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The effects of increased nitrogen deposition and CO_2 on *Sphagnum angustifolium* and *S. warnstorfii*

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The differences in response to four levels of N deposition rates 0, 10, 30 and 100 kg ha^{-1} a^{-1} and ambient CO_2 concentrations 350, 700, 1 000 and 2 000 ppm were studied in a greenhouse with Finnish material: *Sphagnum angustifolium* (Russow) C. Jens., a species occurring over a wide nutrient regime, and *S. warnstorfii* Russow, a meso-eutrophic species. With increased N deposition rate, capitulum density, capitulum and stem dry masses per unit length increased in *S. warnstorfii*. Length increments differed statistically among the N treatments, but in the highest experimental N deposition rate there was no fall in *S. angustifolium* comparable to that found in *S. warnstorfii*. In both species, raised CO_2 concentrations caused increasing trends in capitulum and stem dry masses as well as length increments. Dry mass production of *S. angustifolium* increased at raised CO_2 concentrations. Interaction between the two treatments was not so clear as their individual effects.

Keywords: bryophyte ecology, carbon dioxide, dry mass, growth parameters, production

INTRODUCTION

The presence or absence of many *Sphagnum* species on mires has been found to correlate with N and P availability (Malmer 1962b, 1986, Damman 1986). The chemistry of mire water, mainly the concentration of Ca and pH, has also been found to correlate with the presence of *Sphagnum* species (Heikkilä 1987, Hayati & Proctor 1990, Vitt & Chee 1990). Some *Sphagnum* species are used as indicators in the classification of mire types ecologically based on ombrotrophy-minerotrophy (Sjörs 1948, Malmer 1962a, 1986, Pakarinen & Ruuhijärvi 1978, Pakarinen 1979). Many *Sphagnum* species have adapted to ombrotrophic conditions, in which the usually low supply of nitrogen is derived from deposition by air, fixation of atmospheric N by cyanobacteria, or from insects captured by carnivorous plants. Mosses in minerotrophic mires have additional N available through nutrients from the so-called telluric waters (surface run-off and ground waters).

As *Sphagnum* species are clearly different in their ionic concentrations (Aulio 1980, Clymo & Hayward 1982), tolerance to high ionic concentrations among *Sphagna* may vary and thus affect growth and species composition. In Finland the amount of nutrient deposition from the atmosphere has increased markedly over recent decades (Kauppi *et al.* 1990) and the distribution pattern of the *Sphagnum* species may well be affected because of changes in growth conditions. Laboratory measurements with ombrotrophic *S. fuscum* (Schimp.) Klinggr. (nomenclature follows Koponen *et al.* 1977) showed that high N deposition rates may have serious vitality weakening effects on the mosses by causing an imbalance in tissue nutrient contents (Jauhiainen *et al.* 1998) and diminished production (Jauhiainen *et al.* 1994, 1997). This kind of change has already been observed in the southern Pennines, on raised bogs with high sulphur and nitrogen depositions (Press *et al.* 1986, Lee *et al.* 1987).

Ever since the pre-industrial age, CO_2 concentration in the atmosphere has increased due to human activities and the increase is predicted to continue into the next century (Watson *et al.* 1996). *Sphagna* constitute an important CO_2 sink via peat formation, because there is an imbalance between dry mass production and decay in the sites where they usually grow. CO_2 released by below-ground respiratory processes may often expose mosses to CO_2 concentrations above those in bulk air, regardless of the general increase in the atmospheric concentration (Silvola 1985, Hogg 1993). This would mean that the increase in atmospheric CO_2 concentration would have a lesser effect on peat mosses. A short-term increase in CO_2 concentration has clearly increased the rate of net CO_2 exchange in *S. fuscum* (Silvola 1985, 1990). Therefore, responses to enhanced CO_2 concentrations in various production parameters have differed greatly from expectations. Length increments decreased slightly when *S. fuscum* was grown at enhanced CO_2 concentrations and the CO_2 treatment had no statistically significant effect on the dry mass production in this species (Jauhiainen *et al.* 1994, 1997). Consequently, further experiments on *Sphagna* representing different taxonomic groups and nutrient levels were found necessary.

