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Raised atmospheric CO_2 levels and increased N deposition cause shifts in plant species composition and production in *Sphagnum* bogs

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Abstract

Part of the missing sink in the global CO_2 budget has been attributed to the positive effects of CO_2 fertilization and N deposition on carbon sequestration in Northern Hemisphere terrestrial ecosystems. The genus *Sphagnum* is one of the most important groups of plant species sequestrating carbon in temperate and northern bog ecosystems, because of the low decomposability of the dead material it produces. The effects of raised CO_2 and increased atmospheric N deposition on growth of *Sphagnum* and other plants were studied in bogs at four sites across Western Europe. Contrary to expectations, elevated CO_2 did not significantly affect *Sphagnum* biomass growth. Increased N deposition reduced *Sphagnum* mass growth, because it increased the cover of vascular plants and the tall moss *Polytrichum strictum*. Such changes in plant species composition may decrease carbon sequestration in *Sphagnum*-dominated bog ecosystems.

Keywords: bogs, carbon dioxide, nitrogen, peatlands, *Sphagnum*

Introduction

An important part of the missing sink in the global CO_2 budget has been attributed to the positive effects of CO_2 fertilization and N deposition on carbon sequestration in Northern Hemisphere terrestrial ecosystems (Schimel 1995; Walker & Steffen 1997). The exact nature of these effects, however, is still a matter of debate (Myneni *et al*. 1997; Fan *et al*. 1998; Nadelhoffer *et al*. 1999). Carbon in Northern peatlands equals about 25% of all atmospheric CO_2-C (Schlesinger 1991). *Sphagnum* species sequester more carbon in temperate and northern ecosystems than any other group of plants. In many of these ecosystems, particularly in rain-fed bogs, *Sphagnum* species create conditions that strongly favour carbon sequestration (Van Breemen 1995). *Sphagnum* produces material that is rich in phenolics and therefore far more resistant to microbial decomposition than litter of vascular bog plants (Verhoeven & Liefveld 1997). The genus-specific p-hydroxy-β-carboxymethyl-cinnamic-acid strongly retards the decay of litter of both *Sphagnum* and other neighbouring plants (Clymo & Hayward 1982; Bartsch & Moore 1985; Verhoeven & Toth 1995). Moreover, by creating anoxic and acid conditions, *Sphagnum* strongly reduces microbial degradation of the litter of co-occurring plant

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Table 1 Location, climate summary and atmospheric N deposition of the four sites. Climatic data comprise: mean daily temperature in warmest and coldest month, annual precipitation and number of days with snow cover

Country	Name and location field site	Climate	N deposition (g N m^{-2} y^{-1})
Finland (FI)	Salmisuo, in Ilomantsi, eastern Finland (62°47′ N, 30°56′ E)	16 °C, –10 °C, 650 mm 150–200 snowdays	0.4
Sweden (SW)	Kopparåsmyren, south Sweden (57°8′ N, 14°30′ E)	16 °C, –2 °C, 800 mm 80–120 snowdays	0.8
Switzerland (CH)	La Chaux-des-Breuleux, Swiss Jura (47°13′ N, 7°3′ E)	15 °C, –5 °C, 1390 mm 80–120 snowdays	1.8
Netherlands (NL)	Peat from Dwingeloo (52°49′ N, 6°25′ E) transplanted to Wageningen (51°99′ N, 5°70′ E)	18 °C, 3 °C, 750 mm < 10 snowdays	3.9

species. Therefore, carbon sequestration in peatlands strongly depends on *Sphagnum* mass growth. It is hypothesized that (i) raised CO_2 concentrations cause increased *Sphagnum* growth, but that (ii) higher N inputs would have an opposite effect by stimulating the growth of vascular plants. These hypotheses were tested by two simultaneous experiments in four different bog sites under different climates across Western Europe. This study was part of the BERI (Bog Ecosystem Research Initiative) project that was carried out in close cooperation between research groups from Finland, Sweden, UK, Switzerland and the Netherlands.

