

Effects of water level and temperature on performance of four *Sphagnum* mosses

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Received: 20 December 2005 / Accepted: 1 July 2006 / Published online: 23 July 2006
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Abstract To evaluate the effects of changes in water level and temperatures on performance of four *Sphagnum* mosses, *S. magellanicum*, *S. rubellum*, *S. imbricatum* and *S. fuscum* were grown at two water levels, –5 cm and –15 cm, and at two temperatures, 15°C and 20°C. These species differ in their position along the microtopographical gradient and in their geographical distribution. Height increment, subcapitulum bulk density, biomass production, capitulum water content and cumulative evaporation were measured. Height increment and biomass production of *S. magellanicum* was lower at low water table than at high water table, whereas height increment and biomass production of *S. rubellum*, *S. imbricatum* and *S. fuscum* were unaffected. Height increment of *S. magellanicum*, *S. rubellum* and *S. imbricatum* was higher at high temperature than at low temperature. Biomass production of only *S. magellanicum* and *S. rubellum* was higher at

high temperature than at low temperature, corresponding with their more southern distribution. Cumulative evaporation of *S. magellanicum* and *S. rubellum* was lower at low water table and could be explained by hampered water transport towards the capitula. We conclude that changes in water table and temperature may alter the *Sphagnum* composition on raised bogs, which may result in changes to important ecosystem processes. Therefore, it is important that species composition and changes therein are taken into account when evaluating global change effects on raised bog ecosystems.

Keywords Biomass production · Climate change · Raised bogs · Peatlands · *Sphagnum* · Water table

Introduction

Raised bogs play an important role in the global carbon cycle owing to their ability to sequester large amounts of atmospheric carbon (Gorham 1991; Clymo et al. 1998; Hilbert et al. 2000). Apart from being potential carbon sinks, raised bogs have the ability to store great quantities of water, making them important water retaining ecosystems (Moore 2002). Global increases of temperature and changing patterns of precipitation are believed to impact upon the functioning

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of raised bog ecosystems (Moore 2002; Dorrepaal et al. 2003).

Sphagnum mosses are important in the ecology of bogs, since they are the dominant species in these systems. Because of their biomass production and rather slow decay rate (Clymo and Hayward 1982; Moore 2002; Limpens and Berendse 2003a; Rydin et al. 2003), *Sphagnum* species are largely responsible for the peat accumulation. Furthermore, *Sphagnum* mosses regulate the hydrological and hydrochemical conditions at the bog surface to a high degree (Clymo and Hayward 1982; Van der Schaaf 2002; Rydin et al. 2003). Raised bogs show a typical pattern of microtopographical habitats, ranging from wet depressions (hollows) and relatively dry (but regularly inundated) lawns to dry hummocks, with a different set of *Sphagnum* species occupying each microhabitat. The tight correlation between *Sphagnum* species and the position along the hydrological gradient (from hollow to hummock) is likely the result of a combination of morphological and physiological constraints (Andrus et al. 1983). Among species there seems to be a trade off between maximum growth rate, the ability to transport water to the capitula and the ability to minimize evaporative water loss (Titus and Wagner 1984; Rydin and McDonald 1985a, b; Rydin et al. 2003). *Sphagnum* species can differ in growth rate and water holding capacity, implying a different influence on ecosystem functioning (i.e. carbon sequestration and water retention). As such, the impact of environmental changes on the functioning of the ecosystem may depend on species composition and on changes therein.

Numerous papers report on the effects of environmental changes like nutrient deposition and elevated atmospheric CO₂ (e.g. Heijmans et al. 2002; Limpens and Berendse 2003b; Limpens et al. 2003; Bragazza et al. 2004), yet the number of papers reporting on the effects of changes in water level and temperature on the performance of different *Sphagnum* species is limited (e.g. Wallén et al. 1988; Dorrepaal et al. 2003; Gunnarsson et al. 2004) and to our knowledge no study describes the effect of these changes on the performance of the main peat forming species of oceanic Europe. The aim of this study was to investigate the potential effects