The specific questions of this study were: (i) What kind of responses in various production parameters do increased nitrogen deposition rates and CO_2 concentrations elicit in *S. angustifolium* (Russow) C. Jens. and *S. warnstorfii* Russow? (ii) Is there some limit to the increase of production under conditions of increased N deposition rates and ambient CO_2 concentrations? (iii) Are there interactions between the effects of increased CO_2 concentration and N deposition on the measured parameters in these species?

MATERIAL AND METHODS

The species

Both of the *Sphagnum* species studied prefer lawns or low hummocks in which the availability of water does not extensively restrict growth. Both are medium-sized peat mosses and form more or less dense, structured moss carpets. They belong to different taxonomic sections: *S. angustifolium* to *Cuspidata* Lindb. and *S. warnstorfii* to *Acutifolia* (Russow) Schimp. (Isoviita 1966, Daniels & Eddy 1984), and they are also ecologically different, especially in relation to nutrient status. *Sphagnum angustifolium* has quite a wide niche and mostly occurs in reasonably dry oligotrophic fens and bogs (Daniels & Eddy 1984). However, it may also grow as a lawn-level species in moderately wet places or even under forest canopy (Daniels & Eddy 1984). *Sphagnum warnstorfii* is a meso-eutrophic species with higher requirements for nutrient availability (Kivinen 1933, Horton *et al.* 1979, Pakarinen 1979 and references therein, Lindholm & Vasander 1990).

2.2. Material collection

Samples were taken from sites in eastern Finland representing characteristic habitats of the species. In the beginning of the growing season in May 1992, samples of *Sphagnum angustifolium* were collected from pure stands on two mires, the Raatesuo tall-sedge pine fen (62°38´N, 29°46´E) and the Salmisuo low-sedge *Sphagnum papillosum* pine fen (62°47´N, 31°56´E). Samples of *S. warnstorfii* were collected in the beginning of May 1993 from the Huurunlampi-Sammakkolampi *Sphagnum warnstorfii* fen (63°01´N, 29°54´E), cf. Ruuhijärvi (1983) for the Finnish mire site types.

Several microplots, 3 × 3 cm, were chosen from pure stands of both *Sphagna*, and the number of shoots was counted. Sixty-four cores (15 cm in diameter and 11–12 cm thick) of both species were then cut from the surface of the mire using a cylindrical corer with a sharpened wave shaped edge. Each of the cores was cut longitudinally open with a knife and a plastic strip 6 cm × 15 cm was fixed in the slit with two sharp wooden sticks, which were pressed through the strip to the lower part of the core. Part of the plastic strip, 6–7 cm in length, was left above the moss surface to serve as a reference mark for the length increments. Then the cores were placed in identical cylindrical plastic containers. The containers were transported to a greenhouse at the University of Joensuu for further study.

Control over the treatments

Sixty-four moss containers, grouped in four-sample series, were placed in four sets of trays. Deionized water was added to the trays to maintain the water table height at 7 cm below the capitulae. The water in the trays was replaced weekly before N fertilization treatment. Each of the sample cores was fertilized weekly by spraying the moss surface with a modified Rudolph's nutrient solution (Rudolph & Voigt 1986), so it received a nitrogen deposition rate equivalent to either 0, 10, 30 or 100 kg ha^{-1} a^{-1}. The selected experimental N deposition rates were: control (N_0), equivalent to low N deposition rate in southern Finland (N_{10}), equivalent to moderate N deposition rate in an industrialized area in central Europe (N_{30}), and high N deposition rate (N_{100}) representing a potential situation in a highly N polluted area. The nutrient solution used in this study has been found to be suitable for growing *Sphagna* in a laboratory (Rudolph & Voigt 1986). Non-nitrogenous replacement salts were used in the nutrient solution to maintain constant ionic strength for the nutrients, excluding nitrogen, in each of the four N treatments. An appropriate amount of NH_4NO_3 was added to the solution in order to give the desired fertilization effect. The pH of the water was adjusted to 4.5 for *S. angustifolium* and 6.0 for *S. warnstorfii*, which correspond to the pH of the species' growing sites (Lindholm & Vasander 1990). The volume of the weekly sprayed nutrient solutions per sample container (180 ml) was a proportion of the annual rainfall of 530 mm.

