

Growth, production and interspecific competition in *Sphagnum*: effects of temperature, nitrogen and sulphur treatments on a boreal mire

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Summary

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- Growth and production of *Sphagnum balticum* and interspecific competition between *S. balticum* and either *Sphagnum lindbergii* or transplanted *Sphagnum papillosum*, were studied in a 4-yr field experiment in a poor fen.
- Temperature and influxes of nitrogen (N) and sulphur (S) were manipulated in a factorial design. The mean daily air temperature was increased by 3.6°C with glass-house enclosures. Nitrogen loads were increased 15-fold and S loads seven-fold compared with the natural loads up to influxes observed during the 1980s in south-western Sweden.
- Production of *S. balticum* decreased with increasing temperature and N-influx. The N treatment significantly reduced the incremental length of *S. balticum*, and this reduction was reinforced with time (24% in the first year to 51% in the final year). The area covered by *S. lindbergii* changed with time in all treatments and *S. papillosum* area increased significantly in the temperature-treated plots.
- Growth, production and competitive patterns change if the environmental conditions change. Increased N deposition and raised temperature may transform mires currently dominated by *Sphagnum* into vascular-plant-dominated mires.

Key words: *Sphagnum*, nitrogen deposition, global warming, production, acidification, peatlands, competition.

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Introduction

Boreal mires store in total *c.* 300–455 Gt carbon, equivalent to 20–30% of the global soil carbon (Gorham, 1991). Most of this carbon is stored in *Sphagnum* peat, and it has been suggested that more carbon may be stored in *Sphagnum* than in any other plant genus (Clymo & Hayward, 1982). Mires have been subject to natural environmental changes throughout the Holocene. However, since industrialization, human activities have increased the rate of change. Particularly pronounced changes include the large increases seen in the deposition rates of nitrogen (N) and sulphur (S) and the increased temperatures in boreal regions. These changes may have had major effects on the vegetation and on the biogeochemical cycles in boreal mire ecosystems.

In *Sphagnum*-dominated peatlands *Sphagnum* growth and production are key variables in the interactions between vascular plants and mosses and for the function of the ecosystem as carbon sequesters (Malmer *et al.*, 1994; Svensson, 1995; van Breemen, 1995; Berendse *et al.*, 2001; Ohlson *et al.*, 2001). *Sphagnum* has the ability to engineer its environment, making it acid and nutrient poor, while promoting a high water table with accompanying anoxic conditions (van Breemen, 1995). Very few vascular plants can compete in the resulting environment. Growth of *Sphagnum* on bogs and poor fens is usually not greater than 1–5 cm yr⁻¹ (Rocheffort *et al.*, 1990; Gunnarsson & Rydin, 2000), but this is enough to outgrow most vascular plant seedlings under these conditions (van Breemen, 1995; Gunnarsson & Rydin, 1998; Ohlson, 1999; Ohlson *et al.*, 2001). However, environmental changes may affect *Sphagnum*

growth rates, and reductions in its growth may release the vascular plants from stress by reducing the rate at which they need to grow to match its vertical growth. This may, in turn, increase the likelihood that the mire communities will become more dominated by vascular plants (Berendse *et al.*, 2001; Heijmans *et al.*, 2001; Limpens *et al.*, 2003; Malmer *et al.*, 2003; Tomassen *et al.*, 2003). As the competition for light is asymmetric, favouring large plants, in this case vascular plants, the growth of *Sphagnum* would subsequently be further reduced by shading from the vascular plants and the accumulated litter (Hayward & Clymo, 1983; Chapman & Rose, 1991; Limpens *et al.*, 2003). Thus, reductions in the production of *Sphagnum* may profoundly affect the role of boreal mires as carbon-sequestering ecosystems (Gorham, 1991; Thormann *et al.*, 1999).

Northern mires usually have a clear microtopographic pattern with distinct hummocks and hollows. *Sphagnum* species growing in these ecosystems show clear distinctions in their distribution in relation to variables such as height above the water table and pH (Økland, 1989; Rydin, 1993). Several authors have speculated that the main effects of global warming on mires would be changes associated with a lowering of the water table (Manabe & Wetherald, 1986; Moore *et al.*, 1998). However, it has also been suggested that a warmer climate would increase precipitation in some northern regions (Maxwell, 1992; Mattsson & Rummukainen, 1998), which makes it difficult to predict the outcome of global warming on the water table. Such changes will probably result in larger variations in the ground water table and might change the intricate species composition along the hollow-to-hummock gradient. Raising the air temperature may, by itself, lead to increased evapotranspiration, but the air humidity does not necessarily have to be increased (cf. Granberg *et al.*, 2001). In areas with low summer temperature increased temperatures may be important to raise the relative growth rate of bryophytes as long as the elevated evapotranspiration does not lead to desiccation. *Sphagnum* species growing in hollows often tend to dry out more than hummock-forming species during dry periods, even though they are growing closer to the water table (Rydin, 1993). This drought-pattern is mainly attributable to differences in capillary transport systems, which are more highly developed in hummock-forming *Sphagnum* species than in hollow species (Hayward & Clymo, 1982; Rydin, 1985). Thus, if a warmer climate lowers the ground water table, increases the desiccation rate or gives longer dry periods, hummock-forming *Sphagnum* species may benefit at the expense of hollow-dwelling species.

At N-limited sites an elevated N supply will result in increased growth, up to a certain capitulum concentration (Vitt *et al.*, 2003). Above this point the *Sphagnum* growth will be limited by other factors, such as phosphorus (Aerts *et al.*, 1992), and the high N concentration may result in a nutrient imbalance or even be toxic. In recent N fertilization experiments *Sphagnum* growth decreased when the capitulum N concentrations became

too high, owing to moderate influxes (*c.* $1 \text{ g m}^{-2} \text{ yr}^{-1}$) over long periods (Rocheffort *et al.*, 1990; Gunnarsson & Rydin, 2000) or high influxes ($> 15 \text{ g m}^{-2} \text{ yr}^{-1}$) over a shorter period (van der Heijden *et al.*, 2000b). *Sphagnum* species have no known mechanism for regulating their uptake of N (Jauhiainen *et al.*, 1998b), but can transport N internally from older to younger tissue (Aldous, 2002).

