

# Contrasted effects of increased N and CO<sub>2</sub> supply on two keystone species in peatland restoration and implications for global change

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## Summary

**1** Significant areas of temperate bogs have been damaged by peat harvesting but may regenerate. These secondary mires, if well managed, may act as strong C sinks, regulate hydrology and buffer regional climate.

**2** The potential effects of bog regeneration will, however, depend on the successful establishment of the principal peat formers – *Sphagnum* mosses. The influence of hydrology and microclimate on *Sphagnum* re-growth is well studied but effects of elevated CO<sub>2</sub> and N deposition are not known.

**3** We carried out two *in-situ* experiments in a cutover bog during three growing seasons in which we raised either CO<sub>2</sub> (to 560 p.p.m.) or N (by adding NH<sub>4</sub>NO<sub>3</sub>, 3 g m<sup>-2</sup> year<sup>-1</sup>). The two treatments had contrasting effects on competition between the initial coloniser *Polytrichum strictum* (favoured by high N) and the later coloniser *Sphagnum fallax* (favoured by high CO<sub>2</sub>).

**4** Such changes may have important consequences for bog regeneration and hence for carbon sequestration in cutover bogs, with potential feedback on regional hydrological and climatic processes.

*Key-words*: competition among bryophytes, cutover bog regeneration, global change, growth, *Sphagnum*

## Introduction

Although peatlands cover only an estimated 3.8% of the world's ice-free land area (Gorham 1991), they contain about the same amount of C as the atmosphere (IPCC 1990). Growing peatlands represent an important long-term C sink and thus play a key role in the global C cycle, especially in the context of global warming. Their regulating effect on the hydrology may become increasingly valuable with respect to changes in the precipitation regime, increases of

catastrophic flood frequency and limitation of water resources.

The destruction of peatlands contributes directly to global warming through CO<sub>2</sub> emissions from long-term peat deposits. Peatland drainage and cutting in recent centuries may have turned these ecosystems into net carbon sources or at least reduced their overall carbon sink by at least three quarters (Armentano & Menges 1986). The farming of organic soils oxidizes the remaining peat and contributes significantly to national greenhouse gas budgets in Europe (Kasimir-Klemedtsson *et al.* 1997). Regarding its contribution to the global greenhouse effect, peat is therefore similar to fossil fuel (Rodhoe & Svensson 1995). In the temperate and boreal zones the destruction of peatlands affects the hydrology and most likely the climate at a

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regional scale (Bonan *et al.* 1992; Stohlgren *et al.* 1998; Pielke *et al.* 1999) and may even affect global climate (Chase *et al.* 2000; Pielke *et al.* 1998).

Significant bog areas have been exploited for peat, mostly in the temperate zone, and are now either destroyed or slowly regenerating. In recent years, considerable effort has been made towards improving peatland restoration and especially *Sphagnum* re-establishment (Rocheftort 2000). On the one hand, the peat industry has a direct interest in showing that peat extraction may be considered as a sustainable economic activity. On the other hand, countries in which over 90% of their original peatland areas have disappeared due to land reclamation are making tremendous efforts to conserve and restore their remaining peatlands. In those countries the main goal is the conservation of rare ecosystems and species and in some cases also of archives preserved in the peat. Present incentives to reduce greenhouse gas emissions have led politicians, not only to preserve the remaining peatlands, but also to initiate restoration of damaged peatlands (European Commission 2000).

