

Sphagnum modifies climate-change impacts on subarctic vascular bog plants

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Summary

1. Vascular plant growth forms in northern peatlands differ in their strategies to cope with the harsh climate, low nutrient availability and progressively increasing height of the *Sphagnum* carpet in which they grow. Climate change may therefore affect growth forms differentially, both directly and through changes in the length growth of *Sphagnum* mosses. However, the role of mosses as modifiers of climate-change effects on vascular plants has been largely overlooked so far. We investigated the direct and *Sphagnum*-mediated effects of experimental changes in summer, winter and spring climate on four species of contrasting growth forms (evergreen and deciduous shrubs, graminoid, forb) in a subarctic bog, by studying their biomass and nitrogen losses through leaf litter, and the length growth of the two shrubs.

2. Direct and indirect effects of summer warming differed among the growth forms. Enhanced *Sphagnum* overgrowth of leaves due to summer warming initially stimulated leaf litter losses of the evergreen shrub *Empetrum nigrum*. However, changes in its shoot morphology, related to an apparent small increase in its length growth, prevented further effects. A stronger increase in stem growth of the deciduous shrub *Betula nana* in response to summer warming directly reduced its leaf litter mass, N concentration and N losses. The changed allocation prevented indirect, *Sphagnum*-mediated effects on its leaf and N dynamics through overgrowth of buds. In contrast, leaf litter mass, N concentrations or N losses of the forb *Rubus chamaemorus* and the graminoid *Calamagrostis lapponica* were not affected by summer warming or enhanced *Sphagnum* growth.

3. Increases in winter snow cover, with or without spring warming, did not affect shrub growth, nor the total shoot leaf litter mass or N dynamics of any of the growth forms.

4. Altogether, summer warming is likely to enhance *Sphagnum* overgrowth of small shrubs with a limited growth response such as *Empetrum*. Moreover, increased vertical growth may allow *Sphagnum* to keep pace with inclined growing, responsive shrubs such as *Betula*. This might prevent net longer-term positive effects of summer warming on the vascular plant canopy height. However, leaf litter and N losses are more likely to be affected by direct warming effects on shoot morphology and allocation than by *Sphagnum* growth. The different responses of the growth forms to summer warming suggest that both direct and *Sphagnum*-mediated climate effects have the potential to change the vascular plant community and N dynamics in peatlands.

Key-words: global warming, leaf litter, peatlands, plant growth form, snow cover

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Introduction

Plant growth and survival in high-latitude ecosystems are constrained by adverse environmental conditions, such as low temperatures and irradiance throughout a large part of the year, a short growing season, and low nutrient availability (Bliss 1956; Sonesson & Callaghan 1991; Arft *et al.* 1999). In northern peatlands, vascular plant performance is further controlled by the presence of *Sphagnum*, which often dominates the bottom layer and the peat deposits in which the plants grow (Clymo & Hayward 1982). *Sphagnum* mosses strongly reduce the availability of nutrients to vascular plants by efficiently accumulating nutrients from atmospheric deposition and reducing decay and mineralization rates (Lee & Woodin 1988; Malmer *et al.* 1994; Van Breemen 1995; Li & Vitt 1997). At the same time, however, they force vascular plants to keep pace with their progressively increasing height, in order not to become buried (Back us 1985; Malmer *et al.* 1994; Rydin 1997). The abiotic and biotic environments thus place extreme demands on vascular plant growth and nutrient-use efficiency in northern peatlands. Arctic and subarctic areas are expected to experience above global-average increases in year-round temperatures and winter precipitation during this century (Maxwell 1992; Houghton *et al.* 2001; McCarthy *et al.* 2001). This may directly alleviate climatic and possibly nutritional constraints on vascular plants (Chapin *et al.* 1995; Rustad *et al.* 2001). However, strongly enhanced *Sphagnum* growth as a result of climate change (Sonesson *et al.* 2002; Dorrepaal *et al.* 2004) may modify the net effects on community structure and nutrient dynamics in northern peatlands.

The growth strategies that enable vascular plants to cope with the contrasting abiotic and biotic demands in northern peatlands might also be indicative of their sensitivity to the direct and *Sphagnum*-mediated effects of climate change. Deciduous and evergreen shrubs, which make up a major part of many vascular plant communities of peatlands, have long-lived, woody stems with low nutrient concentrations, which limit their nutrient requirements (Berendse *et al.* 1987; Berendse & Jonasson 1992). Evergreen shrubs reduce their litter and nutrient losses even further by having extended leaf longevity and very low litter nutrient concentrations (Aerts 1995; Eckstein & Karlsson 1997). However, above-ground woody shoots carry a great risk of winter frost damage to apical buds and branches or to overwintering leaves if the protection of a snow cover is limiting (Sonesson 1969; Weih & Karlsson 2002). Moreover, shrubs must compensate for the yearly decrease in branch height (relative to the vertically up-growing *Sphagnum* carpet) by new growth at the top of their usually inclined branches (Back us 1985; Malmer *et al.* 1994). Clonal graminoids and forbs, on the other hand, avoid frost damage or *Sphagnum* overgrowth of their shoots by abandoning their above-ground tissues (including the non-resorbed nutrients)

at the end of the growing season. During the coldest part of the year, they thus keep their growing points just below the moss surface, and efficient elongation of their below-ground rhizomes enables their shoots to keep pace with the *Sphagnum* surface in summer (Back us 1985; Malmer *et al.* 1994; Svensson 1995). However, as a consequence, graminoids and forbs lose a large proportion of their nutrients annually through the formation of litter (Berendse *et al.* 1987; Berendse & Jonasson 1992; Eckstein & Karlsson 1997).

