

Minor Changes in Vegetation and Carbon Gas Balance in a Boreal Mire under a Raised CO₂ or NH₄NO₃ Supply

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ABSTRACT

Increasing concentrations of carbon dioxide (CO₂) in the atmosphere or continuous nitrogen (N) deposition might alter the carbon (C) cycle in boreal mires and thus have significant impacts on the development of climate change. The atmospheric impact of the C cycle in mires is twofold: C accumulation attenuates and CH₄ release strengthens the natural greenhouse effect. We studied the effects of an increased supply of CO₂ or NH₄NO₃ on the vegetation and annual CO₂ exchange in lawns of a boreal oligotrophic mire in eastern Finland over a 2-year period. Ten study plots were enclosed with mini-FACE (Free Air Carbon Dioxide Enrichment) rings. Five plots were vented with CO₂-enriched air (target 560 ppmv), while their controls were vented with ambient air; five plots were sprayed with NH₄NO₃, corresponding to a cumulative addition of 3 g N m⁻² a⁻¹, while their controls were sprayed

with distilled water only. A raised NH₄NO₃ supply seemed to affect the composition of the moss layer. Raised CO₂ did not affect the vegetation, but gross photosynthesis increased significantly. The change in net CO₂ exchange depended on the annual weather conditions. Our results suggest that C accumulation may increase in wet years and compensate for the warming effect caused by the increase in CH₄ release from this mire. In contrast, a relatively dry and warm growing period favors decomposition and can even make the CO₂ balance negative. Along with the increased CH₄ release under raised CO₂, the decreased C accumulation then increases the radiative forcing of boreal mires.

Key words: raised CO₂; NH₄NO₃ addition; CO₂ exchange; CH₄ release; boreal mire; climate change.

INTRODUCTION

A mire is an ecosystem in which, over the long term, primary production is higher than decomposition and thus organic matter accumulates as peat. It is estimated that boreal wetlands accumulate 44–70 Tg of carbon (C) annually (Clymo and others 1998; Turunen and others 2002). In Finland, the

long-term average C accumulation rate has been 24 g m⁻² a⁻¹ in bogs and 15 g m⁻² a⁻¹ in fens (Tolonen and Turunen 1996). This accumulation rate, however, is not constant. Depending on the prevailing weather conditions, the C balance in certain regions varies from positive (gain) to negative (release) in individual years (Alm and others 1997, 1999a). In the future, the ongoing increase in the atmospheric concentration of carbon dioxide (CO₂) (Houghton and others 1996) and the continuous, although now decreasing, N deposition (Kulmala

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and others 1998; Ruoho-Airola and others 1998) may alter the present functioning of mire ecosystems.

The increase in both CO₂ and nitrogen (N) supply can be expected to augment C cycling in mire ecosystems. The current atmospheric CO₂ concentration is a limiting factor for the growth of C₃ plants. Many studies have shown that photosynthesis and biomass accumulation in both the above- and belowground parts of plants increases under raised CO₂ concentrations (see, for example, van Ginkel and others 1997; Reich and others 2001). Increased litter production and C supply to decomposers is the most probable reason for the enhanced release of CH₄ from wetlands under raised CO₂ concentrations (Dacey and others 1994; Hutchin and others 1995; Megonigal and Schlesinger 1997; Saarnio and others 2000). However, under future atmospheric CO₂ concentrations, the increase in both net primary production (Oberbauer and others 1986; Tissue and Oechel 1987) and CH₄ efflux rate (Saarnio and Silvola 1999; Saarnio and others 2000) could remain clearly lower in northern regions compared to the situation in warmer climates.

Nitrogen is another factor that is often limiting for the growth of plants. In mire ecosystems, an elevated N supply should favor vascular plants rather than the peat mosses adapted to nutrient-poor conditions (Berendse and others 2001). However, a moderate increase in N availability also promotes the growth of many *Sphagnum* species (Press and others 1986; Aerts and others 1992; Jauhiainen and others 1994, 1999). Increasing growth of plants increases the rate of CO₂ uptake, respiration, and litter production. In addition, a decrease in the C/N ratio of litter would promote decomposition (Coulson and Butterfield 1978; Aerts and others 1995). Elevated N supply may have antagonistic effects on CH₄ release. The addition of N compounds has been observed to decrease both CH₄ production (for example, see Bollag and Czlonkowski 1973; Kimura and others 1992) and oxidation (for example, Steudler and others 1989; Kravchenko 1999) in the soil. According to Saarnio and Silvola (1999) and Saarnio and others (2000), N deposition, comprising both ammonium and nitrate, will not significantly affect CH₄ release from boreal mires.

We studied the effects of a raised CO₂ or NH₄NO₃ supply on the dynamics of the vegetation and net ecosystem CO₂ exchange in a boreal oligotrophic fen. The annual C gas (CO₂, CH₄) exchange balance was reconstructed for the study plots to assess possible future changes in the radiative forcing of boreal fens due to the ongoing increase in the atmospheric concentration of CO₂ and continuous N

deposition. The estimates for the annual CH₄ release were adopted from Saarnio and others (2000).

METHODS

Experimental Conditions

In May 1996, 20 study plots (1 m diameter) with similar vegetation were selected subjectively in the Salmisuo mire complex (62°47'N, 30°56'E) in eastern Finland. The study area was a minerogenic, oligotrophic low-sedge *S. papillosum* pine fen, that is, a mire ecosystem with low nutrient availability. All the study plots were located on lawn, which represents a microsite with intermediate moisture conditions; the average water table is 5–20 cm below the peat surface (Eurola and others 1984). Aluminum collars (60 × 60 cm) were permanently installed in each study plot for CO₂ and CH₄ exchange measurements.

Five study plots were enclosed with mini-FACE (Free Air Carbon Dioxide Enrichment) rings consisting of a circular arrangement of about 70 18-cm-high venting pipes. The rings were vented with CO₂-enriched air, and the CO₂ concentration above the mire surface was monitored with an infrared gas analyzer. The CO₂ supply was adjusted via a PC and a mass-flow controller to maintain the target concentration (560 ppmv) on the plots with raised CO₂ (for more details, see Miglietta and others 2001). In 1996, 1997, and 1998, the 95% confidence intervals for the daily mean CO₂ concentration were 551–562 ppmv, 534–543 ppmv, and 522–533 ppmv, respectively. The other five plots were also enclosed with mini-FACE rings, but they were vented with ambient air only. In both treatments, the mini-FACE rings were functioning only during the snow-free period (about May–October).

Five other plots received NH₄NO₃ on six occasions during the growing season; the cumulative total amount of N was 3 g m⁻² a⁻¹. Ammonium nitrate was dissolved in 2000 ml distilled water and sprayed on the appropriate plots. The atmospheric bulk deposition in the study area is 0.2–0.3 g N m⁻² a⁻¹, and the proportions of NH₄⁺ and NO₃⁻ ions in deposition are about one-third and two-thirds, respectively (Ruoho-Airola and others 1998). The five control plots received the same amount of distilled water at the same time as the N treatment. In 1998, only four of the six additions (2 g N/m²) were applied before the experiment was terminated at the end of July (the time of maximum biomass).

