Interspecific competition between *Sphagnum* mosses at different water tables

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Summary

1. Effects of climate change may affect the *Sphagnum* species composition in bogs, and ultimately the functioning of the whole ecosystem. We investigated the effect of different water tables on the competition between six *Sphagnum* species in the glasshouse. The amount of precipitation (234 mm year^{-1}) and precipitation frequency (every 2 weeks) were kept low to encourage water-table effects. Relevant species combinations and monocultures were grown at different water tables for a 16-month period. We studied changes in cover, height increment and capitulum water content (WC_{cap}) in order to understand competitive responses.

2. Species naturally occurring further above the water table generally showed higher competitive strength than species naturally occurring closer to the water table. Surprisingly, this effect was irrespective of the water table, indicating a minor role for capillary water transport. Cover change seemed to be related to differences in length growth, but not to water table or WC_{cap}.

3. The WC_{cap} of species within a mixture did not differ, but was lower than the WC_{cap} of the individual species growing in monoculture, indicating differences in ability to supply water to the capitula between mono- and mixed cultures. Subcapitulum bulk densities between mono- and mixed cultures did not differ, or were even lower in monocultures, but did differ between species within mixed cultures.

4. Our results indicate that structural heterogeneity of the peat in mixed cultures has a negative effect on WC_{cap} of both species. Furthermore, we show that sustained periods of drought cause species that naturally occur further above the water table to oust species that naturally occur closer to the water table, even if the water table remains high. Ultimately, the *Sphagnum* vegetation in raised bogs may shift from hollow to hummock species, evening out the natural microtopography of raised bogs.

Key-words: anisotropy, capillary water transport, climate change, peatlands, species composition, *Sphagnum*

Introduction

Peatlands play an important role in the global carbon cycle due to their ability to sequester large amounts of atmospheric carbon (Gorham 1991; Hilbert, Roulet & Moore 2000). Additionally, peatlands have the ability to store great quantities of water, making them important water-retaining ecosystems (Moore 2002). In ombrotrophic peatlands, such as raised bogs, *Sphagnum* mosses dominate the vegetation, playing a crucial role in these ecosystems. Due to their considerable biomass

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production and relatively slow decay rate (Johnson & Damman 1991; Limpens & Berendse 2003), *Sphagnum* mosses are largely responsible for the formation of peat, and hence the sequestration of carbon. Furthermore, *Sphagnum* regulates the hydrological and hydrochemical conditions at the raised bog surface to a high degree (Van Breemen 1995; Van der Schaaf 2002). The extent to which *Sphagnum* mosses affect their environment may depend on the identity of the dominant species. Consequently, the *Sphagnum* species composition and changes therein may affect the functioning of the bog ecosystem.

Species composition seems to be determined mainly by differences in water table, with different sets of

Sphagnum species occupying specific positions above the water table. The distribution of species along the hydrological gradient is thought to be related to differences in growth rate (as reviewed by Gunnarsson 2005), the efficiency of their capillary system, and their ability to hold water (Hayward & Clymo 1982; Titus & Wagner 1984; Rydin & McDonald 1985a). Because *Sphagnum* species lack stomata or roots, the ability to keep their active apical parts (capitula) moist is related to the efficiency of transporting water from the water table to the capitula and of avoiding water loss. Because of their dense growth (Clymo & Hayward 1982), hummock species are believed to be efficient in transporting and holding water in their capillary system, which enables them to supply water to the capitula even at relatively low water tables (Hayward & Clymo 1982). However, water transport to the capitula may also be related to physical properties other than bulk density, such as porosity and carpet structure. Interspecific differences in physical properties, which affect water transport, may result in differences in height increment and in horizontal expansion, and may ultimately influence the outcome of interspecific competition.

Much of the above has been deduced from experiments with monocultures or field measurements (Hayward & Clymo 1983; Schipperges & Rydin 1998; Dorrepaal *et al*. 2003), but has not yet been tested in mixed cultures under controlled conditions. In order to predict how bogs will respond to environmental change, we need to know the underlying mechanisms that determine the outcome of interspecific competition. Studies that focus on the response of *Sphagnum* species to water-table and temperature changes, which are a logical consequence of the drier and warmer summer conditions predicted for large parts of north-west Europe (Houghton *et al*. 2001), are scarce (Gunnarsson & Rydin 2000; Dorrepaal *et al*. 2003; Dorrepaal *et al*. 2006). Moreover, there is a lack of knowledge about the competitive interactions among bryophytes (Mulligan & Gignac 2002), and to our knowledge no study describes the effect of environmental changes on competition between the main peat-forming *Sphagnum* species of (sub)oceanic raised bogs in Europe.

