

Effects of nutrient addition on vegetation and carbon cycling in an ombrotrophic bog

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Abstract

We measured net ecosystem CO₂ exchange (NEE), plant biomass and growth, species composition, peat microclimate, and litter decomposition in a fertilization experiment at Mer Bleue Bog, Ottawa, Ontario. The bog is located in the zone with the highest atmospheric nitrogen deposition for Canada, estimated at 0.8–1.2 g N m⁻² yr⁻¹ (wet deposition as NH₄ and NO₃). To establish the effect of nutrient addition on this ecosystem, we fertilized the bog with six treatments involving the application of 1.6–6 g N m⁻² yr⁻¹ (as NH₄NO₃), with and without P and K, in triplicate 3 m × 3 m plots. The initial 5–6 years have shown a loss of first *Sphagnum*, then *Polytrichum* mosses, and an increase in vascular plant biomass and leaf area index. Analyses of NEE, measured *in situ* with climate-controlled chambers, indicate that contrary to expectations, the treatments with the highest levels of nutrient addition showed lower rates of maximum NEE and gross photosynthesis, but little change in ecosystem respiration after 5 years. Although shrub biomass and leaf area increased in the high nutrient plots, loss of moss photosynthesis owing to nutrient toxicity, increased vascular plant shading and greater litter accumulation contributed to the lower levels of CO₂ uptake. Our study highlights the importance of long-term experiments as we did not observe lower NEE until the fifth year of the experiment. However, this may be a transient response as the treatment plots continue to change. Higher levels of nutrients may cause changes in plant composition and productivity and decrease the ability of peatlands to sequester CO₂ from the atmosphere.

Keywords: bog, carbon cycling, net ecosystem CO₂ exchange, nitrogen deposition, nutrients, peatland, plant biomass, *Polytrichum* moss, *Sphagnum* moss

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Introduction

The increase in atmospheric nitrogen (N) deposition is of major concern in northern ecosystems, which are typically nutrient-limited with slow rates of decomposition and N mineralization (Bobbink *et al.*, 1998). N deposition has been hypothesized to increase the carbon dioxide (CO₂) sink potential of ecosystems by stimulating plant productivity (Walker & Steffen, 1997). Some studies have suggested that N deposition may account for a significant portion of the missing CO₂ sink in the northern hemisphere carbon (C) budget (Schimel *et al.*, 2001). Alternatively, recent evidence

suggests higher rates of peat decomposition with atmospheric N deposition (Bragazza *et al.*, 2006). With increasing temperatures, particularly at high latitudes, it is important to understand the contribution of N deposition to net CO₂ exchange and C cycling in order to quantify the ecosystem feedbacks to global climate change.

Peatlands store approximately one-third of the global soil C pool (Gorham, 1991), but have low rates of plant production and decomposition owing to nutrient limitation, and cold, waterlogged soils (Clymo, 1984; Frohling *et al.*, 1998). Vegetation structure, however, strongly influences the C sink capacity of peatlands (Belyea & Malmer, 2004). In Europe, where N deposition ranges from 0.2 to 4 g N m⁻² yr⁻¹ (Berendse *et al.*, 2001), peatland and tundra studies have reported changes in plant

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species composition in response to high N deposition. These studies have also documented increases in vascular plant biomass, and decreases in moss abundance (Berendse *et al.*, 2001; Graglia *et al.*, 2001; Van Wijk *et al.*, 2003), particularly the genus *Sphagnum*. This unique moss is a critical plant functional type in bogs with its ability to absorb and retain moisture and nutrients from the atmosphere, and to retard vascular plant growth and to slow peat decomposition leading to C sequestration (Clymo & Hayward, 1982; van Breemen, 1995; Verhoeven & Liefveld, 1997; Williams *et al.*, 1999; Malmer *et al.*, 2003).

The mechanisms for these plant species and community shifts include an inability of *Sphagnum* to retain the additional N, thereby allowing vascular plants access to these nutrients through mineralization in shallow-rooted peats (Malmer *et al.*, 2003), as well as through regeneration by rotifers (Bledzki & Ellison, 2002). As *Sphagnum* mosses depend on airborne sources of nutrients in raised bogs, they are particularly sensitive to atmospheric deposition (Malmer & Wallén, 2005). Low levels of N stimulate *Sphagnum* growth, but at high levels *Sphagnum* can no longer retain added N, losing its filtering ability (Lamers *et al.*, 2000; Berendse *et al.*, 2001; Nordbakken *et al.*, 2003). Once vascular plants have access to the excess N, *Sphagnum* growth and biomass are further reduced by shading from increased vascular plant biomass and litter accumulation (Hayward & Clymo, 1983; Heijmans *et al.*, 2001; Limpens *et al.*, 2003a). Finally, P availability affects the impact of N deposition on both vascular plants and mosses (Aerts *et al.*, 1999; Bragazza *et al.*, 2004; Limpens *et al.*, 2004). The type of nutrient limitation as assessed by N:P, N:K and K:P ratios affects species composition and diversity, as well as productivity in a wide range of wetlands (Bedford *et al.*, 1999; Gusewell & Bollens, 2003; Venterink *et al.*, 2003).

In North America, atmospheric N deposition ranges from 0.2 to 1.2 g N m⁻² yr⁻¹, much lower than in Europe. In a study of boreal peatlands from Ontario to the Maritimes in Canada, Turunen *et al.* (2004) reported a positive correlation between wet N deposition (ranging from 0.3 to 0.8 g N m⁻² yr⁻¹) and C accumulation using peat cores from a range of ombrotrophic bogs. However, it is not clear whether this pattern would continue under higher N deposition levels in light of European observations (e.g. Lamers *et al.*, 2000) and North American experiments (Thormann & Bayley, 1997; Vitt *et al.*, 2003). Our study site Mer Bleue Bog in eastern Ontario is in the zone of highest atmospheric wet N deposition for Canada (0.8–1.2 g N m⁻² yr⁻¹). Most of the peatlands in Canada occur in the boreal/subarctic zone and have been long-term sinks of C since deglaciation because of their cold, waterlogged soils with slow decomposition.

But with a warmer and perhaps drier climate, without the effect of N deposition, bog communities are likely to shift (Weltzin *et al.*, 2001, 2003) and could become weaker C sinks or even C sources (Shurpali *et al.*, 1995; Moore *et al.*, 1998).

Although much research has been conducted on responses of plant communities to N deposition in Europe, and studies have speculated on the implications for the C balance (Williams & Silcock, 1997; Berendse *et al.*, 2001; Heijmans *et al.*, 2001; Malmer & Wallén, 2005), there has been very little research on the changes in net ecosystem CO₂ exchange (NEE) in response to N deposition. Saarnio *et al.* (2003) reported only minor changes in NEE with N addition in a Finnish peatland; however, that study lasted only 3 years. With increasing N deposition, the questions are how will changes in atmospheric N affect the ability of peatlands to sequester carbon and what are the feedbacks to climate?

To address some of these issues, we established a 6-year fertilization experiment at the Mer Bleue Bog in eastern Ontario. In addition to a control treatment, we established triplicates of five treatments using summer additions of N, as NH₄NO₃, with/without P and K. The range of N additions are from five times the current summer ambient atmospheric deposition at Mer Bleue to those experienced in the regions of high N deposition in Europe. We initially set out to test four hypotheses arising from our understanding of this bog system. We predicted the following responses to nutrient addition: (1) increases in gross photosynthesis and NEE, with smaller increases in ecosystem respiration (ER) resulting in a stronger net sink of CO₂; (2) a positive response in vascular plants (dominantly shrubs), with increased cover, biomass and leaf area index (LAI); (3) a decrease in moss growth and cover, through either the direct effects of the fertilizer additions or the indirect effects of the changes in shrub cover; and (4) faster litter decomposition of the major plant species.

Materials and methods

Study site

The Mer Bleue peatland is primarily a large ombrotrophic bog located in the Ottawa River Valley, 10 km east of Ottawa, Ontario, Canada (45.40°N latitude, 75.50°W longitude). Mean annual temperature is 6.0 °C ranging from -10.8 °C in January to 20.9 °C in July. Mean annual precipitation is 944 mm, 342 mm of which falls from May to August (Environment Canada; 1971–2000 climate normals). Peat began to form approximately 8500 years ago and the peat depth now

ranges from 2 m at the edge to >5 m in the center near the fertilization area (Roulet *et al.*, 2007).

Plant communities are dominated by the ericaceous shrubs *Chamaedaphne calyculata* (L.) Moench, *Ledum groenlandicum* Oeder and *Kalmia angustifolia* L. Clusters of the deciduous shrub *Vaccinium myrtilloides* Michx. and the tufted sedge *Eriophorum vaginatum* L. are also fairly common. Sparsely scattered tree species include *Larix laricina* (Duroi) K. Koch., *Betula populifolia* Marshall and *Picea mariana* (Miller) BSP. Total above-ground biomass ranges from 147 to 1011 g m⁻² across the bog, with shrubs contributing between 42% and 72% of the total. The ground layer is dominated by mosses, mainly *S. magellanicum* Brid., *S. capillifolium* (Ehrh.) Hedw. and *Polytrichum strictum* Brid. (Bubier *et al.*, 2006).