Vegetation Analyses

The abundance of individual plant species was measured using the point-quadrat method (for exam-

ple, see Buttler 1992). In each ring, a permanent plot was chosen subjectively to be representative of the vegetation type. The plot was marked in the corners with plastic tubes inserted into the peat. A Plexiglas plate with four metal pins (fitting into the corner tubes) and 150 holes (2.5 cm grid size within a 25 × 37.5 cm area) was used for the measurements. At each point, contacts between a thin, pointed pin and the shoots of vascular plants, litter, and peat mosses were counted. *Sphagnum* mosses were measured in July 1996, September 1997, and July 1998. Vascular plants and litter were measured at the time of maximum biomass in late July each year.

Species coverage within the gas exchange collars was estimated visually in 1996. In addition, the aboveground vascular vegetation was harvested from the point-quadrat areas at the end of the experiment in July 1998 (time of maximum biomass). Individual species were separated, dried (70°C), and weighed. One 50-cm-deep peat sample was taken from each study plot using a box sampler (8 × 8 × 100 cm) to estimate the amount of living belowground biomass of the vascular plants. The monolith was divided into 10-cm slices and stored for a number of days (2–3°C) before the roots were washed out from the peat. Living roots were dried (70°C), weighed, and sorted into two classes (aerenchymatous and nonaerenchymatous).

Nutrient Analyses

At the end of the experiment, two peat samples from each study plot were taken for the nutrient analyses with a box sampler (8 × 8 × 100 cm) from a depth of 25–30 cm. The upper layers (0–25 cm) were used for the aerobic decomposition potential measurements (data not shown). The samples were frozen. The samples were ashed at 550°C, and the residue was extracted with 1 M HCl. Total potassium (K), calcium (Ca), and magnesium (Mg) were determined on an atomic absorption spectrophotometer (Zeeman 6000; Hitachi, Japan), and total phosphorus (P) was determined colorimetrically (U-2000 spectrophotometer, Hitachi). The Kjeldahl method (Vapodest 30; Gerhardt, Germany) was used for determination of the total N content.

CO₂ Exchange

Instantaneous net CO₂ exchange was measured using chambers and a portable infrared gas analyzer (Alm and others 1997, 1999b) from 1 July to 24 October in 1996, from 15 May to 6 October in 1997, and from 18 May to 23 July in 1998. Measurement pairs consisted of the net CO₂ exchange measurement in natural irradiance and temperature condi-

tions and the dark ecosystem respiration (that is, combined respiration of soil and vegetation) measurement in natural temperature conditions using a transparent, thermostated chamber (60 × 60 × 17 cm) and an opaque chamber (60 × 60 × 20 cm) respectively. On the plots with raised CO₂, the CO₂ concentration at the beginning of the measurement was adjusted, when necessary, to near 560 ppmv by blowing gently into the chamber through the compensation air tube. To prevent the cooling unit on the front side of the chamber from damaging the ventilating pipes in the mini-FACE rings, an extension collar (60 × 60 × 38 cm) with an extra fan was fitted onto the permanent collar during the measurements with the transparent chamber.

Measurements were made one to five times per week in each collar during daytime, mainly between 7 AM and 4 PM. The light intensity and air temperature inside the gas exchange collar and peat temperatures (surface, -2 cm and -5 cm) and water table next to the gas exchange collar were measured simultaneously. The rates of net CO₂ exchange and dark ecosystem respiration (mmol CO₂ m⁻² h⁻¹) were calculated from the linear ($r^2 \geq 0.9$) change in CO₂ concentration during the measurement period of 2–4 min. In addition, small fluxes (change ≤ 4 ppmv min⁻¹) were accepted despite low r^2 values. The gross photosynthesis was calculated from the measured net CO₂ exchange and dark CO₂ release.

Winter Effluxes

During periods with snowcover (December–April), the release of CO₂ from the peat into the atmosphere was measured every 2 (or 3) weeks using a snowpack diffusion method (Sommerfeld and others 1993). More frequent sampling was not needed because CO₂ release during snow-covered periods is relatively constant (Lafleur and others 2001; Laurila and others 2001). The snowpack diffusion method assumes that diffusion is the major mechanism for gas transport through the snow and that the porosity of the snowpack is homogeneous. In practice, however, ventilation of the snowpack by wind when the snow cover is thin or the presence of ice layers in the melting snow may distort the results, especially in early and late winter (Alm and others 1999a). Some disjointed ice layers were observed in the spring, but the snowpack had become completely frozen over only one collar. This collar could not be sampled from the beginning of February to the middle of April 1998.

In each collar, three 15-ml gas samples were drawn into polypropylene syringes from the bottom of the snowpack and above the snow through a thin

metal pipe. The CO₂ concentrations were determined within 6 h on an infrared analyzer (HB URAS 3E; Hartmann & Braun AG, Germany) connected to an integrator (HP 3396A; Hewlett Packard, USA). In connection with each sampling, five to six (on two occasions only, three), volumetric samples were taken for the determination of the snow porosity (for details, see Saarnio and others 2000). The CO₂ release rate was calculated using Fick's first law (the diffusion coefficient, 0.139 cm²/s, for CO₂ was taken from Sommerfeld and others 1993). The peat temperature at depths of 10, 30, and 50 cm was measured in connection with sampling using thermocouple sensors installed in the peat in autumn 1996.

Reconstructions

Gross photosynthesis, dark ecosystem respiration, and net CO₂ exchange were reconstructed separately for each of the 20 collars for 1997 using the statistical relationships between gas exchange and environmental variables (compare Alm and others 1997, 1999b). This procedure enabled us to derive the CO₂ exchange rates for the whole growing season by using instantaneous daytime measurements and recorded day-round time series of environmental variables. Gross photosynthesis (P_g = measured net CO₂ exchange + dark ecosystem respiration) was dependent on the irradiance and peat temperature; respiration (R) was dependent on peat temperature and the water table depth. These dependences were modeled by means of the following equations:

$$P_g = Q \cdot I \cdot t2 / (k + I) \quad (1)$$

$$R = \exp(a + b \cdot t2 + c \cdot wt) \quad (2)$$

where I = irradiance ($\mu\text{mol m}^{-2} \text{s}^{-1}$), $t2$ = peat temperature at the depth of 2 cm, ($^{\circ}\text{C}$), wt = water table (cm), and Q , k , a , b , and c are regression parameters. Stepwise regression ($P < 0.05$) was used in selecting variables $t2$ and wt in the models for respiration. The hourly values of peat temperature and irradiance were obtained from the weather station (GroWeather; Davis Instruments, USA) at the study site. The same series were used for all the collars. However, the hourly water table series were obtained from manual measurements made about one to three times a week for each collar using cubic spline interpolation (routines CSAKM and CSVAl, IMSL 1989).

Individual regression parameters for each collar and series of environmental factors were used to reconstruct the hourly gross photosynthesis and respiration from 5 May to 20 October 1997. Each

estimate for gross photosynthesis was calculated by averaging the outcomes from two evaluations of Eq. (2) with mean hourly irradiance + and - SD to account for the hourly variation in irradiance (Smolander 1984). Net CO₂ exchange was then calculated from $P_g - R$. The modeled net CO₂ exchange was integrated over the summer for the estimation of the annual C balance.