Materials and methods

Sites

The experiments were located in predominantly ombrotrophic peatbog-lawns in Salmisuo, eastern Finland (FI); Kopparåsmyren, South Sweden (SW); La Chaux-des-Breuleux, Switzerland (CH); and Dwingeloo, the Netherlands (NL). The fifth BERI site, Roudsea bog in NW England, was not included in this study, because data for *Sphagnum* mass growth were not available at Roadsea. The experiments at FI, SW and CH were carried out *in situ*, but at NL peat cores (1.1 m diameter and 60 cm deep) were collected in frozen condition and transferred to 0.6-m deep containers near Wageningen (NL). These containers were buried to a depth of 0.5 m in an area that was fenced to exclude grazing by rabbits. Climatic data for each site are summarized in Table 1. The initial vascular plant and moss species composition in the control plots is given in Table 2. The peat moss layers at the FI, SW, CH and NL sites were dominated by *Sphagnum balticum* + *S. papillosum*, *S. magellanicum*, *S. fallax* and *S. magellanicum*, respectively. At the FI, SW, CH and NL sites, N inputs through atmospheric deposition were 0.4, 0.8, 1.8 and 3.9 gN m^{-2} y^{-1}, respectively (RAINS 7.2 1997). These N inputs include wet and dry deposition.

Experimental design

In the CO_2 experiment the atmospheric CO_2 concentration was either kept at ambient (360 ppmv) levels or increased to 560 ppmv in mini-FACE rings (Miglietta *et al.* 2001). Each mini-FACE ring (diameter 1 m at FI, SW and CH; 1.1 m at NL) had approximately 70 venting tubes, supplying either ambient or CO_2-enriched air. The tubes were 18 cm tall with two holes, at 6 and 12 cm above the moss surface. Blowers located next to the MiniFACE rings supplied ambient air to the rings. CO_2 supply was adjusted automatically on the basis of wind speed and CO_2 concentrations that were measured continuously with an infrared gas analyser in the centre of each plot at 7.5 or 10 cm above the moss surface. Measured CO_2 concentrations were within 20% of the target concentration between 93 and 99% of operational time (Miglietta *et al.* 2001). In the winter months the MiniFACE system was turned off because of the low rates of biological activity in this period.

In a parallel experiment, N deposition was increased by adding aqueous dissolved NH_4NO_3 six times per growing season (about every three weeks) as small (2 mm) simulated rain events, with control plots receiving equal quantities of deionized water. Annual N deposition was increased by 3 gN m^{-2} y^{-1} at the FI, SW and CH sites and by 5 gN m^{-2} y^{-1} at the NL site.

Each treatment was replicated five times. The plots were assigned randomly to each of the treatments. The elevated CO_2 plots were located at least 6 m from other plots to prevent cross contamination (Miglietta *et al.* 2001). In order to avoid edge effects, no measurements were taken in the outer 15 cm of each plot. The experiments lasted three growing seasons, starting in spring 1996 until the final harvest at the end of summer 1998. For all sites the final harvest was taken immediately after the peak biomass of vascular plants, but before major senescence and reallocation of nutrients.

Table 2 Average estimated cover (percentage of area) of vascular plants, mosses and hepatics in the control plots (N0) at the four sites during the growing season of the first year of the experiment (1996). + : < 0.5%

	FI	SW	CH	NL
Vascular plants				
Andromeda polifolia	4	3	+	+
Betula pubescens	–	+	–	–
Calluna vulgaris	–	4	+	+
Carex lasiocarpa	+	–	–	–
C. limosa	+	–	–	–
C. nigra	–	–	2	–
C. pauciflora	1	–	–	–
C. rostrata	–	–	1	+
Drosera rotundifolia	1	5	–	1
Empetrum nigrum	–	–	–	+
Erica tetralix	–	–	–	4
Eriophorum angustifolium	–	17	1	2
E. vaginatum	11	3	1	–
Narthecium ossifragum	–	3	–	–
Picea abies	–	1	–	–
Pinus sylvestris	–	1	–	+
Potentilla erecta	–	–	1	–
Rhynchospora alba	–	1	–	+
Scirpus cespitosus	–	+	–	–
Scheuchzeria palustris	1	–	–	–
Vaccinium oxycoccos	4	3	2	4
Mosses/hepatics				
Aulacomnium palustre	–	–	1	+
Calliergon stramineum	–	–	–	+
Odontoschisma sphagni	–	–	–	+
Polytrichum strictum	–	–	54	–
P. commune	–	–	+	–
Sphagnum balticum	60	3	–	–
S. capillifolium	–	–	+	–
S. fallax	–	–	90	+
S. magellanicum	1	86	–	97
S. papillosum	39	6	–	1
S. rubellum	–	2	–	–