The record of CO₂ exchange from an eddy covariance tower near the fertilization area shows annual sums that can be either positive or negative, with extreme inter-annual and seasonal variability. The modern C accumulation (which includes DOC, CH₄ as well as NEE) is similar to the long-term average rate of 20 g C m⁻² yr⁻¹ (Roulet *et al.*, 2007). NEE is the most variable component of the C budget and in many years the C balance is close to zero or negative. Therefore, slight changes in environmental conditions can switch the bog from a net C sink to a source.

Experimental design

We established triplicate 3 m × 3 m plots in areas of homogenous hummock vegetation for each of six treatments, following a stratified random design to avoid hollows within the plots. The 10NPK and 20NPK treatments were started 1 year later, after abandoning this treatment on smaller plots due to disturbance, and these treatments were aligned adjacent to each other to minimize contamination. Treatments were made by adding nutrients dissolved in the equivalent of 2 mm of water seven times from early May to early September, effectively the growing season. The treatments were:

Control, distilled water; 5N – five times the ambient summer N deposition, or 1.6 g N m⁻² yr⁻¹; PK, 5.0 g P m⁻², 6.3 g K m⁻² yr⁻¹; 5NPK, N as above plus PK; 10NPK, 10 times the ambient summer N deposition, or 3.2 g N m⁻² yr⁻¹ plus PK as above; 20NPK, 20 times the ambient summer N deposition, or 6.4 g N m⁻² yr⁻¹ plus PK as above.

N was added as NH₄NO₃ and P and K as KH₂PO₄. Applications were made from 2000 to 2005; the 10NPK and 20NPK applications started in 2001 and, thus, lag by 1 year. Treatment plots were separated by at least a 1 m buffer zone. We measured gas exchanges,

plant biomass and species composition in a 0.6 m × 0.6 m collar located in the center of the 3 m × 3 m plots. Moss growth, LAI, litter accumulation, bulk density, and litter decomposition were measured in the remainder of the plot.

Net ecosystem CO₂ exchange

We measured NEE, photosynthetically active radiation (PAR), relative humidity (RH) and chamber temperature with a LI-COR 6200 (LI-COR, Lincoln, NE) portable photosynthesis system, which includes a LI-6250 infrared gas analyzer, thermistor, hygrometer, quantum sensor and data logger. Whole ecosystem measurements were made with clear, climate-controlled chambers, as described in Bubier *et al.* (2003). The chamber walls were constructed of clear lexan with a removable top to allow equilibration of plant communities to ambient conditions between sampling runs. The climate-control system consisted of a heat exchanger and a cooler to store cold water, which was pumped to and from the exchanger through hoses. Air was circulated by fans inside the chamber as required to maintain steady temperatures (±1 °C) relative to outside air temperature and to reduce changes in relative humidity in the chamber. Although the LI-COR 6200 system tends to underestimate NEE due to vapor pressure effects (Hooper *et al.*, 2002), the system used in this study minimizes these effects with the climate-control component.

Chamber dimensions were 0.6 m × 0.6 m at the base and 0.45 m in height, which enclosed all the vegetation at each plot. Aluminum collars (0.6 m × 0.6 m) with a groove for chamber placement were installed in the center of each 3 m × 3 m plot in 1999 and 2000, to allow 1 year for recovery of any damaged roots and disturbance caused by collar insertion, before gas exchanges were measured. The collar (0.2 m depth) was inserted by pre-cutting the peat so that the top was level with the moss surface and did not disrupt the flow of water. Collars were accessible from moveable ladders to avoid disturbance while making chamber measurements. An opaque shroud was placed over the chamber to eliminate all light for measuring dark ER (autotrophic and heterotrophic combined). Change in headspace CO₂ concentration was measured every 5 s and averaged every 30 s for 2.5 min. Two sampling runs at full light (PAR > 1000 μmol photons m⁻² s⁻¹) and dark conditions were conducted at each collar location every 7–14 days from May to August in 2000, 2001, 2003 and 2005. We measured air and peat temperature at 5 and 10 cm below the peat surface with a Reotemp digital thermometer at the same time as the NEE sampling runs. We also measured the level of the water table in PVC tubes installed at each plot.

Vegetation sampling

Plant species composition was recorded in each 0.6 m × 0.6 m collar during July and August of each year from 2000 to 2005 by visually estimating percent cover of vascular plant and bryophyte species. Nomenclature follows Anderson *et al.* (1990) for true mosses, Anderson (1990) for *Sphagnum* moss species, and Fernald (1950) for vascular plant species. In addition, we measured presence/absence of each moss species by subdividing the larger plots into 36 subplots. A combined measure of percent cover and frequency for *Sphagnum* and *Polytrichum* mosses was determined by multiplying the frequency data from the 36 subplots by the percent cover in the larger collar.

As an estimate of biomass, we measured the density and height of all vascular plant stems within each NEE collar. We also clipped three random stems outside the collar, but within each larger plot, from each of the three major shrub species (*C. calyculata*, *L. groenlandicum* and *V. myrtilloides*, 27 stems/treatment), dried and weighed them at 80 °C. We measured LAI of vascular plants at each plot in August 2005 with nine replicate measurements per plot with a LI-2000 (LI-COR). We also collected vascular plant leaf litter samples in triplicate 10 cm × 10 cm quadrats within each 3 m × 3 m plot during August 2005. These litter samples were dried at 80 °C and weighed. We measured growth of *Sphagnum* and *Polytrichum* mosses each year with a cranked wire technique (Clymo, 1970), as the difference in height of 10 stems/plot (30/treatment) between the spring (early May) to fall (late September). We also measured moss growth in a hummock outside the experimental area for comparison.

Decomposition

We measured decomposition of leaves of *C. calyculata*, the dominant evergreen shrub, and stems of *S. capillifolium*, the dominant moss. We collected senesced tissues in the fall, air-dried and placed them in litter bags in the field in triplicate samples per plot in 2000 at the beginning of the experiment. A subsample of each litter type was oven-dried to determine the air-dry to oven-dry conversion. Litter bags were made of fiberglass mosquito netting, mesh size 1.5 mm × 2 mm and placed on the peat surface for *Chamaedaphne* leaves and 5 cm beneath the surface for *Sphagnum* stems, the position in which they would start decomposing. Bags were retrieved after 5 years, oven dried at 70 °C and mass remaining calculated.

We also measured bulk density and volumetric soil water content in duplicate 10 cm × 10 cm × 10 cm samples collected within each plot in August, 2005. The

Sphagnum capitulum, *Polytrichum* stems and leaf litter were removed, the sample weighed fresh and then oven dried at 70 °C to calculate volumetric water content and bulk density.

Data analyses

Gas flux calculations were performed on the CO₂ concentration data collected during each 2.5 min run. On several occasions, we used a shorter measurement period (usually 1.5 min) for the flux calculation if the rate began to change during the sampling run. This situation occurred under full light conditions when plants may have been stressed due to particularly warm weather with high relative humidity. As the maximum observed value of PAR was usually 2000 μmol photon m⁻² s⁻¹ in mid-summer and maximum photosynthesis for most plants occurs at PAR > 1000 μmol photon m⁻² s⁻¹, maximum NEE (NEE_{max}) and maximum gross photosynthesis (PSN_{max}) were calculated for PAR ranging from 1000 to 2000 μmol photon m⁻² s⁻¹. We adopted the sign convention of CO₂ uptake by the ecosystem as positive and CO₂ loss to the atmosphere as negative. The dark chambers measured ER, the total of enclosed plants, roots, and soil microbes. As light and dark measurements were made within a few minutes of each other, the difference between NEE at full light and NEE with a dark chamber (ER) was considered to represent the gross photosynthesis at that light level for the vegetation within the chamber.

One-way analysis of variance [ANOVA and Tukey's honestly significant different (HSD) post hoc test for multiple comparisons among means] was used to test for significant differences ($P < 0.05$) among treatments for the first (2000) and latest (2005) year of the experiment (using statistical software S-PLUS 6.0, Insightful Corp., 2001). Repeated measures ANOVA (RM ANOVA) with nutrient addition (Treatments – Control, 5N, PK, 5NPK, 10NPK, 20NPK), temperature at 10 cm below the peat surface ($T_{10\text{cm}}$) and the level of the water table (WT) were performed to find the main and interactive effects for years 2001, 2003 and 2005. As two new treatments were added in 2001, we did not include 2000 in the multi-year analysis. However, one-way ANOVA of the 2000 data showed no significant differences in CO₂ exchange among treatments. Temperature and water table were treated as covariates, while testing for the differences between treatments and within years in repeated measures. RM ANOVA was performed with SPSS 12.0 (SPSS Inc., 2003) using the generalized linear model, repeated measures ANOVA procedure and the type III sum of squares. The design of the experiment and the low degree of freedom (df) due to small sample size (three seasonal means per treatment) does not

permit all the possible interactions with covariates. For NEE_{max} , PSN_{max} and ER data, all measurements of individual collars can not be used for the test with RM ANOVA unbalanced model type IV (to avoid the low df) because of temporal autocorrelation and high residual error (A. Ellison, pers. comm.). Analyses were provided according to methods and assumptions (especially regarding the normal distribution, sphericity and circularity of the data) described by Zar (1999), Motulsky (1995), von Ende (2001) and Gotelli & Ellison (2004). All data were $\ln(x + 1)$ transformed before statistical analyses to stabilize and normalize variance, and analyzed using the Kolmogorov–Smirnov goodness-of-fit test, which is especially useful with small samples (Sokal & Rohlf, 1995) without correction (see discussion in Zar, 1999).

