpets in the wet environment (Moore 1989, Gunnarson 2005, Rydin *et al*. 2006).

Besides its effect on biomass production, the water status of the microhabitats strongly influences also the conditions for populations of soil decomposers and, consequently, the litter decomposition. Hummocks provide a higher decomposition potential than waterlogged hollows (Farrish and Grigal 1985, 1988, Santelmann 1992). Reciprocal *Sphagnum* litter transplants, used for separating the effects of the environment and species-characteristic litter quality, showed that the litter quality of typical hollow species, *S. cuspidatum*, exceeds that of typical hummock species, *S. fuscum* (Johnson & Damman 1991, Belyea 1996). These findings promoted the hypothesis that *Sphagnum* litter quality, as an intrinsic, species-controlled factor, is responsible for the initiation and maintenance of the hummock–hollow microtopography.

Thus, peat accumulation in hummock and hollow is controlled by the biomass production rate as well as the litter quality that affect the decomposition rate in these microhabitats (Johnson and Damman 1991, Van Breemen 1995, Belyea 1996, Malmer and Wallén 1999). Because the growth potential is lower and decomposition potential higher in hummocks than in hollows, I hypothesize that the hummock-forming *Sphagnum* species have a greater biomass production and/or a lower litter quality in comparison with hollow species. This is a way how hummock sphagna may control the long-term persistence of own microhabitat. In the present study, I investigate the production and decomposition characteristics of six dominant *Sphagnum* species in a bog with a well-developed surface microtopography. The objectives were: (i) to study relationships between the basic production parameters (i.e. bulk and shoot density, annual height increment, annual net production) in order to evaluate the general pattern in *Sphagnum* growth traits along the hummock–hollow gradient; (ii) to asses the seasonal growth dynamics in *Sphagnum*; (iii) to quantify the decomposition rate of *Sphagnum* litter within the six species' microhabitats separating the effect of microhabitat and the decomposability of *Sphagnum* litter (iv) and finally to relate the discovered production, decomposition and litter quality to the hummock–hollow dynamics.

Materials and methods

Site description and species

I carried out the experiments in Rokytecká slať (49°01.3´N, 13°25.1´E; 1115 m a.s.l.), a mountain raised bog in the Bohemian Forest — Šumava National Park and Biosphere Reserve, Czech Republic. The annual mean air temperature is 3.5 °C, the warmest month is July (12.2 °C). The mean total annual precipitation of 1486 mm is uniformly distributed during the year. Snow cover persists, on average, for 140 days.

I performed the study within a 3-ha mire area which consisted of a narrow strip of sparse lagg spruce forest of *Picea abies*, a broader zone of tall *Pinus* × *pseudopumilio* shrubs and large mire expanse. The understorey of the woody mire edge was dominated by dwarf shrubs such as *Vaccinium uliginosum* and *V. myrtillus* with *Sphagnum capillifolium* in the moss layer. The treeless mire expanse was covered by lawns with *Eriophorum vaginatum* and *Trichophorum cespitosum*. Some parts were dominated by low *Pinus* × *pseudopumilio* shrubs with *S. magellanicum*. Other moss species, namely *S. fuscum*, *S. rubellum* and *Polytrichum strictum* built flat hummocks, elevated microhabitats inhabited the ericaceous dwarf shrubs *V. uliginosum*, *Andromeda polifolia* and *Oxycoccus palustris*. The slightly sloping mire expanse was patterned into elongated depressions, flarks, which are filled with water or seasonally inundated. The shallow flarks and hollows were inhabited by *S. majus* with *Scheuchzeria palustris* and *Carex limosa*, the deeper flarks and bog pools hosted floating *Sphagnum cuspidatum*.

I studied all the *Sphagnum* species listed above in their typical microhabitats. The aver-

age water table was estimated in all *Sphagnum* microhabitats (Table 1) using the method of PVC tape discoloration (Belyea 1999). Strips of red PVC insulating tape were attached to bamboo stalks and inserted vertically into the peat. The discoloration indicated the depth of occurrence of anoxic conditions, which corresponds particularly with the seasonally high water table (Booth *et al*. 2005, Navrátilová and Hájek 2005). Based on the mean water table, *S. fuscum*, *S. rubellum* and *S. magellanicum* are referred to as hummock sphagna, *S. majus* as a hollow species and *S. cuspidatum* as an aquatic, pool species.