The aim of this study is to elucidate the effects of water table on competition between peat mosses. We focus on two types of response: effect responses and mechanistic responses. We define cover change as an effect response, whereas capitulum water content (WC$_{cap}$), height increment and subcapitulum bulk density (BD$_{subcap}$) were defined as mechanistic responses. Under drought, the ability to transport water towards the capitula may become an important factor in determining competitive strength. Therefore, we mimicked a situation where water supply to the capitula was influenced not by precipitation, but by capillary water transport. Species that naturally occur further above the water table (hummock) are better at maintaining water supply to the capitula than species

that occur closer to the water table (hollow). As a result, hummock species were expected to be less negatively affected by low water tables than hollow species in their water content and growth response. We expected that (i) in a mixture, decreased water table would lead to increased cover of species that naturally occur further above the water table; and (ii) these changes in cover would be associated with differences between competing species in height increment, BD$_{subcap}$ and WC$_{cap}$.

Methods

EXPERIMENTAL DESIGN AND SAMPLING

In May 2004, 135 intact peat cores (16 cm diameter; 30 cm depth) of six peat mosses (*Sphagnum cuspidatum* Ehrh. Ex. Hoffm., *Sphagnum papillosum* Lindb., *Sphagnum magellanicum* Brid., *Sphagnum rubellum* Wilson, *Sphagnum fuscum* (Schimp.) H. Klinggr. and *Sphagnum austinii* Sull. in Aust. were collected at Clara bog (53°19′ N, 007°58′ W), an Irish midland raised bog with a relatively intact hydrology and extensive *Sphagnum* cover (Cross 1990). Cores were taken from monospecific stands (95% of one species) with sparse vascular plant cover (<5%) at the natural microsites of the species. The natural occurrence of these species along the water table in Clara bog is: *S. cuspidatum* < *S. papillosum* ≤ *S. magellanicum* < *S. rubellum* < *S. fuscum* ≤ *S. austinii*. Thereafter, the peat cores were placed in PVC cylinders and enclosed in plastic bags. Care was taken to avoid disturbing the natural packing density of the species. The cylinders were placed in large boxes and transported to Wageningen, the Netherlands. Before storing the peat cores at 1 °C for 3 weeks, the few above-ground vascular plants were cut flush with the *Sphagnum*. Drying out of peat cores was prevented by covering the cylinders with plastic. The mosses were not visibly affected by the storage period.

In early June, the peat cores were transported to the glasshouse facilities. The peat cores were randomly assigned to the mixture and water-level treatments, which were arranged in a randomized block design with five replicates per treatment. Mixture treatments consisted of two levels: monocultures of each species; and mixed cultures of species that co-occur in the field, comprising hollow–lawn, lawn–lawn, lawn–low hummock, low hummock–hummock and hummock–hummock combinations (Fig. 1). Mixed cultures were made by inserting two equally sized half-cores of two species in one PVC cylinder. Care was taken to minimize disturbance of the moss and underlying peat structure, and to ensure the surfaces of both species made uniform connection. Water-table treatments consisted of two or three levels (Fig. 1). Monocultures of *S. cuspidatum*, *S. papillosum* and *S. magellanicum* were grown at water levels of –5 and –15 cm below the *Sphagnum* surface, whereas *S. rubellum*, *S. fuscum* and *S. austinii* were grown at –15 and –25 cm. Mixtures of hollow–lawn
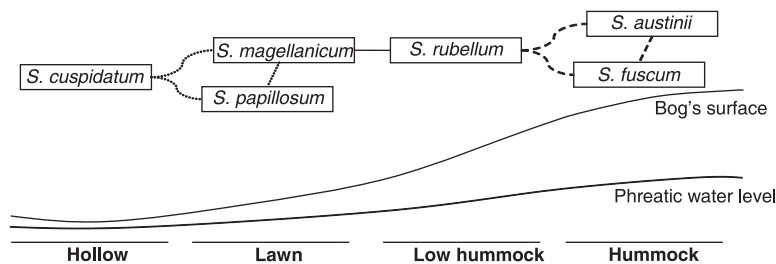
Fig. 1. Schematic view of the experimental set-up, representing the position of the *Sphagnum* species at their natural habitat along the hydrological gradient from hollow to hummock. Connecting lines indicate species combinations at the applied experimental water tables: –5 and –15 cm (dotted line); –5, –15 and –25 cm (solid line); –15 and –25 cm (dashed line) below the *Sphagnum* surface.

