Effects of elevated CO_2 and N deposition on CH_4 emissions from European mires

J. Silvola,[1] S. Saarnio,[1] J. Foot,[2] I. Sundh,[3] A. Greenup,[4] M. Heijmans,[5] A. Ekberg,[6] E. Mitchell,[7,8] and N. van Breemen[9]

[1]   Methane fluxes were measured at five sites representing oligotrophic peatlands along a European transect. Five study plots were subjected to elevated CO_2 concentration (560 ppm), and five plots to NH_4NO_3 (3 or 5 g N yr^{-1}). The CH_4 emissions from the control plots correlated in most cases with the soil temperatures. The depth of the water table, the pH, and the DOC, N and SO_4 concentrations were only weakly correlated with the CH_4 emissions. The elevated CO_2 treatment gave nonsignificantly higher CH_4 emissions at three sites and lower at two sites. The N treatment resulted in higher methane emissions at three sites (nonsignificant). At one site, the CH_4 fluxes of the N-treatment plots were significantly lower than those of the control plots. These results were not in agreement with our hypotheses, nor with the results obtained in some earlier studies. However, the results are consistent with the results of the vegetation analyses, which showed no significant treatment effects on species relationships or biomass production.   INDEX TERMS: 1055 Geochemistry: Organic geochemistry; 1040 Geochemistry: Isotopic composition/chemistry; 0330 Atmospheric Composition and Structure: Geochemical cycles; 0322 Atmospheric Composition and Structure: Constituent sources and sinks; KEYWORDS: elevated CO_2, N deposition, methane, European peatlands

Citation: Silvola, J., S. Saarnio, J. Foot, I. Sundh, A. Greenup, M. Heijmans, A. Ekberg, E. Mitchell, and N. van Breemen, Effects of elevated CO_2 and N deposition on CH_4 emissions from European mires, *Global Biogeochem. Cycles*, *17*(2), 1068, doi:10.1029/2002GB001886, 2003.

1.   Introduction

[2]   Peatlands are generally considered to be sinks for CO_2 and sources for CH_4 [*Gorham*, 1991; *Bartlett and Harriss*, 1993]. The fluxes and balances of these two biogenic greenhouse gases are tightly interconnected in the biospheric carbon cycle [*Mosier*, 1998]. The climatic net effect of the fluxes from an individual mire or peatland area may vary from warming to cooling depending on the mire type, weather conditions and timescale under consideration [*Korhola et al.*, 1996; *Laine et al.*, 1996]. During the industrial period, the greatest increase in biogenic greenhouse gases has been in the concentration of methane, ∼145%. In the anticipated climatic change, the contribution of methane has been estimated to be ∼25% [*Houghton et al.*, 1996]. The level of global methane emissions to the atmosphere is now about 540 Tg yr^{-1}, of which ∼40% originates from soils, and half of this is emitted from natural wetlands [*Mosier*, 1998]. The emission estimate for northern peatlands is about 40 Tg CH_4 yr^{-1} [*Bartlett and Harriss*, 1993].

[3]   The characteristics of peatlands vary due to regional and local environmental factors [*Overbeck*, 1975; *Gore*, 1983; *Succow and Jeschke*, 1990], and these differences are also reflected in their methane emissions. Important regulating factors are temperature, the water level and nutrient status [*Moore and Dalva*, 1993; *Nykänen et al.*, 1998; *Bellisario et al.*, 1999]. The rate of primary production and CH_4 fluxes have been shown to correlate across different types of wetland [*Whiting and Chanton*, 1993]. In recent decades the human impact on wetlands has been very strong, especially in densely populated areas [*Bragg et al.*, 1992]. In western and central Europe, for instance, only a small proportion of the peatlands (originally millions of hectares) are still in a natural state [*Succow and Jeschke*, 1990]. Various human activities have either increased soil CH_4 emissions (e.g., rice paddies [*Cole et al.*, 1996]) or decreased them (e.g., as a result of peatland drainage

[1]Department of Biology, University of Joensuu, Joensuu, Finland.
[2]Scottish Environmental Protection Agency, Stirling, Scotland, UK.
[3]Department of Microbiology, Swedish University of Agricultural Sciences (SLU), Uppsala, Sweden.
[4]Department of Animal and Plant Sciences, University of Sheffield, Sheffield, UK.
[5]Wageningen University, Nature Conservation and Plant Ecology Group, Wageningen, Netherlands.
[6]Lund University, Department of Physical Geography and Ecosystem Analysis, Lund, Sweden.
[7]Department of Plant Ecology, Institute of Botany, University of Neuchâtel, Neuchâtel, Switzerland.
[8]Now at Department of Biological Sciences, University of Alaska Anchorage, Anchorage, Alaska, USA.
[9]Wageningen Agricultural University, Department of Soil Science and Geology, Wageningen, Netherlands.