Growth and production measurements

In order to estimate seasonal variation in *Sphagnum* growth, I measured the apical height increments in five periods: Summer 2000 (15 June–28 Aug.; 74 days), Autumn 2000 (29 Aug.–28 Oct.; 60 days), Spring 2001 (29 Oct. 2000–9 June 2001; 70 days since 31 Mar. 2001 when the snow melted), Summer 2001 (10 June–28 Aug.; 79 days) and Autumn 2001 (29 Aug.–30 Oct.; 63 days). Spring 2001 included also growth during the preceding very late autumn and winter, but no growth was assumed to have occurred before spring. I chose three monospecific plots (replicates) of each of the six species. I measured the growth increment of their shoots using white thread as a marker, tied around the stem 10 mm below the shoot apices (Clymo 1970). I marked 15 *Sphagnum* shoots from each plot and inserted them carefully back into the moss vegetation of the same replicates. At the end of each period, I harvested the marked plants and inserted new sets of 15 marked individuals to each plot. The height increment was calculated from the distance to the thread below the shoot apices and the average growth rate was expressed as shoot increment in μm day^{-1} for each season.

After finishing the growth measurements in October 2001, I removed a *Sphagnum* block (50 cm^2 and 4 cm deep) from each investigated plot and determined the *Sphagnum* bulk and shoot density. Shoot density of adult plants was expressed as the shoot number per m^2 (tiny juveniles lacking differentiated branches were neglected). Few shoots of other *Sphagnum* spe-

Table 1. List of *Sphagnum* species, depth of the water table in their typical microhabitats (n = 13–24), production and decomposition parameters, and cation exchange capacity (CEC; means ± SE). Production characteristics (n = 3) were determined at the end of the growth season of 2001. Relative rates of decomposition (k; parameter of the negative exponential model of decomposition) were determined for *Sphagnum* litter and cellulose. Relative litter quality (Q_L) of *Sphagnum* was expressed as *Sphagnum k* in % of cellulose k. Data of CEC (n = 5) were estimated in 2005 (Hájek and Adamec 2009) in mosses from the same microhabitats where the growth and decomposition measurements were conducted. Values in columns with different letters differed at α = 0.05 (ANOVA, Tukey's HSD test; Extra sum-of-squares F-tests, α = 0.0033 in case of k).

Sphagnum species	Water table (cm)	Shoot density ($\times$ 1000 m^{-2})	Bulk density (g m^{-2} cm^{-1})	Increment (mm y^{-1})	Net production (g m^{-2} y^{-1})	*Sphagnum k* (k_S)	Cellulose k (k_C)	*Sphagnum* Q_L $k_S\,k_C^{-1}$ (%)	CEC (μeq g^{-1})
ANOVA P	< 0.0001	0.0002	0.0062	< 0.0001	0.52			< 0.0001	< 0.0001
fuscum	18.1 ± 1.2^{a}	102.3 ± 20.5^{a}	444 ± 64^{a}	12.4 ± 0.4^{a}	365 ± 58	0.22^{ab}	1.42^{a}	15.6^{ab}	918 ± 9^{a}
rubellum	16.1 ± 1.9^{a}	60.7 ± 10.3^{ab}	304 ± 46^{ab}	14.3 ± 2.6^{a}	229 ± 17	0.18^{abc}	1.31^{ab}	14.0^{ab}	860 ± 20^{b}
capillifolium	43.6 ± 1.3^{b}	46.4 ± 14.0^{bc}	204 ± 56^{b}	27.3 ± 5.3^{ab}	310 ± 122	0.15^{ac}	0.64^{bc}	24.2^{bc}	859 ± 10^{b}
magellanicum	15.5 ± 1.1^{a}	38.5 ± 7.6^{bc}	303 ± 65^{ab}	14.0 ± 3.5^{a}	251 ± 35	0.18^{ac}	1.80^{a}	9.7^{a}	831 ± 10^{b}
majus	4.1 ± 1.3^{c}	21.1 ± 2. 6^{bc}	207 ± 63^{b}	41.1 ± 4.1^{b}	242 ± 60	0.26^{b}	0.55^{c}	47.7^{c}	461 ± 9^{c}
cuspidatum	0.2 ± 0.1^{c}	9.7 ± 4.2^{c}	104 ± 61^{b}	91.9 ± 13.4^{c}	199 ± 116	0.11^{c}	0.13^{d}	85.5^{d}	469 ± 12^{c}

cies were included among those of the dominant species. *Sphagnum* bulk density was determined in the apical 10-mm moss layer (in g m^{-2} cm^{-1}). Bulk density of the second 10-mm shoot segment multiplied by the mean annual height increment in 2001 (in cm y^{-1}; sum of three measurements) gives the net primary production (NPP in g m^{-2} y^{-1}) (Weltzin *et al*. 2001). The method of NPP estimation assumes that the bulk density of the apical and subapical 10-mm shoot segments is constant in time.