The climatic and nutritional conditions, together with the growth rate of *Sphagnum*, control the relative importance of the benefits and disadvantages of each of the growth strategies. However, in contrast to the direct effects of higher summer temperatures on plant performance at high latitudes, the effects of changes in climate outside the growing season and indirect, *Sphagnum*-mediated effects of summer warming in northern peatlands have received little attention so far. Summer warming may directly increase the growth of deciduous and evergreen shrubs (Parsons *et al.* 1994; Shevtsova *et al.* 1997; Hobbie *et al.* 1999; Bret-Harte *et al.* 2002), but their response tends to be smaller than observed for *Sphagnum* (Sonesson *et al.* 2002; Dorrepaal *et al.* 2004). Summer warming may therefore increase the risk of shrubs becoming overgrown. The performance of small evergreen shrubs may be further suppressed by enhanced senescence of basal leaves overgrown by *Sphagnum* (Back us 1985). Furthermore, enhanced overgrowth of the basal leaf buds of deciduous shrubs may prevent net positive effects of increased temperatures on their leaf and biomass production (Chapin & Shaver 1985; Hobbie *et al.* 1999; Suzuki & Kudo 2000), and thus potentially on carbon sequestration in peatlands. Changes in climatic conditions outside the growing season do not appear to affect *Sphagnum* length growth (Dorrepaal *et al.* 2004). However, positive relations between *Betula nana* shrub height (Sonesson 1969) or *Betula pubescens* seedling leaf biomass (Weih & Karlsson 2002) and winter snow thickness indicate that the above-ground overwintering shoots of tall shrubs, in particular, may benefit from the increased protection of a thicker snow layer. Higher spring temperatures may accelerate vascular leaf development and early season growth, although the responsiveness of species varies (Back us 1985; Chapin & Shaver 1996; Shevtsova *et al.* 1997; Arft *et al.* 1999; Suzuki & Kudo 2000). It remains uncertain, however, whether these spring effects alone will increase total growing-season shoot elongation and leaf production, without additional warming during the rest of the summer (Back us 1985; Shevtsova *et al.* 1997; Kudo *et al.* 1999).

In this study we investigated the responses of different vascular plant growth forms to experimentally imposed changes in summer, winter and spring climate (temperatures, snow-cover thickness) in a subarctic bog in northern Sweden. We explicitly attempted to differentiate between direct and *Sphagnum*-mediated

effects of summer warming, and particularly examined potential, negative, *Sphagnum*-mediated effects on shrubs. In order to do this, we related shoot biomass and nitrogen dynamics through leaf litter of four species of contrasting growth strategies – *Empetrum nigrum* (short evergreen shrub); *Betula nana* (taller deciduous shrub); *Rubus chamaemorus* (forb); and *Calamagrostis lapponica* (graminoid) – and length growth of the two shrubs, to *Sphagnum* length growth in the second and third years of the experiment. We tested the following hypotheses. (i) Summer warming and higher spring temperatures will stimulate the length growth of shrubs, but relatively less than *Sphagnum* length growth. (ii) Summer warming and higher spring temperatures will enhance leaf production and thus directly increase leaf litter and N losses of deciduous species (deciduous shrub, forb and graminoid), but not of evergreen shrubs. (iii) Increased *Sphagnum* growth will (a) reduce basal bud development and thus leaf litter and N losses of deciduous shrubs; (b) stimulate basal leaf senescence and thus leaf litter and N losses of evergreen shrubs by overgrowth of the basal parts of shrubs; and (c) not affect forbs and graminoids. (iv) Increased winter snow accumulation will enhance growth and leaf (litter) production of taller shrubs more strongly than that of shorter shrubs, forbs and graminoids.

Methods

STUDY SITE AND EXPERIMENTAL DESIGN

The climate-manipulation experiment was established on a slightly sloping bog on the southern shore of Lake Tornerträsk, Abisko, northern Sweden (68°21' N, 18°49' E). The vegetation is dominated by a continuous and homogeneous carpet of *Sphagnum fuscum* (Schimp.) H. Klinggr. Other bryophytes and lichens are sparse. The vascular plant community is low and open (maximum shrub height 15 cm, average cover 20%), and consists mainly of *Empetrum nigrum* ssp. *hermaphroditum* (Hagerup) Böcher; *Rubus chamaemorus* L.; *Andromeda polifolia* L.; *Vaccinium microcarpum* (Turcz. ex Rupr.) Schmalh.; *Betula nana* L.; *V. uliginosum* L.; and *Calamagrostis lapponica* (Wahlenb.) Hartm. The water table depth increases up-slope from ≈20 to 40 cm below the soil surface (July 2001), while permafrost depth is approximately –45 cm.

Since June 2000, 30 plots have been subjected to experimental manipulations of summer, winter and spring climate, with six fully factorial combinations of two summer treatments (ambient, warming) and three treatments during winter and spring. For brevity, the latter are referred to as winter treatments (ambient, snow addition, snow addition plus spring warming, $n = 5$; Table 1). Large, transparent, hexagonal ITEX open-top chambers (OTCs, 50 cm high, 2.2–2.5 m bottom diameter; cf. Marion *et al.* 1997) were used to manipulate the climate throughout the year. They

Table 1. Experimental design and treatment codes used for the climate manipulations

Winter treatment	Summer treatment	
	Ambient	Warming
Ambient	AA	WA
Snow addition	AS	WS
Snow addition plus spring warming	AS+	WS+

increased the average air temperature (+5 cm) in June–July by 0.9 °C. Air temperatures in August–September, average soil temperatures (–5 cm) throughout the summer, and vapour pressure deficit were not significantly affected by the OTCs. During winter (October–April) the OTCs passively accumulated snow, thereby doubling the ambient snow-cover thickness and increasing the average temperatures at +5 and –5 cm by 0.5–2.8 and 0.5–2.2 °C, respectively. In spring (May), before the start of the growing season, OTCs increased the average air and soil temperatures in the AS+ and WS+ treatments by 0.3–1.0 and 0.7–1.2 °C, respectively, but did not affect snow-melt timing (for treatment codes see Table 1). Full details of the experimental procedures and their effects on summer and winter microclimate are presented by Dorrepaal *et al.* (2004).