Results

Net ecosystem CO₂ exchange

During the 5–6 years of the experiment, NEE_{max} , PSN_{max} and ER responded to treatment and natural variations in water table and temperature (Fig. 1). Fertilization treatment had a stronger influence than interannual variability on CO₂ exchange, but there was a strong interaction ($P < 0.10$) between treatment and year for NEE_{max} and PSN_{max} in the RM ANOVA (Table 1). This indicates that the treatments had different temporal trajectories over the 5-year period. No inherent variability was apparent in the treatments based on local patterns of wetness or temperature as shown by lack of significant variability and additive or interactive effects with years and $T_{10\text{cm}}$ or WT. The residual error (unexplained variability) was also very low (mean square = 0.003, 0.03 and 0.004, respectively for NEE_{max} , ER and PSN_{max} ; Table 1). The interaction between $T_{10\text{cm}}$ and 2001 for ER occurred during a year with exceptionally low precipitation and WT at the warmest part of the season (Lafleur *et al.*, 2003).

The decline in NEE_{max} in all treatments between 2000 and 2001 was in response to the relatively greater increase in ER than PSN_{max} between the two years owing to dry, warm conditions (Bubier *et al.*, 2003; Lafleur *et al.*, 2003). In 2001, 5N, 5NPK and PK all showed higher rates of PSN_{max} and ER than the controls after 1 year of fertilization (Fig. 1; Basiliko *et al.*, 2006). In that same year, 10NPK and 20NPK were similar to controls as that was the first year of the high nutrient treatments (Fig. 1). NEE_{max} in the controls increased three-fold from 2001 to 2005, similar to trends observed at the eddy covariance tower (E. Humphreys, personal communication). NEE_{max} increased substantially in all treatments except PK in 2003 (two-fold in control, 5N

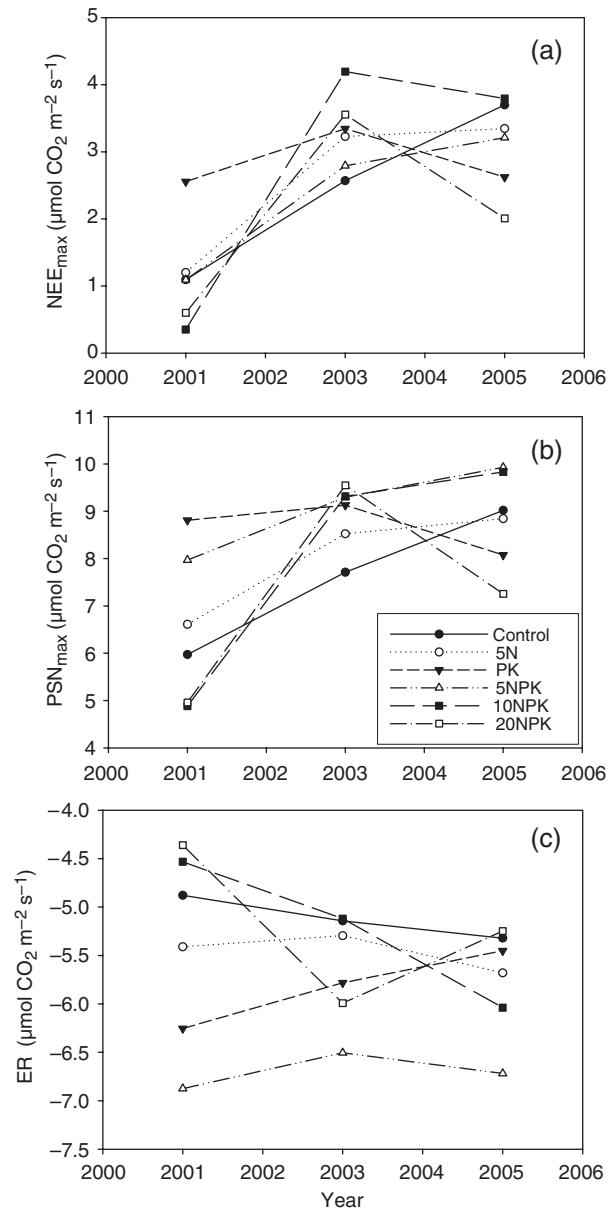


Fig. 1 (a) Net ecosystem CO₂ exchange at photosynthetically active radiation (PAR) > 1000 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ [maximum net ecosystem CO₂ exchange (NEE_{max})], (b) gross photosynthesis at PAR > 1000 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ [maximum gross photosynthesis (PSN_{max})], and (c) ecosystem respiration (ER) for the six treatments in 2001, 2003 and 2005. Year 2001 was the second year of treatment for control 5N, PK and 5NPK plots, and the first year for 10NPK and 20NPK plots.

and 5NPK; 10-fold in 10NPK; six-fold in 20 NPK plots), but the response diverged in 2005 with 5N and 5NPK increasing slightly, and PK, 10NPK and 20NPK all declining. PSN_{max} followed similar trends as NEE_{max} with all treatments increasing through the study period, except PK and 20NPK, which increased in 2003, then

Table 1 Repeated measures analysis of variance (RM ANOVA) for treatment effects on NEE_{max} , PSN_{max} , and ER

	Source	Type III sum of squares	df	Mean square	F	Significance
NEE_{max}	Treatment	0.025	5	0.005	2.354	0.163
	Error (between)	0.013	6	0.002		
	Years	0.003	2	0.002	0.518	0.608
	Years \times treatment	0.077	10	0.008	2.349	0.082*
	Error (within, years)	0.039	12	0.003		
PSN_{max}	Treatment	0.048	5	0.010	2.614	0.137
	Error (between)	0.022	6	0.004		
	Years	0.003	2	0.002	0.434	0.658
	Years \times treatment	0.100	10	0.010	2.685	0.054*
	Error (within, years)	0.045	12	0.004		
ER	Treatment	0.677	5	0.135	3.711	0.071*
	Error (between)	0.219	6	0.036		
	Years	0.072	2	0.036	1.104	0.363
	Years \times treatment	0.375	10	0.037	1.154	0.401
	Years \times T10 _{cm} ₂₀₀₁	0.519	2	0.260	7.999	0.006**
	Error (within, years)	0.390	12	0.032		

Covariates T_{10cm} and WT were tested and found to be non-significant except as noted above. Residual error (between treatments, within years) also noted.

Treatments – Control, 5N, PK, 5NPK, 10NPK, 20NPK.

Years – repeated measurements at 2001, 2003, 2005 (interannual variability) for NEE_{max} , maximum net ecosystem CO₂ exchange; PSN_{max} , maximum gross photosynthesis; ER, ecosystem respiration; WT, water table level; T_{10cm}, temperature at 10 cm below the peat surface.

**Significant at $P < 0.05$; *Strong trend $P < 0.10$; df, degree of freedom.

declined in 2005. After an initial increase (more negative) in ER for all treatments in 2001, the response to nutrient addition was more variable in subsequent years. ER in the 10NPK and 20NPK increased in 2003, but diverged in 2005 with further increases in the 10NPK treatment and decreasing trends in the 20NPK plots.

Results of the one-way ANOVA in 2005, the latest year of the experiment, show that NEE_{max} was significantly lower in the 20NPK plots at $2.0 (\pm 0.3) \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ compared with $3.7 (\pm 0.5) \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in the controls (Fig. 2a). This was contrary to our prediction that nutrient addition would enhance CO₂ uptake in the nutrient-limited bog. Even more surprising was that the differences in NEE_{max} were explained by lower rates of PSN_{max} (Fig. 2b), not higher rates of ER (Fig. 2c) in the high nutrient plots. PSN_{max} was $9.0 (\pm 1.1) \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in the controls compared with $7.2 (\pm 1.1) \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in the 20NPK plots. Although the 20NPK plots did not have significantly different rates of ER than the controls ($-5.3 (\pm 0.5) \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), the 5NPK plots had significantly higher rates ($-6.7 (\pm 0.8) \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). However, the 5NPK plots had been fertilized for one more year than the 10NPK and 20NPK plots.