I will discuss the seasonal growth rate dynamics with the respect to seasonal precipitation dynamics (by months). The precipitation data were collected by the Czech Geological Survey at a site located 40 km to the east at 795 m a.s.l. Because of the lower altitude, the absolute precipitation was lower at the meteorological station, but the seasonal dynamics is assumed to be comparable with that at the study site.

Decomposition measurement

I measured *Sphagnum* and cellulose decomposition rate using litter bags. I collected shoots of the six *Sphagnum* species from their typical microhabitats in May 2000. Parallel to Johnson and Damman (1991), I removed the capitula (about 5 mm of the shoot apices) and dried the next 15 mm shoot segment for 10 days at 24 °C and RH of about 40%. Subsamples of the air-dried shoots were oven-dried (80 °C, 4 hours) to calculate the oven-dry weight of the air-dried samples.

I sealed 70.0–150.0 mg of air-dried shoots into nylon mesh bags (55 × 55 mm, 0.6-mm mesh with 63% of openings; 50 bags per species). Similarly, I prepared 300 bags with cellulose (squares of ash-free filter paper, 50 × 50 mm, 80 g m^{-2}, one layer). Each *Sphagnum* bag was coupled with a cellulose bag and such bag-pairs (55 × 110 mm) were provided with a nylon thread. In total, I prepared 300 bag-pairs for the six species, ten replicates and five incubation periods. The bags were buried horizontally, about 5 cm below the moss surface of each species in June 2000. The nylon threads were anchored above the moss surface.

I collected a bag-pair of each replicate (60 altogether) at the end of each incubation period (0.4, 1.0, 1.4, 2.0, 2.4 years). In the laboratory, I removed roots and stolons grown into the bags and air-dried and weighted the incubated substrates. Mass loss was expressed as the remaining fraction of the original substrate.

For simplification, I consider the *Sphagnum* and cellulose mass loss from the litter bags as decomposition losses due to microbial respiration. According to the results of Coulson and Butterfield (1978) I assume negligible losses of solid particles due to mesh size, soil fauna and leaching of water-soluble organic compounds.

Data processing

I performed the statistics using STATISTICA ver. 7 (StatSoft Inc.), unless otherwise indicated. If necessary, the data were normalized (log-transformed) after which general linear models ANOVA was used to test the differences within each factor. Tukey's HSD mean separation test compared factor levels. All data are presented without transformation.

To test the relationships between the species characteristics and water table I used linear regression. I analyzed the *Sphagnum* growth rate using hierarchical ANOVA with interactions. The model expression was: GrowthRate = Species + Season + Plot(Species) + Species × Season.

I expressed the relative rates of *Sphagnum* (k_S) and cellulose (k_C) decomposition as the parameter k of the negative simple exponential model $R_t = e^{-kt}$, where R_t is fraction of the remaining *Sphagnum* (R_S) or cellulose (R_C) in time t (cf. Wieder and Lang 1982). I used the simple exponential model because it facilitates the comparison between litter types and the environment. To estimated k_S and k_C, I fitted the model to all 50 values of remaining litter (5 incubation periods and 10 replicates). I tested k_S and k_C for statistically significant differences between the six species with the extra sum-of-squares F-test (15 analyses in total) using Prism ver. 5 (GraphPad Inc.) for Windows. I used the Bonferroni correction to reduce the standard α-level of 0.05 by a factor of 15. Cellulose decomposition was used as a proxy for the decomposition potential at the species' microhabitats. For quantifying rela-

tive litter quality of *Sphagnum*, I standardized k_S by k_C ($Q_L = k_S k_C^{-1}$) and plotted k_S against k_C to visualize Q_L as a slope. To test Q_L for statistical differences I calculated it for each pair of litter bags and tested it using repeated measures ANOVA: $\log(R_S + 1.5)\log(R_C + 1.5)^{-1}$ = Species + Time + Species × Time, where Time was the repeated measures factor (5 levels). The constant 1.5 enabled division by a positive divisor. I used the same model of repeated measures ANOVA to test if k changed during the litter exposition. I calculated k_S and k_C values for all samples and exposition times (k_t): $k_t = -\log(R_t + 0.001)t^{-1}$; the constant 0.001 makes it possible to take the logarithm of zero values of cellulose R_t.