Sphagnum growth, vascular plant cover and biomass measurements

For all measurements a detailed protocol was applied that was nearly identical for all sites. *Sphagnum* height increment was measured using four stainless steel wires in each plot anchored in the peat by small brushes (modified from Clymo 1970). The length of the wire extending above the moss surface was measured at the beginning and the end of each growing season. Mass growth was calculated by *Sphagnum* length growth (cm y^{-1}) times the *Sphagnum* dry weight (g cm^{-1} m^{-2}) in the upper 3 cm (including the capitula). These dry weights were measured in 7- or 8-cm diameter samples around each wire at the end of the growing season in 1998. The sampled moss mass was dried at 70° C for at least 48 h and weighed.

At the end of the experimental period, cover by living and dead vascular plant parts was measured in point quadrats (25×37.5 cm, with grid interval 2.5 cm resulting in 150 points). At each point a sharpened knitting needle was lowered into the vegetation to the top of the moss vegetation, and its contact with all species was noted.

Immediately after these cover measurements, aboveground vascular plant biomass was harvested in the same subplot (25×37.5 cm). Plants were clipped off at the moss surface. The litter on top of the moss surface was also collected. Belowground biomass (including roots, rhizomes and buried stems) was measured in three 11-cm diameter samples per plot to a depth of 30 cm. From these peat columns belowground stems, rhizomes and roots were extracted. All plant parts were dried at 70° C for at least 48 h and weighed. Nitrogen concentrations in the living *Sphagnum* were measured in dry, ball-milled samples using an automatic element analyser. Dry weight and organic matter contents were determined in subsamples that were dried at 105° C and ignited at 550° C.

Results

Sphagnum growth

In 1996 and 1997, no significant treatment effects on *Sphagnum* length growth were found in either of the two experiments (using ANOVA with site and treatment as factors). In 1998 the overall CO_2 and $CO_2 \times$ site interaction effects were not significant, but there was a significant positive CO_2 effect at the NL site ($P = 0.048$). In the N experiment there was an overall negative impact of N addition on *Sphagnum* length growth during the last year ($P = 0.005$).

Sphagnum dry weight production in 1998 was calculated by multiplying *Sphagnum* length growth by the measured bulk density per unit of depth. In the CO_2 experiment there were no significant treatment effects on *Sphagnum* mass production (Fig. 1). The CO_2 effect on length growth at the NL site did not result in an increased biomass production. There was a clear CO_2 effect on *Sphagnum* stem morphology, including strongly increased distances between branches at this site. In the N experiment, increased N inputs had a significant overall effect on *Sphagnum* productivity ($P = 0.016$; Fig. 1). At the NL and the CH sites, peat moss production was reduced in the N-addition treatments (NL: $P = 0.011$; CH: $P = 0.002$), but at the SW and the FI sites there were no effects.

In both experiments the N concentrations in the living *Sphagnum* in the control plots at CH and NL were ≈ 30% higher than those at FI and SW ($P < 0.05$; Fig. 2). The