LENGTH GROWTH, LEAF LITTER PRODUCTION AND LITTER N CONCENTRATION

To compare the effects of changes in summer and winter climate on shrub growth and on vascular plant leaf litter production and N losses, we selected one species of each of four growth forms: *E. nigrum* (short evergreen shrub), *B. nana* (taller deciduous shrub), *R. chamaemorus* (forb) and *C. lapponica* (graminoid). At the experimental site these four species comprise ≈85% of the above-ground vascular plant biomass (S. Bokhorst and J.H.C.C., unpublished results). The species are referred to hereafter by their genus names. Because these species are long-lived perennials, the ramets of which are connected below the moss layer through overgrown stems (shrubs) or rhizomes (forbs and graminoids), we defined a shoot as a stem or tiller that emerged above the moss layer (Chapin & Shaver 1985). In the second and third years of the experiment, in mid-July 2001 and 2002, we randomly selected and marked 10 *Empetrum* shoots, five *Betula* shoots (2001 only) and five *Calamagrostis* shoots in the central area of each plot. *Empetrum* has a lower branching rate in *Sphagnum* carpets than at drier, more exposed sites (Bell & Tallis 1973; Backéus 1985). We thus confined ourselves to unbranched shoots to reduce heterogeneity. *Betula* normally also grows along one main axis (long shoots) and rather infrequently shows conversion of short side branches (short shoots) into new

long shoots (Bret-Harte *et al.* 2002). For this species we therefore included the main axis with short shoots, and all long shoots that had been converted from short shoots since the start of the experimental treatments. The selected shoots of *Calamagrostis* were all solitary ramets 1–2 years old, as indicated by the small number of attached, overwintering dead leaves (Chapin & Shaver 1985). For *Rubus* we included all shoots within a fixed area of 55 × 55 cm in the centre of each plot.

Because of the inherent differences in growth and leaf senescence among the growth forms, we had to apply different methods for each species to assess length growth and leaf litter losses. To measure the annual length increment and leaf litter production of *Empetrum*, we used the clearly spatially separated distribution of green (live) and brown (dead) leaves along the shoots. This pattern is caused by the progressive overgrowth and senescence of basal leaves, which remain attached to the stem for more than a year. We marked each shoot with a piece of thin, plasticized iron wire, just above the uppermost brown leaves, and measured the length of the remaining green part of the branch. In mid-July of the following year we cut off each shoot at the marking point, measured the total length and the length of the part covered with brown leaves, and harvested all brown leaves of each shoot. To avoid underestimating litter production owing to losses of senesced leaves during the year, we discarded the few shoots that had lost leaves just below or above the marking. For *Betula* we used the same five shoots in each plot in both years, and measured the length of the current-year growth of the main axis. This part was identified using colour differences and scars of the terminal bud. To estimate leaf litter production per shoot, we counted the number of leaves on each shoot cohort: main axis parts formed in 2002, 2001, 2000 or earlier, including their short shoots, and cohort parts of short shoots converted to long shoots in 2002, 2001 or 2000. We randomly collected 40 dead leaves per plot directly after leaf senescence, in September 2001 and 2002. Leaf litter production per shoot was calculated by multiplying the number of leaves per shoot by the average mass per dead leaf. For *Rubus* we counted the number of leaves of each shoot within the fixed area in July, and randomly collected 10 senesced leaves per plot in September 2001 and 2002. Leaf litter production per shoot was calculated as indicated for *Betula*. The five marked *Calamagrostis* shoots per plot were also harvested after senescence in September 2001 and 2002. All leaf litter material was oven-dried (70 °C, 48 h), weighed and ground. Total N concentration was determined by dry combustion on a Carlo Erba NA1500 CNS analyser for the second leaf litter collections only. The N losses through leaf senescence per shoot were calculated by multiplying the N concentration by leaf litter production per shoot in the corresponding year. All measurements of individual shoots within each plot were averaged for each species before statistical analyses.

STATISTICAL ANALYSES

The effects of the summer and winter climate manipulations on *Empetrum* annual stem-length increment and *Betula* current-year stem length in the second and third year of the experiment were analysed using repeated-measures multivariate ANOVAS (Pillai's trace). Year was the within-subject factor, and summer treatment and winter treatment the between-subject factors. The overall effects of the climate manipulations on leaf litter production per shoot in the two subsequent years were also analysed for each of the four species using repeated-measures multivariate ANOVAS. These were followed by two-way ANOVAS for separate years if significant interactions between year and summer treatment, winter treatment or summer × winter treatment were found. The overall relation between vascular plant leaf litter production and *Sphagnum* length growth was analysed for separate years by calculating Pearson's correlation coefficients (Spearman's ρ in case of non-homogeneous variances) and using the *Sphagnum* data from Dorrepaal *et al.* (2004). These *Sphagnum* length-growth data were collected using a modification of the cranked wire technique (Clymo 1970) in the same plots and over the same years as the vascular plant measurements. The total range of *Sphagnum* growth in all plots was partly the result of the summer warming treatments. We therefore assessed the relative contribution of direct climate effects and indirect effects via *Sphagnum* growth on vascular plant leaf litter production, in those cases where both the overall summer climate treatment and the overall correlation with *Sphagnum* growth were significant. In order to do this, we performed an analysis of covariance (ANCOVA), with summer and winter treatments as fixed factors and *Sphagnum* growth as a covariate, and compared the *F* values of the summer factor and *Sphagnum* growth. Leaf litter N concentrations and total N losses through leaf litter formation per shoot were analysed for main effects and interactions of the summer and winter treatments using two-way ANOVAS. All data were tested for homogeneity of variances with Levene's test. For *Betula* length growth, *Betula* older shoot leaf litter production, and *Rubus* total N loss per shoot, ln-transformation improved the homogeneity of variances considerably, but this had no effect on *Empetrum* length increment in 2002–03. As ANOVA is robust to considerable heterogeneity of variances as long as the sample sizes are nearly equal (Zar 1999), we included the untransformed data for *Empetrum*. All analyses were performed with SPSS for Windows 10.1.