Field studies in the southern Pennines, UK, have shown that high influxes of S (as SO_2 , HSO_3^{2-} and SO_4^{2-}) can dramatically reduce the occurrence and growth of *Sphagnum* (Tallis, 1964; Ferguson *et al.*, 1978). Inter- and intra-specific differences in the growth responses of *Sphagnum* species to HSO_3^{2-} and SO_4^{2-} additions have also been observed (Ferguson & Lee, 1980; Austin & Wieder, 1987; Lee *et al.*, 1990). There are some reasons to believe that the interactions between the N, S and temperature treatments are different from pure additive effects. For example, the uptake of S might be reduced by high levels of N and intercellular concentrations of the physiologically active substances may very well interfere with each other. Thus, the combination of high N and high S might be positive for growth in some situations. Increased levels of N influx might be extra harmful for *Sphagnum* when the air temperature is increased and the mosses are dry.

Sphagnum species have been shown to coexist in 1 dm^2 plots for many hundreds or even thousands of years (Rydin & Barber, 2001). Such species coexistence in a community can be explained either by species occupying different niches or being competitive equivalents (Bengtsson *et al.*, 1994). If species coexistence is explained by niche differentiation, the environment has to be spatially or temporally heterogeneous. By contrast, if coexisting species are similar enough in their competitive abilities, no competitive exclusion will occur, even in the absence of niche differentiation (Hubbel & Foster, 1986). If the environment change and species is niche differentiated the competitive relations will change and the prerequisites for species coexistence will be altered. Several studies have found reduced species coexistence (diversity) following increased N influx (Lütke Twenhöven, 1992; Willems & van Nieuwstadt, 1996; Berendse, 1999). In *Sphagnum* monolayers individual shoots compete for space. Thus, individuals that are well adapted to the new environmental conditions following changes will successively occupy larger surface areas and eventually monopolize the area.

To our knowledge this one of the first large-scale field experiments on boreal mire ecosystems where the effects of a raised temperature and increased influxes of N and S on *Sphagnum* communities have been studied in a full factorial design. In this study we test the following hypotheses: (1) for the lawn species *Sphagnum balticum*, length growth and production will be reduced at increased temperature, increased influxes of N and S and there are interactions between these factors; (2) as the environmental conditions change (i.e. as temperature or N and/or S influxes increase) the competitive relations between naturally coexisting species will change;

(3) a transplanted hummock species will increase in the temperature treatments at the expense of the naturally occurring hollow species.

Materials and Methods

The site

The experimental site is a poor fen lawn community (*sensu* Sjörs, 1948) at Degerö Stormyr is at 64°11' N, 19°33' E, 270 m above sea level, c. 60 km north-west of Umeå (northern Sweden). The mire was described by Malmström (1923). The site was selected to be as uniform as possible in terms of vegetation and water chemistry, and there were no microtopographical patterns of hummocks and hollows in the area. The precipitation is c. 520 mm yr⁻¹ and the mean temperature is 14.7°C in July and -12.4°C in Jan. (Alexandersson *et al.*, 1991). The dominant vascular plants are *Eriophorum vaginatum* L., *Vaccinium oxycoccos* L., *Andromeda polifolia* L., *Scheuchzeria palustris* L. and *Carex limosa* L. These species grow in a continuous carpet dominated by *Sphagnum balticum* Russ. C. Jens. and *Sphagnum lindbergii* Schimp. The pH of all experimental plots was c. 4.0, in June 1997 with no significant differences between plots allocated to different treatments (Granberg *et al.*, 2001).

Species studied

Sphagnum balticum and *S. lindbergii* taxonomically belong to section Cuspidata (Isoviita, 1966) and both occur in carpets and lawns (Rydin, 1993). The transplanted species, *S. papillosum* Lindb., belongs to section Sphagnum and occurs over a wide range of water levels. It is most frequently found in low hummocks and lawns (Rydin, 1993).

Experimental design

The experimental set-up was a full factorial design with two levels of each of temperature, N and S. Each experimental combination was duplicated, and in addition there were four replicates of N and S midpoint treatments, with half the N and S additions applied in the N and S treatments under ambient temperature, and a control without a surrounding plastic frame, giving a total of 21 experimental plots (size 2 × 2 m). There were no obvious effects of the inserted frames, thus we used the unframed plot as an additional untreated control. Midpoint treatments were placed in the corners of the experimental area and the other treatments were distributed randomly over the remaining plots (see Granberg *et al.* (2001) for further information about the experimental design). The experiments were established in summer 1994, when plastic frames (0.5 m deep) were inserted into the ground to prevent horizontal movements of the added elements.

The experimental treatments were started in 1995, when transparent plastic screens (0.5 m high) were set up around the plots that were to be temperature-treated, to raise the temperature. However, soil temperatures at 18 cm depth were not found to be significantly affected in the first year by the plastic screens, so these plots were covered with perforated plastic films to further increase the temperature. These films were removed during the winter. Following this measure, the average soil temperature difference at 18 cm depth between the temperature plots and the other plots was 2°C during the snow-free period late May to late Sept., in 1996–97, whereas the air temperature at 25 cm above the moss surface was increased by 3.6°C (Granberg *et al.*, 2001). The plastic films reduced the irradiance (20–25% of PAR), but the radiation spectrum (325–700 nm) was not changed (Granberg *et al.*, 2001). The holes in the perforated plastic film also changed the spatial distribution of the rain, and the plastic film might have reduced dry deposition in these plots. However, this reduction was probably negligible given the low background deposition at this site, and the more important wet deposition was probably not reduced by the film.