The sets of trays with samples for nitrogen deposition treatment were placed in four growth chambers, the ambient CO_2 concentration of which was automatically controlled. These CO_2 concentrations were the reference (350 ppm) and common doubling scenario (700 ppm), while the two highest concentrations (1 000 and 2 000 ppm) were selected in order to study growth response to CO_2 treatment on a wider scale. The temperature in the chambers was adjusted to automatically maintain the appropriate conditions, i.e. 10–15°C at night and below 25°C during the day. The samples were illuminated by natural summer-time sunlight, which shone through the transparent plastic walls of the growth chambers. The duration of direct sunlight was somewhat lower than it would have been on open terrain because of shade from trees and buildings. Although the light conditions were found to be about similar in the four growth chambers during the experiment, the four CO_2 concentrations and respective samples were exchanged biweekly between the growth chambers. A computer (IBM PS/model 30) controlled the CO_2 concentration through a data acquisition system (HP 3421 A) by sampling gas from the growth chambers in an infra-red gas analyzer (Uras 3T, Hartmann & Braun) and, if needed, regulated the gas flow from a CO_2 source.

Measurements of *Sphagna*

At the start and end of the experiment, the total number of capitulae per unit area was counted in each sample core in 3×3 cm areas ($n = 3$). Before the treatments, a comparison was made between the number of capitulae counted in the field and in the collected samples in order to confirm that sampling had caused no change.

Dry mass in capitulum (0–1 cm) and stem dry mass (per mm of stem) were calculated at the end of the experiment. Individual *Sphagnum* shoots were first cut from the cores and divided into capitulum (top 1 cm of the shoot) and stem (next 2 cm below the capitulum). A pooled sample consisted of 20 capitula or 20 stems. Four pooled samples were prepared from each of the sample cores. The samples were oven dried for 12 h at 60°C and weighed.

Length increment was measured by the plastic strip method (Lindholm 1990). In this method the change in the distance between moss apex and the horizontal reference line, drawn near the upper margin of the plastic strip, is measured with calibration calipers. Length increments of five shoots per sample core were measured biweekly over a period of 71 d for *Sphagnum angustifolium* and 98 d for *S. warnstorfii*. The experiment was terminated when the light flux in the autumn was reduced to such an extent that, combined with relatively high night temperatures in the growth chambers, its effect was assumed to affect the mosses unfavourably. Dry mass production was calculated by multiplying the total length increment of shoot by the average stem dry mass and by the average number of capitulae per unit area in each of the sample cores.

For both species, the total number of sample cores was 64 and the experiment was conducted under four levels of CO_2 times four levels of N deposition, i.e. a total of 16 treatments with four replicate cores per treatment. For each sample core, the mean value was calculated from the values of pooled sub-samples in the case of capitulum density, shoot dry masses and length increment, thus resulting in four replicates for the statistical analysis. Two-way analysis of variance (ANOVA) was used for the statistical analysis and all statistical analyses were done by SPSS for Windows (SPSS Inc.), release 6.1 program package.

RESULTS

Capitulum density
(Fig. 1, Table 1)

The N treatment did not have a statistically significant effect on the capitulum density of *Sphagnum angustifolium*. In *S. warnstorfii* the number of capitulae was significantly higher at increased N deposition rates and the increase was especially clear in comparison of the N_{30} and N_{100} treatments with the N_0 treatment.

The CO_2 treatment had no effect on the *Sphagnum angustifolium* capitulum density. Although statistically significant differences were found in the capitulum density of *S. warnstorfii* with CO_2

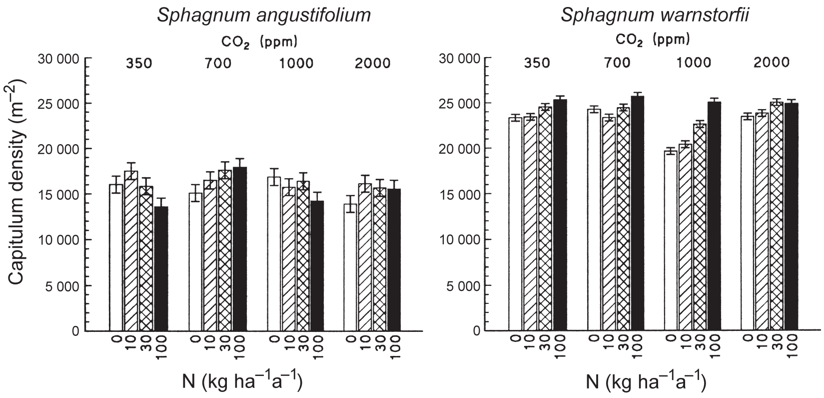

Fig. 1. The capitulum density (shoots m^{-2}) of *Sphagnum angustifolium* (Russow) C. Jens. and *S. warnstorfii* Russow at four N deposition rates and at four CO_2 concentrations. The growth period was 71 d for *S. angustifolium* and 98 d for *S. warnstorfii*. Mean ± S.E. presented (n = 4).

treatment, these were mostly due to low capitulum densities in *Sphagna* grown at a CO_2 concentration of 1 000 ppm at the three lowest N deposition rates.