and lawn–lawn species were grown at –5 and –15 cm; mixtures of lawn–low hummock species at –5, –15 and –25 cm; and mixtures of low hummock–hummock and hummock–hummock at –15 and –25 cm (Fig. 1). These water levels are comparable with the field water levels at which species can (co)occur (Rydin, Sjörs & Löfroth 1999). To analyse the effect of cutting on the WC_{cap}, in an additional experiment monocultures of *S. magellanicum* and *S. rubellum* were either left intact, or cut in half and put together again ($n = 5$). Samples were grown at intermediate water level (–10 cm). The WC_{cap} was analysed 15 days after applying the water-table treatment, which corresponds to one cycle of rainwater addition in the competition experiment. Moreover, the effect of cutting on WC_{cap} was expected to be immediate.

All cylinders, which were closed at the bottom and perforated on the sides to facilitate water movement, were suspended in 50-l containers (25 cm diameter; 100 cm depth) containing an artificial rainwater solution (Garrels & Christ 1965), by hanging them from a lid. The lid also covered the water surface between the large and small containers, preventing evaporative water loss via the open water surface. Water tables were kept by weekly addition of artificial rainwater below the *Sphagnum* surface, mimicking prolonged rainless periods. To avoid complete chronic drying out, the capitula in all containers were moistened once every 2 weeks by sprinkling ≈ 9 mm (234 mm year^{-1}) artificial rainwater over the capitula. The last addition of water to the moss capitula was applied 1 week before harvest.

The experiment lasted from early June 2004 until early October 2005. Temperature in the glasshouse was 20 °C day/15 °C night and relative humidity $\approx 80\%$. Natural light was supplemented by high-pressure sodium lamps (Philips Master SON-T PIA agro 400 W E E40 SLV, Luminous flux EM [Lm] 55000), to induce a 16 h photoperiod. During the winter period (October 2004 to April 2005), cores were kept in an open greenhouse with a transparent roof and walls of coarse shade mesh, as an earlier experiment had shown that in the glasshouse in winter, when natural light is reduced but temperature remains relatively high, liverworts overgrow *Sphagnum* (Robroek *et al.* 2007).

MEASUREMENTS

To estimate the competitive strength of the species within a mix, we calculated the change in cover during the experiment. At the end of the experiment, a photograph was taken of the moss surface. The area of each species in the mixed culture was analysed using an image-processing and analysis program (IMAGEJ 1·33u; National Institutes of Health, USA, http://rsb.info.nih.gov/ij).

Sphagnum height increment was measured using a variation on the cranked wire method (Clymo 1970). Plastic rods were inserted, to a depth of ≈ 10 cm, into every species in a combination and in the monocultures. In monocultures, two rods were anchored so that the treatment resembled that of the mixed cultures. The rods were anchored in the *Sphagnum* substrate by broom bristles and did not visibly interfere with *Sphagnum* growth.

To measure WC_{cap} and BD_{subcap}, cores with a diameter and depth of 5 cm were cut around every cranked wire, at harvest. Every core was separated into a capitulum section (0–0·5 for species with small capitula or 0–1·0 cm for species with large capitula) and a subcapitulum section, defined as the centimetre directly under the capitulum section (cf. Dorrepaal *et al.* 2003), after which fresh weight was measured. Next, dry weight was determined by oven-drying both sections for 48 h at 70 °C. WC_{cap} was expressed as the FW : DW ratio. BD_{subcap} was expressed as DW (g) cm^{-3}.

STATISTICAL ANALYSIS

Data were tested for normality and equality of variance prior to further analysis. Some data on WC_{cap}, height increment and cover change did not meet the assumptions of homogeneity of variances. Transformations did not improve the homogeneity of variances. However, ANOVA appears not to be greatly influenced if the assumptions of equality of variances or normal distribution are not met, as long as sample sizes are more-or-less equal (Heath 1995). Since sample sizes were equal in our experiment, we decided to perform our analyses without transformations.