Results

Production characteristics

The six *Sphagnum* species differed greatly in shoot and bulk density (Table 1). These parameters correlated with the position of *Sphagnum* apices above the water table, i.e., along the gradient from pools and hollows to hummocks (Fig. 1). Although the aquatic species *S. cuspidatum* had the lowest shoot and bulk density, it had clearly the highest apical increment in 2001. *Sphagnum majus*, occupying wet hollows, behaved similarly but less markedly. On the contrary, the densely growing hummock species *S. fuscum*, *S. rubellum* and also *S. magellanicum* had small annual height increment but, due to their higher bulk density, they had similar or higher NPP than the two species from wet habitats (Fig. 1). *Sphagnum capillifolium* had intermittent growth characteristics (Table 1).

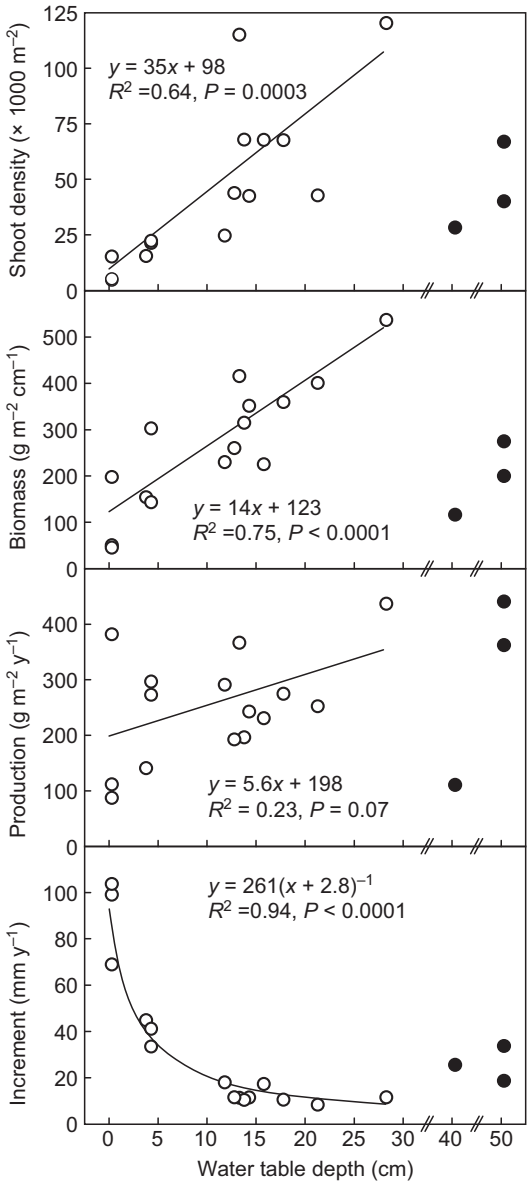

Fig. 1. Production characteristics of five *Sphagnum* species (three sites per species) along the gradient of water-table depth, which represents the hummock–hollow gradient (open symbols). *Sphagnum capillifolium* (filled symbols) grew in lagg forest, out of the hummock–hollow patterning, and therefore it was excluded from the regression models.

Seasonal variability of growth rate

There were significant differences in growth rate between species and seasons, and also in species' seasonal growth dynamics (interaction Species × Season; Table 2). *Sphagnum majus* and *S. cuspidatum*, the species of water-saturated habitats, both grew fastest in the summers and slowly in the autumns (Fig. 2). The two typical hummock species, *S. fuscum* and *S. rubellum*, grew slowly in summer 2000 but 1.5–2 times as fast in the autumn and 2–4 times as fast in summer 2001. The seasonal growth pattern of *S. magellanicum* resembled the species of wet habitats while *S. capillifolium* had strong increase in