The release of CO₂ during snowcover periods was estimated by multiplying the monthly average CO₂ release rate ($\text{mmol CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) by the number of hours in the month. No measurements were made at three air ventilation and two water addition collars at the beginning of 1997 (January–April). The missing values were replaced with the average CO₂ release from the other collars of the same treatment. The CO₂ release in the beginning of May (1–4), prior to snowmelt, was calculated by extending the monthly averages in April. The late autumn (21 October–30 November) CO₂ release was interpolated from the December measurements and the estimates for early October. Finally, the total CO₂ balance in 1997 was calculated for each collar by summarizing all the monthly values.

Statistical Analyses

Repeated measures analysis was used to test the effects of treatments on the abundance of plant species and litter on the study plots. The relative proportion (%) of litter and main vascular plant and moss species in the point-quadrat areas during years 1996–98 was used as a test datum. Differences in the above- or belowground biomasses of aerenchymatous and nonaerenchymatous vascular plants, aboveground necromass and nutrient concentrations in the peat between treatments, and their controls were tested using a t -test.

Effects of the treatments on CO₂ fluxes were tested using a repeated-measures analysis with covariance. Measurements from two consecutive calendar weeks (odd and the following even) in 1997 and 1998 were pooled, and the average rate of net CO₂ exchange, ecosystem respiration, and gross photosynthesis at light-saturated conditions was calculated separately for each collar. This procedure led to eight comparable measurement times for the CO₂ experiment (week pairs 21–22, 23–24, 25–26, 27–28, and 29–30 in 1997 and week pairs 21–22, 27–28, and 29–30 in 1998) and nine measurement times for the NH₄NO₃ experiment (week pairs 21–22, 23–24, 25–26, 27–28, and 29–30 in 1997 and week pairs 23–24, 25–26, 27–28, and 29–30 in 1998). Only measurements made at light-saturated conditions (irradiation $> 500 \mu\text{mol m}^{-2} \text{s}^{-1}$) (Long and Hällgren 1987) were accepted to ensure that

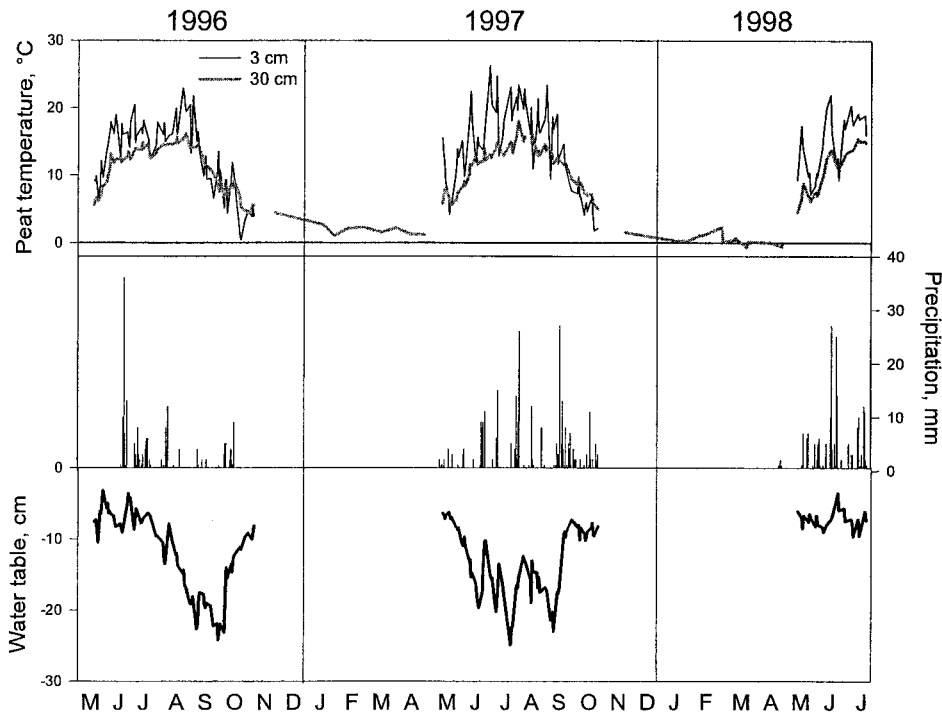


Figure 1. Average peat temperature at depths of 3 and 30 cm, summarized daily rainfall, and average depth of the water table in the study area during the experiment.

possible differences between a treatment and its control could be assumed to be caused by the treatment and not to differences in irradiation (or temperature) during the measurements. The visually estimated summarized coverage of all vascular plants in the collars in 1996 was used as a covariate in the raised CO_2 experiment. In the raised NH_4NO_3 experiment, the amount of vascular plants was so similar in all the collars that there was no correlation between CO_2 exchange and vascular plant coverage; therefore, the repeated-measures analysis was made without the covariate. The similarity of environmental conditions (water table, peat temperature at the depth of 2 cm, and irradiation) during CO_2 measurements included in the repeated-measures data was also tested with the repeated-measures analysis.

Differences between the treatments and their controls in the estimated CO_2 exchange and the total C gas exchange in 1997 were tested using a *t*-test in the raised NH_4NO_3 experiment and a covariance analysis in the raised CO_2 experiment. The coverage of all vascular plants in the collars in 1996 was also used as a covariate in this analysis.

RESULTS

Environmental Variables

The weather varied between the three study years (Figure 1). In 1996, the early summer was wet,

whereas the end of the growing season was warm (August) and dry (August–September). The summer of 1997 was exceptionally warm, and rainfall remained 17%, 23%, 9%, and 52% below the long-term (1960–90) averages in the study region in May, June, July, and August, respectively (Finnish Meteorological Institute 1997a, b, c, d). By contrast, the whole growing season was exceptionally wet in 1998.

Vegetation Dynamics

The moss layer inside the gas exchange collars consisted mainly of *Sphagnum balticum* (Russow) C. Jens and *S. papillosum* Lindb., accompanied by some *S. magellanicum* Brid. The dominant vascular plant species were *Eriophorum vaginatum* L., *Vaccinium oxycoccus* L., *Andromeda polifolia* L., *Carex pauciflora* Lightf., and *Drosera rotundifolia* L., with *Scheuchzeria palustris* L. in the wettest places. The coverage of litter (mainly old *E. vaginatum* leaves) was also high (5%–20%).

S. balticum declined during the experiment but retained its dominance, whereas both *S. papillosum* and *S. magellanicum* became more abundant in all treatments (Figure 2). The change was most prominent on the plots given NH_4NO_3 , in which the proportion of *S. balticum* decreased by almost 30% over the 2-year period. The decline of *S. balticum* (within subject factor) was statistically significant in both CO_2 supply and its control ($P = 0.027$) and in