The natural regeneration of cutover bogs is a clear example of the steering effect of species on ecosystem processes. Shifts in species composition cause important modifications in ecosystem functioning when the species differ in their effect on ecosystem processes (Chapin *et al.* 1997). The plant succession observed in regenerating cutover bogs in Central Europe (Grosvernier *et al.* 1995) illustrates this concept very well. The bare peat is first colonized by *Polytrichum strictum* or *Eriophorum vaginatum*. Then *Sphagnum fallax* invades the *Polytrichum* moss carpet or the space between *Eriophorum* tussocks, where microclimatic conditions allow it to grow. Following a period of interspecific competition, *Sphagnum* out-competes the initial coloniser. *Sphagnum* re-establishment increases water storage and peat accumulation in cutover peatlands and turns these ecosystems back into a carbon sink. Furthermore, regenerating peatlands have an ability to regulate the water cycle through aquifer recharge and to increase air moisture (Eggelsmann 1964). These effects would feed back negatively to both the current increase in atmospheric carbon dioxide concentration and to global warming. But potential effects of peatland restoration on climate need to be considered in the context of increased atmospheric CO<sub>2</sub> level and also, at least regionally, of elevated N deposition levels.

The dominant producers of peat in temperate latitudes, the peat mosses (*Sphagnum*), are adapted to extremely low levels of N (Van Breemen 1995), and lose their competitive advantage over vascular plants under increased N deposition (Berendse *et al.* 2001). A potential obstacle for successful peatland restoration may be the high rate of N deposition often occurring in regions where most peatlands have been lost to mining and farming. It is also possible that future concentrations of atmospheric CO<sub>2</sub> may influence the

interaction between peat mosses and other species during restoration.

We hypothesized that atmospheric CO<sub>2</sub> enrichment and nitrogen addition would influence bog regeneration at our study site by affecting the competition between two moss species, *Sphagnum fallax* (Klinggr.) Klinggr. and *Polytrichum strictum* Menzies ex Bridel. Elevated CO<sub>2</sub> often causes N dilution in plant tissues because the CO<sub>2</sub>-induced increase in photosynthesis causes an accumulation of non-structural carbohydrates (Van der Heijden *et al.* 2000b). In order to compensate for this imbalance, plants increase their uptake of N, which decreases the N content in the soil. Such an effect, if also observed within the moss carpet – as suggested by Van der Heijden *et al.* (2000b), would affect *Sphagnum* less than *Polytrichum* because of the tolerance of *Sphagnum* to low nutrient conditions (Van Breemen 1995). Conversely, N addition is likely to affect *Sphagnum* more than *Polytrichum* because N addition often has a negative effect on ombrotrophic *Sphagnum* species (Press *et al.* 1986; Thormann & Bayley 1997; Gunnarsson & Rydin 2000). To test these hypotheses, we set up two parallel experiments in a cutover bog in the Swiss Jura mountains to determine how an increase in atmospheric CO<sub>2</sub> concentration and a higher rate of N deposition may affect the success of peatland restoration and hence the possible feedback on climate forcing and carbon sequestration. We think that this is the first experimental study of the effects of elevated CO<sub>2</sub> and N deposition on the regeneration of cutover bogs.

## Methods

The experimental site was a cutover bog in the Jura Mountains of Switzerland (La Chaux-des-Breuleux; 47°13' N, 7°03' E) at an altitude of 1000 m a.s.l. The mire was drained and peat was mined until the 1940s. The vegetation succession at the site was a typical example of facilitation, where a keystone species (such as the moss *Polytrichum strictum* or the sedge *Eriophorum vaginatum*, or both) created favourable microenvironmental conditions allowing *Sphagnum fallax* to re-establish in cutover ombrotrophic bogs (Buttler *et al.* 1998). In the later stages of a successful restoration, *Sphagnum* will out-compete the initial coloniser and the succession will lead to a typical bog vegetation (Grosvernier *et al.* 1995). The vegetation at the site was a mosaic of lawns and drainage ditches. The lawns, in which the experimental plots were set up, were dominated by *Sphagnum fallax* and *Polytrichum strictum*. Other mosses included *Aulacomnium palustre*, *Polytrichum commune* and *Pleurozium schreberi*. The dominant vascular plants in the studied plots were *Eriophorum vaginatum*, *Carex nigra*, *Vaccinium oxycoccus* and *Eriophorum angustifolium* (2.7, 2.9, 1.3 and 0.9% cover on average, respectively). *Andromeda polifolia* and *Calluna vulgaris* each covered only 0.2% of the surface. Approximately 30 cm of new peat had

accumulated over the old cutover peat surfaces. The ditches were colonized by *Carex rostrata*, *Eriophorum angustifolium*, *Potentilla palustris* and *Sphagnum fallax*.