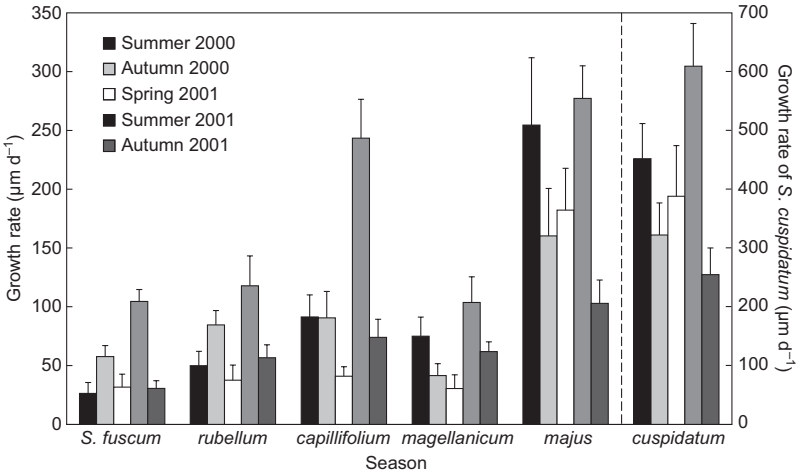

Fig. 2. Seasonal dynamics of growth rate in six *Sphagnum* species. Error bars indicate 95% confidence intervals (n = 19 to 44).

growth rate between the summers of 2000 and 2001 similarly to the hummock species.

Decomposition

The course of decomposition of *Sphagnum* litters and, especially, of cellulose greatly varied within the species' microhabitats (Fig 3). I calculated the mean relative decomposition rate of *Sphagnum* and cellulose (k_C and k_S) for each species (Table 1 and Fig. 4). Cellulose decomposed fastest in the drier habitats of hummocks and, particularly, within *S. magellanicum* where, in several cases, no cellulose litter was recorded after the first year already. Both *Sphagnum* and cellulose were decomposed slowest in pools with *S. cuspidatum*, the only habitat where *Sphagnum* litter decomposed almost at same rate as cellulose. Hollows showed a relatively low decomposition potential, but the litter of *S. majus* was decomposed at the highest rate among the sphagna. The forested habitat of *S. capillifolium* had a transitional character in terms of both k_C and k_S.

Table 2. Results of nested ANOVA for the factorial effects of species and season on *Sphagnum* growth rate.

Source	d.f.	*F*	*P*
Species	5	41.2	< 0.0001
Season	4	94.0	< 0.0001
Plot(Species)	12	9.7	< 0.0001
Species × Season	20	13.7	< 0.0001

In contrast with cellulose, the relative decomposition rate of *Sphagnum* litters was not constant during the whole exposure period (Table 3, factor Time). The decrease after the first year to about a half of that found in the fifth month in all species indicated that the fresh litter contained a significantly large fraction of a labile organic matter.

The relative decomposition rate of *Sphagnum* divided by that of cellulose gave an estimate of the relative *Sphagnum* litter quality, expressed as percentage of k_C (Q_L, Table 1 and Fig. 4). There was a steep increase in *Sphagnum* litter quality from the species of elevated habitats towards those of wet habitats. Accordingly to k_S, also Q_L decreased with decomposition time (Table 3).

Discussion

Growth and production

Although mean NPP of *Sphagnum rubellum* and *S. magellanicum* in this study corresponded to those found in earlier studies (Gunnarsson 2005), my results deviated from the general pattern of *Sphagnum* production along the hummock–hollow gradient. Hollow species of the section Cuspidata are, globally, about 1.9 times as productive as hummock species of the section Acutifolia with a mean NPP of 200 g m^{-2} y^{-1} (Gunnarsson 2005). In his literature review, Moore (1989) constructed a simple linear model of *Sphagnum* NPP as a function of mean annual temperature.

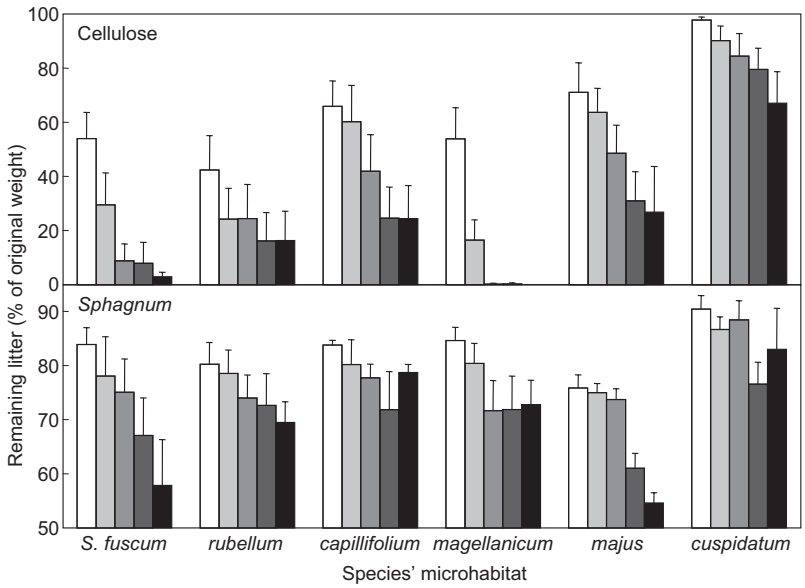

Fig. 3. Course of decomposition of six *Sphagnum* species and cellulose in microhabitats of those species (mean ± SE, n = 7–10). The grouped columns indicate five incubation periods (from the left: 0.4, 1.0, 1.4, 2.0 and 2.4 years).