Results

LENGTH GROWTH

Summer warming strongly increased the current-year stem length of *Betula* (42% in 2001; 51% in 2002), but

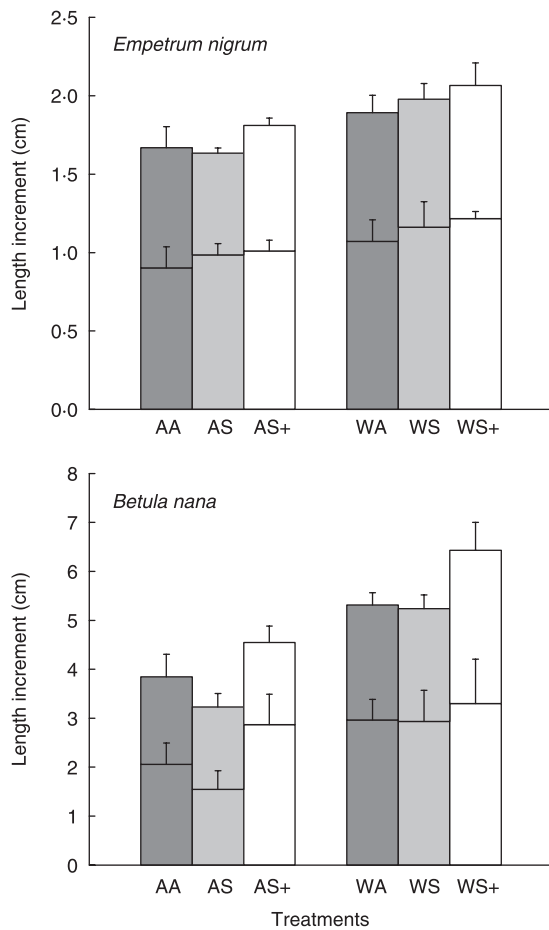


Fig. 1. Annual apical stem-length increment of *Empetrum nigrum* (lower part of each bar, July 2001–July 2002; upper part, July 2002–July 2003), and current-year apical stem length of *Betula nana* (lower part of each bar, July 2001; upper part, July 2002) in response to summer treatments (ambient, warming) and winter treatments (ambient, snow addition, snow addition plus spring warming) in the second and third years of the experiment (mean \pm SEM, $n = 5$). For treatment codes see Table 1.

the apparent positive effect ($P < 0.1$) on *Empetrum* annual stem length increment was less pronounced (19% in 2001–02; 12% in 2002–03) (Fig. 1; Table 2). Although winter snow addition plus spring warming also appeared to enhance the length growth of the shrubs (Fig. 1), this effect was not significant. *Empetrum* length increment was higher in 2001–02 than in 2002–03, but the overall responses of each of the species to the treatments were similar in both years. The relative response of *Betula* to summer warming was almost equal to that of *Sphagnum* (50% increase; Dorrepaal *et al.* 2004). For *Empetrum*, however, the ratio of shrub length growth to *Sphagnum* length growth was lower in the summer warming than in the summer ambient treatments (Fig. 2).

LEAF LITTER PRODUCTION

The direct and *Sphagnum*-mediated effects of climate manipulations on litter production differed among the

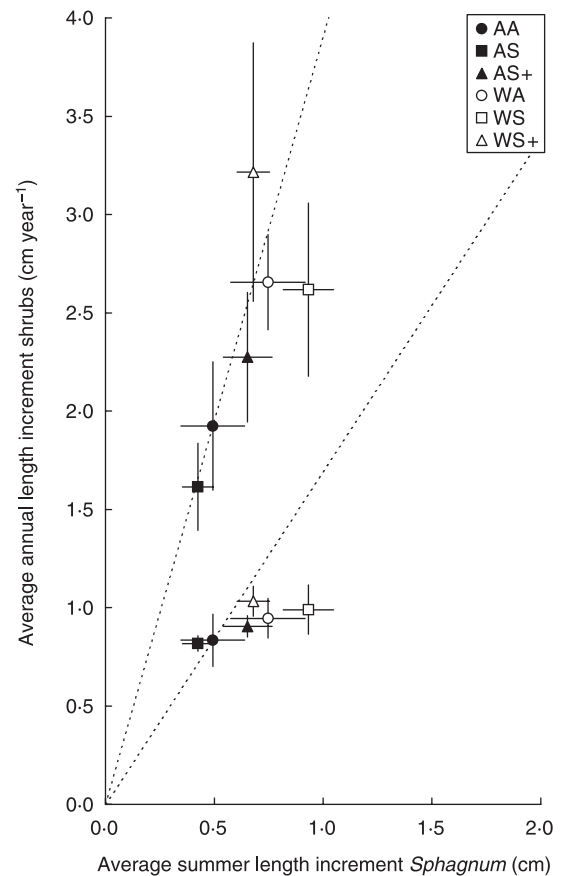


Fig. 2. Average annual apical stem length increment of *Empetrum nigrum* (lower group of points) and average current-year apical stem length of *Betula nana* (upper group of points) relative to average summer length increment of *Sphagnum fuscum* in response to summer treatments (ambient, warming) and winter treatments (ambient, snow addition, snow addition plus spring warming) in the second and third years of the experiment (mean \pm SEM, $n = 5$). Dotted lines indicate ratios of shrub length growth to *Sphagnum* growth equal to the AA treatment of either of the shrub species (for treatment codes see Table 1). All points of a shrub species below the corresponding line showed a response to the treatment relatively smaller than that of *Sphagnum*.

growth forms. Overall, *Empetrum* lost 22% more leaf litter mass in the summer warming treatments than in the ambient treatments in 2001–02, but this effect was not maintained in the next year (Fig. 3; Table 2). Increased winter snow cover and spring warming had no effect on *Empetrum* leaf litter losses (Table 2). The length of the harvested *Empetrum* stem parts covered with brown leaves was positively related to *Sphagnum* growth in both years (2001–02, Pearson's $r = 0.38$, $P < 0.05$; 2002–03, $r = 0.63$, $P < 0.001$), but total leaf litter mass was only significantly, positively related to *Sphagnum* growth in 2001–02 (Table 3). ANCOVA showed that the overall positive effect of the summer warming treatments on *Empetrum* leaf litter production in 2001–02 was primarily via the effects on *Sphagnum* growth (summer treatments, $F = 0.78$, $P > 0.1$; *Sphagnum* growth, $F = 5.49$, $P < 0.05$).