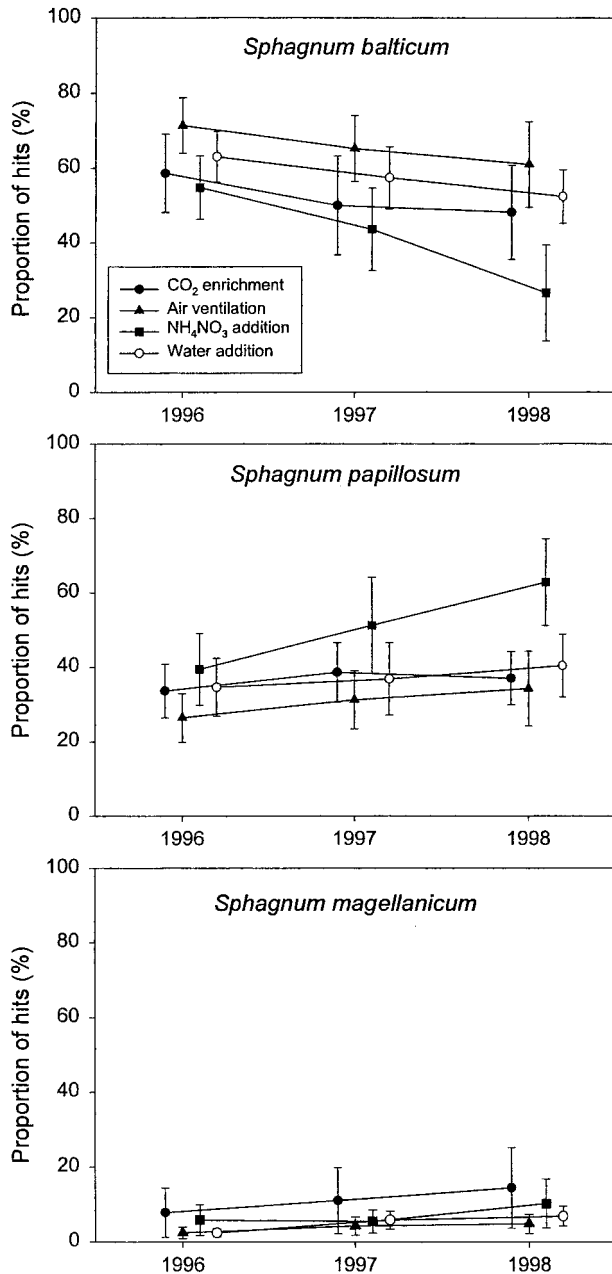


Figure 2. Relative proportions (% \pm SE, $n = 5$) of *Sphagnum* species in the point-quadrat areas during the experiment.

NH₄NO₃ supply and its control ($P = 0.010$) analyses. In the latter case, the increase of *S. papillosum* was also significant ($P = 0.004$).

Although the amount of vascular plants (that is, the number of hits) varied between years in the point-quadrat areas, some general trends were found in the relative proportion of species (Table 1). In all the treatments, the clearest changes were an approximately 10% decrease in litter and an ap-

proximately 5% increase in *V. oxycoccus*. In repeated-measures analysis with data from the CO₂ enrichment and air ventilation plots, the decrease in litter ($P = 0.005$) and the increase in *V. oxycoccus* ($P = 0.004$) and *S. palustris* ($P = 0.036$) were statistically significant. In a comparison of the NH₄NO₃ and water addition plots, the general increase and decrease were significant in the amount of *V. oxycoccus* ($P < 0.0005$) and litter ($P < 0.0005$), respectively. None of the differences between the treatment and their control were statistically significant. Correspondingly, no significant differences in either the above- or belowground biomasses harvested at the end of the experiment or the total K, Ca, Mg, P, and N concentrations in the peat were found between the treatments (Table 2).

CO₂ Exchange

After snowmelt at the beginning of May, the gross photosynthesis (Figure 3), ecosystem respiration (Figure 4), and net CO₂ uptake (Figure 5) increased up until their summer maximum in July–August. In 1996, the warm and dry weather in August caused the water table to drop down to 25 cm (Figure 1) which enhanced the ecosystem respiration, and the instantaneous net CO₂ uptake decreased rapidly during August–September. The warm and dry growing period in 1997 with a low water table (13–23 cm below the peat surface) promoted ecosystem respiration, which reached its maximum rate for the whole experiment. Although respiration had already started to decrease in August, the daytime net CO₂ uptake occasionally changed to net CO₂ release in August–September, especially in both mini-FACE treatments. The summer of 1998 was wetter, and the water table was only 5–10 cm below the peat surface. Thus, the rates of gross photosynthesis, ecosystem respiration, and net CO₂ uptake depended mainly on the seasonal development of temperature and vegetation biomass, increasing from May to the end of the experiment in July. The average snow-time CO₂ release varied from -0.2 to -0.8 mmol m⁻² h⁻¹ during the winters of 1996–97 and 1997–98 independent of the treatment (Figure 4).

The covariate, vascular plant coverage, was statistically significant ($P = 0.027$) only in repeated-measures analysis of net CO₂ uptake between the raised CO₂ and air ventilation plots. The covariance-corrected averages differed significantly from the control in the case of gross photosynthesis and net CO₂ uptake in the raised CO₂ experiment (Table 3). Other comparisons indicated no differences between the treatments and their controls.

Table 1. Relative Proportion (%) of Litter and Main Species of All Hits in the Individual Point-Quadrat Areas

Vascular Plant	Treatment	1996	1997	1998
Litter (mainly dead <i>E. vaginatum</i> leaves)	Raised CO ₂	62 ± 3	59 ± 3	51 ± 5
	Air ventilation	61 ± 2	53 ± 2	47 ± 3
	NH ₄ NO ₃ addition	61 ± 3	57 ± 2	47 ± 5
	Water addition	64 ± 2	56 ± 3	45 ± 4
<i>Eriophorum vaginatum</i> + <i>Carex pauciflora</i>	Raised CO ₂	29 ± 2	31 ± 4	31 ± 5
	Air ventilation	32 ± 3	34 ± 2	35 ± 4
	NH ₄ NO ₃ addition	29 ± 4	30 ± 3	32 ± 3
	Water addition	27 ± 2	30 ± 3	31 ± 4
<i>Vaccinium oxycoccos</i>	Raised CO ₂	4 ± 1	5 ± 1	8 ± 2
	Air ventilation	5 ± 1	8 ± 1	9 ± 2
	NH ₄ NO ₃ addition	4 ± 1	6 ± 2	11 ± 2
	Water addition	4 ± 1	7 ± 1	12 ± 3
<i>Scheuchzeria palustris</i>	Raised CO ₂	3 ± 2	2 ± 1	6 ± 3
	Air ventilation	1 ± 1	1 ± 1	3 ± 1
	NH ₄ NO ₃ addition	1 ± 1	3 ± 1	2 ± 1
	Water addition	3 ± 1	3 ± 2	6 ± 3

Mean ± standard error of mean, *n* = 5

Table 2. Average (± SE, *n* = 5) Aboveground Necromass and Biomass in the Point-Quadrat Areas (g DW/m²), Total Belowground Biomass at the Depth of 0–50 cm in the Study Plots (g DW/m²), and Total K, Ca, Mg, P, and N Concentrations at the Depth of 25–30 cm in the Study Plots (µmol/g DW) at the End of the Experiment

	Treatment			
	Raised CO ₂	Air Ventilation	NH ₄ NO ₃ Addition	Water Addition
Aboveground necromass	40 ± 5	41 ± 4	39 ± 5	30 ± 3
Aboveground biomass, aerenchymatous	50 ± 6	45 ± 9	45 ± 9	47 ± 5
Aboveground biomass, nonaerenchymatous	35 ± 8	28 ± 4	38 ± 6	26 ± 6
Belowground biomass, aerenchymatous	131 ± 39	102 ± 26	85 ± 16	150 ± 32
Belowground biomass, nonaerenchymatous	169 ± 36	170 ± 36	201 ± 31	147 ± 30
Potassium (K)	2.9 ± 0.2	3.3 ± 0.2	2.9 ± 0.2	3.0 ± 0.3
Calcium (Ca)	53 ± 3	55 ± 1	57 ± 4	59 ± 1
Magnesium (Mg)	14 ± 1	15 ± 1	14 ± 1	15 ± 0
Phosphorus (P)	21 ± 1	23 ± 1	21 ± 1	21 ± 1
Nitrogen (N)	1099 ± 69	1261 ± 77	1236 ± 96	1243 ± 66

Biomasses are shown separately for aerenchymatous (*Eriophorum vaginatum*, *Carex lasiocarpa*, *C. limosa*, *C. pauciflora*, and *Scheuchzeria palustris*) and nonaerenchymatous (*Andromeda polifolia*, *Vaccinium oxycoccos*, *Drosera rotundifolia*, and *Pinus sylvestris*) species.