[*Roulet and Moore*, 1995; *Nykänen et al.* [1998]). Some drained wetlands have been restored, and the development of a mire vegetation and peat accumulation have started on top of the old dry peat [*Grosvernier et al.*, 1995, 1997; *Tuittila et al.*, 2000b]. However, the reestablishment of biogeochemical soil processes takes a considerable period of time, and restored drained areas may therefore have lower CH$_4$ emissions even though the water table is at the same depth as that in corresponding virgin sites [*Nykänen et al.*, 1998; *Tuittila et al.*, 2000a].

[4] Global change can affect methane emissions in several ways. Climate warming may increase methanogenesis, but the reduction in soil moisture predicted by some scenarios would nevertheless depress emissions [*Manabe and Wetherald*, 1986; *Mitchell*, 1989; *Roulet et al.*, 1992]. Increased nitrogen deposition may cause a shift toward more fertile mire types, with higher CH$_4$ emissions, while in some sites it may lead to a decrease in CH$_4$ production or oxidation [*Crill et al.*, 1994; *Aerts and de Caluwe*, 1999].

[5] Elevated atmospheric CO$_2$ has been shown to increase photosynthesis and plant biomass production in the short term [*Eamus and Jarvis*, 1989], but less so in the longer term [*Tissue and Oechel*, 1987; *Jauhiainen and Silvola*, 1999]. In addition to the peaty organic matter itself, fresh plant litter and root exudates are important substrates for methane production in peatlands [*Schütz et al.*, 1991]. Thus the link between the atmospheric CO$_2$ concentration and methanogenesis via photosynthesis is theoretically obvious. In some recent experiments a doubling of the CO$_2$ concentration increased methane emissions by as much as 145% [*Hutchin et al.*, 1995]. A decrease in methane oxidation has also been observed at elevated CO$_2$ concentration [*Ineson et al.*, 1998]. As concluded by *Megonigal and Schlesinger* [1997], this would mean a dramatic increase in the CH$_4$ load, since soils account for $\sim$40% of globally emitted CH$_4$, and soil methane oxidation plays an important role in the global CH$_4$ balance [*Whalen and Reeburgh*, 1990; *Mosier*, 1998]. *Saarnio et al.* [1998], in contrast, found only a small effect of doubled CO$_2$ concentrations on methane emission from mire microcosms kept at temperatures prevailing in boreal mires.

[6] In order to test the effects of elevated CO$_2$ concentration and nitrogen deposition on methane emissions from mires in real field conditions, methane fluxes were measured in five experimental sites representing mires along a European transect.

[7] Our hypotheses were that (1) an elevated CO$_2$ concentration increases methane emissions; (2) the CO$_2$ effect increases with increasing temperature; and (3) the effect of N application on CH$_4$ emissions depends on the nutrient status and level of N deposition on peatlands. We tested these hypotheses in the BERI project [*Hoosbeek et al.*, 1996], in which we studied the responses of mire vegetation and biogeochemical soil processes to elevated CO$_2$ and N during three successive growing seasons.

2. Material and Methods
2.1. Study Sites
[8] Experimental sites were established in Switzerland (CH), Finland (FIN), the Netherlands (NL), Sweden (SE)

and the United Kingdom (UK) (Figure 1). The aim was to find as similar sites as possible in all the countries: an ombrotrophic to slightly minerotrophic mire habitat with a vegetation cover of *Sphagnum magellanicum*/*S. papillosum* and *Eriophorum vaginatum*/*E. angustifolium*. For practical reasons (electricity and CO$_2$ supply), the Dutch group had to use peat + vegetation sods, transported from the mire site and installed outdoors close to the laboratory. The locations and some physical and chemical characteristics of the sites are shown in Table 1.