of temperature and water level on growth of four *Sphagnum* species that are mainly responsible for peat accumulation in raised bogs in Western Europe, *Sphagnum magellanicum* Brid., *S. rubellum* Wils., *S. imbricatum* Hornsch. and *S. fuscum* (Schimp.) Klinggr. These species differ in their position above the water table in the field and in their distribution across Europe. In the field, *S. magellanicum* occupies microhabitats that are relatively close to the water table (lawns), whereas *S. rubellum*, *S. fuscum* and *S. imbricatum* occupy microhabitats that range from relatively dry lawns to dry hummocks. Furthermore, *S. magellanicum* and *S. rubellum* extend further southward in Europe than the other two species, which are constrained to more temperate regions (Daniels and Eddy 1990). *S. magellanicum* and *S. rubellum* may be able to profit more from higher temperatures than *S. fuscum* and *S. imbricatum*, improving the competitive strength of *S. magellanicum* and *S. rubellum* towards the south.

We hypothesized that (I) productivity of lawn species (*S. magellanicum*) will decrease with decreasing water level, whereas biomass production of hummock species (*S. rubellum*, *S. fuscum* and *S. imbricatum*) will not be affected. (II) Because of the efficient capillary water transport of hummock species, we expected that capitulum water content and evaporation of hummock species would be less affected by decreased water tables than capitulum water content of lawn species. Furthermore, we expected (III) species that extend further southward (*S. magellanicum* and *S. rubellum*) to perform better at higher temperatures than species with a more northern distribution (*S. fuscum* and *S. imbricatum*). In order to test these hypotheses, peat cores of the four *Sphagnum* species were placed in a glasshouse under two different temperatures, while keeping the water table at two constant levels.

Methods

Plant material

In June 2003, 20 intact peat cores (16 cm diameter and approximately 20 cm depth) of four peat

mosses, *Sphagnum magellanicum*, *S. rubellum*, *S. imbricatum* and *S. fuscum*, were collected from two raised bog in the Irish midlands. *Sphagnum magellanicum* and *S. rubellum* were collected at Clara bog (53°19' N, 007°37' W), whereas *S. imbricatum* and *S. fuscum* were collected at Mongan bog (53°19' N, 007°58' W), Co. Offaly, Ireland; for detailed site descriptions see Schouten (2002). The two bogs are both classified as true midland raised bogs with a similar age and developmental history. Furthermore, they both have a relatively intact hydrology and an extensive *Sphagnum* cover (Cross 1990; Parkes and Mitchell 2000; Connolly unpublished results summarised in Schouten 2002). Cores were taken from mono-specific *Sphagnum* stands (> 95% of one species) with a sparse vascular plant cover (< 5%). The peat cores were cut with a sharp knife and put into PVC pipes (16 cm diameter) for transport. Aboveground vascular plant parts were removed (seedlings were pulled out and older specimens were clipped) before storing the peat cores in the PVC pipes for 3 months at 1°C. To prevent drying out, the pipes were covered with plastic. The mosses were not visibly affected by the storage period.

Experimental design

Late September 2003, the PVC pipes containing the peat cores were placed in the glasshouse in 50 l containers (25 cm diameter and 100 cm height), containing an artificial rainwater solution (Garrels and Christ 1965). The area between the PVC pipes and the containers was covered by a tight fitting lid. We applied four treatment combinations which comprised two temperature regimens (15°C and 20°C) and two water table regimens (–5 cm and –15 cm below the top of the capitula). The water tables in this experiment represented average water tables at lawn and hummock microhabitats in Clara bog (Kelly and Schouten 2002). Temperatures represented Irish mean summer temperature (15–16.7°C; Met Éirann—The Irish Meteorological Service) and a hypothetical temperature increase of 5°C; the rounded upper limit of temperature increase for the next century as projected by the IPCC (1996). This study was conducted as a nested randomised

block design with four treatments for every species in five replicated blocks. The four treatments were arranged in a 2 × 2 × 4 nested arrangement (i.e., two adjacent temperature compartments). The weekly mean humidity in the glasshouse ranged from 68% to 80%, but did not differ between the two compartments (paired sample *t*-test: $t = 2.36$, $P = 0.11$). Light conditions in both glasshouse compartments were assumed to be similar; natural light was supplemented with high pressure sodium lamps (Philips MASTER SON-T PIA Agro 400W E E40 SLV; Luminous flux EM [Lm] 55000, 1 lamp · 4 m²), to induce a-16 h photoperiod. Water level in the containers was adjusted to the experimental height below the moss surface once a week, using the same artificial rainwater solution as described above. To avoid complete, chronic (i.e., detrimental) drying out, the capitula in all containers were moistened once every 2 weeks to simulate natural rain events by adding 20 mm (=175 ml) rainwater solution. This corresponds with 520 mm precipitation per year. During the experiment, regrowth of vascular plants was regularly removed. The mosses were harvested after 6 months.