Dry mass in capitulum and stem
(Fig. 2, Table 1)

N treatment did not have a significant effect on the capitulum or stem dry masses of *Sphagnum angustifolium*. N treatment had a significant effect on the dry masses in both capitulum and stem of *S. warnstorfii*, however, they were highest at the 100 kg ha^{-1} a^{-1} N deposition rate.

An increase in CO_2 concentration increased the capitulum dry mass in *Sphagnum angustifolium*. The stem dry mass also rose in enhanced CO_2 concentrations. However, this increase in higher CO_2 concentrations was not uniform in the four N deposition rates. In *S. warnstorfii*, a marked increase in the dry mass of both capitulum and stem was statistically significant at enhanced CO_2 concentrations, while the increase was clearest among mosses grown at CO_2 concentrations of 1 000 ppm and 2 000 ppm.

Length increment and production
(Fig. 3, Table 1)

Statistically marked differences were found in length increments in both treatments, although the effect of CO_2 treatment on length increments was smaller than that of N treatment. In *Sphagnum angustifolium* the clearest increase in length increment was generally between the N_0 and N_{10} treatments. For mosses grown at 1 000 and 2 000 ppm CO_2 concentrations, length increments remained surprisingly low in the N_{30} treatment when compared with those for the next lower and next higher N deposition rates. In general, length increments in *S. warnstorfii* grew more in the N_{10} or N_{30} treatments than in the N_0 treatment. The lowest length increments were always in the N_{100} treatment and they were also significantly lower than to the length increments in the N_0 treatment.

Generally speaking, the length increments of *Sphagnum angustifolium* increased at raised CO_2; thus the differences were clearest between the extreme concentrations: 350 and 2 000 ppm CO_2. In *S. warnstorfii* there was an increasing trend in length increments at raised CO_2 concentrations up to 1 000 ppm, but length increments remained relatively low in mosses grown at 2 000 ppm CO_2.

The dry mass production in *Sphagnum angustifolium* was clearly higher if there was additional nitrogen in the treatment, but the highest dry mass production was always found at low or moderate N deposition rates. There were no statistically marked differences in the dry mass production of *S. warnstorfii* in the N deposition treatment.

In *Sphagnum angustifolium*, markedly differing amounts of dry mass production were found in the CO_2 treatment, while the response mainly showed an increasing trend in higher CO_2 concentrations. The dry mass production in *S. warnstorfii* was variable among the four CO_2 concentrations with no statistically significant differences in the treatment.

Combined effect of the N and CO_2 treatments (Table 1)

Responses in the production parameters measured showed few statistically significant interactions between the N and CO_2 treatments, i.e. in capitulum density of *Sphagnum warnstorfii* and length increment of *S. angustifolium* (Table 1). However, such effects can not be easily interpreted because response to these treatments, even within a treatment, seldom follows linear trends. In *S. warnstorfii* there was a clearly increasing trend in capitulum density, which corresponded with increased N deposition rates; no such trend, however, was found in *Sphagna* among the four CO_2 concentrations. In *S. angustifolium*, the effect of increased

Table 1. Results of two-way ANOVAs for measured parameters in *Spahgnum angustifolium* (Russow) C. Jens. and *S. warnstorfii* Russow. Degrees of freedom (DF), sum of squares (SS), mean square (MS), *F*-value and *F*-probability (*P*) presented. Values in boldface are significant at 0.05 probability level.