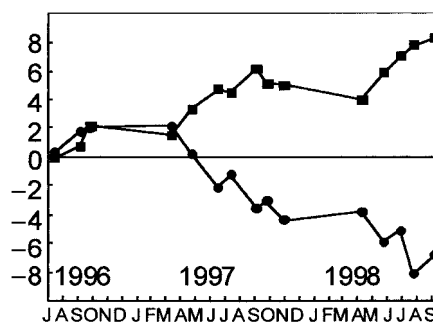
We set up two parallel experiments to determine how an increase in atmospheric CO<sub>2</sub> concentration and higher N deposition rates in cutover bogs may affect the success of peatland restoration and hence the possible feedback on climate forcing and carbon sequestration. (i) We raised atmospheric CO<sub>2</sub> concentrations to 560 p.p.m. during the growing period (March to October) in five 1-m diameter plots using mini-FACE rings (small Free Air CO<sub>2</sub> enrichment systems) (Miglietta *et al.* 2001). The control plots were ventilated with ambient air (360 p.p.m.). Each mini-FACE ring had 72 venting tubes, supplying either ambient or CO<sub>2</sub>-enriched air. The tubes were 18 cm tall and had two holes, at 6 and 12 cm above the moss surface. Blowers located next to the mini-FACE rings supplied ambient air to the rings. The CO<sub>2</sub> supply was adjusted automatically on the basis of wind speed and CO<sub>2</sub> concentrations in the centre of each plot at 7.5 cm above the moss surface (canopy level) that were continuously measured with an infrared gas analyser. To avoid CO<sub>2</sub> contamination, the elevated CO<sub>2</sub> rings were located at least 3.5 m from the nearest ambient CO<sub>2</sub> ring. Measured CO<sub>2</sub> concentrations were within 20% of the target concentration between 93 and 99% of the operational time (Miglietta *et al.* 2001). In the winter months the mini-FACE system was turned off because of the low rates of biological activity in this period. (ii) We fertilized a second set of plots with a NH<sub>4</sub>NO<sub>3</sub> solution sprinkled over the vegetation as simulated rain in six applications per year during the growing season (equivalent to 2 mm precipitation per application), corresponding to an increased annual N deposition of 3 g m<sup>-2</sup> year<sup>-1</sup>. We watered the control plots with equal amounts of deionized water. The background N deposition in the Swiss Jura Mountains is estimated at 1.5 g m<sup>-2</sup> year<sup>-1</sup> (NABEL 1995). All treatments were replicated five times and the experiment lasted from June 1996 to August 1998.

We measured the moss length increment using a modified cranked wire method (Clymo 1970). We inserted miniature bottle brushes into the moss carpet at the beginning of the experiment. We then determined at regular intervals during the growing seasons the length increment by measuring the length of the wire emerging above the mosses. Four wires were inserted into each plot. The height differences represent the vertical distance from the tip of *Polytrichum* growing above the *Sphagnum* to the capitula of *Sphagnum*. Through repeated measurements during the course of the experiment we followed the growth of the mosses and the changes in height differences. We determined percentage cover using the point frame method (Buttler 1992). The quadrats measured 25 by 37.5 cm with a grid interval of 2.5 cm resulting in 150 sampling points. There was one quadrat per plot. Total cover was higher than 100% because *Polytrichum* overtops