Sphagnum growth and biomass production

Once a month, height increment of the *Sphagnum* species was measured using a method slightly modified after the one described by Limpens and Berendse (2003b). Two metal rods were placed at fixed points on the PVC pipes edge. A bar fitted between the rods was used as a stable horizontal benchmark above the *Sphagnum* carpet. At five fixed points we measured the distance between the *Sphagnum* surface and the traverse, using a ruler. Subsequently, the two metal rods and the benchmark were rotated 90°, after which we repeated the measurements. Before statistical analysis, the measurements for the ten distances were averaged. At final harvest we cut a vertical *Sphagnum* slice (3 × 9 cm and 1.5 cm deep) from the middle of each peat column. Next, every slice was cut into two sections: a capitulum (0–0.5 cm) section and a subcapitulum (0.5–1.5 cm) section (c.f. Dorrepaal et al. 2003). After determining fresh weight, the two sections were oven dried at 70°C for a least 48 h. Here-

after we were able to calculate capitulum water content ratios and subcapitulum bulk density. Biomass production (P) per column was calculated by multiplying the subcapitulum bulk density (B_{Subcap}) with the height increment (L) of the *Sphagnum* carpet: $P = L \times B_{\text{Subcap}}$. Since at harvest, capitulum dry weight within species did not differ significantly between the treatments (Table 1), we assumed that capitulum dry weight also was not different at the start and did not change over the experimental period as a response to treatment. Consequently, we did not correct for changes in the capitulum dry weight when calculating biomass production.

In the course of the experiment, liverworts (*Mylia anomala* and *Odontoschisma sphagni*) appeared on the peat moss surface. To correct for possible effects of liverwort presence on *Sphagnum* performance, we measured liverwort cover using a transparent sheet that was placed over the *Sphagnum* layer. This sheet had a grid, which constituted 710 intersections. Liverwort cover was expressed as follows:

$$\text{Liverwort cover} = (\text{number of intersections coinciding with liverworts}/710) \times 100\%$$

Sphagnum water loss

To assure that water loss could only take place from the *Sphagnum* surface, the area between the PVC pipes that contained the peat cores and the containers was covered with a tight fitting lid. The cumulative amount of water, lost during

the experiment, was used as a proxy for the evaporative water loss. As a measure for the capitulum water content at harvest, we used the capitulum fresh weight · dry weight⁻¹ (FW · DW⁻¹) ratio.

Data analysis

Data were tested for normality (Shapiro–Wilks W -test) and equality of variance (Levene test) prior to further analysis. Our data did not always meet the assumptions of homogeneity of variances (Subcapitulum bulk density: $F = 1.95$, $P = 0.034$; Capitulum water content: $F = 2.03$, $P = 0.027$), even after ln-transformation. Since analysis of variance appears not to be greatly influenced if the assumptions of equality in variances or normal distribution are not met, as long as sample sizes are more or less equal. (Heath 1995), we proceeded our analyses without transformations. The effects of the fixed factors Species (S), Temperature (T) and Water table (W) on the variables height increment, subcapitulum bulk density, biomass production, cumulative evaporation and capitulum water content were analysed using GLM multivariate analysis of covariance. We included liverwort cover as a co-variable in the model. Since we did not find an effect of block, we omitted block from the model. After omitting liverwort as a co-variable from the analyses, overall differences between the *Sphagnum* species were determined by multiple LSD post-hoc tests.