Nitrogen was applied as NH₄NO₃ and sulphur as Na₂SO₄. The chemicals to be added to each 4 m² plot were dissolved and applied in 10 dm³ of mire water at each application event, equivalent to 2.5 mm of rain. Mire water was also added to the control plots. One-third of the yearly dose was applied after snowmelt, and one-sixth was applied each month from June to Sept. The amounts of N and S applied were 2.8 g m⁻² yr⁻¹ and 1.7 g m⁻² yr⁻¹, respectively. These inputs, together with the ambient deposition in the area (i.e. 0.2 g m⁻² yr⁻¹ and 0.3 g m⁻² yr⁻¹), equal the maximum annual depositions found in Sweden (3 g m⁻² yr⁻¹ N and 2 g m⁻² yr⁻¹ S; Lövblad *et al.*, 1994). For the midpoint-treatments half the maximum doses of N and S were applied (i.e. ambient deposition plus the addition of 1.3 g m⁻² yr⁻¹ and 0.7 g m⁻² yr⁻¹, respectively). In a recent article Granberg *et al.* (2001) presented results from methane emission studies at the same experimental site.

Measurements of growth and competition

To measure *Sphagnum* growth and production we used Clymo's (1970) cranked wire method, as modified by Gunnarsson & Rydin (2000) (i.e. a short brush, 1 cm long, was attached to a metal wire, c. 15 cm long, and inserted into the moss matrix so that the wire was extending vertically upwards, providing dynamic reference points). In each plot, three patches (c. 15 × 15 cm) in which *S. balticum* was the only species of *Sphagnum* present were located and three wires were inserted per patch.

To test the treatment effects on interspecific competition between *S. balticum* and *S. lindbergii*, one patch per plot, with as equal proportions of the species as possible, was visually located and marked. The vascular plants were removed from the patches and the areas covered by each species were mapped

on a circular transparency (diameter, 10 cm) and later measured using a digitizing pad (Rydin, 1986).

In a transplant experiment, we tested how the hummock and lawn-forming species *S. papillosum* affected *S. balticum*. We used transplants of *S. papillosum*, because it was the only hummock-forming species growing in this fen. The transplants were collected from a low hummock c. 50 m outside the experimental area. Cylindrical cores, 8 cm in diameter and 10 cm deep, were transplanted into each plot after removing cores of the same size of *S. balticum* growing in the plot. Areas covered by the transplanted *S. papillosum* were drawn on a transparency and the area was measured with a digitizing pad.

All experiments were established at the end of June 1995. The first measurements were performed 3 wk after their establishment. The wires and the area covered by *S. lindbergii* and *S. papillosum* were then measured twice each year, at the end of June and in mid Sept., until 1998. From each *S. balticum* patch a core (7 cm diameter) was sampled at the end of the experiment. The cores were divided into capitula (the top 1 cm) and stems (the next 2 cm). The fractions were dried at 70°C for 48 h and weighed. To convert length increments into biomass production we multiplied the length increment by the bulk density of the stem fraction and corrected for treatment changes in capitula weights (Gunnarsson & Rydin, 2000).

The height above the water table was measured weekly in plastic tubes during the experiment, and the position of the ground water table and the temperature were monitored daily at a climate station located in the experimental area (Granberg *et al.*, 2001).

Statistical analysis

To evaluate the treatment effects on production, capitulum weight and length increment we used multiple linear regressions, which can use the full power of the applied experimental design, including the midpoint treatments (Box & Draper, 1987). Thus, N and S influx were treated as continuous variables in the analyses. For the change in area of the *Sphagnum* species we used repeated measures analyses (SAS Institute Inc., 1989; Wolfinger & Chang, 1995); if the time interactions were significant we also performed multiple regression for changes within separate periods. The following response variables were used in the analysis: plot means of production and capitulum dry mass, plot means of length increment for each growing season and the measured area of *S. lindbergii* and *S. papillosum*. In the multiple regression analyses no nonlinearity was found using lack of fit tests (Box & Draper, 1987). Since the height above the ground water table may influence the water balance of *Sphagnum*, and thus its production (Rydin, 1993; Vitt *et al.*, 2003), we used the overall mean plot heights above the water table as a covariate in the analyses; in the length increment analyses the yearly means were used. In all analyses we included the main experimental factors (N, S and temperature); only significant interactions ($P < 0.05$) were included in the models.

Results

Growth and production of *S. balticum*

The average production of *S. balticum* over the 4-yr period was 115 g m⁻² yr⁻¹ (± 6.0 SE) for the controls and was significantly reduced by both the increased N influx and raised temperature regime (Table 1, Fig. 1). Compared with the

Table 1 Summary of multiple regression models of *Sphagnum balticum* production and capitulum dry mass sampled in September 1998

Production (g m ⁻² yr ⁻¹)			Capitulum dry mass (g m ⁻²)		
Factor	Coefficients	P	Factor	Coefficients	P
Intercept	62 (25)	0.022	Intercept	121 (39)	0.006
WT	5.1 (2.4)	0.049	WT	5.9 (3.8)	0.14
N	-15 (3.1)	< 0.001	N	-12 (4.9)	0.023
T	-37 (8.2)	< 0.001	T	-59 (13)	< 0.001
S	-3.5 (4.8)	0.47	S	11 (7.6)	0.15
r ²	0.72		r ²	0.63	

Model coefficients (SE in parentheses) are shown with corresponding *P*-values for the significance of the factors. WT, the height above the water table; N, nitrogen; T, temperature; S, sulphur; r², the total variance explained by the model.