		Sphagnum angustifolium				*Sphagnum warnstorfii*			
Source of variation	DF	SS	MS	*F*	*P*	SS	MS	*F*	*P*
Capitulum density									
Main effects	6	31.8	5.3	1.2	0.314	116.3	19.4	19.7	**0.000**
N	3	21.5	7.2	1.6	0.191	60.9	20.3	20.7	**0.000**
CO_2	3	9.8	3.3	0.8	0.527	55.4	18.5	18.8	**0.000**
N × CO_2	9	57.8	6.4	1.5	0.184	22.7	2.5	2.6	**0.017**
Explained	15	88.3	5.9	1.4	0.210	139.1	9.3	9.4	**0.000**
Residual	48								
Capitulum DM									
Main effects	6	39.2	6.5	2.7	**0.025**	26.6	4.4	4.8	**0.001**
N	3	8.9	3.0	1.3	0.310	14.6	4.9	5.3	**0.003**
CO_2	3	29.6	9.9	4.1	**0.012**	12.0	4.0	4.4	**0.008**
N × CO_2	9	29.3	3.3	1.3	0.240	4.0	0.4	0.5	0.877
Explained	15	67.9	4.5	1.9	0.052	30.6	2.0	2.2	**0.019**
Residual	48								
Stem DM									
Main effects	6	14 913.3	2 485.6	2.5	**0.034**	49 653.9	8 275.6	5.9	**0.000**
N	3	2 286.0	762.0	0.8	0.516	19 605.2	6 535.1	4.7	**0.006**
CO_2	3	12 477.8	4 159.3	4.2	**0.010**	300 048.6	10 016.2	7.2	**0.000**
N × CO_2	9	15 005.0	1 667.2	1.7	0.119	6 507.0	723.0	0.5	0.854
Explained	15	29 441.5	1 962.8	2.0	**0.038**	56 160.9	3 744.1	2.7	**0.005**
Residual	48								
Length increment									
Main effects	6	4 196.9	699.5	4.7	**0.001**	8 371.6	1 395.3	6.4	**0.000**
N	3	3 008.0	1 002.7	6.7	**0.001**	6 414.2	2 138.1	9.7	**0.000**
CO_2	3	1 352.2	450.7	3.0	**0.039**	1 957.3	652.4	3.0	**0.041**
N × CO_2	9	3 060.6	340.1	2.3	**0.033**	1 478.2	164.2	0.7	0.665
Explained	15	7 366.8	491.1	3.3	**0.001**	9 849.8	656.7	3.0	**0.002**
Residual	48								
Production									
Main effects	6	54 344.2	10 724.1	6.4	**0.000**	43 487.8	7 248.0	1.3	0.284
N	3	35 382.2	11 794.1	7.1	**0.001**	40 729.4	13 576.5	2.4	0.080
CO_2	3	31 760.1	10 586.7	6.3	**0.001**	2 758.4	919.5	0.1	0.921
N × CO_2	9	24 567.7	2 729.7	1.6	0.133	33 232.7	3 692.5	0.7	0.747
Explained	15	85 154.2	5 676.9	3.4	**0.001**	76 720.5	5 114.7	0.9	0.566
Residual	48								