As we often found interactions between species and temperature or species and water table, these overall analyses were followed by

Table 1 Mean capitulum dry weight (± 1 Standard Error) in g m⁻² at harvest for all treatments and species

Treatment	Code	Species			
		<i>S. magellanicum</i>	<i>S. rubellum</i>	<i>S. fuscum</i>	<i>S. imbricatum</i>
15°C, -5 cm	tW	248.0 \pm 46.8*	321.7 \pm 37.2	407.9 \pm 118.5*	470.9 \pm 42.4
15°C, -15 cm	tw	209.5 \pm 24.6	382.0 \pm 11.4	539.5 \pm 77.8	511.2 \pm 57.7
20°C, -5 cm	TW	222.6 \pm 12.1	305.1 \pm 43.7	342.7 \pm 35.5*	384.8 \pm 35.9
20°C, -15 cm	Tw	301.1 \pm 40.1*	292.0 \pm 18.2	448.0 \pm 51.4	508.4 \pm 71.1

Unless indicated, $n = 5$. Four data points were omitted from the analyses because the containers were leaking and as a consequence constant water levels could not be guaranteed. Treatment effect was tested within every species using PROC GLM in SAS 9.1. Within species, we did not find any treatment effects

* $n = 4$

ANOVA's for each *Sphagnum* species. Temperature and water table were included in the model as fixed factors. Since liverwort cover affected subcapitulum bulk density, we included liverwort as a co-variable if testing the effects of our variables on subcapitulum bulk density. Liverwort cover was omitted from the analyses not dealing with subcapitulum bulk density. We tested the effects of the fixed factors Species (*S*), Temperature (*T*) and Water table (*W*) on the liverwort cover using GLM univariate analysis.

All statistical analyses have been carried out using SAS 9.1 (SAS Institute, Windows version 5.1.2600). Four data points were omitted from the analysis, because of leaking containers.

Results

Overall effects

We found main effects of species, temperature and water on height increment and of species and temperature on subcapitulum bulk density and biomass production. Overall height increment was highest for *S. imbricatum*, *S. fuscum* and *S. rubellum* and lowest for *S. magellanicum* (LSD post-hoc test; Fig. 1A, Table 2). Furthermore, subcapitulum bulk density and biomass production of *S. imbricatum* and *S. fuscum* exceeded that of *S. magellanicum* and *S. rubellum* (LSD post-hoc test; Fig. 1B,C; Table 2). Overall capitulum water content and cumulative evaporation did not differ between species (LSD post-hoc test; Fig. 2A,B; Table 2).

Cover of *Mylia anomala* and *Odontoschisma sphagni* was more pronounced in *S. fuscum* and *S. imbricatum* than in *S. magellanicum* and *S. rubellum* ($F = 16.25$, $P < 0.001$; Table 3). Overall, liverwort cover was an important factor explaining subcapitulum bulk density (Table 2). Higher liverwort cover resulted in higher bulk density only in *S. fuscum* and *S. imbricatum* (Table 4). Liverwort cover was affected by the water table, resulting in higher cover at low water tables ($F = 4.33$, $P = 0.042$). Nonetheless, these liverworts had no effect on *Sphagnum* height increment, dry weight production, capitulum

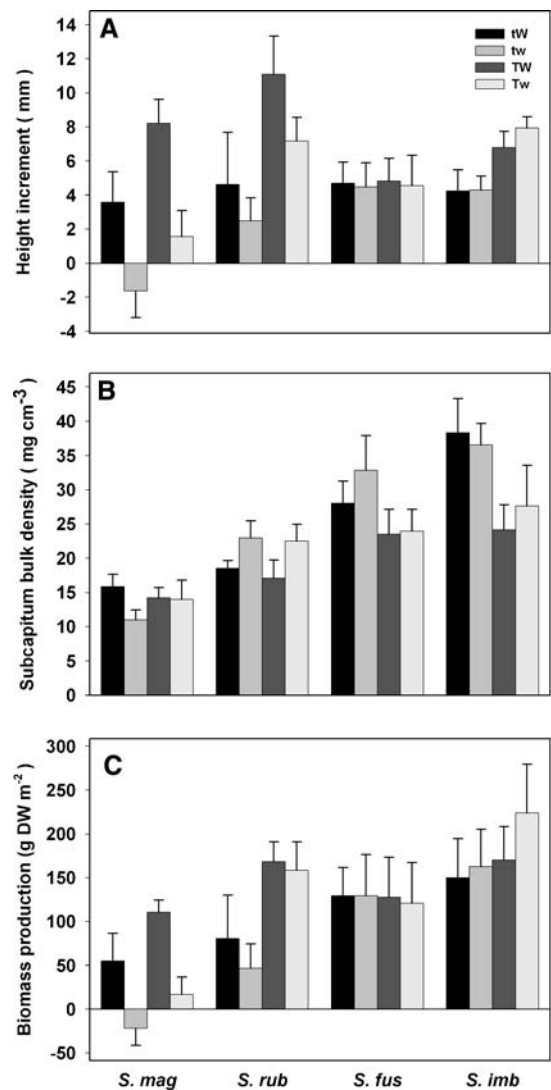


Fig. 1 The effects of temperature and water table treatments on (A) height increment, (B) subcapitulum bulk density at harvest and (C) biomass production (means \pm SEM). For treatment codes and replicate numbers, see Table 1. For statistics, see Tables 2 and 3

water content and cumulative evaporation (Table 2).