Vascular plant and moss biomass and growth

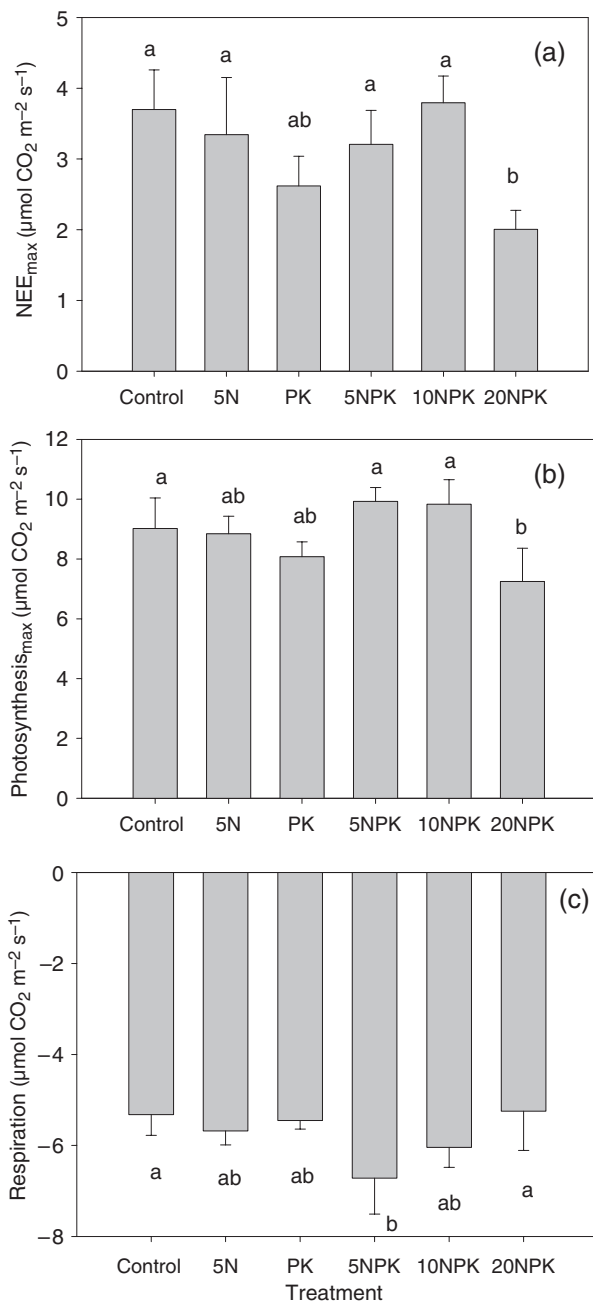
Although there was a trend toward greater vascular plant biomass (as measured by stem density \times average height of stems) in the fertilized plots, the treatments were not statistically different from controls after 5 years (Fig. 3a). However, biomass of randomly selected stems from the three major shrub species was significantly greater in the 10NPK and 20NPK plots (Fig. 3b). Also, vascular plant leaf area increased significantly with treatment (Fig. 6a). This made the chamber NEE and gross photosynthesis results even more surprising. However, the moss cover declined significantly in the high nutrient plots (Fig. 4), suggesting that loss of moss photosynthesis had a greater effect on gross photosynthesis than the increase in vascular plant foliar biomass. The controls had nearly 90% cover of *Sphagnum* mosses (mostly *S. capillifolium* and *S. magellanicum*), with less than 17% cover of *P. strictum*, a small hummock moss that does not have the ability to hold water as does *Sphagnum* in the large hyaline cells (Fig. 4a). Beginning with the 5N plots, *Polytrichum* cover increased to 70% and *Sphagnum* cover decreased to 27%. This reversal of moss dominance progressed to the point where *Sphagnum* disappeared in the 10NPK

plots with 51% *Polytrichum* cover, and all moss was gone in the 20NPK plots (Fig. 4a, b).

Sphagnum moss linear growth as measured by cranked wires declined with treatment from 2001 to 2005 (Fig. 5a). The increase in growth rate in the control plots, 2000 to 2005, compared with the similar growth rates in the hummock located 150 m south of the fertilizer plots, cannot be easily explained by precipitation during May to August, which was highest in 2000 (466 mm) and lowest in 2005 (285 mm), nor by the number of days in which at least trace precipitation

was recorded, though 2001 and 2002 showed the smallest number (43 and 41 days, respectively) and the largest number occurred in 2000 (66 days) and 2003 (62 days) (Table 2). There is no clear explanation for the increased growth in the control plots, unless it is a response to the additional 14 mm of water added in the nutrient solutions, though this is a small proportion (4%) of the average May–August precipitation.

Starting as early as 2002, we measured significant declines in *Sphagnum* growth in the PK and NPK treatments, possibly owing to the toxic effects of fertilization. Growth rates declined in all the PK and NPK treatments until no growth was observed in 2004. However, the 5N treatment had neither a negative or positive effect on *Sphagnum* growth throughout the five years as there was no significant difference between the controls and 5N plots (Fig. 5a). We did not measure *Polytrichum* growth until 2003, but observed higher growth in the 5N treatment compared with the NPK treatments that year. There was no difference in growth rates among treatments in 2004 and little difference in 2005 with the exception of the PK treatment (Fig. 5b), and all *Polytrichum* disappeared in the 20NPK plots.



Shading

LAI of vascular plants in 2005 ranged from 2.3 to 3.9 and increased with treatment, with 5NPK, 10NPK and 20NPK plots having significantly higher LAI than the controls, 5N, or PK plots (Fig. 6a). Vascular plant leaf litter accumulation in 2005 increased 10-fold with treatment with the highest accumulation of 410 g m⁻² in the 20NPK plots compared with 49 g m⁻² in the controls (Fig. 6b). The combination of high LAI and litter cover blocked light from reaching the peat surface, thereby reducing or eliminating radiation for the mosses.

Microclimate of peat surface and decomposition

We hypothesized that the increase in shrub biomass and loss of *Sphagnum* would change the moisture and temperature regime in the surface layers of the peat owing to increased shrub evapotranspiration and the loss of large water-holding capacity in *Sphagnum*. We found that the volumetric soil water increased slightly

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Fig. 2 (a) Net ecosystem CO₂ exchange at PAR > 1000 μmol photon m⁻² s⁻¹ (NEE_{max}), (b) gross photosynthesis at photosynthetically active radiation (PAR) > 1000 μmol photon m⁻² s⁻¹ [maximum gross photosynthesis (PSN_{max})], and (c) ecosystem respiration (ER) for the six treatments in 2005 after 6 years of fertilization for all treatments except 5 years for 10NPK and 20NPK plots. Treatments with no letters in common are significantly different at P < 0.05. Bars represent mean fluxes from May through August; error bars are standard deviations.

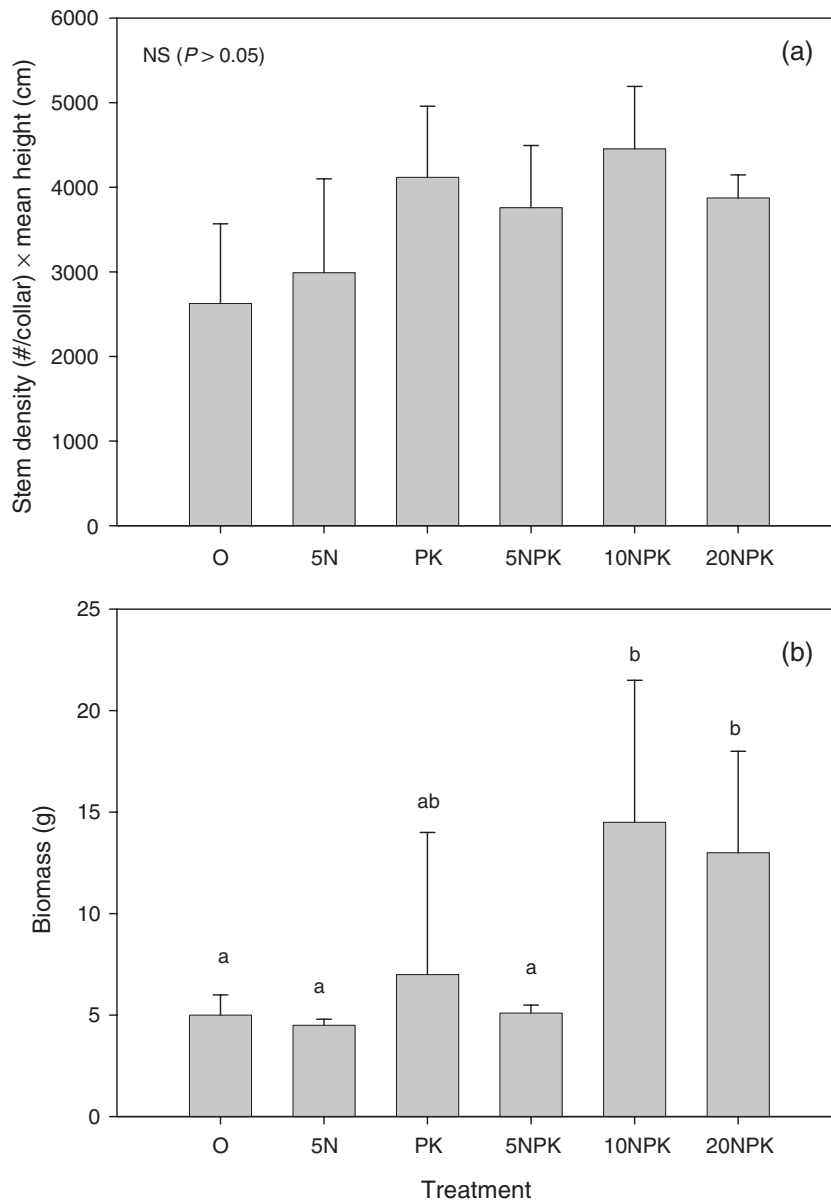


Fig. 3 (a) Stem density × height for all vascular plants in each 0.60 m × 0.60 m collar in 2005, and (b) biomass of three randomly selected plants per plot of the three major shrub species (27 stems/treatment). Treatments with no letters in common are significantly different at $P < 0.05$. Bars represent means and error bars are standard deviations.

instead of decreasing, although the PK and 5NPK treatments were the only ones significantly different than the controls (Fig. 7a). However, the 10NPK and 20NPK plots had been fertilized for one less year than the other treatments. There was no change in water table position (data not shown). Mean summer 2005 peat surface temperature was 1.8 °C cooler in the 20NPK plots (data not shown) at 24.4 °C compared with 26.2 °C in the controls, probably due to increased shading. Temperature at 10 cm depth was 1 °C cooler in both

the 10NPK and 20NPK plots at 18.9 °C compared with 19.9 °C in the controls. Surface and 10 cm temperatures in the other treatments were not significantly different from control plots in 2005.