Reconstructed C Gas Balance for 1997

Irradiance and peat temperature at the depth of 2 cm (Eq. [1]) explained 39%–73% of the variation in gross photosynthesis in each plot (Table 4). Correspondingly, peat temperature and the depth of the water table (Eq. [2]) explained 52%–82% of the variation in ecosystem respiration. For the period from 5 May to 20 October, both the reconstructed gross photosynthesis and respiration were

higher for the raised CO₂ and NH₄NO₃ treatments than for their controls, but only the increase in gross photosynthesis under raised CO₂ and raised NH₄NO₃ supply were statistically significant (Table 5). The off growing season estimates of net CO₂ release in 1997 (1 January–4 May and 21 October–31 December) were rather similar for all the treatments. The estimated annual CH₄ release for 1997 in Table 5 has been taken from Saarnio and

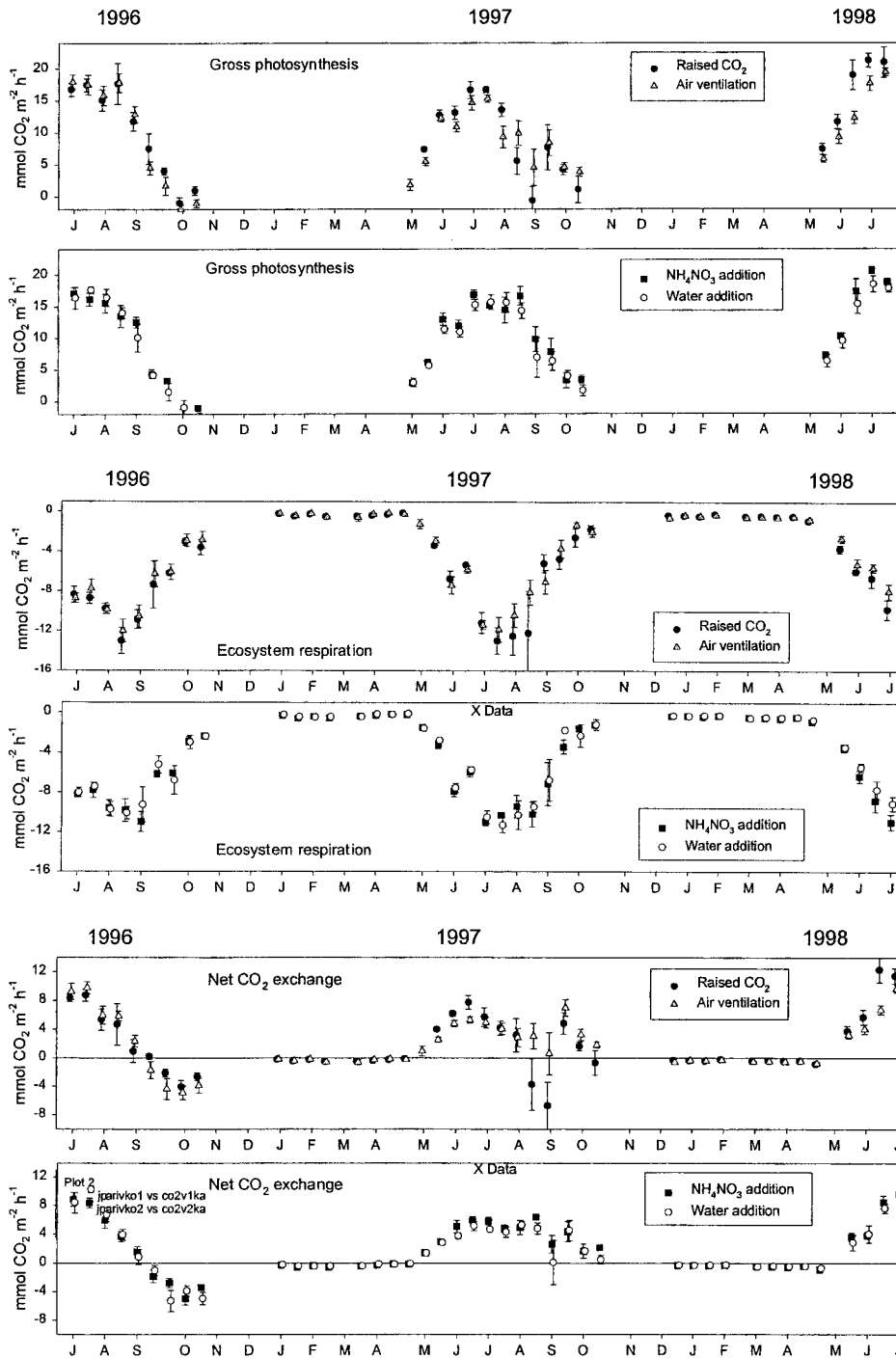


Figure 3. Two-week average (\pm SE) gross photosynthesis in the raised CO₂ and air ventilation plots (*upper panel*) and in the raised NH₄NO₃ supply and water addition plots (*lower panel*) during 1996–98. Positive values indicate C gain to the ecosystem.