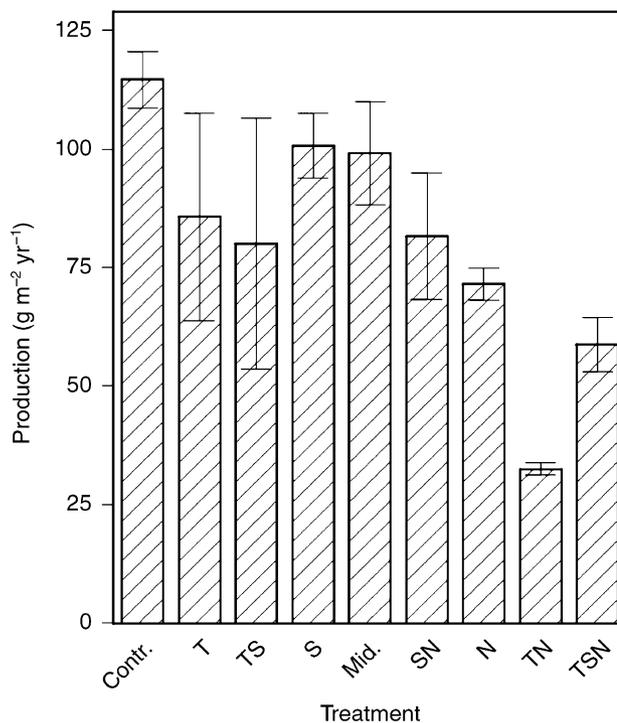


Fig. 1 Mean annual dry mass production (\pm SE) of *Sphagnum balticum* during 1995–98 for the different treatments. Contr., controls; T, temperature; S, sulphur; Mid., midpoint (see text for explanation); N, nitrogen; and the combined treatments T \times S (TS), S \times N (SN), T \times N (TN) and T \times S \times N (TSN).

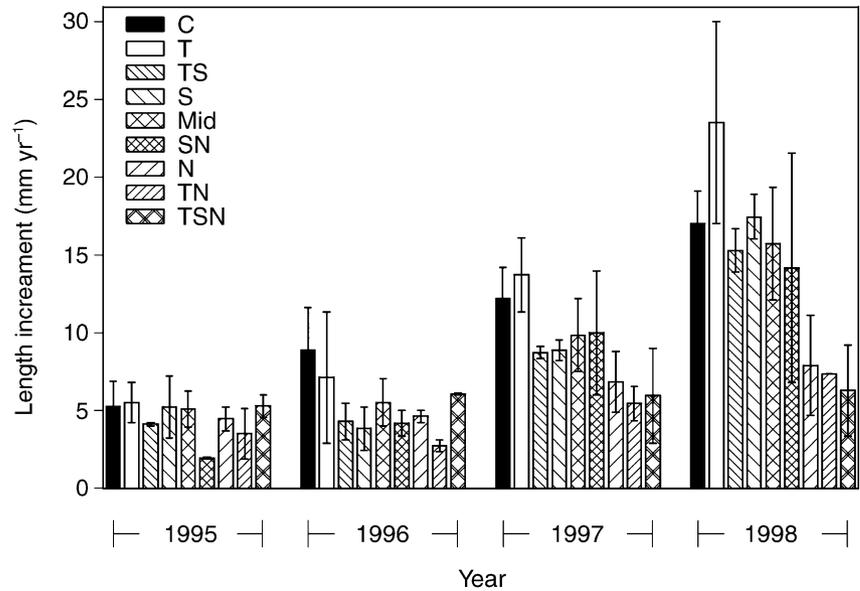


Fig. 2 Mean annual length increments (\pm SE) of *Sphagnum balticum* during 1995–98 for the different treatments: C, controls; T, temperature; S, sulphur; Mid, midpoint (see text for explanation); N, nitrogen; and the combined treatments T \times S (TS), S \times N (SN), T \times N (TN) and T \times S \times N (TSN).

Table 2 Mean height above the ground water table and mean air temperature (SD in parentheses) and air temperature sum (threshold 0°C) during the period June–September in 1995–98 from the experimental site at Degerö Stormyr, northern Sweden

	1995	1996	1997	1998
Mean height (cm)	17 (3.9)	13 (4.7)	13 (4.4)	5 (3.3)
Mean temperature (°C)	11 (4.3)	12 (3.7)	14 (3.9)	12 (3.0)
Temperature sum (degree days)	825	1077	1183	906

controls, the high N treatment and the temperature treatment had reduced production by 47% and 43%, respectively. The combined N and temperature treatment had only 26% of the production measured in the controls (Fig. 1). Sulphur had no

significant effect on *S. balticum* production, and we found no significant interactions (Table 1).

The overall mean length increment of *S. balticum* increased during the experiment from 5 mm in 1995 to 17 mm in 1998 (controls in Fig. 2) and was negatively correlated with the height above the mean annual water table (Pearson $r = -0.93$, $n = 4$, $P = 0.07$, Table 2). Because of the strong time effect we performed models for each separate growing season (1995–98). The effect of N became increasingly negative during the experiment (i.e. the annual growth rates declined increasingly strongly with time in the high N treatments, from a 24% reduction in 1995 to a 51% reduction in 1998, compared with the controls and the regression coefficient for N decreased from -0.48 in 1995 to -3.5 in 1998; Table 3). In 1995 the midpoint treatment had about the same length growth as the control plots (Fig. 2), but in later stages the N addition

Table 3 Summary of multiple regression models of *Sphagnum balticum* length growth during the vegetation periods in 1995–98

Factor	<i>Sphagnum balticum</i> growth in length (mm)							
	1995		1996		1997		1998	
	Coefficients	<i>P</i>	Coefficients	<i>P</i>	Coefficients	<i>P</i>	Coefficients	<i>P</i>
Intercept	3.6 (3.5)	0.31	-3.6 (5.2)	0.50	1.0 (6.9)	0.88	13 (4.8)	0.013
WT	0.22 (0.38)	0.57	1.3 (0.50)	0.021	1.1 (0.66)	0.10	1.8 (1.1)	0.13
N	-0.48 (0.35)	0.19	-2.4 (0.72)	0.005	-1.6 (0.6)	0.018	-3.5 (1.0)	0.002
T	-0.04 (0.95)	0.96	-1.5 (1.2)	0.21	-1.2 (1.5)	0.44	-2.5 (2.6)	0.36
S	-0.24 (0.60)	0.69	-2.6 (1.0)	0.025	-0.16 (1.0)	0.87	0.43 (1.6)	0.79
S \times N	-	-	1.4 (0.51)	0.017	-	-	-	-
<i>r</i> ²	0.12		0.52		0.38		0.47	