Within species response to water table

Height increment and biomass production of *S. magellanicum* were depressed at low water table, whereas height increment and production of *S. fuscum*, *S. rubellum* and *S. imbricatum* remained unaffected (Fig. 1A,C; Table 4). Subca-

Table 2 Values for the overall effects of the fixed factors species, water table and temperature treatment and the covariable liverwort cover on height increment,

Source	d.f.	Height increment		Subcap. bulk density		Biomass production		Cap. water content		Cum. evaporation	
		F-value	P-value	F-value	P-value	F-value	P-value	F-value	P-value	F-value	P-value
LW cover	1	0.39	0.533	27.71	< 0.001	2.09	0.153	1.22	0.274	0.25	0.617
Species	3	3.58	0.019	6.36	0.001	4.26	0.009	1.30	0.284	1.62	0.196
Water	1	5.76	0.020	0.14	0.713	1.84	0.180	64.58	< 0.001	25.74	< 0.001
Temperature	1	14.75	< 0.001	7.71	0.007	6.35	0.014	3.83	0.055	1.32	0.256
<i>S</i> × <i>W</i>	3	3.40	0.023	1.23	0.306	1.33	0.275	4.07	0.011	3.34	0.025
<i>S</i> × <i>T</i>	3	2.06	0.115	2.81	0.047	1.11	0.353	0.21	0.887	0.47	0.703
<i>W</i> × <i>T</i>	1	0.14	0.714	0.59	0.446	0.11	0.745	0.32	0.573	0.24	0.627
<i>S</i> × <i>W</i> × <i>T</i>	3	0.17	0.917	0.21	0.889	0.17	0.916	0.56	0.641	1.90	0.139

Values in bold indicate significant *P*-values (<0.05)

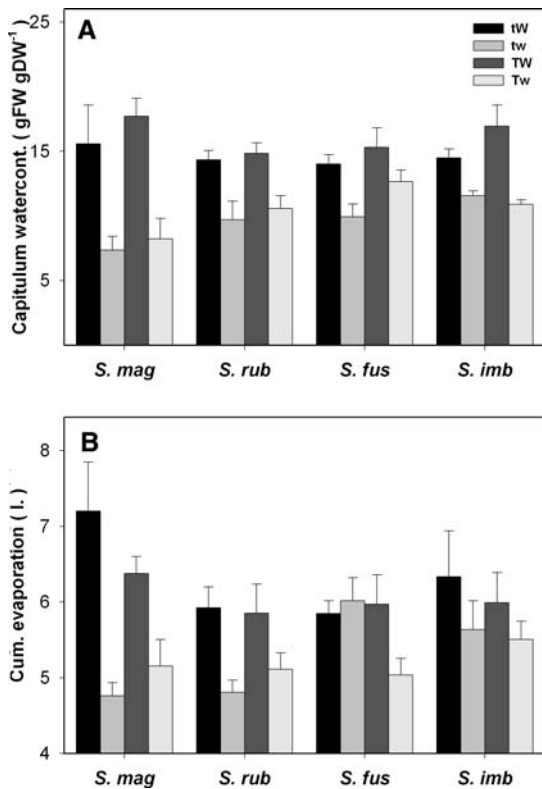


Fig. 2 The effect of temperature and water table treatments on (A) capitulum water content and (B) cumulative evaporation (means ± SEM). For treatment codes and replicate numbers, see Table 1. For statistics, see Tables 2 and 3

pitulum bulk density was not affected by water table for any of the species. Capitulum water content was lower at the -15 cm treatment than at the -5 cm treatment for all *Sphagnum* species

subcapitulum bulk density, biomass production, capitulum water content and cumulative evaporation