The overall effect of water table and mixture type (the identity of the species combination) on cover change was tested by two-way ANOVA models. In our analysis, we used data for only the species within the mixture that naturally occur closest to the water table. Although the interaction between water table and mixture type was not significant ($F = 1\cdot75$, $P = 0\cdot126$), further analyses of the effect of water table on cover change of species were carried out within each mixture, to enable analysis of whether cover change differed to zero (one-way ANOVA). Two-way ANOVA was used to test the effects of competing species and water table on the height increment of each individual species, and to test the effects of species and water table on the WC_{cap} and BD_{subcap} of the species within a mixture. One-way
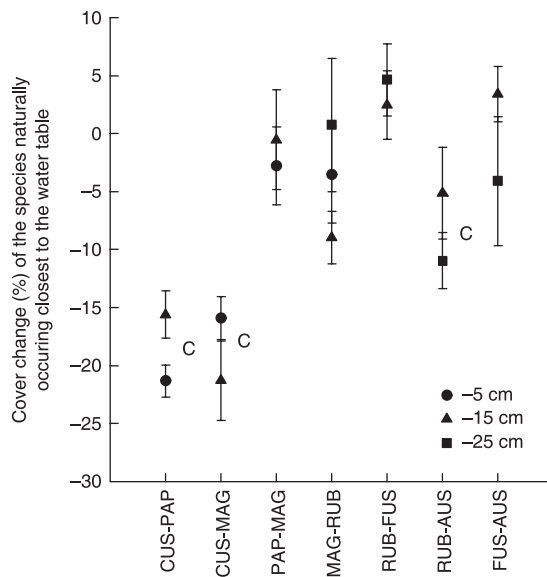
Fig. 2. Cover change at different water tables within the experimental species combinations. Values are mean cover change (±1 SE) for the species that naturally occurs closest to the water table (see Fig. 1). C, overall change in cover (ANOVA, $P < 0.05$). For statistics see Table 1.

ANOVA was used to test the effect of cutting on WC_{cap} of *S. magellanicum* and *S. rubellum*. Pearson correlation analysis was used to outline the relationship between differences in height increment and change in cover of the fastest-growing species. Paired-sample *t*-tests were used to test for differences in WC_{cap} and BD_{subcap} between monocultures and the corresponding species in a mixture.
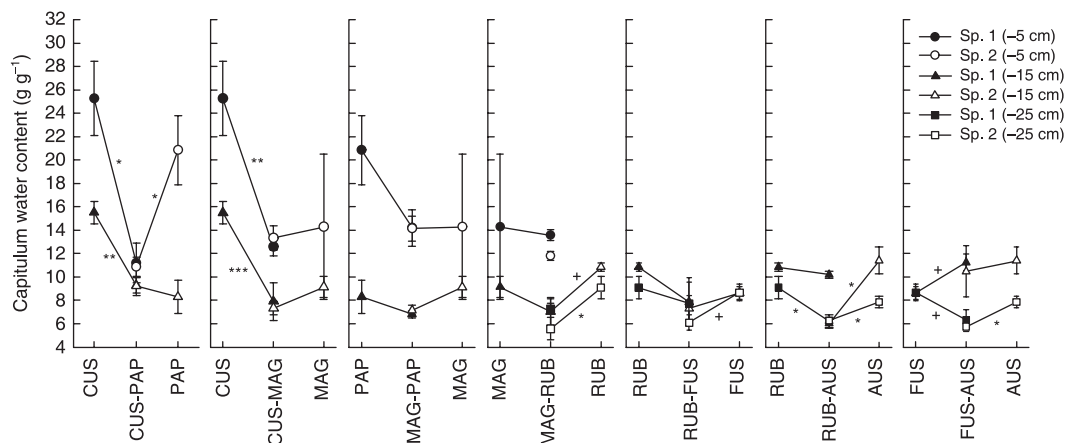
Results

COVER CHANGE

Over all treatments, water table did not affect cover change of species growing in a mixture ($F = 0.04$,

$P = 0.97$), but there was an effect of mixture type ($F = 10.73$, $P < 0.001$). Among the seven species mixtures examined in this study, three showed overall shifts in relative cover, all at the expense of the species naturally occurring lower on the hummock–hollow gradient (Fig. 2; Table 1). Cover change seemed to be most pronounced when hollow and lawn species were grown in competition (Fig. 2). Water table did not play an important role in determining the outcome of competition; it only affected cover change in the CUS–PAP combination, but counterintuitively, *S. cuspidatum* cover decrease was largest at the highest water table (Table 1).