*Sphagnum*. We measured the density and biomass of both moss species on material collected at the final harvest. A 7-cm diameter, and 15-cm long core was taken around each bottle brush (i.e. four samples per plot). The cores were then cut into slices as follows. The 0 level was defined for both *Sphagnum* and *Polytrichum* as the top of *Sphagnum* capitula. (i) We first cut the top centimetre of the *Sphagnum* mosses together with any other plants (0–1 cm sections). Since *Polytrichum* mosses grew taller than *Sphagnum*, this section represented one centimetre for *Sphagnum*, but more (1.1–6.6 cm) for *Polytrichum*. (ii) We cut each core 2 cm lower (1–3 cm sections). Individual plant biomass measurements represent averages over 10 plants for each core. We calculated *Sphagnum* and *Polytrichum* production over the three growing seasons by multiplying the total length increment by the average biomass per unit length in the top three centimetres (0–1 + 1–3 cm sections). Percentage CO<sub>2</sub> and N effects are the percentage difference between treatment and controls. We compared values using an ANOVA (nested model with treatment and plot).

## Results

Increased CO<sub>2</sub> and N had contrasted effects on *Polytrichum* and *Sphagnum*. Over three growing seasons, elevated CO<sub>2</sub> reduced the growth in length of both *Polytrichum* and *Sphagnum* as compared to the control, but this effect was less pronounced for *Sphagnum*. This difference caused a 28% reduction of the height difference between the usually overgrowing *Polytrichum* and the *Sphagnum* mosses under elevated CO<sub>2</sub> (Fig. 1). Density, cover and total plant biomass were unaffected. The biomass per unit length and per plant of the upper part of *Polytrichum* was increased by 26%. Both *Sphagnum* and *Polytrichum* production decreased, but this effect was not significant (Table 1, Fig. 1).



**Fig. 1** Effect of increased CO<sub>2</sub> (circles) and N (squares) supply on the average height difference from the tip of overgrowing *Polytrichum strictum* to the capitulum of *Sphagnum fallax* ( $\Delta h$ , mm). The values represent the differences between the treatment and control in each experiment: CO<sub>2</sub> effect =  $\Delta h_{\text{elevated CO}_2} - \Delta h_{\text{ambient CO}_2}$ ; N effect =  $\Delta h_{\text{fertilized}} - \Delta h_{\text{ambient N}}$ . Positive values indicate an increase in height difference (i.e. *Polytrichum* growing more in length than *Sphagnum*). Negative values indicate a decrease in height difference (i.e. *Sphagnum* catching up on *Polytrichum*).

**Table 1** Effect of three years of increased CO<sub>2</sub> and N on *Sphagnum fallax* and *Polytrichum strictum* in La Chaux-des-Breuleux cutover bog in the Swiss Jura Mountains

	Elevated CO <sub>2</sub>	Ambient CO <sub>2</sub>	Percent CO <sub>2</sub> effect	P-value	Elevated N	Ambient N	Percent N effect	P-value
Length increment (mm) 1996–98								
<i>Sphagnum fallax</i>	53	66	–19	0.082	41	43	–3	0.818
<i>Polytrichum strictum</i>	54	74	–27	0.005	51	43	17	0.217
Final height difference (Δh, mm)								
<i>Polytrichum–Sphagnum</i>	21	29	–28	0.008	25	18	42	< 0.001
Density (number × 1000 m <sup>–2</sup> )								
<i>S. fallax</i>	37	34	8	0.383	28	38	–25	0.003
<i>P. strictum</i> living	44	44	1	0.957	88	48	83	< 0.001
Percentage cover (point intercept)								
<i>S. fallax</i>	78	83	–6	0.473	65	86	–24	0.039
<i>P. strictum</i>	45	52	–15	0.367	89	61	46	< 0.001
Biomass per plant (mg)								
<i>S. fallax</i> (0 to –3 cm)*	10.8	10.2	6	0.487	8.5	10.2	–17	0.019
<i>P. strictum</i> (top to –3 cm)*	10.6	10.1	5	0.382	9.0	9.3	–3	0.570
Biomass per unit length (mg mm <sup>–1</sup> )								
<i>S. fallax</i> (–1 to –3 cm)*	0.19	0.18	7	0.522	0.16	0.18	–12	0.205
<i>P. strictum</i> alive (top to –1 cm)*	0.18	0.14	26	0.046	0.16	0.16	0	0.948
<i>P. strictum</i> all (–1 to –3 cm)*	0.23	0.21	6	0.369	0.17	0.23	–25	< 0.001
Production (g m <sup>–2</sup> ) 1996–98								
<i>S. fallax</i>	604	702	–14	0.255	279	539	–48	< 0.001
<i>P. strictum</i>	525	629	–17	0.193	931	535	74	0.001