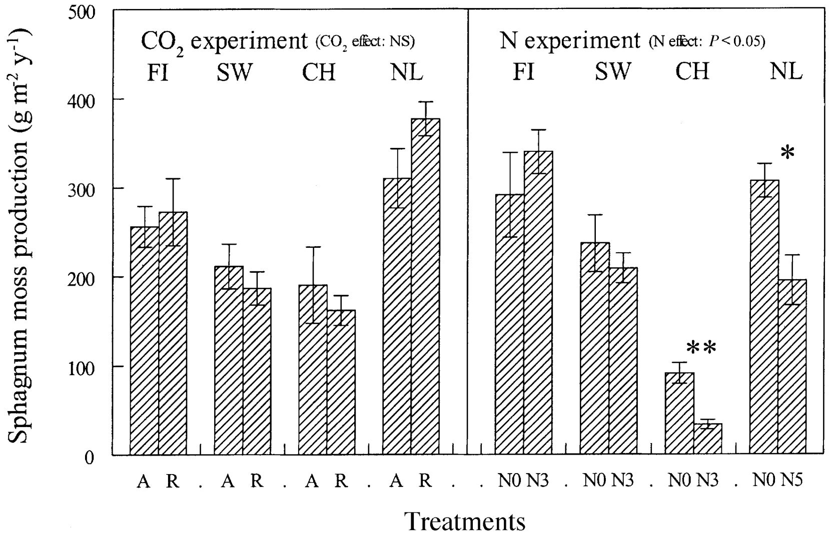

Fig. 1 Mass growth of *Sphagnum* during 1998 in the CO_2 and in the N addition experiment. In the CO_2 experiment *Sphagnum* growth is given at ambient (A, 360 ppmv) and raised (R, 560 ppmv) CO_2 concentrations. In the N experiment *Sphagnum* growth is compared between the control (N0) and the N addition treatments N3 (3 g N m^{-2} y^{-1}) or N5 (5 g N m^{-2} y^{-1}). Bars represent means ± SE. NS, not significant; $*P < 0.05$; $**P < 0.01$.

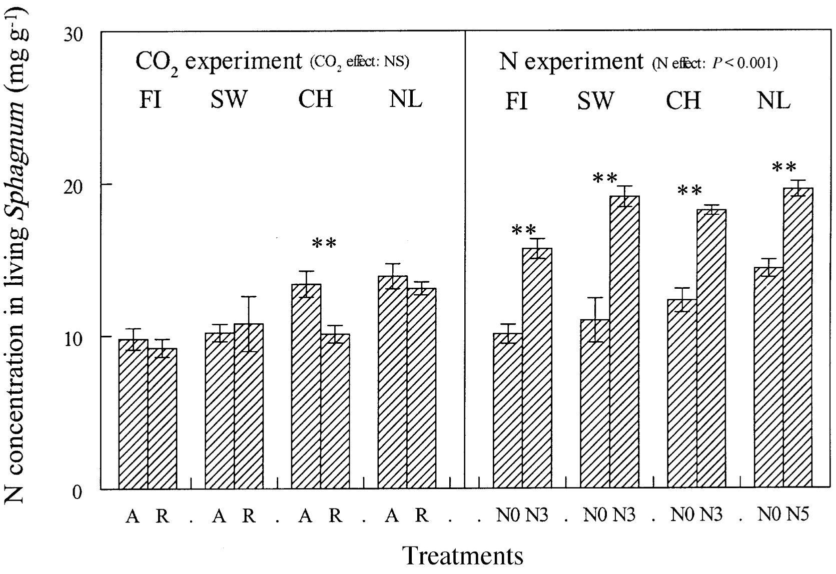

Fig. 2 Nitrogen concentrations in living *Sphagnum* (upper 3 cm) at the end of the summer of 1998 in the CO_2 and in the N addition experiment. A, ambient (360 ppmv); R, raised (560 ppmv) CO_2 concentration. N0, no N addition; N3, 3 g N m^{-2} y^{-1}; N5, 5 g N m^{-2} y^{-1}. Bars represent means ± SE. NS, not significant; $*P < 0.05$; $**P < 0.01$.

elevated CO_2 treatment had no significant overall effect, but per site analysis revealed that this treatment significantly reduced the N concentration in *Sphagnum* at the CH site ($P < 0.001$). N addition resulted in higher N concentrations in living *Sphagnum* at all sites ($P < 0.001$), but they never exceeded 20 mg g^{-1}. Despite the higher N addition at the NL site, there was no difference between the N concentration in the *Sphagnum* material in the N-fertilized plots at NL (19.6 mg g^{-1}) and SW (19.1 mg g^{-1}).