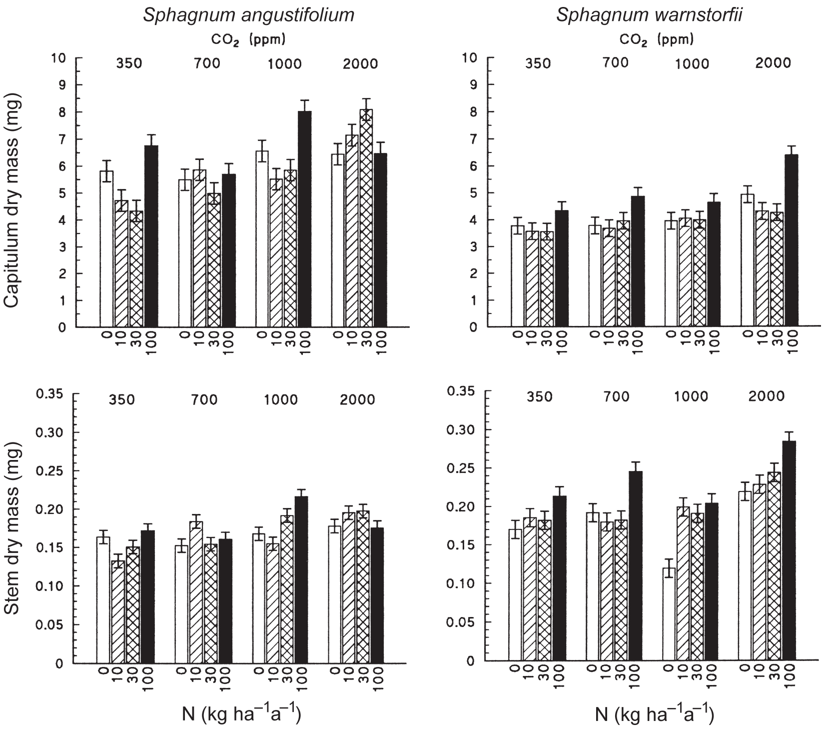

Fig. 2. Dry mass of capitulum (mg) and stem dry mass (mg) of *S. angustifolium* (Russow) C. Jens. and *S. warnstorfii* Russow at four N deposition rates and at four CO_2 concentrations. The growth period was continued 71 d for *S. angustifolium* and 98 d for *S. warnstorfii*. Mean ± S.E. presented (n = 4).

N deposition rates was initially an increase in length increment, whereas low length increments were found at the highest N deposition rates in the two lowest experimental CO_2 concentrations. However, CO_2 concentrations of 1 000 and 2 000 ppm resulted in high length increments even in the N_{100} treatment.

DISCUSSION

Capitulum density and shoot dry mass

The change in capitulum density may be considered an indicator of stress or altered growth conditions caused by the treatments. In this study, the observed change in the number of capitula occurred only if the growth circumstances were greatly changed, due either to increased N deposition or CO_2 concentration, and the change took place only in the ecologically more restricted *Sphagnum warnstorfii*. It is worth noting, that although the capitulum density in *S. warnstorfii* remained low at 1 000 ppm CO_2, at the start of the experiment the capitulum densities in the samples did not exhibit statistically marked differences**.** A similar kind of increase as found in the capitulum density of *S. warnstorfii* in this study has been reported for *S. fuscum* grown at high CO_2 concentrations (Jauhiainen *et al.* 1994). Tissue and Oechel (1987) found an increase in the number of new tillers in cottongrass at enhanced CO_2 concentrations. Our results also compare well with those of Aerts *et al.* (1992), who noticed an increase in the capitulum density of *S. balticum* (Russow) C. Jens. on a high nitrogen deposition field site.

Wide tolerance of nutrient status in *Sphagnum angustifolium* was clearly indicated by a low sensitivity to N treatment in the capitulum density and shoot dry masses, while *S. warnstorfii* had clearly higher responses to N treatment. At the highest experimental N deposition rate in particular, the *S. warnstorfii* shoot dry masses were high, indicating a variety of reasons: heavier cell structures, a shorter distance between branches on the stem caused by low length increments, longer branches or a combination of all of these. Of these potential causes, low length increments were found in this study. A similar kind of lowered dry mass of shoots subsequent to increased nitrogen deposition was found in *S. balticum* (Aerts *et al.*