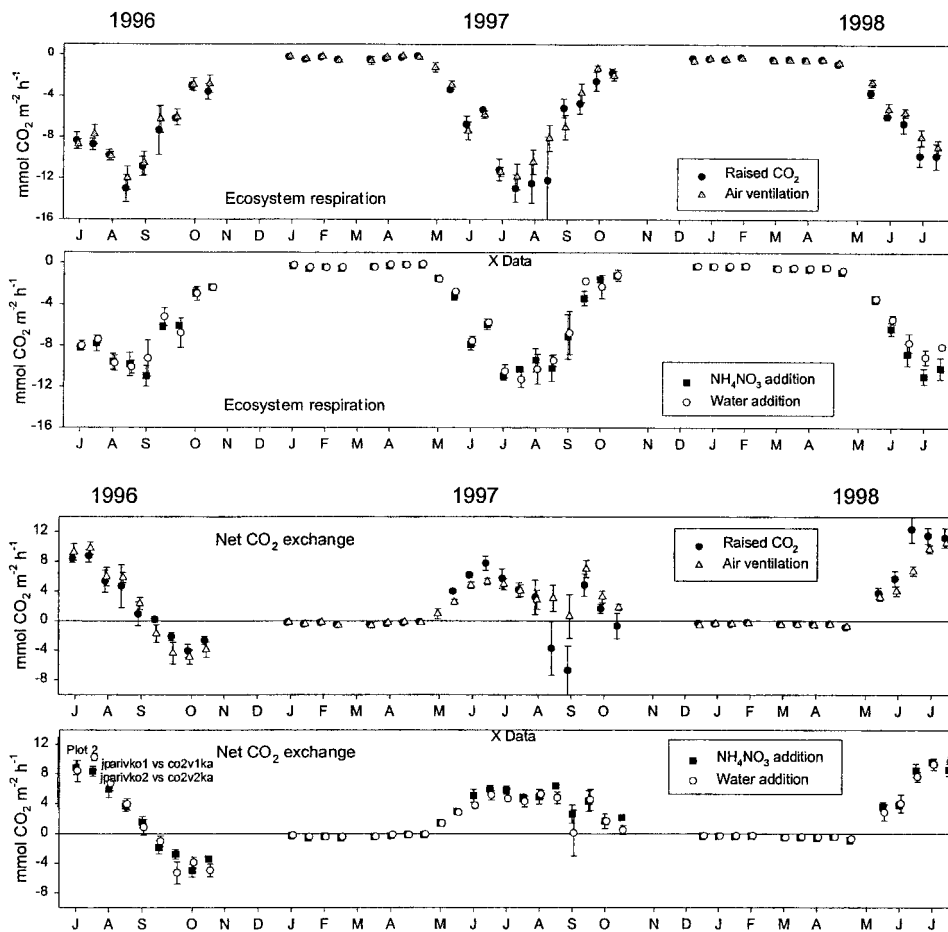


Figure 4. Two-week average (\pm SE) daytime ecosystem respiration in the raised CO₂ and air ventilation plots (*upper panel*) and in the raised NH₄NO₃ supply and water addition plots (*lower panel*) during 1996–98. Negative values indicate C loss from the ecosystem.

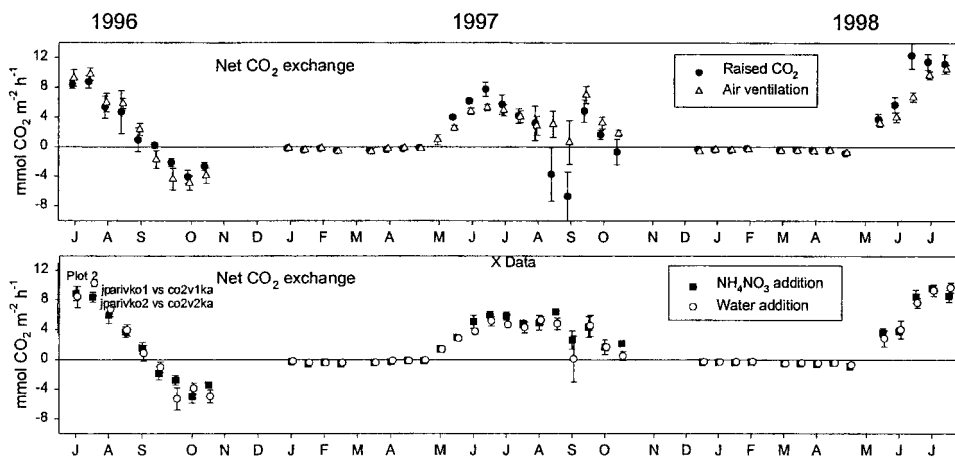


Figure 5. Two-week average (\pm SE) net CO₂ exchange in the raised CO₂ and air ventilation plots (*upper panel*) and in the raised NH₄NO₃ supply and water addition plots (*lower panel*) during 1996–98. Positive and negative values indicate C gain to and C loss from the ecosystem, respectively.

others (2000). The summarized whole-year net CO₂ and total C gas exchange was negative in both mini-FACE treatments and positive in the NH₄NO₃ and water addition treatments. The differences between the treatments and their controls in the annual C gas balance were statistically nonsignificant, although raised CO₂ increased both the CO₂ and CH₄ fluxes.

DISCUSSION

A Raised CO₂ Supply Slightly Amplified C Gas Exchange

The relative proportion of individual plant species (Figure 2, Table 1) and the amount of aboveground vegetation (Table 2) did not change significantly under raised CO₂ conditions, as has also been ob-

Table 3. Average Rate of Gross Photosynthesis, Ecosystem Respiration, and Net CO₂ Uptake (mmol m⁻² h⁻¹) and Average Water Table, Peat Temperature at a Depth of 2 cm, and Irradiation in the Data of the Repeated-Measures Analysis

Variables	Treatment			
	Raised CO ₂	Air Ventilation	NH ₄ NO ₃ Addition	Water Addition
Gross photosynthesis	17.5 ^a	14.3	16.4	15.7
Ecosystem respiration	8.8	8.2	9.0	8.8
Net CO ₂ uptake	8.8 ^a	6.4	7.4	7.0
Water table, cm	-15.6	-16.5	-16.6	-16.3
Peat temperature (-2 cm), °C	19.5	19.7	19.8	20.7
Irradiation μmol m ⁻² s ⁻¹	946	1026	955	1010

Within-subject factor, measurement time, was always significant ($P \leq 0.05$), except in the case of irradiation in the CO₂ experiment; whereas within-subject by between-subject interaction, measurement time* treatment, and within-subject by covariate interaction, measurement time* vascular plant coverage, were never significant. The covariate, vascular plant coverage, was significant only in the case of net CO₂ uptake in the CO₂ experiment. Between-subject factor, treatment, was significant in the case of gross photosynthesis and net CO₂ uptake in the CO₂ experiment.

Italics indicate covariance-corrected average.

^aSignificant ($P < 0.05$) difference from appropriate control

Table 4. Parameter Values for the Regressions of Gross Photosynthesis (Eq. [2]) and Ecosystem Respiration (Eq. [3]) for Each Study Plot

Treatment	Collar	Gross Photosynthesis				Ecosystem Respiration				
		Q	K	R ²	df _{reg, res}	a	b	c	R ²	df _{reg, res}
Raised CO ₂	1	1.39	369	0.67	2,43	0.289	0.106		0.76	1,43
	2	0.94	109	0.53	2,45	-0.299	0.112	-0.050	0.69	2,44
	3	1.12	181	0.68	2,54	-0.093	0.087	-0.043	0.79	2,53
	4	1.05	209	0.63	2,45	0.209	0.112		0.59	1,45
	5	1.27	171	0.49	2,44	0.461	0.077	-0.024	0.61	2,43
Air ventilation	6	1.18	217	0.65	2,67	0.167	0.107		0.69	1,67
	7	1.08	233	0.39	2,52	0.014	0.129		0.69	1,52
	8	0.76	125	0.53	2,58	-0.467	0.099	-0.053	0.72	2,57
	9	1.01	127	0.52	2,64	-0.263	0.107	-0.025	0.67	2,63
	10	1.01	138	0.51	2,66	0.078	0.124		0.73	1,66
NH ₄ NO ₃ addition	11	1.19	175	0.73	2,66	-0.292	0.138		0.80	1,66
	12	1.06	196	0.61	2,65	0.130	0.109		0.64	1,65
	13	0.92	89	0.57	2,61	-0.081	0.115		0.74	1,61
	14	0.98	83	0.42	2,57	0.398	0.100		0.52	1,57
	15	1.02	112	0.63	2,48	0.155	0.140	0.031	0.74	2,47
Water addition	16	1.24	336	0.67	2,50	-0.109	0.128		0.80	1,50
	17	0.91	96	0.73	2,59	-0.270	0.135		0.82	1,59
	18	0.87	77	0.49	2,58	-0.414	0.127		0.65	1,58
	19	0.90	88	0.67	2,49	-0.032	0.118		0.72	1,49
	20	0.88	97	0.62	2,54	-0.084	0.116		0.73	1,54