Table 2. Repeated-measures ANOVA and two-way ANOVA F statistics ($n = 5$) for effects of summer (ambient, warming; SUM) and winter treatments (ambient, snow addition, snow addition plus spring warming; WIN) on *Empetrum nigrum* annual stem length increment and *Betula nana* current-year stem length; and on leaf litter production per shoot of *E. nigrum*, *B. nana* (total shoot and current-year, previous-year and older parts separately), *Rubus chamaemorus* and *Calamagrostis lapponica* in the second and third years of the experiment (Y = year)

Variable and species	Source (df)						
	Y (1)	Y × SUM (1)	Y × WIN (2)	Y × SUM × WIN (2)	SUM (1)	WIN (2)	SUM × WIN (2)
Apical growth							
<i>Empetrum</i>	43.11***	1.27	1.06	0.30	3.12 ⁺	0.40	0.06
<i>Betula</i>	1.26	0.14	0.24	1.28	7.77**	0.85	0.14
Leaf litter mass							
<i>Empetrum</i> 2 years	12.47**	5.59*	1.82	1.22	1.96	0.33	0.12
<i>Empetrum</i> 2001–02	–	–	–	–	4.38*	0.94	0.30
<i>Empetrum</i> 2002–03	–	–	–	–	0.18	0.68	1.14
<i>Betula</i> total shoot	24.41***	0.71	2.07	0.29	5.04*	0.71	0.19
<i>Betula</i> current-year shoot	1.86	0.14	0.85	0.45	0.19	5.34*	0.16
<i>Betula</i> previous-year shoot 2 years	59.84***	4.38*	0.71	1.64	1.50	2.28	0.88
<i>Betula</i> previous-year shoot 2001	–	–	–	–	5.55*	1.19	0.03
<i>Betula</i> previous-year shoot 2002	–	–	–	–	0.00	2.33	1.79
<i>Betula</i> older part shoot	2.50	0.32	0.08	0.37	8.74**	0.14	0.01
<i>Rubus</i>	0.02	0.31	0.18	1.63	0.86	0.89	1.44
<i>Calamagrostis</i>	0.64	0.28	1.01	1.22	0.00	1.46	0.54

Analyses include data for both 2001 and 2002 (*Empetrum* 2001–02 and 2002–03) unless otherwise indicated.

Error df = 24.

⁺, $P < 0.1$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

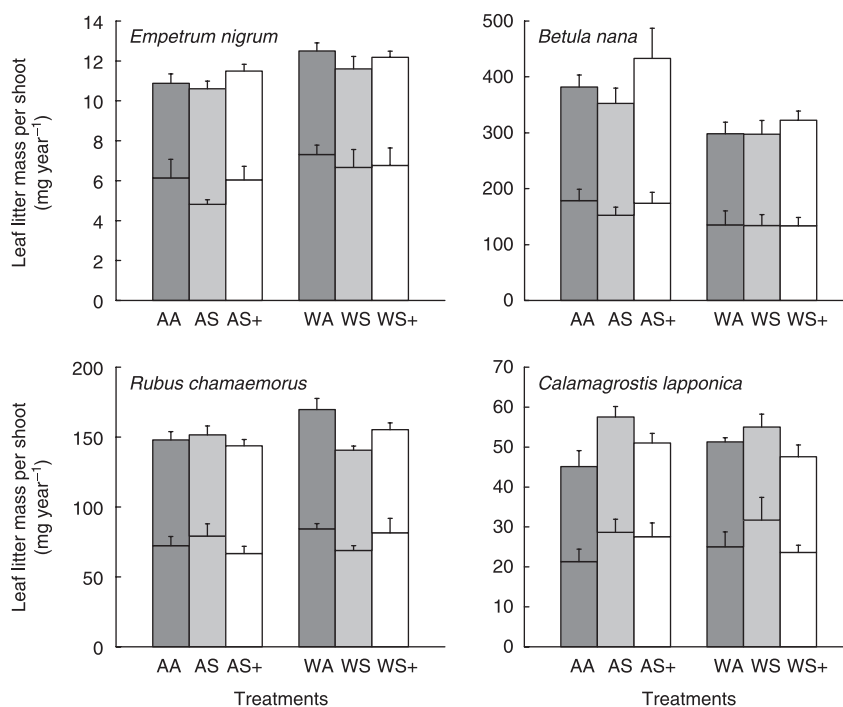


Fig. 3. Annual leaf litter production of *Empetrum nigrum*, *Betula nana*, *Rubus chamaemorus* and *Calamagrostis lapponica* in response to summer treatments (ambient, warming) and winter treatments (ambient, snow addition, snow addition plus spring warming) in the second and third years of the experiment. Indicated are mean + SEM ($n = 5$) for each treatment in 2001 (lower part of each bar, July 2001–July 2002 for *Empetrum nigrum*) and 2002 (upper part of each bar, July 2002–July 2003 for *Empetrum nigrum*). For treatment codes see Table 1.

Betula leaf litter production was clearly reduced by the summer warming treatments in both years (–20% in 2001; –22% in 2002), but was not affected by the winter and spring treatments (Fig. 3; Table 2). This was primarily the result of a (non-significant) reduction in the total number of leaves per shoot (data not

shown). On a total shoot basis, leaf litter production was negatively related to *Sphagnum* growth, although the correlation coefficients were not significant (Table 3). Analyses of the separate shoot cohorts showed that the climate manipulations and increased *Sphagnum* growth had different effects on the basal