Table 3 Mean liverwort cover (± 1 Standard Error) in % at harvest on *S. magellanicum*, *S. rubellum*, *S. fuscum* and *S. imbricatum*

<i>Sphagnum</i> spp.	Liverwort cover (%)
<i>S. magellanicum</i>	2.82 ± 1.01a
<i>S. rubellum</i>	5.18 ± 1.33a
<i>S. fuscum</i>	20.44 ± 3.65b
<i>S. Imbricatum</i>	21.44 ± 2.59b

Means with the same letter do not significantly differ

(Fig. 2A; Table 4), but the response of *S. magellanicum* to water level exceeded that of the other three species (Table 2). Cumulative evaporation was lower at the -15 cm treatment than at the -5 cm treatment for *S. magellanicum* and *S. rubellum*, whereas cumulative evaporation was similar between water table regimens for *S. fuscum* and *S. imbricatum* (Fig. 2B; Table 4).

Within species response to temperature

Height increment of *S. magellanicum*, *S. rubellum* and *S. imbricatum* was larger at high temperature, whereas height increment of *S. fuscum* remained unaffected (Fig. 1A; Table 4). Subcapitulum bulk density of *S. magellanicum* and *S. rubellum* was not affected by temperature, whereas subcapitulum bulk density of *S. imbricatum* was lower at high temperature. *S. fuscum* subcapitulum bulk density showed a similar, albeit weaker, response to temperature (Fig. 1B; Table 4). As a result increased temperature en-

Table 4 Values for the effects of water table and temperature treatment on height increment, subcapitulum bulk density, biomass production, capitulum water content and cumulative evaporation within every species separately

Source	Height increment		Subcap. bulk density		Biomass production		Cap. water content		Cum. evaporation	
	F-value	P-value	F-value	P-value	F-value	P-value	F-value	P-value	F-value	P-value
<i>S. magellanicum</i>										
LW cover*	–	–	0.08	0.776	–	–	–	–	–	–
Water	14.07	0.002	1.68	0.218	16.20	0.001	24.36	< 0.001	26.06	< 0.001
Temperature	6.10	0.027	0.12	0.737	4.94	0.043	0.70	0.418	0.367	0.555
W × T	0.22	0.648	0.76	0.401	0.16	0.698	0.13	0.727	2.89	0.111
<i>S. rubellum</i>										
LW cover	–	–	2.95	0.106	–	–	–	–	–	–
Water	2.00	0.177	3.79	0.070	0.40	0.536	18.64	0.001	11.70	0.004
Temperature	6.83	0.019	0.29	0.600	8.22	0.011	0.43	0.519	0.19	0.667
W × T	0.17	0.692	0.39	0.543	0.12	0.735	0.03	0.864	0.49	0.496
<i>S. fuscum</i>										
LW cover	–	–	7.66	0.016	–	–	–	–	–	–
Water	0.03	0.954	0.14	0.714	0.01	0.940	9.57	0.008	1.793	0.202
Temperature	0.00	0.952	2.64	0.128	0.01	0.910	3.39	0.087	2.285	0.153
W × T	0.00	0.984	0.04	0.838	0.01	0.941	0.45	0.513	3.8	0.072
<i>S. imbricatum</i>										
LW cover	–	–	11.15	0.004	–	–	–	–	–	–
Water	0.41	0.531	0.54	0.473	0.53	0.477	23.61	< 0.001	1.93	0.183
Temperature	10.96	0.004	6.95	0.019	0.80	0.384	0.93	0.350	0.32	0.582
W × T	0.33	0.572	0.55	0.470	0.20	0.658	2.86	0.110	0.06	0.807

We included liverwort as a co-variable only if testing the effects of our variables on subcapitulum bulk density. Numbers in bold indicate significant *P*-values (< 0.05)

* Liverwort cover had effect only on subcapitulum bulk density and was therefore omitted from the other analyses.

hanced biomass production of only *S. magellanicum* and *S. rubellum*. The combination of low temperature and low water table was detrimental to *S. magellanicum* production; this species lost 21.8 g DW m⁻² under these circumstances (Fig. 1C). In general, capitulum water content at harvest was higher at high temperature, but within species this effect was masked by the effects of water table (Tables 2 and 4). Cumulative evaporation did not change as a response to increased temperature for any *Sphagnum* species (Fig. 2B; Table 4).