Even though the chamber CO₂ flux data showed no difference in ER after 5 years in the high nutrient plots, there are suggestions that peat decomposition rate is increasing with fertilization. The 5NPK treatment was the only one with significantly higher ER rates, and the 10NPK and 20NPK treatments lagged behind the others

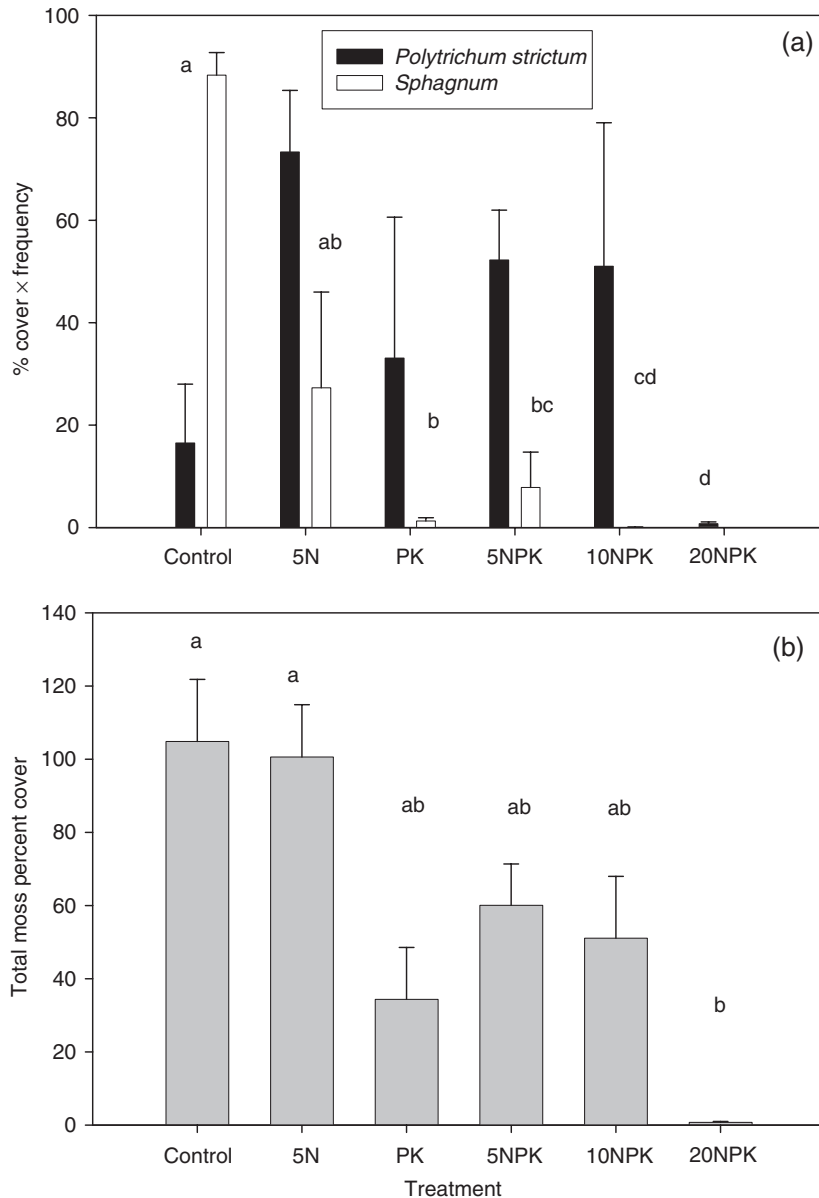


Fig. 4 (a) *Sphagnum* and *Polytrichum* moss percent cover × frequency (% present in 36 subplots) and (b) total moss percent cover in 2005. Treatments with no letters in common are significantly different at $P < 0.05$. Bars represent means and error bars are standard deviations.

by 1 year. Bulk density was significantly greater in all treatments ($0.024\text{--}0.026\text{ g cm}^{-3}$) than the controls (0.017 g cm^{-3}) except 5N (0.019 g cm^{-3}) (Fig. 7b), owing perhaps to higher peat decomposition with fertilization or to greater compaction with the loss of *Sphagnum* moss, which contributes to low bulk density with its rigid stems.

The litter decomposition data using unfertilized plant tissues showed slightly slower, not faster, decomposition after 5 years in the leaves of the dominant shrub *C. calyculata*, and no change in *Sphagnum* mass loss with nutrient addition (Fig. 8). However, the loss of

moss cover is changing the litter quality from very recalcitrant *Sphagnum* tissues to more easily decomposable vascular plant leaves (Table 3).

Discussion

Gas exchanges, plant biomass and species composition

Nutrient addition initially raised the rates of PSN_{max} compared with controls in the first 3 years of the experiment (Fig. 1). However, this trend reversed in the high nutrient plots after 5 years of fertilization. The

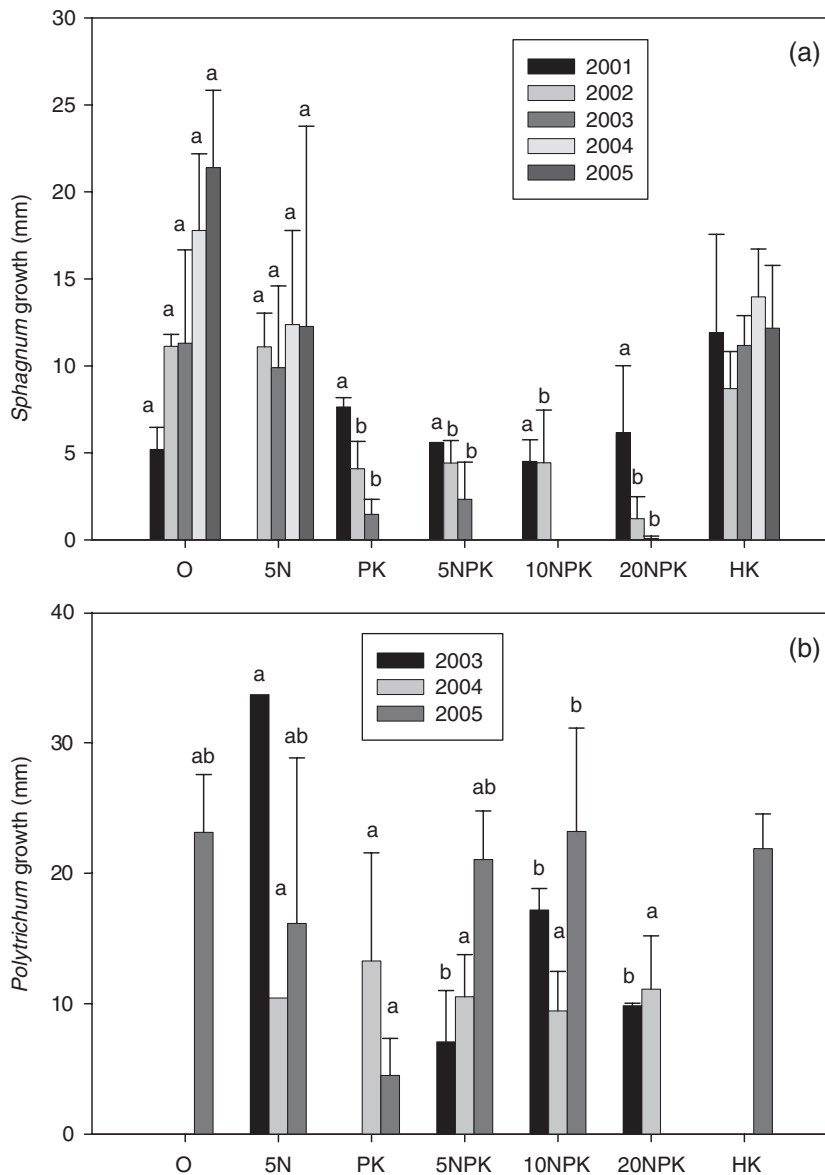


Fig. 5 (a) *Sphagnum* and (b) *Polytrichum* moss growth by treatment from 2001 to 2005. Growth data are also presented for an adjacent hummock (HK) outside the fertilization area. Treatments with no letters in common for each year are significantly different at $P < 0.05$. Bars represent mean growth from late April to mid-October for each year, and error bars are standard deviations.

strong interaction between treatment and year in the RM ANOVA and lack of significant effect of treatment alone (Table 1) suggests that the treatments had different effects on CO₂ exchange over time (Fig. 1) and that several additional years of measurement will be necessary for further clarification of the effect of treatment on CO₂ exchange.