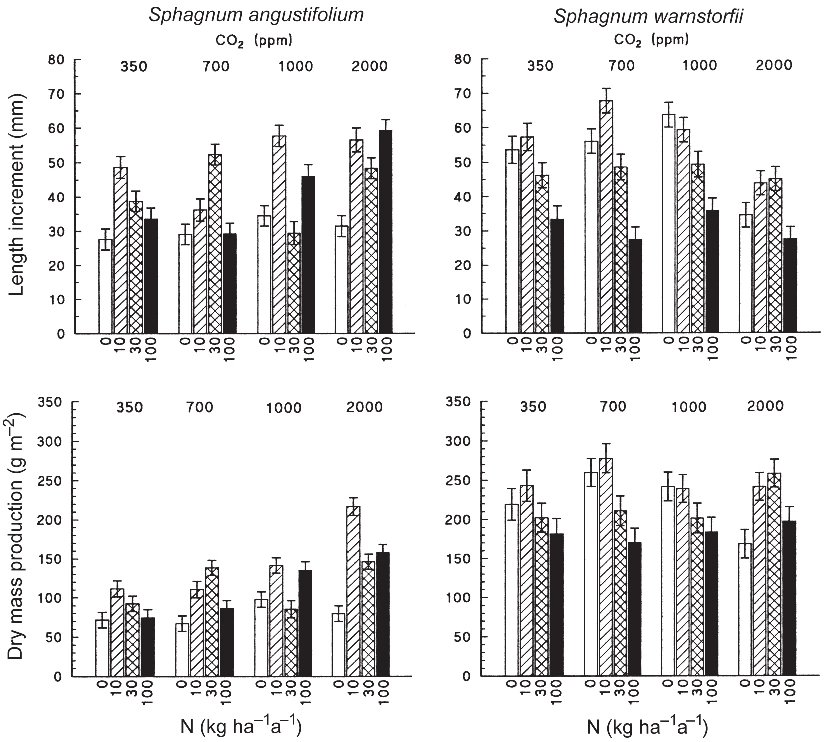

Fig. 3. Length increment (mm) and dry mass production (g m^{-2}) in *S. angustifolium* (Russow) C. Jens. and *S. warnstorfii* Russow at four N deposition rates and at four CO_2 concentrations. The growth period was continued 71 d for *S. angustifolium* and 98 d for *S. warnstorfii*. Mean ± S.E. presented (n = 4).

1992) and also in *S. fuscum* (Jauhiainen *et al.* 1994), but no such changes were found in the dry mass of *S. cuspidatum* Hoffm. (Paffen & Roelofs 1991) nor in *S. magellanicum* Brid. (Aerts *et al.* 1992). However, dry masses in capitulum and stem were higher in samples grown at raised CO_2 concentrations and a similar change has been noticed in *S. fuscum* (Jauhiainen *et al.* 1994) and *S. papillosum* Lindb. (van der Heiden *et al.* 1998). The plant dry mass in *S. cuspidatum* also increased if the CO_2 concentration in the growth solution was raised (Paffen & Roelofs 1991).

Length increment and dry mass production

The response of dry mass production to these treatments may be quite similar in the species studied, but the mechanisms differ because it was calculated as a product of responses in length increment, stem dry mass and capitulum density. Both *Sphagnum angustifolium* and *S. warnstorfii* tolerated the applied N deposition reasonably well and no collapse in length increment or dry mass production at the highest N deposition rate as that reported in ombrotrophic *S. fuscum* (Jauhiainen *et al.* 1994) was observed. In the N treatment of this experiment, the resulting differences in dry mass production in *S. angustifolium* are clearly merged from the amount of length increment at the four experimental N deposition rates. *Sphagnum angustifolium* tolerated even the highest N deposition rate, while the dry mass production in *S. warnstorfii* was at its lowest in the N_{100} treatment. This is obviously related to the wider ecological amplitude of *S. angustifolium*, as the growth and dry mass production of pure *S. angustifolium* carpets may differ among different site types within a single mire (Lindholm & Vasander 1990).

Many plant communities are considered to be nitrogen limited (Lee *et al.* 1983) and this is applicable to northern ombrotrophic bogs, which receive their nutrients solely from atmospheric deposition (Roswall & Granhall 1980). Changes in plant growth, which may take place at an increased nitrogen deposition rate, are therefore thought to arise most distinctly at these ombrotrophic sites. Increased N deposition rates seem to cause changes in the ability of *Sphagnum* species growing in more minerotrophic areas to keep up competitive growth. For example, an increased NH_4^+ and NO_3^-

deposition rate was found to benefit *S. fallax* (Klinggr.) Klinggr. growth at least in hollows, while growth accelerating effects were not observed in species such as *S. magellanicum* (Twenhöven 1992). *Sphagnum warnstorfii* may have higher demands for nitrogen availability, but it is probably also adapted to a narrower range of nitrogen supply. *Sphagnum warnstorfii* tolerates relatively high concentrations of Ca ions (Crum 1976, Pakarinen & Ruuhijärvi 1978) and high pH in growing sites, which indicates specialization. However, high tolerance to Ca ions does not necessarily result in high tolerance to increased concentration of N, which was demonstrated in *S. warnstorfii* through the responses in all the production parameters included in this study. The meso-eutrophic character of *S. warnstorfii* is also probably more closely connected with the pH and Ca concentration of peat than with the N deposition rate alone, the factors of which are usually intercorrelated (Waughman 1980, Daniels & Eddy 1985).