Discussion

Water level

As hypothesised, a low water level resulted in depressed height growth and biomass production for the lawn species *S. magellanicum*, whereas the three hummock species remained unaffected (Fig. 1A,C). This implies that hummock species

are less sensitive to changes in water level than lawn species. Although Lindholm (1990) found that *Sphagnum* growth in hummocks is strongly related to moisture conditions, it is believed that hummock species are less subject to interseasonal changes in the moisture regime than lawn and hollow species (Hayward and Clymo 1982; Gerdol 1995; Asada et al. 2003). In our glass house study, *S. magellanicum* had lower biomass production than *S. imbricatum* and *S. fuscum* (Fig. 1C), even at the favourable water level for this species. These results contradict with mean productivity values derived from field studies or from outdoor field-like studies, which revealed that differences in average productivity rates between *S. magellanicum* (257 g m⁻² year⁻¹), *S. rubellum* (237 g m⁻² year⁻¹) and *S. fuscum* (170 g m⁻² year⁻¹) were positively correlated to the height of the water table in the field (Gunnarsson 2005). Thus, hummock species had lower productivity than hollow or lawn species in their respective microhabitats. In our experiment, overall *S. magellanicum* productivity was ex-

tremely low. Yet, under natural circumstances water levels are subject to some fluctuations and precipitation events may occur more frequently. Hollow and lawn species may have a higher production during wet periods when the water table is close to the moss surface. Since water tables in our experiment were kept constant, the low production of *S. magellanicum* can be explained by its deficiency to keep a positive capitulum water balance, when both water table and frequency of precipitation are low (c.f. Gerdol 1996). This suggests that *S. magellanicum* is sensitive to periods of prolonged drought.

In accordance with our second hypothesis, a decrease in water table depressed capitulum water content of the lawn species *S. magellanicum* more than that of the hummock species *S. fuscum*, *S. imbricatum* and *S. rubellum*. Surprisingly, the decrease in capitulum water content was not reflected in decreased height increment and biomass production for hummock species. Apparently, the decrease in capitulum water content was not enough to trigger a reduction in height increment and biomass production in these peat mosses. For the lawn species *S. magellanicum*, however, the decrease in capitulum water content seems to have hampered height increment and biomass production. *Sphagnum* plants depend more or less on water supply via capillary rise (Clymo and Hayward 1982). The dense growth form (i.e., high subcapitulum bulk density) of the hummock species, *S. fuscum*, *S. imbricatum* and, to a lower extent, *S. rubellum* (Fig. 1B) is often associated with an efficient capillary system (Clymo and Hayward 1982; Grosvernier et al. 1997; Asada et al. 2003), making them less sensitive to changes in the water table. At the lowest water table, capitula of *S. magellanicum* were often observed to be dry, which indicates a poor capillary water transport. At low water tables, this poor capillary system probably resulted in the stronger decrease of the capitulum water content of *S. magellanicum* than the capitulum water content of *S. fuscum*, *S. imbricatum* and *S. rubellum* (c.f. Wallén et al. 1988). On account of the latter, height increment and biomass production of *S. magellanicum* decreased. For *S. fuscum* it has been shown that changes in water supply to the capitula can lead to

changes in bulk density (Dorrepaal et al. 2003). This implies that, given enough time, *Sphagnum* can adapt its morphology to some extent, if faced with a decrease in capitulum water content. In our experiment, however, *S. magellanicum* subcapitulum bulk density did not change. Perhaps the constant low water level and the inability of *S. magellanicum* to transport water to its capitula resulted in hampered growth. Consequently, *S. magellanicum* has been unable to adapt its morphology to cope with low capitulum water content. Additionally, we did not find changes in subcapitulum bulk density as a response to water table in any of the other species. Since height increment and biomass production of *S. rubellum*, *S. fuscum* and *S. imbricatum* were not affected by water table, even though capitulum water content decreased, we assume that there was no necessity for these species to change their subcapitulum bulk density.