The 2005 decline in NEE_{max} and PSN_{max} in the 20NPK plots (Figs 1 and 2) was surprising given the increase in vascular plant biomass (Fig. 3) and LAI of the shrub layer (Fig. 6a). We expected the increase in vascular foliar biomass in response to nutrient addition

Table 2 Precipitation data for Mer Bleue (P. Lafleur and E. Humphreys, personal communication)

Year	Days with P	Total M–A	Long-term
2000	66	466	342
2001	43	288	
2002	41	327	
2003	62	301	
2004	54	364	
2005	53	285	

The number of days with precipitation (P), and total May (M)–August (A) precipitation (mm) are compared with the long-term (30-year) average (mm) for this site.

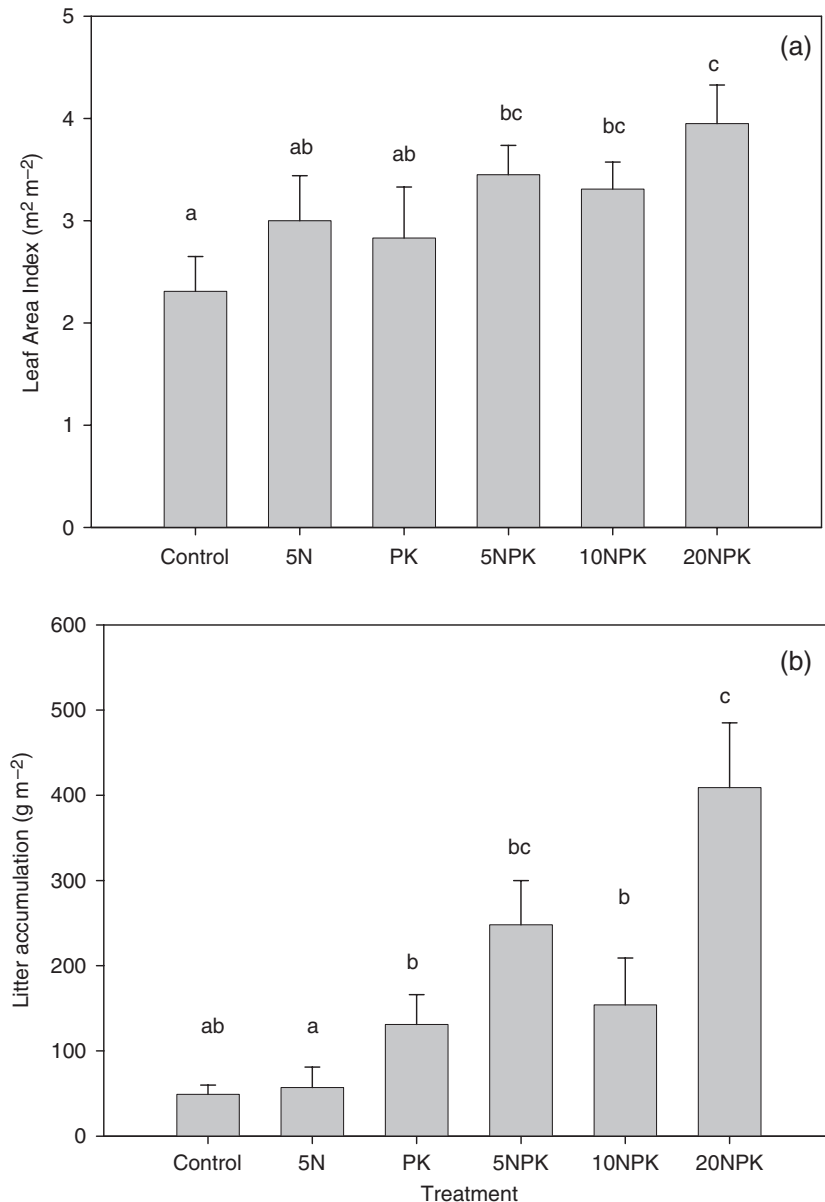


Fig. 6 (a) Leaf area index (LAI) and (b) litter accumulation of vascular plants in 2005. Treatments with no letters in common are significantly different at $P < 0.05$. Bars represent means and error bars are standard deviations.

to increase gross photosynthesis in the treatment plots. Possible explanations for the decline in PSN_{max} include loss of moss photosynthesis and a reduction in vascular plant photosynthetic capacity. There is some indication that leaf-level photosynthesis declined in the high nutrient plots (lower V_{max} ; L. Brunie, personal communication). However, the increase in shrub LAI by about 60% suggests that the increase in photosynthetically active tissues in the vascular plant layer would more than compensate for a lower photosynthetic capacity. The reduction in PSN_{max} is more likely due to the loss of moss photosynthesis. *Sphagnum* moss cover and growth

declined steadily with treatment and time, while *Polytrichum* moss increased with lower levels of nutrient addition, then decreased until all moss was eliminated in the 20NPK plots (Figs 4 and 5).

Toxic effects of fertilization, particularly treatments with PK, and shading from the combination of increased shrub biomass, leaf area, and litter accumulation probably resulted in reductions in moss photosynthesis (Fig. 6; Van der Wal *et al.*, 2005). In unfertilized areas of the bog, the capitula of *Sphagnum* moss comprise 46% of total foliar biomass (Bubier *et al.*, 2006), so that the contribution of moss to gross PSN_{max}

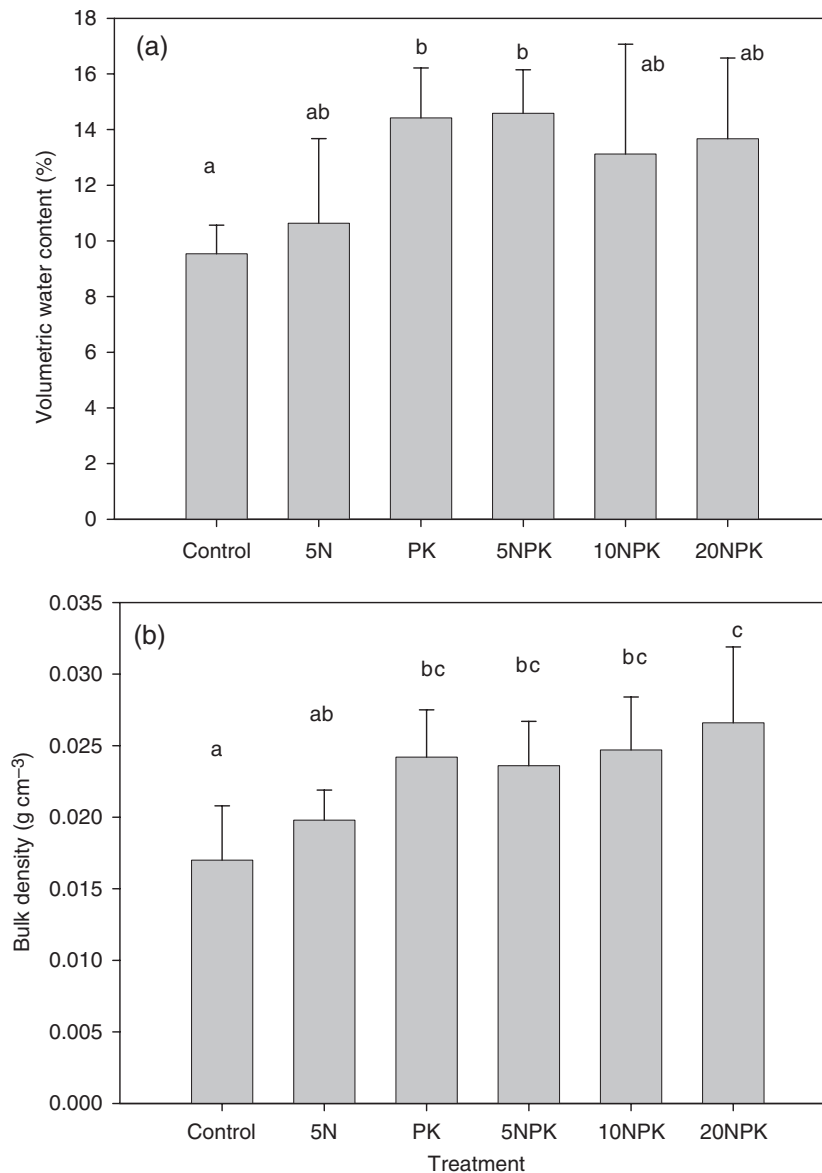


Fig. 7 (a) Volumetric soil water content and (b) bulk density of organic material in 2005. Treatments with no letters in common are significantly different at $P < 0.05$. Bars represent means and error bars are standard deviations.

is significant. Photosynthesis for 20NPK in 2005 was 80% of control PSN_{max} , so loss of moss photosynthesis may have accounted for a 20% reduction in gross PSN_{max} , even with an increase in shrub LAI. Limpens *et al.* (2003a) reported a threshold level of 53% light interception by the canopy as detrimental to *Sphagnum* moss growth. Berendse *et al.* (2001) reported no effect of treatment on living above ground vascular plant biomass; however standing dead biomass and litter was higher in fertilized plots, thereby reducing light intensities for *Sphagnum*. In addition to peatland studies in Europe that have reported increases in vascular plant biomass and declines in moss cover with nutrient

addition, several tundra studies have shown similar trends (Jonasson, 1992; Chapin *et al.*, 1995; Shaver *et al.*, 2001).