Degree of determination (R²) and model degrees of freedom (df) for regression (reg) and residuals (res)

served in similar experiments in the Netherlands, Sweden, and Switzerland (Berendse and others 2001; Heijmans and others 2001). However, during the second and third growing season, both the uptake and release of CO₂ (Figures 3 and 4) and the release of CH₄ (Saarnio and others 2000) increased on the plots with raised CO₂. Correspondingly, in

two laboratory experiments with wetland species, enhanced CO₂ assimilation was not seen as an increase in biomass, whereas CH₄ release was promoted by 100%–150% (Hutchin and others 1995; Megonigal and Schlesinger 1997). In other types of ecosystems (rice paddy, grasslands, prairie), the effects of raised CO₂ on C cycling have remained

Table 5. Estimated Average (\pm SE, $n = 5$) Gross Photosynthesis, Ecosystem Respiration, Net CO₂ Exchange, and CH₄ Release in 1997 under the Raised CO₂, Air Ventilation, NH₄NO₃ Addition, and Water Addition treatments

	Treatment			
	CO ₂	Air	NH ₄ NO ₃	Water
1 January–4 May				
Respiration	<i>-1.0 ± 0.1</i>	<i>-1.0 ± 0.1</i>	<i>-1.0 ± 0.1</i>	<i>-0.9 ± 0.0</i>
5 May–20 October				
Gross photosynthesis	<i>25.5 ± 0.8^a</i>	<i>21.9 ± 0.8</i>	<i>24.8 ± 0.6^a</i>	<i>23.1 ± 0.2</i>
Respiration	<i>-24.0 ± 1.2</i>	<i>-21.4 ± 1.2</i>	<i>-20.5 ± 0.8</i>	<i>-19.1 ± 1.2</i>
Net CO ₂ exchange	<i>1.5 ± 0.8</i>	<i>0.4 ± 0.8</i>	<i>4.4 ± 0.6</i>	<i>4.0 ± 1.0</i>
21 October–31 December				
Respiration	<i>-1.1 ± 0.2</i>	<i>-1.1 ± 0.2</i>	<i>-0.8 ± 0.1</i>	<i>-0.6 ± 0.1</i>
Whole year 1997				
Net CO ₂ -C exchange	<i>-0.5 ± 0.8</i>	<i>-1.7 ± 0.8</i>	<i>2.6 ± 0.7</i>	<i>2.5 ± 1.1</i>
CH ₄ -C release	<i>-1.3 ± 0.1</i>	<i>-1.0 ± 0.1</i>	<i>-0.9 ± 0.1</i>	<i>-0.9 ± 0.1</i>
Total C gas exchange	<i>-1.8 ± 0.8</i>	<i>-2.7 ± 0.8</i>	<i>1.7 ± 0.7</i>	<i>1.7 ± 1.1</i>

All estimates expressed as mol C/m²

Italics indicate covariance-corrected value.

Annual estimates for CH₄-C release taken from Saarnio and others (2000)

^aSignificant ($P < 0.05$) difference from appropriate control

relatively small and varied according to the weather or between subsites dominated by different species (Williams and others 2000; Craine and others 2001; Grünzweig and Körner 2001; Reich and others 2001; Sakai and others 2001).

The small increase in the ecosystem respiration, which consists mainly of decomposition (for example, see Glenn and others 1993; Silvola and others 1996), and the increase in CH₄ efflux (Saarnio and others 2000) under raised CO₂ may be explained by a change in the C allocation pattern and decomposition conditions. Different plant species have been shown to increase C allocation to the roots and into the adjacent soil (for example, see van Ginkel and others 1997; Williams and others 2000; Reich and others 2001) and to accelerate the turnover of roots (Pregitzer and others 1995) under raised CO₂. In addition to new, easily degradable substrates for the microbes, the living roots make the conditions in the rhizosphere more favorable for microbes and thus may promote the decomposition of the surrounding organic material (Cheng and Coleman 1990; Mary and others 1993). New litter produced under a raised supply of CO₂ has often been assumed to be more resistant to decomposition due to the decrease in N content and the increase in lignin content; however, according to the synthesis of Norby and others (2001), neither mass loss nor respiration rates from litter produced in raised CO₂ concentrations have shown any consistent pattern

or differences compared to litter from plants grown in ambient CO₂.

The change in the net CO₂ exchange depended on the depth of the water table, as also reported in a study by Billings and others (1983) of monoliths cored from tundra. During wet periods, the net CO₂ uptake was highest under a raised supply of CO₂. In contrast, the net CO₂ exchange was often negative (that is, C was lost from the ecosystem) during the daytime, especially in the raised CO₂ and air ventilation plots during the warm and dry midsummer in 1997 (Figure 5). Similar daytime net CO₂ release with low water tables has also been observed in different microsites of an *S. fuscum* bog (Alm and others 1999b).

The Mini-FACE Effect

Some of the changes in gas exchange under the raised CO₂ treatment seem to have been caused by the air venting procedure. In the case of CH₄ release, the air flow appeared to account for one-half of the increase observed in the raised CO₂ treatment (Saarnio and others 2000). Because the whole growing season of 1997 was exceptionally dry, the net CO₂ uptake was lowered in all treatments (Figure 5). The water table had already begun to fall in May, but the lower temperature and some rainfall episodes (Figure 1) probably helped to keep the moss layer moist during June. In July, there were six rainfall episodes of over 5 ml d⁻¹ that occurred

both in the beginning and at the end of the month. In August, the rainfall was only 56% of that in July, and only two episodes were over 5 ml d⁻¹. During this period, gross photosynthesis declined drastically in both the raised CO₂ and air ventilation treatments (Figure 3).

One possible explanation could be enhanced evaporation under a continuous air flow. In addition, the mini-FACE plots were not sprayed with 2000 ml water every 3 weeks, as was the case for the NH₄NO₃ and water addition plots. When the water table is low and evaporation is high, the *Sphagnum* mosses, especially the lawn and hollow species, may suffer from a water deficit, even though they can retain water and transport it externally from deeper in the peat. The decrease in CO₂ assimilation is steep when the water content of *Sphagnum* species decreases below the optimum for photosynthesis (Silvola and Aaltonen 1984; Schipperges and Rydin 1998). Thus, even a small reduction in the water content of peat mosses could have caused the decline in photosynthesis in both mini-FACE treatments, even though the depth of the water table did not differ significantly between the treatments.

Minor Effects of NH₄NO₃ Addition

The composition of the moss layer changed during the experiment (Figure 2). *S. balticum* may have suffered more than *S. papillosum* from the low water tables in 1996 and especially in 1997, showing a general decline in all treatments, even though Økland (1990) describes *S. balticum* as a stress-tolerant competitor. All three species have a rather broad, overlapping niche, but *S. papillosum* and *S. magellanicum* prefer higher nutrient availability than *S. balticum* (Økland 1990). This could explain why *S. magellanicum* and especially *S. papillosum* became more abundant at the expense of *S. balticum* in the NH₄NO₃ addition plots.