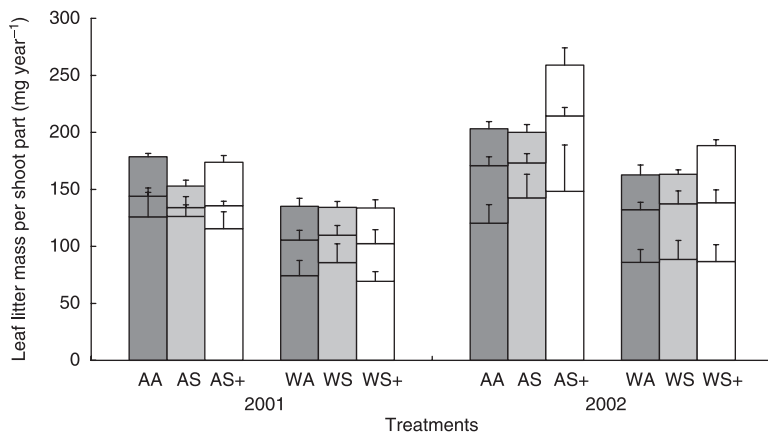
Table 3. Correlation ($n = 30$) between leaf litter production per shoot of *Empetrum nigrum*, *Betula nana* (total shoot and >2-year-old part of shoot), *Rubus chamaemorus* and *Calamagrostis lapponica*, and *Sphagnum fuscum* length growth

Species	Period	Correlation coefficient
<i>Empetrum</i>	2001–02	0.52**
<i>Empetrum</i>	2002–03	0.04
<i>Betula</i> total shoot	2001	-0.24
<i>Betula</i> total shoot	2002	-0.29
<i>Betula</i> older part shoot	2001	-0.31 ⁺
<i>Betula</i> older part shoot	2002	-0.48**
<i>Rubus</i>	2001	0.10
<i>Rubus</i>	2002	0.03
<i>Calamagrostis</i>	2001	-0.21
<i>Calamagrostis</i>	2002	0.27

⁺, $P < 0.1$; **, $P < 0.01$.

Sphagnum data from Dorrepaal *et al.* (2004).

and apical parts of the shoots (Fig. 4; Table 2). The production of leaf litter by the current-year parts of the shoots showed a significant, positive response to the winter treatments, in particular to higher spring temperatures (Tukey's HSD, AS+/WS+ vs AS/WS, $P < 0.01$). The parts of the shoots that had been

**Fig. 4.** Annual leaf litter production (mean + SEM, $n = 5$) of *Betula nana* current-year (upper), previous-year (middle) and older shoot parts (lower part of each bar) in response to summer treatments (ambient, warming) and winter treatments (ambient, snow addition, snow addition plus spring warming) in the second (2001) and third (2002) years of the experiment. For treatment codes see Table 1.**Table 4.** Leaf litter N concentration and total shoot N losses through leaf senescence (mean ± SEM, $n = 5$) of *Empetrum nigrum* (2002–03), *Betula nana*, *Rubus chamaemorus* and *Calamagrostis lapponica* (2002) in response to summer (ambient, warming) and winter treatments (ambient, snow addition, snow addition plus spring warming) in the third year of the experiment

	<i>Empetrum</i>		<i>Betula</i>		<i>Rubus</i>		<i>Calamagrostis</i>	
	N (mg g ⁻¹)	N (µg per shoot)	N (mg g ⁻¹)	N (mg per shoot)	N (mg g ⁻¹)	N (mg per shoot)	N (mg g ⁻¹)	N (mg per shoot)
AA	4.3 ± 0.3	20.2 ± 1.8	5.5 ± 0.3	1.12 ± 0.12	8.0 ± 0.3	0.60 ± 0.05	3.8 ± 0.3	0.09 ± 0.02
AS	3.4 ± 0.1	19.8 ± 1.4	6.0 ± 0.3	1.21 ± 0.19	8.2 ± 1.1	0.57 ± 0.06	4.4 ± 0.3	0.13 ± 0.01
AS+	3.5 ± 0.1	19.4 ± 1.3	5.7 ± 0.2	1.45 ± 0.29	7.6 ± 0.4	0.58 ± 0.04	4.5 ± 0.2	0.11 ± 0.01
WA	3.9 ± 0.4	20.1 ± 1.8	4.9 ± 0.2**	0.80 ± 0.12*	8.1 ± 1.1	0.71 ± 0.14	4.3 ± 0.5	0.11 ± 0.01
WS	4.1 ± 0.2	19.9 ± 2.7	5.3 ± 0.2**	0.86 ± 0.13*	6.3 ± 0.2	0.45 ± 0.03	3.9 ± 0.1	0.09 ± 0.01
WS+	3.8 ± 0.1	20.3 ± 1.1	5.1 ± 0.3**	0.96 ± 0.10*	6.9 ± 0.5	0.51 ± 0.06	3.9 ± 0.2	0.09 ± 0.01

Note different unit for N loss per shoot for *Empetrum*. For treatment codes see Table 1.

Asterisks indicate significance level of differences compared with values without asterisks within the same column (two-way ANOVA): *, $P < 0.05$; **, $P < 0.01$.

formed in the previous year produced more leaf litter in response to summer warming in 2001, but not in 2002 (Table 2). In contrast, the leaf litter production of the older, lowest parts of the *Betula* shoots, which represented 50–80% of the total leaf litter production, showed a strong negative response to the summer warming treatments (-38% in 2001; -37% in 2002; Fig. 4; Table 2). The leaf litter production of the older parts of the *Betula* shoots was also negatively related to *Sphagnum* growth (Table 3), as was the stem length of this part of the shoot (2001, Pearson's $r = -0.46$, $P < 0.01$; 2002, $r = -0.51$, $P < 0.01$). ANCOVA showed, however, that the indirect effect of the summer warming treatments, via enhanced *Sphagnum* growth, on leaf litter production of the older shoot parts of *Betula* was limited compared with the direct climate effect (summer treatments, $F = 4.48$, $P < 0.05$; *Sphagnum* growth, $F = 1.01$, $P > 0.1$).

In contrast to the two shrubs, leaf litter production of *Rubus* and *Calamagrostis* was not affected by any of the climate manipulations, nor was it related to the length growth of *Sphagnum* (Fig. 3; Tables 2 and 3).

LEAF LITTER N LOSSES

By the end of the third summer of the experiment (2002), summer warming appeared to have reduced leaf litter N concentrations, but this effect was significant only for *Betula* (Table 4). In combination with the negative effects of summer warming on leaf litter production, this reduced the total N losses of *Betula* shoots by 31%. The leaf litter N concentrations and total N losses through leaf litter production of the three other growth forms were not affected significantly by summer warming, nor was there a significant effect of the winter treatments on N concentrations or N losses of any of the growth forms (Table 4).