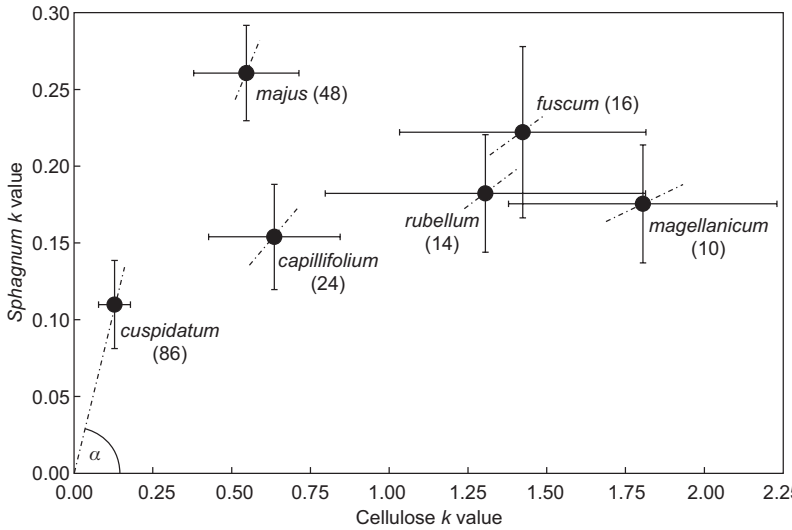

Fig. 4. Relative rates of decomposition (k; parameter of the negative exponential model of decomposition) of six *Sphagnum* species plotted against those of cellulose in the six *Sphagnum* microhabitats. The model was fitted to five successive measurements of remaining litter in ten replicates (n = 44 to 50). Relative litter quality of *Sphagnum* was expressed as Q_L (*Sphagnum k* in percentage of cellulose k; numbers in parentheses) and is shown as a slope (tg α) with the dash-and-dot lines. Error bars indicate 95% confidence intervals.

Table 3. Results of repeated measures ANOVA for the factorial effects of species and duration of decomposition (repeated-measure factor Time) on relative decomposition rate (k_t) of *Sphagnum* and cellulose and *Sphagnum* relative litter quality (Q_L). Q_L is k of *Sphagnum* litter standardized by k of cellulose. *See* Materials and methods for details.

		Sphagnum k_t		*Cellulose* k_t		Q_L	
Source	d.f.	*F*	*P*	*F*	*P*	*F*	*P*
Species	5	1.4	0.2588	7.6	< 0.0001	8.4	< 0.0001
Time	4	20.8	< 0.0001	1.1	0.3515	12.3	< 0.0001
Species × Time	20	0.7	0.8641	1.0	0.4534	0.8	0.6688

According to the model prediction using the mean annual temperature of 3.5 °C, the NPP of hummock and hollow sphagna in the study should be 195 and 300 g m^{-2} y^{-1}, respectively. On the contrary, the typical hummock species *S. fuscum* had the highest measured NPP while *S. cuspidatum*, which has been observed to be generally the most productive hollow species (Gunnarsson 2005), had the lowest NPP, comparable to the NPP expected for hummock species (Moore 1989, Gunnarsson 2005). These two species occupying the extreme ends of the hummock–hollow gradient were responsible for the deviation from the general pattern of NPP. The aquatic environment of *S. cuspidatum* may be suboptimal for NPP, probably due to lack of water limitation which normally constrains mosses to form dense covers. On the other hand, *S. fuscum* is able to grow in low shoot densities of about 10 000 m^{-2} (Wallén *et al*. 1988) as well as to form compact cushions with tenfold shoot density if the water table is low, which also leads to higher bulk density (Luken 1985). Water availability seem to be the factor constraining shoot and bulk density and thus also NPP of hummock species. Nevertheless, a higher or equal *Sphagnum* NPP in hummocks compared to hollows has been also reported from bogs (Lindholm and Vasander 1990) and fens (Bartsch and Moore 1985, Rochefort *et al*. 1990, Vitt 1990, Asada *et al*. 2003).