In principle, increased N availability should favor vascular plants at the expense of *Sphagnum* mosses adapted to nutrient-poor conditions (Press and others 1986; van Breemen 1995), increase C allocation into the aboveground parts of vascular plants (Hocking and Meyer 1985; Reich and others 2001), increase growth and litter production (for example, see Jauhiainen and others 1994, 1999; Reich and others 2001), and lower the C/N ratio in the litter (Coulson and Butterfield 1978; Aerts and others 1992; Aerts and de Caluwe 1999). All these possible changes suggest that gas exchange rates should increase. However, no other changes in the vegetation, except for the pronounced replacement of *S. balticum* by *S. papillosum*, were seen during the ex-

periment (Table 1 and Figure 2). This is in agreement with the small differences in CO₂ fluxes between the NH₄NO₃ and water addition plots. Similarly, the weekly average CH₄ efflux varied both above and below the control value throughout the experiment in the NH₄NO₃ treatment (Saarnio and others 2000). Correspondingly, Nykänen and others (2002) did not find any significant increase in ecosystem respiration on a *Sphagnum fuscum* pine bog after 6 years of addition of 3 or 10 g N m⁻² a⁻¹. However, CH₄ release increased during the final 2 years, most probably due to the increase in the coverage of *E. vaginatum*. In contrast, Granberg and others (2001) found a significant decrease in CH₄ release despite the increase in sedge cover under 3-year exposure to N addition of 3 g m⁻² a⁻¹.

Probably the moderate amount of extra N, even though it was about 10 times higher than the estimated wet deposition in the study area (Ruoho-Airola and others 1998), low ambient N deposition, that is, no N saturation in mosses (Berendse and others 2001),—and the relatively short exposure time (Nykänen and others 2002) are the main reasons for the minor changes in the vegetation and gas exchange. *Sphagnum* mosses are known to effectively accumulate N in their capitula (Damman 1978; Press and others 1986; Jauhiainen and others 1998); thus, it is possible that they hinder vascular plants and microbes from benefiting from the enhanced N supply. The peat mosses themselves seemed to benefit from the N addition, because their chlorophyll content increased under the elevated NH₄NO₃ supply compared to that in the control (data not shown).

Annual C Gas Exchange

At the beginning of the 1997 growing period, the rates of gross photosynthesis and dark ecosystem respiration were of the same order of magnitude as earlier measurements made in a similar microsite on the same mire in 1993 (Alm and others 1997). In July–August, the weather was exceptionally warm and dry (Finnish Meteorological Institute 1997c, Finnish Meteorological Institute 1997d) compared to the long-term (1960–90) averages in the study region, resulting in a greatly decreased gross photosynthesis, increased ecosystem respiration, and thus diminished net C accumulation. Although the summertime CH₄ release in 1997 (Saarnio and others 2000) was lower than that during the very wet growing season in 1993 (Saarnio and others 1997), and the winter respiration in 1997 was lower than that in winter 1994–95 (Alm and others 1999a), the estimated C accumulation rate for the whole of 1997 remained much lower than

that for 1993 (Alm and others 1997) independent of the treatment.

The average net C gas exchange in 1997 showed a net loss in the raised CO₂ and air ventilation treatments, and a net gain in the NH₄NO₃ addition and water addition treatments (Table 5). The negative C balance in both mini-FACE treatments was a result of decreased gross photosynthesis during August and September (Figure 3). The significantly higher gross photosynthesis in the raised CO₂ and NH₄NO₃ treatments compared to their control was compensated by an increase in decomposition, and the annual C gas balance for 1997 did not differ from the control in either treatments (Table 5). To obtain an estimate of the total C balance in the mire, C gas exchange in the other microsites and C losses through leaching should be included in the calculations.

Methane is 6.5–56 times more effective than CO₂ as a greenhouse gas, depending on the time scale (Houghton and others 1996). The increase in net CO₂ uptake should thus be as many times higher compared to the increase in CH₄ release before it can compensate for the effects on radiative forcing. In this study, both gross photosynthesis and ecosystem respiration increased under CO₂ enrichment, resulting in a lowered net CO₂ uptake in 1997; whereas the CH₄ release increased by about 16% (Saarnio and others 2000). This suggests that the feedback for an increasing CO₂ concentration would be positive—that is, the radiative forcing in the atmosphere would increase, and thus the greenhouse effect would strengthen. However, in years with a wet growing period (for example, 1998), the small increase in net CO₂ uptake (Figure 5) might be sufficient to compensate for the increase in CH₄ release. This was tested by assuming, on the basis of measurements made in the wet year 1998, that the gross photosynthesis, ecosystem respiration, and CH₄ release increases during the summertime by 12.5%, 8%, and 16%, respectively, and that the C gas exchange in the air ventilation would have been equal to the wet-year estimate for a similar microsite in the same mire (Alm and others 1997). The annual net CO₂-C uptake increased by 2.3 mol/m², and the CH₄-C release increased by 0.3 mol/m². Thus, the net effect of changes on the radiative forcing would have been decreasing with a time horizon of 500 years (coefficient 6.5).

Other Ecosystems

The response of different ecosystems to similar changes in the regulating factors varies depending on the climatic (for example, rainfall, temperature, irradiation) and geographical (for example, latitude,

exposition, soil type) conditions regulating and limiting the function of the ecosystem, and the time scale of the experiment. Uniform response to the increasing atmospheric CO₂ concentration or N supply cannot be expected across all the ecosystems on the planet. In some experiments, the response of the ecosystem to an increase in the availability of CO₂ has been a significant increase in production (desert, *Bromus madritensis* and *Eriogonum inflatum*, Huxman and Smith 2001; forest, *Pinus taeda*, Hamilton and others 2002) or small/no response (semi-aridgrassland, Grünzweig and Körner 2001; lake shore, *Equisetum fluviatile*, Ojala and others 2002). Correspondingly, decomposition has either increased (tallgrass prairie, Williams and others 2000) or the response has remained negligible (pasture, *L. perenne*, Ineson and others 1998; forest, *P. taeda*, Hamilton and others 2002) under a raised CO₂ supply. A raised N supply may also either increase production (field, *L. perenne*, Daepf and others 2001; field, *Oryza sativa*, Kim and others 2001) or decomposition (deciduous forest, Phillips and others 2002) or have no effect (subarctic health and arctic drained fen, Christensen and others 1998; forest, *Pinus sylvestris*, Sjöberg and Persson 1998). The coexistent change in both the CO₂ and N availability or other factors further complicates any estimates of how the global C balance will change in the future.

SUMMARY

Our results indicate that, under increased NH₄NO₃ deposition, the change in vegetation and increase in C gas exchange in lawns of boreal oligotrophic mires would be very small, at least over the short term. In addition, they suggest that gross photosynthesis, as well as CH₄ release (Saarnio and others 2000), would increase under increasing atmospheric CO₂ concentration in boreal oligotrophic mire lawns. In contrast, the change in the net CO₂ uptake would depend on the prevailing weather conditions. In wet years, C accumulation would probably increase, whereas a relatively dry and warm growing period would favor (aerobic) decomposition and thus diminish the net C gain or even turn the balance negative. Along with the increased release of CH₄, the decreased C accumulation would increase the radiative forcing of boreal mires. In wet years, on the other hand, the increased C accumulation would probably compensate for the increased CH₄ release, and radiative forcing might remain unchanged or even decrease. This kind of relatively short-term experiment with a step change, in comparison with a long-term tran-

sitional change in atmospheric CO₂, probably reveals the maximal response of the ecosystem. However, long-lasting experiments are needed to verify the long-term changes in the C balance.

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