SPHAGNUM HEIGHT INCREMENT, WC_{CAP} AND BD_{SUBCAP}

Cumulative height increment was relatively small and varied between –2.20 and 2.28 cm over the experimental period, but was smaller than 1 cm in 76% of observations. In some species (especially *S. cuspidatum*), we found negative height increment (data not shown), possibly caused by the slight subsidence of the peat material. Despite the low height increment, we did find differences in height increment between species growing together. Difference in height increment between the species in the mixture was affected by water table only in the CUS–PAP mixture ($F = 5.41$; $P < 0.05$). In all cases but one, cover change of the fastest-growing species was significantly correlated with the difference in height increment (Table 2).

The WC_{cap} of individual species in a mixture was affected by water table (two-way ANOVA, $P < 0.1$). Lower water tables resulted in lower WC_{cap}, especially for the hollow and lawn species (Fig. 3). Interestingly, WC_{cap} between individual species in a mixture did not differ, except for the RUB–AUS combination at –15 cm (two-way ANOVA, species × water, $F = 27.54$, $P < 0.001$; Fig. 3). For individual species in a mixture, WC_{cap} was generally lower than when growing in a monoculture

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Fig. 3. Capitulum water content (WC_{cap}) of the individual species in a mix at the applied water tables compared with WC_{cap} of monocultures. Mean ± 1 SE is indicated for each species in monoculture and in a mixture ($n = 5$). Differences in WC_{cap} between species in monocultures and similar species in a mixture at definite water tables are indicated (paired-sample *t*-tests: +, $P < 0.1$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$). Sp. 1 = first species on the *x*-axis; Sp. 2 = second species on the *x*-axis.

Table 1. Values for effects of water table on cover change within each mixture (one-way ANOVA). For the analysis we used only data for the species within the mixture that naturally occur closest to the water table (first-mentioned in table)

Mixture	Source	Type III SS	df	MS	F	P
CUS–PAP	Intercept	3411·668	1	3411·668	223·211	<0·001
	Water	81·447	1	81·447	5·329	0·050
	Error	122·276	8	15·285		
	Corrected total	203·724	9			
CUS–MAG	Intercept	3464·028	1	3464·028	90·284	<0·001
	Water	73·057	1	73·057	1·904	0·205
	Error	306·945	8	38·368		
	Corrected total	380·002	9			
PAP–MAG	Intercept	27·636	1	27·636	0·373	0·558
	Water	12·522	1	12·522	0·169	0·692
	Error	592·896	8	74·112		
	Corrected total	605·418	9			
MAG–RUB	Intercept	231·265	1	231·265	2·485	0·141
	Water	238·516	2	119·258	1·282	0·313
	Error	1116·553	12	93·046		
	Corrected total	1355·068	14			
RUB–FUS	Intercept	125·741	1	125·741	2·742	0·136
	Water	11·964	1	11·964	0·261	0·623
	Error	366·807	8	45·851		
	Corrected total	378·771	9			
RUB–AUS	Intercept	647·140	1	647·140	12·107	<0·01
	Water	85·328	1	85·328	1·596	0·242
	Error	427·598	8	53·450		
	Corrected total	512·926	9			
FUS–AUS	Intercept	1·184	1	1·184	0·013	0·912
	Water	141·263	1	141·263	1·546	0·249
	Error	730·913	8	91·364		
	Corrected total	872·176	9			

CUS = *S. cuspidatum*, PAP = *S. papillosum*, MAG = *S. magellanicum*, RUB = *S. rubellum*, FUS = *S. fuscum*, AUS = *S. austinii*.

Table 2. Correlation between the difference in height increment between two species in a mixture and cover change of the fastest-growing species (Pearson correlation analysis)

Mixture	Water table	Correlation coefficient	P
CUS–PAP	–5 cm	0·781	0·119
	–15 cm	0·905	<0·005
CUS–MAG	Overall	0·821	<0·005
PAP–MAG	Overall	0·934	<0·001
MAG–RUB	Overall	0·880	<0·001
RUB–FUS	Overall	0·746	<0·05
RUB–AUS	Overall	0·862	<0·005
FUS–AUS	Overall	0·940	<0·001

(paired sample *t*-tests; Fig. 3). It is unlikely that this could be attributed to the different handling of the cores, as an additional experiment with cut and uncut *S. magellanicum* and *S. rubellum* monocultures showed no difference in WC_{cap} (one-way ANOVA: *S. magellanicum*, $F = 1·51$, $P = 0·235$; *S. rubellum*, $F = 2·07$, $P = 0·167$).