Discussion

To our knowledge, this is the first report of the vegetative responses of vascular peatland plants to realistic and independent climate manipulations inside and

outside the growing season, which, moreover, explicitly includes *Sphagnum*-growth-mediated effects. The role of mosses as modifiers of climate change effects on vascular plant communities has been largely overlooked so far. Our results showed that 2–3 years' experimental manipulation of summer and winter climate in a subarctic bog had several strong effects on two shrubs, but not on a forb and a grass. Increased *Sphagnum* growth in response to summer warming, however, counteracted several of the potentially positive effects of higher summer temperatures and thicker winter snow cover on those shrubs.

DIRECT AND *SPHAGNUM*-MEDIATED EFFECTS OF SUMMER WARMING ON GROWTH, LEAF LITTER PRODUCTION AND N LOSSES

The species of the four growth forms investigated here responded differently to the climate manipulations. Relatively small increases in summer temperatures enhanced the apical stem growth of the deciduous shrub *Betula* by up to 50%. This is high compared with the responses of most deciduous shrubs in other short-term as well as longer-term studies (Parsons *et al.* 1994; Hobbie *et al.* 1999; Bret-Harte *et al.* 2002; Kudo & Suzuki 2003). The length growth response of the evergreen shrub *Empetrum* to the summer warming treatments was less than that for *Betula*, and less than that for *Empetrum* and other evergreen shrubs in previous warming experiments (Parsons *et al.* 1994; Shevtsova *et al.* 1997; Suzuki & Kudo 2000). Positive growth responses of shrubs to enhanced temperatures strongly increased the total canopy height in a tussock tundra (Chapin & Shaver 1996; Bret-Harte *et al.* 2001) and a dwarf shrub heath (Press *et al.* 1998). However, in support of our hypothesis (i), the relative response of *Betula* in our subarctic bog was in the same range as, or slightly weaker than, the response of *S. fuscum*, while the relative response of *Empetrum* was much weaker (see also Sonesson *et al.* 2002). The *Sphagnum* growth measurements from Dorrepaal *et al.* (2004) were taken at positions not overgrown by vascular plants. Because *Sphagnum* growth is usually stimulated by mild shading (Clymo & Hayward 1982), we may thus have slightly underestimated the growth rate of *Sphagnum* below the small shrubs. Furthermore, in contrast to *Sphagnum*, the length growth of shrubs is not vertical due to the clear inclination of their stems. It therefore seems unlikely that summer warming in subarctic peatlands, despite its positive effects on shrub growth, will increase the height of the vascular canopy above the *Sphagnum* carpet. Short, slow-growing shrubs such as *Empetrum* may even get bogged down by *Sphagnum* as the summers become warmer.

In contrast to our hypotheses (ii) and (iii), summer warming effects on leaf litter biomass and N losses differed among the growth forms, were negative or neutral, and were affected only marginally by changes in *Sphagnum* growth. For the two shrubs, the small to

moderate growth response seemed to play an important role in those effects. The summer warming treatments caused a strong reduction in leaf litter production of the deciduous shrub *Betula* by reducing the number of leaves per shoot. However, ANCOVA indicated that *Sphagnum* growth was a less important factor than warming itself. This contrasts with an earlier report, that the presence of living *Sphagnum* significantly reduced the leaf biomass of *Betula* compared with a *Sphagnum*-removal treatment (Hobbie *et al.* 1999). In tussock tundra, summer warming enhanced *Betula* leaf production and biomass (Chapin & Shaver 1985; Chapin & Shaver 1996; Hobbie *et al.* 1999), while it was relatively unresponsive in a subarctic heath (Graglia *et al.* 1997; Jonasson *et al.* 1999). Positive responses of above-ground biomass and N content in warming experiments have been ascribed to increased nutrient acquisition because of higher mineralization rates (Chapin *et al.* 1995; Chapin & Shaver 1996; Rustad *et al.* 2001), or greater early season competitive ability of *Betula* for nutrients, owing to advanced leaf phenology (Hobbie & Chapin 1998). The summer warming treatments in our experiment did not affect *Betula* leaf phenology (S. Berg and E.D., unpublished results), and reduced its leaf litter N concentrations. This suggests that summer warming did not substantially enhance N availability, probably because our large OTCs resulted in realistic, small increases in average air temperature in summer, but did not significantly enhance average summer soil temperatures (Dorrepaal *et al.* 2004). The increase in apical stem growth of *Betula* in response to summer warming therefore appears to have reduced the growth and maintenance of older shoot parts and short shoots (Chapin & Shaver 1996; Bret-Harte *et al.* 2001), and reduced the allocation to leaves compared with stems (Parsons *et al.* 1994).

For the evergreen shrub *Empetrum*, the length of the stems covered with brown leaves was positively related to *Sphagnum* growth, confirming earlier reports that overgrowth of basal leaves is a major cause of leaf senescence for small evergreen shrubs in peatlands (Backéus 1985). However, increased overgrowth by *Sphagnum* only initially enhanced total leaf litter losses of *Empetrum*. The leaf life span of *Empetrum* at our site (2.4 years, calculated as the ratio of the length of the harvested stem covered with green leaves to the length covered with senesced leaves) suggests that this applied to leaves that had actually been produced before the start of the experiment. In the third year, leaf litter production in the summer warming treatments was reduced to ambient level because enhanced stem elongation had reduced the number of leaves per stem length (data not shown). The distance between leaves on *Empetrum* shoots is known to vary (Mentz 1921; Bell & Tallis 1973). It may increase on enhanced length growth because a considerable part of the new shoot is produced from preformed winter buds without cell division (Bell & Tallis 1973; Backéus 1985).

The length growth response of *Empetrum* to increased summer temperatures may therefore have been limited, but was crucial in avoiding negative impacts of enhanced *Sphagnum* growth on leaf mass and nutrient losses.