Plant cover

At the CH site an important part of the vegetation consists of patches of the relatively tall moss *Polytrichum strictum* that overtop the neighbouring *Sphagnum* patches. In the CO_2 experiment, there were no significant treatment effects on total vascular plant cover, but in the N experiment a strongly significant positive effect of N addition was found both on vascular plant cover and on vascular plant + *Polytrichum strictum* cover (N: $P < 0.001$; N × site: $P < 0.001$; Fig. 3). The per site increase in overstorey cover resulting from N addition was significant for vascular plants at NL ($P < 0.001$) and for *Polytrichum strictum* at CH ($P < 0.001$). Furthermore, analysis of variance with site as factor and plant cover as covariable showed that *Sphagnum* mass production was affected negatively by overstorey cover (vascular plants + *Polytrichum*

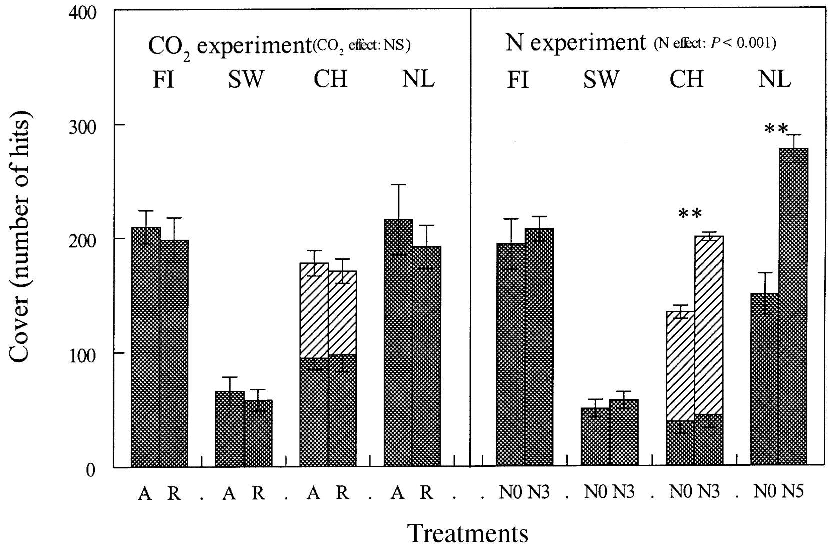

Fig. 3 Cover of vascular plants (black) and *Polytrichum strictum* (hatched) at the end of the growing season of 1998 in the CO_2 and in the N addition experiment. A, ambient (360 ppmv); R, raised (560 ppmv) CO_2 concentration. N0, no N addition; N3, 3 g N m^{-2} y^{-1}; N5, 5 g N m^{-2} y^{-1}. Bars represent means ± SE. NS, not significant; $^{*}P < 0.05$; $^{**}P < 0.01$.

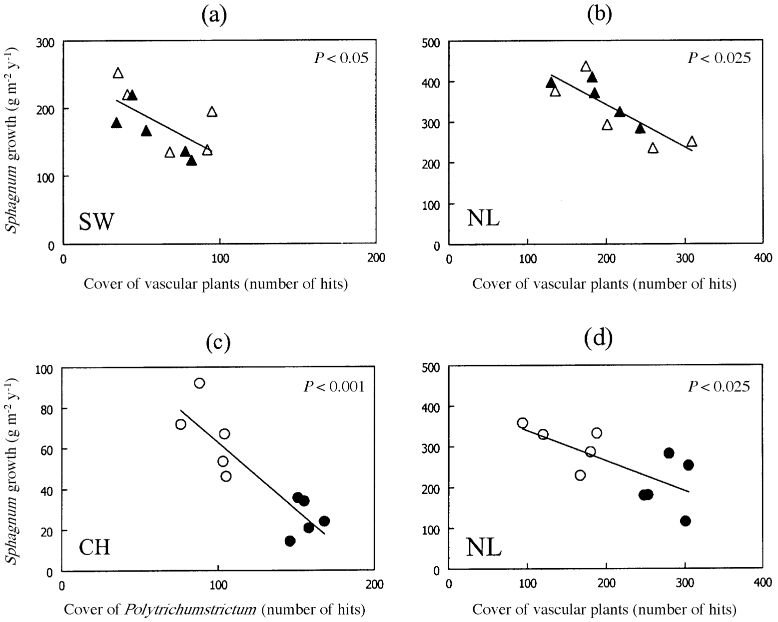

Fig. 4 Relation between *Sphagnum* mass production and vascular plant or *Polytrichum strictum* cover in the CO_2 experiment at the Swedish (a)and the Dutch site (b)and in the N experiment at the Swiss (c)and the Dutch site (d).Levels of significance (two-tailed) are calculated using Pearson's test. The correlations at the other sites were not significant. △, ambient (360 ppmv) CO_2; ▲, raised (560 ppmv) CO_2 concentration; ○, no N addition; ●, 3 g N m^{-2} y^{-1} or 5 g N m^{-2} y^{-1}.