Although many studies have reported changes in vascular plant biomass (e.g. Bartsch, 1994; Thormann & Bayley, 1997; Tomassen *et al.*, 2003), species composition (Bowman *et al.*, 2006) and moss biomass (Graglia *et al.*, 2001; Van Wijk *et al.*, 2003) with nutrient addition, our study is the first to show the negative impact of fertilization on NEE and gross photosynthesis. Shaver *et al.* (1998) reported increased CO_2 fluxes (PSN_{max} and ER) with nutrient addition in wet sedge tundra with minimal moss cover, resulting in a stronger CO_2 sink

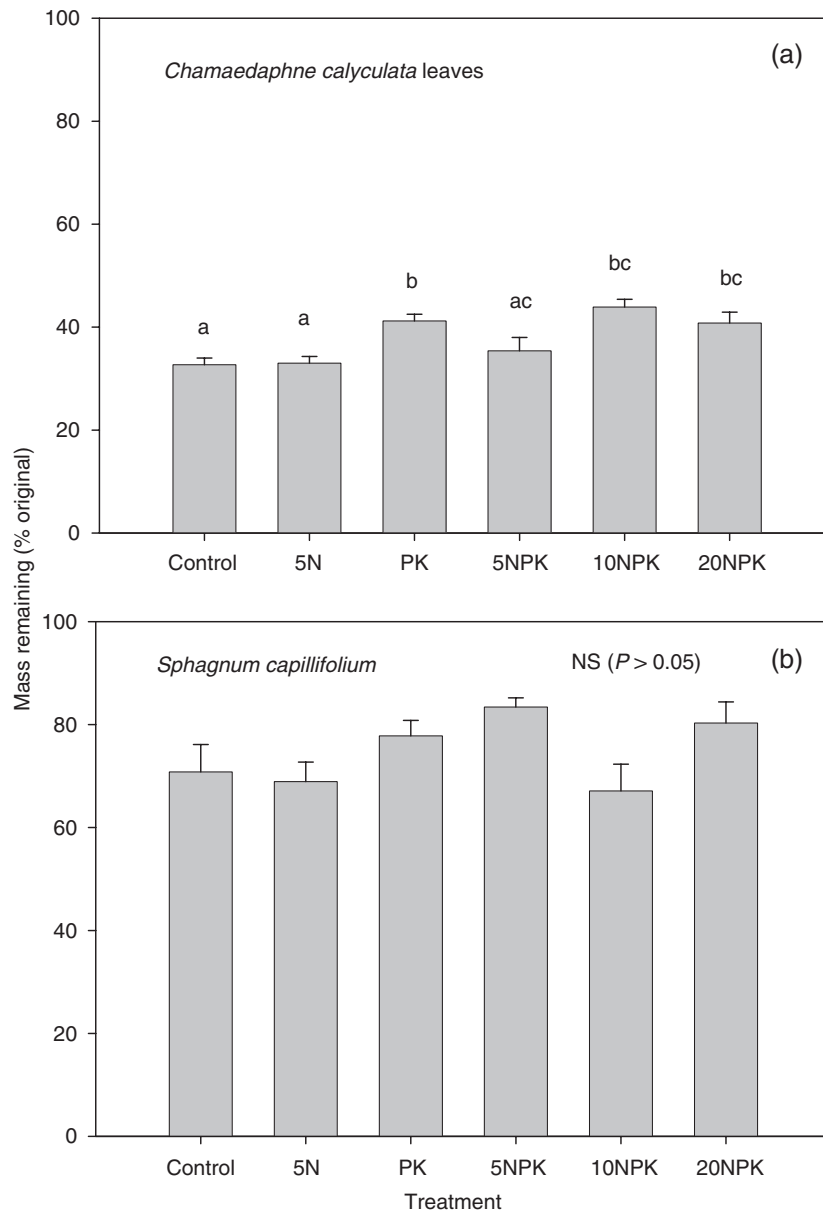


Fig. 8 Surface litter decomposition for (a) *Chamaedaphne calyculata* leaves and (b) *Sphagnum capillifolium* after 5 years of decomposition. Treatments with no letters in common are significantly different at $P < 0.05$. Bars represent means and error bars are standard deviations.

(Johnson *et al.*, 2000). The only other peatland study to measure NEE in a fertilization experiment did not find any differences in NEE after 3 years (Saarnio *et al.*, 2003). There were only minor changes in vegetation, however, probably owing to the short period of treatment.

While we found reductions in gross PSN_{max} , our study did not find differences in ER relative to controls in the high nutrient treatments, even though N and P addition have been shown to increase nutrient cycling (Aerts *et al.*, 2001). We did, however, observe increased ER relative to controls in several treatments in 2001 and

2003 (Fig. 1), and in the 5NPK plots in 2005 (Fig. 2), but the higher nutrient plots had one less year of fertilization. Studies have reported mixed results for ER with some evidence that fertilization lowers ER in fens (Aerts & de Caluwe, 1999), raises ER in bogs (Basiliko *et al.*, 2006), while Finnish peatland studies have reported no differences in ER after 3 years (Saarnio *et al.*, 2003) or 6 years (Nykänen *et al.*, 2002) of N addition. A recent study of peat decomposition across a natural gradient of N deposition in Europe found enhanced CO_2 emissions and dissolved organic carbon release from peat

Table 3 Exponential decay constant (k -value), C:N ratio and lignin content of untreated litter of major species decomposed in the bog for 5-years outside the treatment plots

Species	k -value	C:N ratio	Lignin content
<i>Chamaedaphne</i> leaves	0.184	46.9	10.8
<i>Chamaedaphne</i> stems	0.144	113.0	14.7
<i>Carex oligosperma</i> leaves	0.170	58.5	10.5
<i>Sphagnum capillifolium</i>	0.021	53.2	21.1

accumulated under higher atmospheric N supplies (Bragazza *et al.*, 2006).

We found no significant changes in the emission of methane (CH₄) and nitrous oxide (N₂O) from the plots during 2005 (data not reported). The CH₄ fluxes were small (ranging between averages of 6 and 26 mg m⁻² day⁻¹), as anticipated given the low water table in this bog (Bubier *et al.*, 1995). Others have noted an increase in CH₄ emission with fertilization, usually where the peatland has a sedge cover, such as *E. vaginatum* (e.g. Tuittila *et al.*, 2000; Nykänen *et al.*, 2002; Silvola *et al.*, 2003); sedge cover is less than 3% of the above ground biomass in the Mer Bleue hummocks (Bubier *et al.*, 2006). Average N₂O fluxes were small (ranging from -0.2 to 3.8 µg m⁻² day⁻¹) and showed no significant change with fertilizer treatment. This is contrary to the findings of Christensen *et al.* (1999), but may be related to the dry nature of the Mer Bleue hummocks (Lafleur *et al.*, 2005). Laboratory incubations of Mer Bleue peat have shown significant N₂O production under anaerobic conditions with the addition of NO₃ (M. Kim personal communication), but peat porewater contains small concentrations of NO₃ (J. Ratelle personal communication), and the N added in the fertilizer treatments is probably consumed in the aerobic surface layers and does not reach the anaerobic zone.

Moss growth and decline

Sphagnum has the ability to engineer its environment by making it more acidic, nutrient-poor and wetter with its high cation exchange capacity and large water-holding hyaline cells (van Breemen, 1995; Turetsky, 2003). Few vascular plants can compete successfully with *Sphagnum* in this environment (Ohlson *et al.*, 2001). However, if environmental conditions reduce moss growth rates, vascular plants may thrive. At Mer Bleue Bog, *Sphagnum* moss growth declined with treatment beginning in the second year of the experiment (Fig. 5a), with the exception of the 5N treatment. Toxic effects of nutrient addition may have first caused the decline in *Sphagnum*, while shading from increased shrub LAI and litter

accumulation are the most likely reasons for later reductions in both *Sphagnum* and *Polytrichum* growth (Hayward & Clymo, 1983; Heijmans *et al.*, 2001; Limpens *et al.*, 2003a; see review in Nordbakken *et al.*, 2003).

The studies that have examined the toxic effects of high N deposition on *Sphagnum* growth have shown that *Sphagnum* N metabolism does not adapt fast enough to keep up with enhanced uptake rate. An imbalance between N uptake and assimilation may lead to accumulation of toxic NH₄ in the cell and subsequent reduction in growth (Limpens & Berendse, 2003a; Bragazza *et al.*, 2005). In addition, parasitic fungus infection and epiphytic algae may reduce the volume of photosynthetic tissue (Limpens *et al.*, 2003b). Our study showed a stronger negative response to PK and NPK treatments than N alone (Fig. 5a), so it may be that PK was the most toxic nutrient to *Sphagnum* growth.

In our study, summer of 2001 was warm and dry, which resulted in lower NEE for the controls and all treatments compared with the other years (Fig. 1, Table 2). In year 2002 we began to see declines in moss growth (Fig. 5a), which might be explained by an interaction between the dry climate of 2001 and the toxic effects of fertilization (strong interaction between treatment and year, Table 1). PSN_{max} was actually higher in most treatments compared with controls in 2003, suggesting that at this stage of the experiment, the increase in vascular plant growth outweighed the first signs of moss decline. Our study did not find any significant differences in NEE between the treatments and controls until the fifth year of fertilization (although we only measured NEE in alternate years), emphasizing the importance of long-term experiments and the lag-times in ecosystem processes. The complete loss of moss cover in the 20NPK plots did not occur until the fifth year of the study, the same year we observed declines in NEE_{max} and PSN_{max} for the first time, although moss decline began as early as the second year.