Water availability, i.e. water table (Luken 1985, Weltzin *et al*. 2001) and precipitation (Moore 1989, Asada *et al*. 2003, Gunnarsson 2005, Robroek *et al*. 2007b) are also important seasonal factors promoting *Sphagnum* growth and NPP. The hollow species *S. majus* showed the same seasonal growth dynamics (Fig. 2) as aquatic *S. cuspidatum* that was permanently flooded, but their growth dynamics differed from that in species from elevated microhabitats. This might indicate that during the two study years *S. majus* did not experience a summer drought period that is likely to affect hollow species (cf. Luken 1985, Moore 1989). Contrary to hummock species, summer growth in pools and hollows was probably enhanced by a higher temperature and longer photoperiod than in the spring or autumn. *Sphagnum* growth in elevated microhabitats may have been limited by lack of precipitation. The 2.6 times slower growth rate in summer 2000 than summer 2001 (Fig. 2) was associated with a relatively dry August 2000 when the precipitation was 2.4 time lower than in previous year (64 and 152 mm, respectively). In addition, sunny periods are accompanied by a high irradiance, which exposes *Sphagnum* mosses to photoinhibition that results in reduced growth rate (Murray *et al*. 1993). Moreover, cloudless periods use to be accompanied with night radiation frost that has inhibitory effect on the photosynthetic apparatus and growth (Rudolph *et al*. 1977, Gerdol 1995, Gerdol *et al*. 1998). Conclusively, year-to-year variation of weather conditions seemed to affect sphagna in elevated microhabitats more than sphagna in hollows and pools.

Litter decomposition and litter quality

The observed substantial mass loss in all *Sphagnum* litters during the first five months (Fig. 3) is likely to be attributed to easily metabolized organic compounds (Johnson and Damman 1993, Limpens and Berendse 2003) as well as to the relatively high nitrogen (N) and particularly phosphorus (P) contents in the green subapical shoot segments used in this study instead of brown dead segments (Hájek and Adamec 2009). The importance of litter quality for the initially fast decomposition rate is further supported by a constant relative decomposition rate of cellulose, which is free of mineral nutrients and readily available carbon (Table 3). Consistently with the present study, Farrish and Grigal (1985, 1988) found about three times higher cellulose loss from hummocks than from hollows in a bog after a year. Santelmann (1992) observed a similar pattern only if the water table was within 5 cm of the bog surface, but failed to find differences between hummocks and hollows if the water table in hollows was below 5 cm depth from the soil surface. Thus the differences in water table seem to be responsible for large differences in decomposition potential between microhabitats at the study site. Permanently aerated and still water-saturated (from the viewpoint of water potential) soil conditions make the hummocks more favourable microhabitats for decomposition than the hollows and pools, which are flooded either permanently or temporarily, i.e., limited by oxygen diffusion

(*see* also Clymo 1965, Johnson and Damman 1991, Belyea 1996, Moore *et al*. 2007).

Most of the previous studies compared litter decomposition of *Sphagnum* species in their original microhabitats and found mass losses of hummock sphagna to generally be only half of those of hollow species (Johnson and Damman 1993 for review) or even less (Moore and Basiliko 2006). Also the present study showed that the hollow species *Sphagnum majus* had the fastest relative decomposition rate; but it was only by about 15%–70% faster than that of the species of elevated microhabitats and by almost 250% faster than that of the aquatic *S. cuspidatum*. To separate the effects of the plant litter chemistry from environmental effects, Johnson and Damman (1991), Belyea (1996) and Turetsky *et al*. (2008) transplanted moss litters between the contrasting microhabitats. Their results pointed to the role of litter quality — all the hummock sphagna were intrinsically more decay-resistant than the hollow ones in bogs and poor fens. A similar method used in this study but the reciprocal transplants replaced by cellulose as a standard substrate allows direct comparisons under the assumption that the plant litter and cellulose decomposition is controlled by the same factors. Thus the result here strongly supports the earlier findings of the decay-resistance of the hummock sphagna: their relative litter quality was significantly lower than that of the hollow species *S. majus* and particularly *S. cuspidatum* from pools.