Model coefficients (SE in parentheses) are shown with corresponding *P*-values for the significance of the factors (significant coefficients in bold). -, nonsignificant interaction ($P > 0.05$) not included in the model; WT, the height above the water table; N, nitrogen; T, temperature; S, sulphur; *r*², the total variance explained by the model.

reduced the *S. balticum* length increment (Fig. 2). In 1996, S had a significant negative effect on length increment and a significant interaction between N and S (Table 3). This interaction was caused by a reduction in length only in S-treated plots without additional N-influx (Fig. 2). Height above the ground water table had a significantly positive effect on length increment in 1996 (i.e. in this year length growth benefited by a lower groundwater table).

Raised air temperature and increased N influx had significant negative effects on capitulum dry mass (Table 1). The capitulum dry mass in the controls was, on an average, 170 g m^{-2} ($\pm 16 \text{ SE}$) and the weights in the temperature and N-treated plots were, on an average, reduced by 27% and 20%, respectively, compared with the controls.

Competition between *S. lindbergii* and *S. balticum*

The area covered by *S. lindbergii* was significantly affected by the time interactions with N, S, temperature and $N \times S$ (Table 4), demonstrating that the treatments had different effects on the species interactions during the experiment (Fig. 3). Analysis of separate periods showed that the temperature treatment initially had no effect on the area of *S. lindbergii* until the summer of 1996 when the temperature treatment significantly reduced the area (coefficient = -2.40 , $t = -2.49$, $P = 0.025$, Fig. 3). Thereafter, temperature did not influence the area change. In the high N treatment *S. lindbergii* had increased in area after the 4-yr period by 62%, from an

Table 4 Summary of a repeated measures analysis model of changes in area covered by *Sphagnum lindbergii* from July 1995 to September 1998

Factor	F	P
WT	0.21	0.65
N	0.01	0.93
T	0.97	0.34
S	1.4	0.26
$S \times N$	1.2	0.29
Time	1.9	0.18
Time \times WT	1.8	0.21
Time \times N	9.0	0.002
Time \times T	7.4	0.004
Time \times S	6.6	0.006
Time \times S \times N	4.2	0.024

As the test statistics for the time interactions we present Pillai's trace, where both denominator and numerator $df = 7$; for the other factors $df = 1$ (significant factors in bold). WT, the height above the water table; N, nitrogen; T, temperature; S, sulphur.

average of 9.3 cm^2 ($\pm 2.3 \text{ SE}$) at the start of the experiment to 15.1 cm^2 ($\pm 3.7 \text{ SE}$). However, the only significant main N effect was a decrease during the first summer (coefficient = -1.79 , $t = -2.93$, $P = 0.0103$, Fig. 3). In the succeeding periods, N had positive effects on *S. lindbergii* area, with the largest increase in the summer of 1998 (coefficient = 3.5 , $t = 2.01$, $P = 0.058$, Fig. 3). Sulphur had a positive effect on *S. lindbergii*

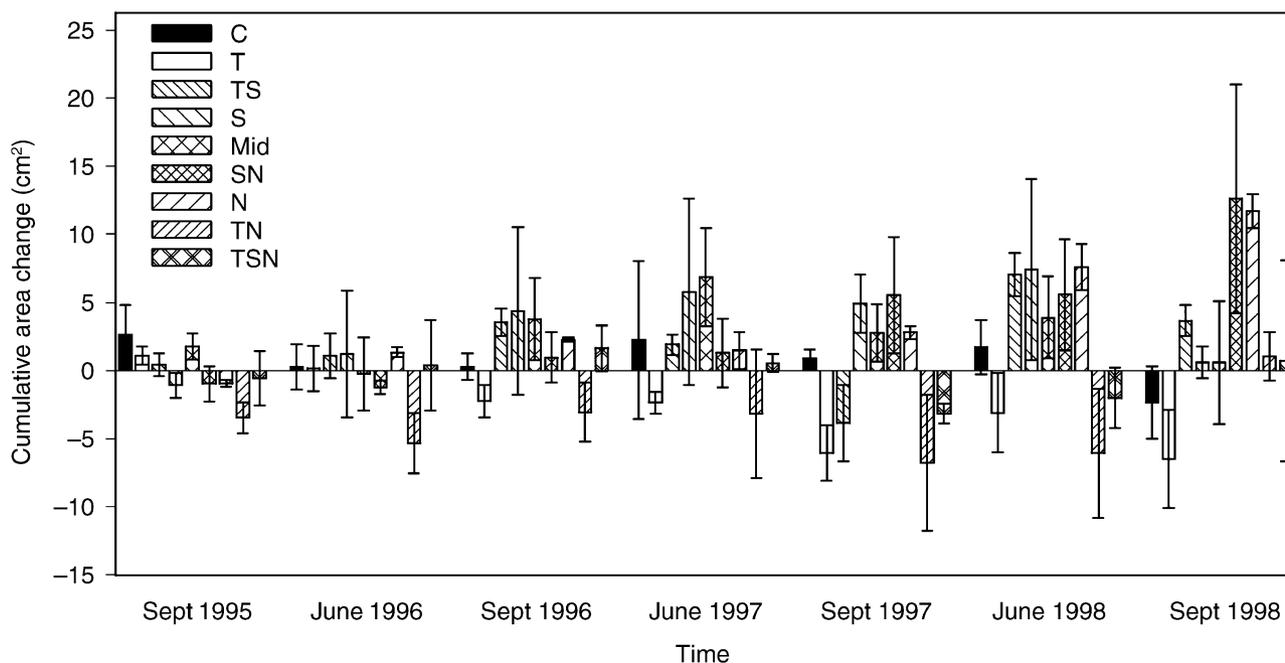


Fig. 3 Cumulative area change ($\pm \text{SE}$) of *Sphagnum lindbergii*, growing in mixture with *Sphagnum balticum*, after the start of the experiment in July 1995. Treatments: C, control; T, temperature; S, sulphur; Mid, midpoint (see text for explanation); N, nitrogen; and the combined treatments $T \times S$ (TS), $S \times N$ (SN), $T \times N$ (TN) and $T \times S \times N$ (TSN).