Lamers *et al.* (2000) and Berendse *et al.* (2001) describe a three stage process where: (1) *Sphagnum* growth is initially stimulated at low levels of N (<1 g N m⁻² yr⁻¹; Jauhiainen *et al.*, 1994; Williams & Silcock, 1997); (2) N no longer limits *Sphagnum* growth, but the *Sphagnum* layer has not yet reached its maximum organic N content, and (3) the *Sphagnum* layer has reached its maximum organic N content and can no longer filter the excess N allowing this additional N to reach the soil solution and the roots of vascular plants (Bragazza *et al.*, 2005). Vitt *et al.* (2003) reported 1.4–3.4 g N m⁻² yr⁻¹ as the critical toxic level for *Sphagnum* in western Canadian bogs. N deposition at our site Mer Bleue Bog is probably in stage 2 as the 5N treatment (equivalent to a total load of 2.4 g N m⁻² yr⁻¹ with ambient levels combined with added N) was neither beneficial nor detri-

mental to *Sphagnum* growth and the concentration of N in the capitulum of *S. capillifolium* in the untreated bog and *S. magellanicum* averaged 0.83–0.86% (Moore *et al.*, 2005) in accord with observations by Lamers *et al.* (2000). Any additional inputs of atmospheric N may put the bog into stage 3 as seen in many European bogs (Berendse *et al.*, 2001). In our study, PK alone, and in combination with higher N levels, was also detrimental to *Sphagnum* growth (Fig. 5a).

Although many studies have reported declines in *Sphagnum* moss with nutrient addition (e.g. Gunnarsson *et al.*, 2004), and differential effects of N addition on various species (Li & Vitt, 1997), very few have discussed the role of *Polytrichum* mosses. NPK fertilizer had a negative impact on growth of *Hylocomium*, but not *P. commune* in a sub-arctic heath in Swedish Lapland (Potter *et al.*, 1995). Individual shoot growth increased in *Polytrichum*, but there was no change in total number of shoots. Therefore, it may be the decline in associated moss species that favors *Polytrichum* growth, rather than the ability of *Polytrichum* to expand its population. With moderately high fertilization levels ($3 \text{ g N m}^{-2} \text{ yr}^{-1}$) at a Swiss bog, the enhanced growth of *P. strictum*, the same species at Mer Bleue, had a negative impact on *Sphagnum* growth (Berendse *et al.*, 2001). Haslinger *et al.* (2006) showed that mosses have different kinetics and uptake rates than vascular plants and that *Polytrichum* is very different from *Sphagnum* in that it has lower uptake rates (possibly due to different cell structure), but similar N content. This could suggest that NPK was more toxic to *Sphagnum* than *Polytrichum* as *Sphagnum* relies more on atmospheric uptake than *Polytrichum*. In our study, individual *Polytrichum* stem growth varied little among treatments (Fig. 5b), unlike the Potter *et al.* (1995) study; but stem density and cover increased as *Sphagnum* growth declined (Fig. 4a). However, at high NPK levels *Polytrichum* died off eventually along with *Sphagnum* (Fig. 4b), probably owing to lack of light from vascular plant and litter shading (Fig. 6). Van der Wal *et al.* (2005) reported that the growth of *P. alpinum*, a montane species, was not influenced by elevated N, but was reduced up to 40% by shading. That study also concluded that different moss species respond in various ways to nutrient addition and shading, as observed in our results.

The effects of microclimate are also important for moss growth (Okland, 1990; Gignac *et al.*, 1991; Rydin, 1993; Weltzin *et al.*, 2001; Groeneveld & Rochefort, 2005). In our study, cooler temperatures and shading might have had some effect on soil moisture, which was somewhat higher in the fertilized plots (Fig. 7a). If moisture had been an important factor in determining moss cover, we would have seen higher, not lower moss cover in the fertilized plots. Potter *et al.* (1995) also

showed that changes in temperature and moisture had less effect on moss growth than nutrient supply.

Finally, Aerts *et al.* (1992) showed that vegetation in bogs with high N deposition becomes P-limited. Malmer & Wallén (2005) reported that increased N deposition might increase mineralization in the acrotelm, increasing the supply of P to the vascular plants; therefore, growth of vascular plants may be as much due to the indirect effect of increased availability of P, as well as the direct effect of N deposition. Williams & Silcock (1997) suggested that *Sphagnum* growth declines because it becomes P-limited at high N levels, and others have also concluded that P availability affects the impact of N deposition (e.g. Limpens *et al.*, 2004). In our high nutrient plots, P and K may have been toxic to *Sphagnum* in the quantities applied, leading to reductions in moss growth. However, the added P was beneficial to vascular plants as the biomass and shrub LAI increased in the PK plots alone, as well as in the combined NPK treatments (Figs 3 and 6a).

Decomposition

We found slightly slower, not faster, decomposition in leaves of the dominant shrub *C. calyculata* and no change in *Sphagnum* mass loss with nutrient addition (Fig. 8), contrary to the findings of Limpens & Berendse (2003b). Increased N availability has variable, species-specific effects on litter mass loss rates (Aerts *et al.*, 2006) and Berg & Matzner (1997) have shown that N addition may increase the initial rate, but slow down the later rates of decomposition.

More importantly in the longer-term, species changes will favor faster decomposing tissues. The mass remaining of the leaves of the dominant shrub *Chamaedaphne* was half that of *Sphagnum* stems after 5 years (Fig. 8). In natural bog environments, *Sphagnum* decomposes much more slowly than any other species (Hobbie, 1996; Dorrepaal *et al.*, 2005) with decay rates a factor of up to ten slower. *Sphagnum* has higher lignin content (Table 3) and is rich in phenolics, and therefore more resistant to microbial decomposition than the litter of vascular bog plants (Verhoeven & Liefveld, 1997). The increase in litter accumulation (Fig. 6b) also suggests an increase in nutrient cycling, which will enhance decomposition. Finally, the loss of *Sphagnum* moss may result in drier and perhaps warmer soils with the loss of moss water holding capacity, which may lead to an increase in aerobic microbial decomposition and CO₂ emission (Moore & Dalva, 1993; Davidson & Janssens, 2006).

Ecosystem feedbacks to climate

Malmer & Wallén (2005) and Bragazza *et al.* (2006) predicted reductions in peatland C accumulation with

nutrient addition as a result of increased decomposition with changes in peat litter quality and plant species composition. Our study shows that reductions in gross photosynthesis are responsible for lower net CO₂ uptake in the high nutrient plots after 5 years, emphasizing the importance of moss photosynthesis to the net C balance. However, we predict that the reductions in C accumulation will become even more severe as more decomposable vascular plant leaf litter replaces the recalcitrant *Sphagnum* moss tissue in the peat. It is not clear whether the increase in shrub growth will be a negative or positive feedback to climate. Shrubs may enhance nutrient cycling in soil organic matter increasing decomposition, or may lead to higher C accumulation because of higher plant production and slowly decomposing woody tissues (Jonasson *et al.*, 1999; Hobbie *et al.*, 2002; Mack *et al.*, 2004; Weintraub & Schimel, 2005). Increased shrub growth also reduces albedo and snow cover, thereby enhancing the positive feedback effect (Sturm *et al.*, 2001; Chapin *et al.*, 2005). In bogs, *Sphagnum* decomposes even more slowly than woody tissues (Table 3). Therefore, it is likely that boreal and sub-arctic bogs will sequester less C with loss of *Sphagnum* and become a positive feedback to climate. The critical role of *Sphagnum* in regulating ER, as well as gross photosynthesis suggests that it is a 'foundation species' (Ellison *et al.*, 2005) or genus, whose loss dramatically disrupts the structure and function of bog ecosystems.

Finally, nutrient addition may have additional negative effects on bogs by facilitating an increase in invasive species (plant and microbial) and making native bog plants more susceptible to secondary stress factors, such as pathogens, frost and drought (Bobbink *et al.*, 1998; Tomassen *et al.*, 2004; Blumenthal, 2005). Wiedermann *et al.* (2006) reported an increase in parasite-plant interactions with N addition after 8 years of fertilization in a boreal peatland. We may also see major changes in vascular plant species composition in the future with sedges/grasses outcompeting ericaceous shrubs, although this may depend on soil pH (Hobbie *et al.*, 2005). As evergreen shrubs have low nutrient loss rates and slow litter decomposition, they help perpetuate low-nutrient environments (Aerts *et al.*, 2006).

Conclusions

Our study highlights the importance of longer-term experiments as we observed varying ecosystem responses to treatment over time, and did not see any decline in net CO₂ exchange until the fifth year of the experiment, the same year that almost complete loss of moss cover occurred in the high nutrient treatments. Shifts in plant species composition led to reductions in

maximum NEE and gross photosynthesis with little change in ER. Loss of moss cover may have had a stronger effect on gross photosynthesis than the increase in vascular plant biomass and leaf area. We predict even more severe reductions in C accumulation with changes in litter quality leading to greater decomposition of soil organic matter.

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