The BD_{subcap} between individual species in a mix was different (Table 3). In general, BD_{subcap} of species was not affected by growing alone or in a mixture (paired-sample *t*-test). In cases where we did find differences in BD_{subcap} ($\Delta CUS/CUS_{MAG}$–15, $t = -4·12$, $P < 0·05$; $\Delta CUS/CUS_{PAP}$–15, $t = -2·97$, $P < 0·05$; $\Delta AUS/AUS_{FUS}$–15, $t = -2·97$, $P < 0·05$; $\Delta RUB/RUB_{AUS}$–15, $t = -3·23$,

$P < 0·05$; $\Delta RUB/RUB_{AUS}$–25, $t = -3·17$, $P < 0·05$) monocultures had lower BD_{subcap}. Surprisingly, we did not find a relation between WC_{cap} and BD_{subcap}, irrespective of water-table treatments (−5 cm, Pearson correlation = −0·110, $P = 0·43$; −15 cm, Pearson correlation = −0·078, $P = 0·44$; −25 cm, Pearson correlation = −0·055, $P = 0·69$).

Discussion

COMPETITION BETWEEN *SPHAGNUM* SPECIES: EFFECT RESPONSE

According to our hypothesis, species that naturally occur further above the water table generally increased in cover at the expense of species that naturally occur closer to the water table. Contrary to our expectations, water table did not seem to be an important factor in influencing cover change. Within a species mixture, in general water table did not affect the outcome of the competition between species. Mixture type, and thus species identity, seems to be much more important. In particular, differences in 'functional type' seemed crucial in determining cover change. The effect was largest when a hollow species was involved. A similar conclusion was drawn from a reciprocal transplantation experiment in the field, where three *Sphagnum* species were transplanted to each other's habitat. Hummock

Table 3. Subcapitulum bulk density (g cm^{-3}) for individual species within every species combination. All values are means ± SE (*n* = 5). Within every species combination, two-way ANOVA models were used to test for the effect of species (S) and water table (W) on subcapitulum bulk density. Species 1 = data for the species first mentioned in the species combination; species 2 = second species in the species combination

Species		Subcapitulum bulk density						
		CUS–PAP	CUS–MAG	MAG-PAP	MAG–RUB	RUB–FUS	RUB–AUS	FUS–AUS
1	−5	0·023 ± 0·001	0·018 ± 0·001	0·018 ± 0·002	0·024 ± 0·003	–	–	–
	−15	0·034 ± 0·006	0·024 ± 0·004	0·022 ± 0·003	0·015 ± 0·001	0·022 ± 0·002	0·027 ± 0·002	0·023 ± 0·002
	−25	–	–	–	0·015 ± 0·002	0·029 ± 0·003	0·026 ± 0·001	0·019 ± 0·001
2	−5	0·024 ± 0·004	0·014 ± 0·002	0·018 ± 0·003	0·026 ± 0·005	–	–	–
	−15	0·017 ± 0·002	0·016 ± 0·002	0·020 ± 0·002	0·020 ± 0·001	0·022 ± 0·001	0·043 ± 0·006	0·037 ± 0·002
	−25	–	–	–	0·024 ± 0·003	0·025 ± 0·004	0·049 ± 0·007	0·030 ± 0·002
	S	†	*	ns	*	ns	***	***
	W	ns	ns	ns	†	†	ns	**
	S × W	**	ns	ns	ns	ns	ns	ns

†P = 0·1; *P = 0·05; **P = 0·01; ***P = 0·001.

species increased in cover at the expense of hollow species, whereas the competitive advantage among more closely related species seemed to be much more variable (Rydin 1993). Our results, however, have to be treated with some caution because our set-up complicates the disentanglement of water table and species mixture effects, as species identity and water table are more-or-less confounding.

COMPETITION BETWEEN *SPHAGNUM* SPECIES: MECHANISTIC RESPONSES

Compared with field values (reviewed by Gunnarsson 2005), height increment was relatively small in our experiment, which was probably a result of the low precipitation rates. Nevertheless, species in a mixture differed in height increment, and in most mixtures this difference was positively correlated to the increase in cover of the faster-growing species. Contrary to our expectations, water table did not seem to play a major role. The competitive outcome seemed to be related to differences in height increment, irrespective of the water table.