During this experiment additional phosphorus was available in the Rudolph's nutrient solution, the quantity being a bit higher (7.2 mg m^{-2}) than in the area's natural deposition (5.1 mg m^{-2}). Therefore a lack of phosphorous was not expected in the experiment. However, the N:P in the *Sphagna* studied were significantly higher in the enhanced N deposition rates and the change indicated more unfavourable conditions. In *S. angustifolium* the N:P was increased from 13 in the N_0 treatment to 35 in the N_{100} treatment while in *S. warnstorfii* the respective values were 27 and 57 (Jauhiainen *et al*. 1998). Such a high increase in N:P would most likely lower the viability of mosses in accordance with species sensitivity, as this study found the responses of *S. angustifolium* and especially of *S. warnstorfii* to high N deposition rates.

Higher atmospheric CO_2 concentration has increased production in most of the C_3 species studied, which, of course, is due to enhanced photosynthesis. As the increase in length and dry mass production have been found to be uncoupled in bryophytes (Rincon & Grime 1989), the relationship between photosynthesis and dry mass production may also differ in mosses grown at enhanced CO_2 concentrations. In *Sphagnum fuscum* the net photosynthesis rate increasing effect of enhanced CO_2 was found to decrease to some extent under prolonged exposure (Jauhiainen & Silvola 1996). Responses to enhanced CO_2 concentration in the length increment and dry mass production of this species also remained relatively low (Jauhiainen *et al.* 1994, 1997). Contrary to hummock-forming *S. fuscum*, floating *S. cuspidatum* grown at increased CO_2 concentration showed a decrease in dry mass, but enhanced length increment and dry mass production (Paffen & Roelofs 1991). The difference in response between these two ombrotrophic species may be partially due to differences in the growth form. It is advantageous for *S. cuspidatum* to have more length to fill the water volume, whereas for *S. fuscum* it is optimal to have denser cushions, which result in a lower length increment but prevent the carpets from drying. The species in this study bear a closer resemblance to *S. fuscum*, as they form well structured plant communities. Further, the response without distinct trend or low response in dry mass production at enhanced CO_2 concentration seems to be similar to *S. fuscum* (Jauhiainen *et al.* 1994, 1997) as well as to responses in the lawn-forming species *S. balticum* and *S. papillosum* (van der Heijden *et al.* 1998).

Photosynthesized carbon may not always be bound in the structural elements of the plant (i.e., capitulum, stem, leaves etc.) but may also be present in non-structural compounds. According to van der Heijden *et al.* (1998), the quantity of soluble sugars in *Sphagnum papillosum* and *S. balticum* showed significant increase if the available CO_2 concentration was doubled, thus accounting for 10%–25% of the increase in the dry mass in capitulum and stem at raised CO_2. Therefore, it may well be that the *Sphagnum* species' response to enhanced CO_2 is not expressed mainly through vegetative growth but via increased concentrations of cell metabolites.

Combined effect of nitrogen and CO_2

The highest nitrogen deposition rate in this study was expected to cause low dry mass production. The effects of CO_2 treatment were assumed to be less dominant but strong enough to increase production at enhanced concentrations, but not in the highest N-deposition treatment. However, the combined effect of the two treatments was weaker than expected, due to the somewhat tangled responses to the CO_2 treatment. In *Sphagnum papillosum*, combined treatments with raised CO_2 of 720 ppm and nitrogen addition of 30 kg ha^{-1} y^{-1} resulted in a clear increase in capitulum and stem structural dry mass and a decrease in length increment (van der Heijden *et al.* 1998). For *S. balticum*, however, the decrease was in length increment only (van der Heijden *et al.* 1998). Baker and Boatman (1990) found that increased concentrations of N, P, K with simultaneously raised CO_2 concentration increased plant dry mass and interfascicle length in an axenic culture of *S. cuspidatum*. However, in their experiment the concentrations of P and K were rather high in the most diluted solution, so the results cannot be regarded as solely due to the effects of N and CO_2. Therefore, the combined effects of CO_2 concentration and N deposition on the vegetative growth of *Sphagna* seem to be species dependent.

CONCLUSIONS

Sphagnum angustifolium seemed to benefit from increased N deposition rates. Although the shoot dry mass was increased in both species at increased N deposition rates, low length increments in *S. warnstorfii* indicated lower tolerance of this species to highly increased N deposition rate. The results showed mainly increasing trends at enhanced CO_2 concentrations. However, due to the somewhat complex responses to CO_2 treatment, the effects of CO_2 may be expressed more clearly through non-vegetative growth. Increased N deposition rates and CO_2 concentrations had clearer effects when they were applied individually than when they were combined.

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