In accordance with our hypothesis (iii), leaf litter biomass of the forb *Rubus* and the graminoid *Calamagrostis* was not related to *Sphagnum* growth. However, in contrast to hypothesis (ii), they did not show direct responses to summer warming either. Above-ground biomass and production responses of graminoids and forbs to experimental warming vary considerably among studies, and may be related more to the effects of higher temperatures on nutrient or light availability (Parsons *et al.* 1995; Press *et al.* 1998; Shaver *et al.* 1998; Jonasson *et al.* 1999). We did not observe that summer warming had closed the low and open vascular plant canopy in our site, nor did the treatment appear to have increased the nutrient availability substantially. This may have contributed to the lack of response of *Rubus* and *Calamagrostis*.

RESPONSES OF VASCULAR PLANTS TO CHANGES IN WINTER AND SPRING CLIMATE

Changes in winter snow cover and higher winter and spring temperatures had few effects on the four species of the growth forms investigated in this study. Our hypothesis (iv), that a thicker snow cover would enhance the growth of taller shrubs such as *Betula* by protecting their apical shoots and buds, was not supported by our data. While winter mortality of the apical part of the main axis or a secondary long shoot was relatively low (8.6%), it was positively associated with the stem length of *Betula* shoots, but not significantly related to any of the treatments (data not shown). The lack of effects of the doubled snow thickness in the OTCs in winter on winter shoot mortality and summer growth may be explained by the relatively small length of the *Betula* shoots (11.1 cm on average), of which more than 70% must have been covered by the shallow, 13-cm-thick ambient snow cover in the coldest part of winter (February–April; cf. Dorrepaal *et al.* 2004; Aerts *et al.* 2004). Although higher summer temperatures enhanced the length growth of *Betula*, the increased overgrowth of the stem bases owing to the continuously rising *Sphagnum* surface are likely to counteract increases in the height of the canopy, as explained above. *Sphagnum* might thus prevent positive interactions between summer warming and increased winter snow cover on vascular canopy height and litter production, as reported in other experiments (Van Wijk *et al.* 2003).

Higher spring temperatures, in addition to the increased snow cover, did not significantly affect shrub growth or total leaf litter production of any of the growth forms. The treatment enhanced the production of leaf litter on the current-year parts of the *Betula* shoots compared with snow addition alone, which indicates that spring warming stimulated development

of the apical leaves and part of the buds. However, on a total shoot basis, growth, leaf and litter production were not affected. Because leaf phenology was also not (*Betula* and *Calamagrostis*) or only slightly (*Rubus*) affected by our spring warming treatments (S. Berg and E.D., unpublished results), it remains unclear how much enhanced leaf phenology might contribute to total leaf and litter production. So far it seems that, although growth and development of some species or shoot parts may be temperature-limited early in the season, limitations by nutrients or other resources later in the summer (Chapin & Shaver 1996) prevent positive effects of increased spring temperatures on whole-shoot growth and production.

CLIMATE CHANGE IMPLICATIONS FOR PLANT INTERACTIONS IN SUBARCTIC PEATLANDS

Experimental manipulation of summer temperatures has been shown to affect the interactions between vascular and non-vascular plants in various arctic and subarctic ecosystems. Declines in moss and lichen production and cover in tussock tundra and dwarf shrub heath have been ascribed to reductions in light availability, due to increased vascular above-ground biomass and litter (Chapin *et al.* 1995; Press *et al.* 1998; Hobbie *et al.* 1999; Cornelissen *et al.* 2001). However, if the vascular vegetation is low and open, such as on fell-fields, wet sedge tundra and ombrotrophic bogs, and moisture conditions are not negatively affected, increased temperatures may enhance moss performance (Callaghan *et al.* 1997; Shaver *et al.* 1998; Jonasson *et al.* 1999; Sonesson *et al.* 2002; Van Wijk *et al.* 2003; Dorrepaal *et al.* 2004). Although mosses usually inhabit the bottom layer of the vegetation, their presence and performance have been shown to affect vascular plants as well, through their effects on moisture and nutrient availability, temperature regime and even light availability through overgrowth of stems, leaves or whole plants (Backéus 1985; Sohlberg & Bliss 1987; Hobbie *et al.* 1999; Ohlson *et al.* 2001; Limpens *et al.* 2003).

Our results indicate that summer warming-enhanced *Sphagnum* growth is likely to have a negative impact on shrubs through the consequences of stem overgrowth for shrub height and functional loss of above-ground stem tissue, but not for leaf litter and N losses. Climate warming, however, determines the ability of woody species to cope with the enhanced stem overgrowth, for which there seems to be a trade-off between resource investments in stem or leaf tissue. If these short-term responses are indicative for longer-term responses as well (Graglia *et al.* 2001; but cf. Chapin *et al.* 1995; Hollister *et al.* 2005), the increased *Sphagnum* growth may thus directly threaten the survival of *Empetrum* because of its weak growth response and short total shoot length (2.0 cm on average). *Betula*, which is known as a shrub with a relatively high plasticity of shoot allocation (Bret-Harte *et al.* 2001), might be able to keep pace with the increasing *Sphagnum* height, but

the resulting reduction in the size of its photosynthetic apparatus is likely to hamper its performance in the long term. In contrast, *Calamagrostis* (graminoid) and *Rubus* (forb) were not affected by either *Sphagnum* growth or enhanced temperatures. These effects of changes in *Sphagnum* growth on woody vs herbaceous species correspond to previously reported responses of growth and survival of *B. pubescens* vs *Molinia caerulea* seedlings (Limpens *et al.* 2003) and *Drosera rotundifolia* plants (Svensson 1995) in relation to N-fertilization effects on *Sphagnum* growth.

Deciduous and evergreen shrubs are important components of the vascular vegetation of peatlands, particularly bogs (Backéus 1985), and represent 80% of the vascular above-ground biomass at our site (S. Bokhorst and J.H.C.C., unpublished results). The structure and stability of moss and peat layers produced by hummock-forming species such as *S. fuscum* depend largely on the support of overgrown shrub stems (Ohlson & Dahlberg 1991; Malmer *et al.* 1994). Decreased relative performance of shrubs due to direct and *Sphagnum*-mediated effects of climate change therefore may not only alter the vascular plant community, but may also affect the stability and functioning of the whole peat-forming system.

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