Temperature

In accordance with our hypothesis, biomass production of the widely distributed species, *S. magellanicum* and *S. rubellum* increased with temperature (Fig. 1C), whereas biomass production of the two species with a more northern distribution, *S. fuscum* and *S. imbricatum*, remained unaffected by temperature (Fig. 1C). Nevertheless, the response of *Sphagnum* to temperature does not seem as straightforward as the above would imply. Other studies may show none, or even an opposite response to the one we are reporting (Gerdol 1995; Gerdol et al. 1998; Weltzin et al. 2001; Sonesson et al. 2002; Dorrepaal et al. 2003; Gunnarsson et al. 2004). This stresses the importance of environmental conditions (precipitation, temperature, etc.) under which the experiments have been carried out (Sonesson et al. 2002). In our experiment, increased temperature did stimulate *S. imbricatum* height increment (Fig. 1A), although, this effect was not reflected in biomass production because of a decrease in bulk density (Fig. 1B). For the widely distributed species *S. magellanicum* and *S. rubellum*, height increment did not occur at the expense of biomass production. Our results raise the question whether the positive response to

increased temperature reflects physiological adaptations or is an effect of changes in nutrient availability caused by increased decomposition and N mineralization (Bergman et al. 1999; Rustad et al. 2001). We found increased growth as a response to increased temperature at both water tables. If nutrients would be limiting then we would have found a temperature effect only at high water table, because growth is not hampered by water here. Consequently, a direct physiological response to increased temperature may be the most plausible explanation for our findings.

In general, we observed a small increase in capitulum water content in response to increased temperature (Table 2). This implies that increased temperature increases capillary water flow. Under these circumstances, evaporation rates can be higher (Gunnarsson et al. 2004). Within species, however, we did not find an effect of temperature on cumulative evaporation. We applied water to the capitula only once every 2 weeks, and water lost by evaporation was only filled up weekly. This may have resulted in higher evaporation at high temperatures just after application. Water tables may have dropped slightly. As a result capitulum water content decreased. Subsequently, evaporation rates at high temperature may have dropped faster than at low temperature, resulting in no difference in cumulative evaporation between the two temperatures.

Liverworts

Although higher liverwort cover resulted in higher subcapitulum bulk density, it did not affect the water balance and the performance of *Sphagnum*. We found that low water tables had a positive effect on the cover of these liverworts. Water level, however, may not directly affect the growth of liverworts. A more likely explanation for our results is that the actively growing *Sphagnum* inhibits the growth of liverworts, whereas liverworts can rapidly overgrow *Sphagnum* that is hampered in growth (Duckett and Clymo 1988). In our experiment, liverworts (*M. anomala* and *O. sphagni*) were more abundant in the hummock species, *S. fuscum* and *S. imbricatum* than in *S. magellanicum* and *S. rubellum* species (Table 3).

Field observations support these results: liverwort abundance is higher in hummock species than in lawn and pool species, suggesting that *M. anomala* and *O. sphagni* prefer drier hummock habitats over the relatively moist lawn habitats.

Implications of climate change

We show that water table draw down and temperature increase can have contrasting effects on peat moss growth and evaporative water loss. Since we did not find interactions between temperature and water table, we conclude that these two factors cause independent responses.

Changes in temperature and water table had differential effects on the four peat mosses. We show that increased temperature will favour the species with a wide geographic range (*S. magellanicum* and *S. rubellum*), whereas lower water tables will be advantageous for hummock species. In time, changes in temperature and raised bog water level might alter the competitive balance between *Sphagnum* mosses, resulting in a change in the species composition of raised bogs. Ultimately, changes in the *Sphagnum* vegetation can have implications on important ecosystem processes. Our results indicate that when temperatures increase, *S. magellanicum* and *S. rubellum* will gain competitive strength whereas *S. rubellum* will likely become dominant when increased temperature would coincide with decreased precipitation.

Acknowledgements We thank R.H.A. van Grunsven, M.M.P.D. Heijmans, F. Kohler, J. Noordijk, J. Verhulst and two anonymous reviewers for their critical comments on earlier versions of the manuscript, which led to significant improvements. We are indebted to An Taisee and the National Parks and Wildlife Service, Department of the Environment, Heritage and Local Government, Ireland for permission to enter their nature reserves and to collect the peat samples. We also acknowledge the practical help of P.H. Crushell (University College Cork), J.M. Gleichman, F. Möller and J.D. van Walsem. This research was supported by the National Forest Service of The Netherlands (Staatsbosbeheer) and a grant from the Dutch Foundation for Conservation of Irish bogs.

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