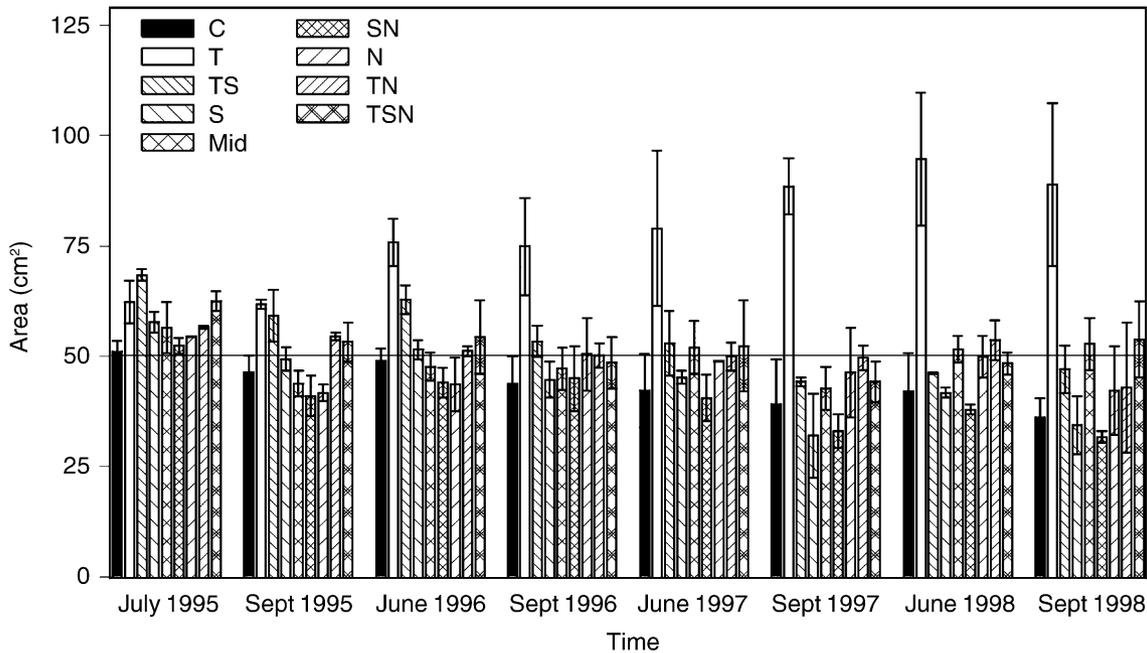


Fig. 4 Area (\pm SE) of transplanted *Sphagnum papillosum* patches, surrounded by *Sphagnum balticum* for July 1995 to September 1998. Treatments: C, controls; T, temperature; S, sulphur; Mid, midpoint (see text for explanation); N, nitrogen; and the combined treatments T \times S (TS), S \times N (SN), T \times N (TN) and T \times S \times N (TSN). The reference line shows the initial transplanted area (50.2 cm²) in June 1995.

area during the summer period 1996 (coefficient = 2.80, $t = 3.32$, $P = 0.005$) and the period September 1997 to June 1998 (coefficient = 3.32, $t = 2.15$, $P = 0.048$, Fig. 3). The only period that the N and S combination had a significant negative effect was during the summer of 1996 (coefficient = -0.93 , $t = -2.33$, $P = 0.033$, Fig. 3).

Competition between *S. papillosum* and *S. balticum*

An initial transplant effect could be seen in the temperature-treated plots, where all transplanted patches increased from the initial area of 50.2 cm² (Fig. 4). The area of transplanted *S. papillosum* was significantly affected by the temperature treatment, the height above the groundwater table and all interactions with temperature (Table 5, Fig. 4). In the control plots *S. papillosum* area decreased by 30% over the experimental period, but at the same time the plots treated using temperature only had increased in area by 42% (Fig. 4). The temperature treatment in combination with N and S reduced this large increase in area (a 7% decrease averaged over all temperature-treated plots). A low water table was beneficial for the area increase of *S. papillosum* (data not shown).

Discussion

We found reductions in *S. balticum* biomass production associated with increases in both temperature and N influx and reduced growth (in terms of length) in the N-treated plots. This may have positive effects on the vascular plants, which

Table 5 Summary of a repeated measures analysis model of changes in area covered by *Sphagnum papillosum* from July 1995 to September 1998

Factor	<i>F</i>	<i>P</i>
WT	5.8	0.032
N	0.09	0.77
T	26	< 0.001
S	2.8	0.11
T \times N	14	0.003
T \times S	6.1	0.028
T \times S \times N	7.3	0.018
Time	0.5	0.81
Time \times WT	2.2	0.16
Time \times N	1.6	0.27
Time \times T	2.0	0.19
Time \times S	1.1	0.46
Time \times T \times N	1.6	0.27
Time \times T \times S	1.4	0.34
Time \times T \times S \times N	0.9	0.55

As the test statistics for the time interactions we present Pillai's trace, where both denominator and numerator $df = 7$; for the other factors $df = 1$ (significant factors in bold). WT, the height above the water table; N, nitrogen; T, temperature; S, sulphur.