As water supply to the capitula becomes more difficult with decreasing water table (Rydin *et al.* 1999; Lafleur *et al.* 2005), the efficiency of the capillary system and interspecific differences therein may become very important in keeping the capitula moist under periodic drought. However, in our experiment, WC$_{cap}$ between the species in a mixture were not different. Therefore interspecific differences in height increment cannot be explained straightforwardly by differences in WC$_{cap}$. This suggests that the competitive outcome may be related to differences in the ability of species to cope with low water availability, either low water tables or low amounts of precipitation. There are indications that species differ in their ability to photosynthesize when water is scarce, yet consensus about differences in physiological response to WC$_{cap}$ between functional types is not evident. Silvola & Aaltonen (1984) found no great differences between *S. fuscum* (hummock) and *S. angustifolium* (hollow). At reduced water contents, *S. fuscum* maintained higher photosynthesis than did *S. angustifolium*, whereas at increased water contents the opposite was found. Titus *et al.* (1983) found an opposite effect when comparing *S. nemoreum* (hummock) with *S. fallax* (hollow); and Rydin & McDonald 1985b) found that *S. balticum* (lawn) and *S. tenellum* (hollow) were more sensitive to reduced water content than *S. fuscum*.

Individual species in mixed cultures generally had lower WC$_{cap}$, and concomitantly lower height increment (data not shown), than in monoculture. BD$_{subcap}$ did not differ for a species growing in mono- or mixed culture, or was even lower in monocultures. Contrary to our assumptions, the above suggests that bulk density may not be a good predictor of the *Sphagnum* vegetation's ability to supply water to the capitula. Other physical properties, such as texture and structure, may play a more important part in the efficiency of the capillary system. An interesting outcome of our experiment was that, in a larger volume of isotropic peat material, water supply to the capitula was more efficient than in a smaller volume. Since WC$_{cap}$ did not differ between cut and uncut monocultures, it is unlikely that the lower WC$_{cap}$ of a species in mixed culture compared with monoculture can be explained as an effect of cutting. Probably the structural heterogeneity of the peat in mixed cultures has a negative effect on the water supply to the capitula of both species. These findings are in accordance with those of Kellner & Halldin (2002), who found anisotropy of peat material to be unfavourable for the hydrological conditions at a bog surface. Our data also suggest that patch size has an effect on competitive strength. The ability of a *Sphagnum* species to supply its capitula with water seems to increase with increasing patch size. More research is required to explain the mechanism(s)

involved, but these findings suggest that a species growing in a peat moss mosaic gains in competitive strength when its patch size enlarges.

EFFECT OF LONG-TERM CHANGES IN CLIMATE

It has been shown that *Sphagnum* species are able to co-occur for prolonged periods (Rydin & Barber 2001; Gunnarsson, Malmer & Rydin 2002), yet changes in the global climate can cause the species composition to change (Mauquoy *et al.* 2001). Rydin & Barber (2001) stated that competition may be intense among species, but as there is no consistent competitive hierarchy over time, competition is not a structuring force that eliminates species from the community. However, this applies only if there are no linear changes in environmental conditions. Investigations of future climate scenarios suggest a slight increase in temperature (Houghton *et al.* 2001; Sweeney & Fealy 2002). Changes in precipitation cannot yet be accurately predicted, but reductions in summer rainfall are likely to occur (Sweeney & Fealy 2002). In addition, higher summer temperatures could increase evaporation rates (Gunnarsson, Granberg & Nilsson 2004) which, if not balanced by precipitation, will result in decreased water tables in raised bogs (Schouten, Streefkerk & Van der Molen 1992). Recently, it has been shown that increased temperature can have a direct positive effect on biomass production of *S. magellanicum* and *S. rubellum*, but not on *S. fuscum* and *S. austinii*, irrespective of the water table, whereas of the four species only *S. magellanicum* was negatively affected by decreased water table (Robroek *et al.* 2007).

Here we show that, under sustained periods of drought, the competitive balance between species seems to shift towards *Sphagnum* species that naturally occur higher on the hummock–hollow gradient, irrespective of the water table depth. These shifts are largest in hollow–lawn species combinations, which indicates that hollow species will not be able to compete with more drought-resistant species when sustained periods of drought occur more frequently. Eventually, this could lead to species loss and the evening out of the typical hollow–hummock pattern of raised bogs.

Acknowledgements

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