strictum) both in the plots of the CO_2 experiment ($P = 0.004$) and of the N experiment ($P = 0.009$). In the CO_2 experiment (Fig. 4a,b), the negative effects of vascular plant cover were significant at SW ($P = 0.048$) and NL ($P = 0.016$; two-tailed levels of probability using Pearson's test). In the N experiment (Fig. 4c,d), vascular plant cover had negative effects at NL (0.016), and *Polytrichum strictum* cover had negative effects on *Sphagnum* growth at CH ($P < 0.001$). The cover of litter and standing dead material had negative effects in the CO_2 experiment at SW ($P = 0.049$) and in the N experiment at NL ($P = 0.028$).

Vascular plant biomass

There was no significant treatment effect on living aboveground vascular plant biomass in both the CO_2 and the N addition experiments (Fig. 5). However, in the N-addition experiment the amount of standing dead material and litter was consistently higher in the N-addition treatment than in the control plots (Fig. 6; overall N effect: $P = 0.012$). In the CO_2 experiment at the Finnish site, there was a significant negative effect of litter mass on *Sphagnum* growth ($P < 0.001$; two-tailed level of probability using Pearson's test).

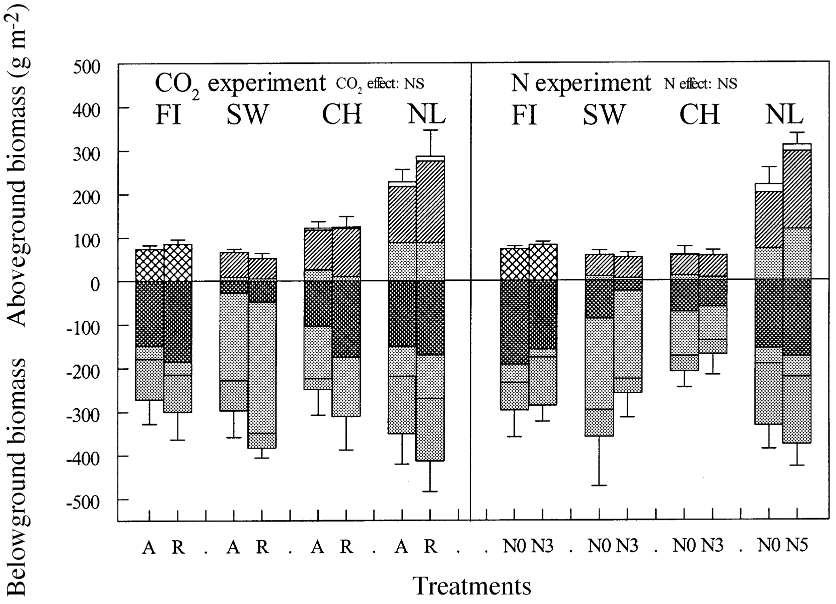

Fig. 5 Aboveground and belowground biomasses at the end of the growing season of 1998 in the CO_2 and in the N addition experiment. Given significance levels refer to aboveground, belowground, and aboveground + belowground biomass; however, in the CO_2 experiment there was a significant positive CO_2 effect on root + rhizome biomass ($P = 0.032$). A, ambient (360 ppmv); R, raised (560 ppmv) CO_2 concentration; N0, no N addition; N3, 3 g N m^{-2} y^{-1}; N5, 5 g N m^{-2} y^{-1}. Aboveground: open, flowers; hatched, leaves; dark grey, stems; cross-hatched, total aboveground biomass (at FI no distinction was made between different above-ground plant parts). Belowground: fine cross-hatched, roots; light grey, rhizomes; dark grey, buried stems. Bars represent means ± SE. NS, not significant.