2.1.1. Swiss Site (CH)
[9] The Swiss site (La Chaux-des-Breuleux) is situated in the Jura in the subalpine zone. The mire has developed on impermeable marl deposits in the bottom of a shallow valley. The site is mostly open with some scattered trees (*Pinus uncinata*, *Picea abies*, *Betula carpatica*). The mire is mainly ombrotrophic, with some minerotrophic influences from the surrounding pasture. The mire has been drained and peat was mined up until the end of World War II. Since then, vegetation has reestablished itself through natural regeneration [*Grosvernier et al.*, 1995], and a layer of young, poorly decomposed peat about 30 cm thick has formed. A mosaic of lawn, hummocks and hollows has now developed well with *Eriophorum vaginatum*, *Carex nigra*, *Calluna vulgaris* and *Vaccinium oxycoccus*. The dominant mosses are *Sphagnum fallax* and *Polytrichum strictum*, with *P. commune* and *Aulacomnium palustre* in places.

2.1.2. Finnish Site (FIN)
[10] The site is situated in the Salmisuo mire, near Ilomantsi, within the transition region of the southern and middle boreal zone. The Salmisuo mire complex is an eccentric bog with some minerotrophic strips, and the site is located in the northernmost, slightly minerotrophic part of the mire. According to the Finnish mire classification system, the site is a low-sedge, *Sphagnum papillosum* pine fen consisting of hummock, lawn and hollow microsites [*Ruuhijärvi*, 1983]. The site is almost open, with only a few small scattered pines (*Pinus sylvestris*) on hummocks. All the study plots are situated in the lawn surface, which represents intermediate moisture conditions. Dominating moss species are *Sphagnum papillosum*, *S. balticum S. angustifolium* and *S. magellanicum*, and the most important vascular plants *Eriophorum vaginatum*, *Carex pauciflora*, *C. lasiocarpa*, *Andromeda polifolia* and *Vaccinium oxycoccus*. The site has been described in more detail by *Saarnio et al.* [1997].

2.1.3. Dutch Site (NL)
[11] The peat sods that were used in Wageningen originated from the Dwingeloo State Forestry, in the province of Drenthe in the north of the Netherlands. The peat in this small mire (<1 ha) has developed in a depression formed by a late glacial brook system. Up to 1955 the site was used for peat cutting and, for this reason, the vegetation nowadays consists of a mosaic of secondary successional stages. The peat sods consist of *Sphagnum magellanicum* rich carpets, the other mosses being *S. papillosum*, *S. fallax*, *Aulacomnium palustre* and *Calliergon stramineum*. The dominant vascular plants are *Erica tetralix*, *Vaccinium oxycoccus*, *Eriophorum angustifolium* and *Drosera rotundifolia*. The

Figure 1. The location of the experimental sites: 1 = SE, 2 = FIN, 3 = UK, 4 = NL, 5 = CH.

mire and experimental plots have been described in more detail by *Heijmans et al.* [2001].

2.1.4. Swedish Site (SE)

[12] The Swedish site (Kopparås mire) is situated in the boreonemoral zone in the middle of the province of Småland in southern Sweden. The underlying acidic mineral soil material is derived mainly from gneiss. The mire is largely open, with scattered *Pinus sylvestris* trees. The mire is mostly minerotrophic, with sporadic smaller ombrotrophic areas, and its surface slopes slightly toward the SSW. All the study plots are situated in a lawn habitat dominated by *Eriophorum angustifolium*, *Calluna vulgaris*, *Andromeda polifolia*, *Narthecium ossifragum* and *Scirpus caespitosus*. The predominant peat mosses are *Sphagnum magellanicum*, *S. papillosum* and *S. rubellum*.

2.1.5. British Site (U.K.)

[13] The British site is situated in the Roudsea Wood National Nature Reserve, North West of England, on the northern edge of Morecambe Bay. The reserve contains an extensive area of open ombrotrophic raised bog that has been partially drained in the past. The drainage ditches have been blocked for over a decade and the mire surface is gradually recovering. The vegetation corresponds to an M18 *Erica tetralix* - *Sphagnum papillosum* raised mire of the UK National Vegetation Classification [*Rodwell et al.*, 1991]. *Sphagnum papillosum* is the predominant *Sphagnum* species in the study area. The lawn also contains *Eriophorum vaginatum*, *Calluna vulgaris*, *Andromeda polifolia* and *Erica tetralix* as major species, with small amounts of

Table 1. Location, Climatic Data and Physical and Chemical Characteristics of the Study Sites