have been shown in a series of studies (Berendse *et al.*, 2001; Heijmans *et al.*, 2001; Weltzin *et al.*, 2001; Limpens *et al.*, 2003; Tomassen *et al.*, 2003), although this question was not addressed in the present study, data on vascular plants show a negative relation between vascular plant biomass and *Sphagnum*

production (unpubl. data). Both the establishment of new vascular plant seedlings (Ohlson *et al.*, 2001) and their nutrient acquisition (Malmer *et al.*, 1994; Heijmans *et al.*, 2002b) may increase, resulting in increased vascular plant biomass production (Heijmans *et al.*, 2002a; Weltzin *et al.*, 2001; Limpens *et al.*, 2003; Tomassen *et al.*, 2003). Since the competition for light (in this study between mosses and higher plants) is asymmetric, the change in dominance from *Sphagnum* to vascular plants may be a relatively fast process. The most efficient peat-accumulating ecosystems are *Sphagnum*-dominated mires (Tolonen & Turunen, 1996) and a shift towards mires dominated by vascular plants may lead to reductions in net regional carbon accumulation. Thus, the role of bryophytes as carbon sequesters in boreal ecosystems may be reduced under increased N and temperature regimes. Negative effects of increases in N concentration and temperature on bryophyte growth have also been found in other boreal ecosystems (Potter *et al.*, 1995; Määkipää, 1998).

Effects of raised temperature and increases in N and S influxes on *Sphagnum* growth

One of the main factors affecting *Sphagnum* growth and photosynthesis is the moss water content (Silvola & Aaltonen, 1984; Rydin & McDonald, 1985). Increased potential evapotranspiration, owing to raised air temperatures, tends to reduce the water content of *Sphagnum* capitula, and experiments by Schipperges & Rydin (1998) have shown that growth is reduced if capitula are dry for extended periods. This may have significantly contributed to the temperature-related growth reductions observed in our study, since we frequently observed dry capitula in the plots with raised temperature when the capitula in the surrounding untreated plots were still saturated (even when the height above the water table was similar). In addition to repeated desiccation of the capitula, etiolation in the raised-temperature plots could have occurred, since these plots usually had a denser vascular plant cover than the other plots. The observed reductions in biomass production and capitulum weights recorded in the temperature treatments, without significantly reducing the length increment fits well to an etiolation response among these *Sphagnum* shoots (Hayward & Clymo, 1983). The height above the groundwater table has been shown to be an important factor for *Sphagnum* growth (Weltzin *et al.*, 2001; Vitt *et al.*, 2003) and the overall growth in length in this study was also enhanced by a high annual water table. However, during the relatively wet year (1996) *S. balticum* was growing the most in plots at high elevations above the groundwater table, which suggest that in some years an optimal groundwater table can be found, above and below which growth is reduced. Unlike the hummock species *Sphagnum fuscum*, *S. balticum* has a rather poor capillary transport of water along the stem, which might explain why Dorrepaal *et al.* (2003) found *S. fuscum* to respond positively by

increasing length growth in a summer warming experiment in a subarctic mire.

Degerö Stormyr is situated in an area with low influx of N. In the control plots at the studied poor fen site, there was a low total N concentration, equivalent to *c.* 0.45% dry wt. in the top 5 cm of the *Sphagnum* (including both capitula and stems, the latter of which usually have lower N concentrations; Granberg *et al.*, 2001). Similarly low concentrations (0.60–0.70% dry wt.) have earlier been measured at N-limited sites in the capitula of *Sphagnum* species growing in ombrotrophic bogs or poor fens (Aerts *et al.*, 1992; Gunnarsson & Rydin, 2000). On the mire we found no clear evidence that the addition of N had initially stimulated growth (Fig. 2), which would have been consistent with expectations at this site since the low capitulum concentrations indicated that growth of the *Sphagnum* was N limited. Several previous studies of *Sphagnum* production have detected an initially increased growth after the addition of N in N-limited ecosystems (Rocheffort *et al.*, 1990; Aerts *et al.*, 1992; Li & Vitt, 1997; Gunnarsson & Rydin, 2000). The lack of distinct growth stimulation by N in our study might have been due to the generally unfavourable growth conditions for *Sphagnum* in the first year, as indicated by the poor growth recorded during the year (Fig. 2) and the very low water table (Table 2). Similarly, drought periods have been found to reduce *Sphagnum* growth in N fertilization experiments (Aerts *et al.*, 2001).

In an experimental study by van der Heijden *et al.* (2000b), capitulum N concentrations as low as 1.5% dry wt. were found to be detrimental for photosynthesis in *Sphagnum recurvum* var. *mucronatum*, and higher concentrations induced necrosis. At our study site we found reduced *Sphagnum* growth when the total N concentration in the top 5 cm of the peat was greater than 0.70% dry wt. (Granberg *et al.*, 2001). *Sphagnum* species retain much of the N added (Malmer, 1988; Li & Vitt, 1997) and store much of the excess N as free amino acids, which have been found to accumulate with the addition of N (Baxter *et al.*, 1992; Nordin & Gunnarsson, 2000). The *Sphagnum* plants in the high N plots in our study site had 70–80% more N stored in the top 5 cm than untreated plots after 2 yr of applications (Granberg *et al.*, 2001), indicating N accumulation. The reduced length increment recorded in the N-treated plots compared with the plots receiving ambient levels of N progressively increased during the four measurement years, and it is likely that these differences in length growth reflected increasing differences in tissue N concentrations.

The high S treatment increased the total S concentration by 70–80% in the top 5 cm of the peat profile (Granberg *et al.*, 2001). However, S had only a significant negative effect on length increment in 1996 (Table 3). In 1-yr field experiments in the UK, very high SO_4^{2-} influxes (*c.* 70 g m⁻² yr⁻¹) reduced the growth of most *Sphagnum* species, except for *S. recurvum* (Ferguson & Lee, 1980). An exclusion mechanism was suggested by Lee *et al.* (1990) to explain S tolerance in *Sphagnum*. They found S tolerance to increase with the degree

of metal saturation of the cation-exchange sites on the *Sphagnum* cell walls, concluding that differences in tolerance were related to differences between habitats rather than to inter- or intra-specific differences in tolerance *per se*. The reduction in length growth 1996 caused by the S treatment was reduced by adding N, which shows that a similar exclusion mechanism could increase S tolerance this year. In this study we used sodium sulphate (to exclude any potential interference from H⁺-ions) but in anthropogenic acid rain sulphate ions are usually associated with hydrogen or ammonium ions, which also have acidifying properties and, more importantly, with HSO₃⁻. The effect of sodium is probably negligible, since sodium generally has no essential function in plants (Kramer & Kozłowski, 1997) and Damman (1978) found sodium to be rapidly leached from ombrotrophic peat.