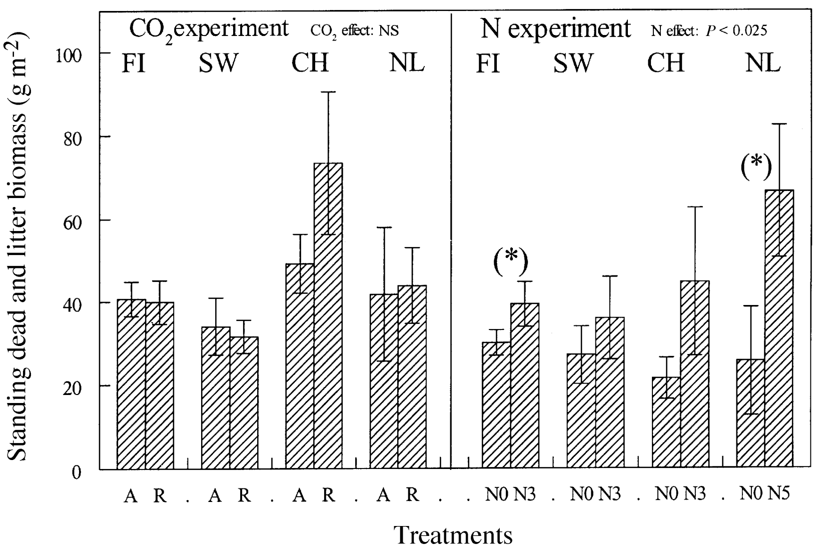

Fig. 6 Litter + standing dead mass at the end of the growing season of 1998 in the CO_2 and in the N addition experiment. A, ambient (360 ppmv); R, raised (560 ppmv) CO_2 concentration. N0, no N addition; N3, 3 g N m^{-2} y^{-1}; N5, 5 g N m^{-2} y^{-1}. Bars represent means ± SE. NS, not significant; (*)$P < 0.1$.

There were no significant N or CO_2 effects on buried stem biomass, but root + rhizome biomass was consistently and significantly higher in the elevated CO_2 treatments than in the controls (Fig. 5; $P = 0.032$). Per site analysis showed only a significant CO_2 effect on root + rhizome mass at SW ($P = 0.04$). In both of the two experiments there were no significant treatment effects on the sum of living above- and belowground biomass.

Discussion

The first hypothesis, that elevated CO_2 would stimulate *Sphagnum* biomass growth, was not confirmed at any of the four sites investigated herein. Although an increased length growth was observed at the NL site, this positive effect was possibly a consequence of CO_2 effects on peat moss morphology. Increased length growth could have important consequences for the dynamics of bog ecosystems, because it may enable *Sphagnum* to overgrow the photosynthesizing parts of low-stature vascular plants (Rydin 1997), such as *Vaccinium oxycoccus* and *Drosera rotundifolia*. It was observed at the NL site that these species had to recover repeatedly after having been overgrown by *Sphagnum*. Here *Drosera* biomass did not increase in the raised CO_2 treatment, while it did increase in all other treatments. Apparently, the increased length growth per unit of mass production at elevated CO_2 increases the competitive vigour of *Sphagnum*, which might affect vascular plant growth over longer periods. Over a long period such an effect might result in an increased sequestration of carbon in the bog ecosystem, because dead *Sphagnum* material decomposes more slowly than the litter of other plants (Coulson & Butterfield 1978; Bartsch & Moore 1985; Verhoeven & Toth 1995). The present data, however, do not provide evidence of such effects at raised atmospheric CO_2 concentrations.

The second hypothesis, that increased N input should depress *Sphagnum* mass growth, is clearly supported by the present data. At two of the four sites (Finland, Sweden) there were no N-treatment effects on *Sphagnum* growth, while at the two other sites (Switzerland, Netherlands) significant negative effects of N addition on peat moss growth were measured. At the two northern sites, nitrogen apparently did not limit the growth of *Sphagnum*. The negative effects of N addition at CH and NL were most likely caused by the increased cover of living and dead parts of other plants that reduced light intensities for *Sphagnum* at the peat surface. This explanation is strongly supported by the negative relationship established herein between the cover of overstorey plants and *Sphagnum* growth, not only in the N experiment, but also in the CO_2 experiment. Other experiments in mire and tundra ecosystems have shown that nutrient additions increase the abundance of vascular plants and reduce the biomass of mosses and lichens (Lütke Twenhöven 1992; Jonasson 1992; Chapin *et al*. 1995; Hogg *et al*. 1995). Hogg *et al*. (1995) showed that removal of aboveground biomass of *Molinia* reduced the negative impact of nutrient addition on *Sphagnum* growth, which strongly supports our conclusions.