\*0 is defined as the top of the *Sphagnum* capitula.

N addition increased the height difference between the two species by 42%. N addition had a negative effect on *Sphagnum* density (number of shoots per surface unit as determined from the analyses of the cores; –25%) and cover (as estimated by point-frame measurements; –24%) and a strong positive effect on *Polytrichum* density (+83%) and cover (+46%). The negative effect on *Sphagnum* density and cover was a combination of reduced biomass per plant and dying out of some of the plants in the high N plots. The biomass per unit length and per plant of the upper part of *Polytrichum* was not affected, but the biomass per unit length and per plant of the lower section decreased by 25%. This is explained by a strong increase in the number of fine new shoots, which are initiated below the surface of the moss carpet. This effect also explains the difference between the effect of N addition on *Polytrichum* density and cover. *Sphagnum* production was reduced by 48% and *Polytrichum* production increased by 74% (Table 1, Fig. 1).

## Discussion

Elevated CO<sub>2</sub> was shown to have some positive effects on *Sphagnum* growth both in the laboratory (*S. angustifolium* and *S. warnstorffii*; Jauhiainen *et al.* 1998; *S. fallax*: Van der Heijden *et al.* 2000a), and in the field (*S. magellanicum*: Heijmans *et al.* 2001), although species-specific responses have been found (Berendse *et al.* 2001). However, the potential effects of CO<sub>2</sub> enrichment on *Polytrichum* were unknown. Although elevated CO<sub>2</sub>

reduced the length growth of *Sphagnum fallax*, our results suggest it may still have a positive effect on bog regeneration at our site because *Polytrichum strictum* was more affected. This paradox illustrates the difference between observations made on a single species and those on multispecies. Indeed had we focused only on the functionally most important species (*Sphagnum*) we would have reached the opposite conclusion. Despite the paradox, we believe our results are clear enough to suggest a positive effect of elevated CO<sub>2</sub> on bog regeneration, at least with the combination of *Sphagnum fallax* and *Polytrichum strictum* and under the climatic and ecological conditions of the studied site, which we believe are representative for many natural regeneration patterns in Central European cutover bogs. By contrast, the effect of N addition on the competition between *Sphagnum* and *Polytrichum* presents no paradox and is straightforward. Our results support those of previous experiments showing a negative effect of N addition on *Sphagnum* growth (Press *et al.* 1986; Gunnarsson & Rydin 2000; Heijmans *et al.* 2001). However N effect on *Sphagnum* was also shown to be species-specific. Jauhiainen *et al.* (1998) observed a negative effect of N addition on the growth of *S. warnstorffii*, but no effect on *S. angustifolium*. Van der Heijden *et al.* (2000a) observed a positive effect of N addition on the growth of *S. papillosum* and no effect on *S. balticum*.

Our results suggest that elevated CO<sub>2</sub> may have some positive effects on bog regeneration processes through a positive influence on *Sphagnum* re-growth. This would feed back negatively to climate warming through

(i) higher rates of C sequestration in secondary bogs, and (ii) increased water storage and evaporation. Counteracting this, raised N depositions will prevent the mechanisms by which *Sphagnum* attains dominance in these ecosystems, and thus may strongly diminish the potential effects of bog regeneration on climate.

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