Regulation of *Sphagnum* litter quality

The differences in the litter decomposability of *Sphagnum* should result from limitations by mineral nutrients and in the content of decay-inhibiting and decay-resistant compounds (Johnson and Damman 1993). According to earlier study (Hájek and Adamec 2009), the studied *Sphagnum* species differ in the litter nutrient contents. *Sphagnum capillifolium*, which grows in the lagg forest and thus receives additional nutrients as dry deposition from the forest canopy, had relatively high contents of N, some cations and particularly P. The enhanced nutrient content in this species was accompanied by the highest decomposability among the species of elevated microhabitats. Although the aquatic *S. cuspidatum* decomposed slowest, its litter quality was about twofold in comparison with the hollow *S. majus*. *S. cuspidatum* also had about twofold N and quadruple P content (Hájek and Adamec 2009), probably due to the rich cyanobacterial flora found in floating mats of this species at the study site (Lederer and Soukupová 2002). Enhanced litter N (Limpens and Berendse 2003, Bragazza *et al*. 2006) and P (Hogg *et al*. 1994) contents have been found to stimulate the decomposition of *Sphagnum* litter. *Sphagnum majus* had, however, lowest N and P contents among the sphagna in the study site (Hájek and Adamec 2009); Similarly to Turetsky *et al*. (2008) the results imply that the contents of N and P alone did not explain the litter quality pattern along the hummock–hollow microtopography.

Cation exchange capacity (CEC) of *Sphagnum* shoots is closely related to the content of uronic acid in cell wall holocellulose, which is generally higher in hummock than in hollow sphagna (Clymo 1963, Spearing 1972). Painter (1991) suggested that uronic acids are responsible for the well-known decay-inhibiting properties of *Sphagnum* litter, although the mechanism has not yet been fully understood (cf. Ballance *et al*. 2008). Johnson and Damman (1993), who compared uronic acid content of five *Sphagnum* species with data of mass loss of the same species from literature, revealed a weak negative correlation between the content of uronic acids and mass loss. The mean relative litter quality presented in this study correlated negatively with the mean CEC (Table 1) across the six *Sphagnum* species ($r = –0.88$, $P = 0.021$, $n = 6$), supporting decay-inhibitor theory. Turetsky *et al*. (2008) found close correlation between *Sphagnum k* and the ratio between metabolic and structural carbohydrates. Consequently, cell-wall carbohydrates such as uronic acids and/or resource partitioning into structural carbohydrates may be responsible for the variation in litter decomposability of hummock and hollow species.

Hummock–hollow dynamics

The development and maintenance of the bog-surface patterning was subjected to discussions

and investigations during the whole 20th century (Zobel 1988 for a review). Although Zobel listed also several abiotic mechanisms, the long-term persistence of the hummock–hollow pattern (Backéus 1972, Svensson 1988, Malmer and Wallén 1999, Rydin and Barber 2001) is assumed to be under the control of biological mechanisms such as litter production (Malmer and Wallén 1999) or decomposition (Johnson and Damman 1991, Moore 1991, van Breemen 1995, Belyea 1996).

It is therefore obvious that the long-term persistence of the bog microtopography must result from equal rates of volumetric peat accumulation across the hummock–hollow pattern (Belyea and Clymo 2001). Peat formation is thus generally the function of the ratio between biomass production and decomposition. In the present study, the *Sphagnum* NPP was generally the same in all microhabitats, with the tendency to be higher in hummock. This resulted from the high bulk density of the compact hummock cushions, despite the smaller annual height increment in these species. The litter of the hummock sphagna had a poorer litter quality. Therefore, it decomposed slightly more slowly than hollow species, despite of the much greater decomposition potential in hummocks. This summarization shows that hummock species possess both principal mechanisms participating in maintaining hummocks above hollows — a sufficient production rate and a limited decomposition rate. The former is connected with species' growth pattern (shoot and bulk density), the latter with the species' litter quality. These properties provide the hummock sphagna with the exclusivity to control the persistence of their own microhabitat, in which they avoid competition with species restricted to wet microhabitats (Rydin 1993). Such a vertical niche separation allows different species to coexist at the mire surface.

The presented data of production and decomposition are based on short-term experiments; an estimation of the final rate of peat formation and accumulation is therefore impossible. Nevertheless, these trends emphasize the role of *Sphagnum* mosses as autogenic ecosystem engineers (*sensu* Jones *et al*. 1994) controlling not only the bog development but also the microhabitat diversification in patterned mires. In the light of on-coming climate warming followed by lowering of water level, hummock species and hummocks are expected to expand at the expense to the species and microhabitats associated with high water table (Laiho 2006, Robroek *et al*. 2007a, 2009, Breeuwer *et al*. 2008). Sufficient input of low-quality litter in such hummock-dominated systems may maintain positive net ecosystem CO_2 exchange (Laine *et al*. 2007) and thus keep the carbon sink character of these peatlands (Laiho 2006).

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