At first glance, it seems inconsistent that there were clear N effects on vascular plant cover, but not on aboveground vascular plant biomass. This difference (only observed at the NL site) was caused by the significantly higher biomass of the shallow-rooting *Vaccinium oxycoccus* in the N-fertilized plots; *V. oxycoccus* produces more cover per unit biomass (9.9 hits g^{-1}) than most other species (e.g. *Eriophorum angustifolium*: 3.1 hits g^{-1}). There was a striking positive effect of N addition on litter and standing dead. This observation agrees with the results of studies in heathlands where increased N inputs did not lead to greater amounts of living biomass, but instead to greater quantities of dead material, resulting from increases both in productivity and in biomass turnover (Aerts 1989). Significant negative effects of litter cover on peat moss growth were measured at the sites in Sweden and the Netherlands, and a significant negative effect of litter mass at the site in Finland. These results suggest that the amount of dead material produced by vascular plants can impact upon the dynamics of the bog community.

That the overstorey cover and *Sphagnum* growth responded to N addition at the NL and CH sites, but not at the FI and SW sites, can be explained by the history of elevated anthropogenic N deposition in the Netherlands (NL) and Switzerland (CH). It is suggested that the *Sphagnum* layer accumulates N until this pool is saturated; only after saturation can the additional N reach the roots of vascular plants or rhizoids of *Polytrichum*. The high ambient N deposition probably resulted in N saturation at the CH and NL sites, so that an additional N input caused increased ammonium concentrations in the interstitial water and subsequently increased N uptake and growth of other plants. A distinction is proposed between three different phases of nitrogen pollution in *Sphagnum* bogs: (i) N is still limiting *Sphagnum* growth, so that N addition leads to increased peat moss growth; (ii) N no longer limits *Sphagnum* growth, but the *Sphagnum* layer has not yet reached its maximum organic N content; and (iii) the *Sphagnum* layer has reached its maximum organic N content, so that additional N input will reach the soil solution. Mires where N still limits peat moss growth (phase 1) have been described for the most northern part of Sweden (Aerts *et al*. 1992), where atmospheric N inputs are extremely low (< 0.2 gN m^{-2} y^{-1}). The present study sites in Finland (0.4 gN m^{-2} y^{-1}) and Sweden (0.8 gN m^{-2} y^{-1}) apparently represent phase 2, whereas our high N deposition sites in Switzerland (1.8 gN m^{-2} y^{-1}) and the Netherlands (3.9 gN m^{-2} y^{-1}) unfortunately have reached phase 3. Bogs that have reached phase 3 will probably enter a positive feedback cycle and finally change into grassland or heathland ecosystems.

The changes in species composition in N-saturated bogs, which result from the competitive advantage of vascular plants and other plant groups that are able to overtop *Sphagnum,* may reduce C sequestration because of the higher decomposability of the dead materials of these groups compared to *Sphagnum* (Coulson & Butterfield 1978; Clymo & Hayward 1982; Bartsch & Moore 1985; Verhoeven & Toth 1995). In addition, increased vascular plant abundance may result in higher C emissions as a consequence of methane transport through aerenchymateous root tissues of some vascular plant species (e.g. *Eriophorum angustifolium*) and exudation of substrates for methanogenic bacteria to the rhizosphere (Joabsson *et al*. 1999). Contrary to earlier expectations (Schimel 1995), the present results suggest that C sequestration is not accelerated by elevated N inputs in one of the dominant northern C-sequestering ecosystems. By contrast, changes in species composition resulting from higher N inputs may substantially lower rates of C sequestration in one of the major pools of terrestrial soil carbon.

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