Interspecific competition

The changes in relative coverage between the naturally coexisting species *S. balticum* and *S. lindbergii* associated with increased temperature, N and S influx were probably caused by shifts in their relative competitive ability or tolerance in combination with different weather conditions. The clearest trend was associated with the increased area of *S. lindbergii* in the N-treated plots during the last two experimental years (Fig. 3). Several studies have suggested that differences between species occur, e.g. in a laboratory study by van der Heijden *et al.* (2000a), in which growth of *S. papillosum* (but not *S. balticum*) was found to respond positively on N applied at 3 g m⁻² yr⁻¹. Furthermore, results from laboratory experiments (Jauhiainen *et al.*, 1998a) suggest that typical minerotrophic *Sphagnum* species will be favoured by still higher N influxes (e.g. 10 g m⁻² yr⁻¹), meanwhile ombrotrophic growing species are reduced by much a lower influx (> 1.4 g m⁻² yr⁻¹, Jauhiainen *et al.*, 1998a; Vitt *et al.*, 2003). In a field experiment similar changes in species composition towards more minerotrophic species was found after increasing N influxes, in which *S. fallax*, a minerotrophic species, was able to outcompete the more ombrotrophic *Sphagnum magellanicum* (Lütke Twenhöven, 1992).

The increase in area covered by *S. lindbergii* in the high N treatment may reflect its higher tolerance to high N influx in relation to *S. balticum*. However, the growth of *S. lindbergii* was probably also reduced by the N treatment, as indicated by the reduced general vigour of its shoots in the N-treated plots. In mid and southern Sweden, *S. lindbergii* is often found in minerotrophic fens and peat pits, which probably have a higher nutrient availability than ombrotrophic hollows (Lönnell *et al.*, 1998; Soro *et al.*, 1999), indicating that this species could be more competitive at higher N levels than the ombrotrophic or extremely poor fen species *S. balticum*. The conclusion that *S. balticum* is relatively intolerant towards high N levels is further supported by its decline in bogs in Britain, following increased atmospheric influx (Church *et al.*, 2001).

The lawn-growing species have lower capillary capacity than hummock-forming sphagna, making the capitula of hollow-forming species more sensitive to any environmental change that increases already negative water balances (e.g. increases in air temperature that cause evapotranspiration to rise or the water table to fall). In accordance with this difference in capillary capacity, the hummock-forming *S. papillosum* transplanted into the *S. balticum* lawn community benefited from raised temperature at the expense of the *S. balticum* plants (Fig. 4). Studies by Rydin (1986, 1993) showed that patches of hollow-growing *S. balticum* species decreased in area over time when transplanted into hummocks; however, this was not a direct effect of competition, but of increased mortality of the transplanted *S. balticum* shoots. According to our results, *S. papillosum* will increase in area at the expense of *S. balticum* under climatic regimes with a more negative water balance (i.e. increased temperature and/or decreased precipitation, presumably because of the low tolerance of *S. balticum* to drier conditions). A warmer climate might lead to changes in microtopographic structure at the mire surface, favouring hummock-forming species, which is exactly what was observed in a study of vegetation changes, over a 40-yr period, in an ombrotrophic bog in south Sweden (Gunnarsson *et al.*, 2002). As the *Sphagnum* species have slightly different rates of decay (Johnson & Damman, 1991) a changed species composition may *per se* have influence on peat production rates, but this influence may largely be overridden by the increased decomposition rates caused by the raised N influx and temperature.

The observed changes in the interspecific competitive relations between *S. lindbergii* and *S. balticum* indicate that the species have slightly different ecological niches with respect to N. Recent studies also suggest that *S. papillosum* should be a better competitor than *S. balticum* under conditions of raised N concentrations (Saarnio, 1999), but this could not be supported by this study. However, the increase in area of the transplanted hummock-forming *S. papillosum* in the raised-temperature *S. balticum* lawn community also indicates niche differentiation. No competitive exclusion did occur: quite significant amounts of all the species studied were still present at the end of the experiment. Therefore, it is too early to exclude the possibility that irreversible changes in competitive relations may occur in periods with different weather conditions. Competitive exclusion in *Sphagnum* communities is probably a slow process, since single shoots of an inferior species can survive together with the superior species for long periods (Rydin, 1993).

Conclusion

We conclude that the growth and production of *S. balticum* in nutrient-poor lawn communities will be reduced if the summer temperature or the N influx increases. This may have profound effects on the ecosystem, since a reduction in

Sphagnum growth could result in increased growth of vascular plants. Further, if the N influx and temperature continue to increase, the *Sphagnum* species composition may shift towards species capable of taking advantage of the increased N regime and hummock-forming species capable of growing under drier conditions. Thus, such changes may also, over several decades, present a threat to *Sphagnum* species diversity on boreal mires. The accumulation of peat depends on both plant biomass production and decomposition. Decomposition was not studied here, but it is also affected by the applied treatments: most studies predict increased decomposition with raised temperature and N influx (Robinson *et al.*, 1995; Malmer & Wallén, 1999; Aerts & Chapain, 2000; Granberg *et al.*, 2001). However, since peat production is dependent on *Sphagnum* production (Clymo & Hayward, 1982), our results suggest that increased influx of N and increases in ambient temperature may reduce the peat accumulation rates in boreal mires.

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