Site	Location	Altitude, m Above Sea Level	Precipitation Annual, mm	Temperature Daily Mean of Warmest and Coldest Month, °C	Snow Cover, Days	Peat Depth, m	Mire Water Quality					
							pH	DOC, mg L^{-1}	NO$_3$, mg L^{-1}	NH$_4$, mg L^{-1}	SO$_4$, mg L^{-1}	Cl, mg L^{-1}
FIN	62°47′N, 30°56′E	150	650	16, −10	150–200	1.5	4.43	18.08	0.38	0.00	0.03	0.00
SE	57°08′N, 14°30′E	225	800	16, −2	80–120	2	4.73	21.55	1.47	0.03	21.51	8.43
UK	54°14′N, 03°01′W	5	1800	13, 1	<20	>2	4.47	41.34	1.55	0.46	16.6	11.64
NL	52°49′N, 06°26′E	13	750	18, 3	<10	1	4.72	39.09	0.13	0.92	0.00	7.98
CH	47°13′N, 07°03′E	1000	1390	15, −5	80–120	1.5	4.8	15.38	0.18	0.00	0.01	1.21

Scirpus caespitosus, Rhynchospora alba, Eriophorum angustifolium and *Narthecium ossifragum.*

2.2. Experimental Design

[14] Twenty circular plots (diameter 1 m) were selected to represent lawn surface with homogeneous vegetation. The plots for the four different treatments with five replicates were selected randomly in blocks, apart from the NL site where 20 monoliths were randomly assigned to the different treatments without blocking. The treatments were CO$_2$ enrichment (CO$_2$), an ambient air control for the CO$_2$ treatment (AIR), nitrogen addition (NITROGEN) and a control for the nitrogen treatment (CONTROL). At the FIN and SE sites every block included one plot of each treatment, the distance between the blocks being 5–20 m. At the UK and CH sites, the plots for the CO$_2$ and NITROGEN treatments with their controls were located in two separate areas with minor ecological differences (e.g., in the water table). At the NL site the peat + vegetation monoliths were placed in plastic containers (1.1 m diameter, 60 cm deep) inserted into the soil. At the FIN, SE and UK sites the water table of the measuring plots followed that of the surrounding mire. In the peat monoliths of the NL site, the water levels were allowed to fluctuate between 5 and 20 cm below the moss surface. The CH$_4$ measuring points of the CH site had 80 cm deep collars that blocked lateral drainage, resulting in a somewhat higher water level at the CH$_4$ measuring points compared to the surrounding mire.

[15] For the CO$_2$ and AIR treatments, the plots were enclosed with miniFACE rings (5-cm-diameter tube) with 70 vertical venting pipes (18 cm long). Ambient air was vented by means of fans to these rings via pipes. CO$_2$ from tanks was added to the air flow in the five rings in order to enhance the CO$_2$ concentration to 560 ppm. The CO$_2$ concentration was controlled by sucking sample air from the middle of the rings to an IRGA, and regulating the CO$_2$ supply by PC-controlled mass-flowmeters (for more detail see *Miglietta et al.* [2001]). The nitrogen plots were not enclosed within a miniFACE ring. Nitrogen was added by spraying NH$_4$NO$_3$ onto the plots every 3 weeks (snow-free period) to give a total addition of 3 g N (5 g in the NL site) m^{-2} yr^{-1}. These N additions resulted in at least a doubling of the annual atmospheric N deposition, which varies from 0.4 g N m^{-2} yr^{-1} (Finland) to 3.9 g N m^{-2} yr^{-1} (the Netherlands) [*Berendse et al.*, 2001]. The CONTROL plots were sprayed with the same amount of deionized water (2000 mL) at the same time as the nitrogen treatment.

2.3. Methane Measurements

[16] The study sites were equipped with boardwalks to prevent disturbance of the soil and vegetation during sampling. At the CH, NL, SE and UK sites, permanent plastic collars (diameter 19 cm) with a groove for a water seal were installed on every plot. For methane sampling, water was added to the groove and cylindrical plexiglass chambers of the same diameter (height 28 cm) were fitted onto the collars. Four 10-mL samples were taken at intervals of 5–8 min with a plastic syringe after careful pumping to mix the air in the chamber and tubing (inner diameter 1 mm, length 1.5 m) between the chamber and syringe. The gas in the syringe was immediately transferred to a preevacuated glass flask (9 mL).

[17] At the FIN site, 60 × 60 cm aluminium collars with a groove for a water seal were used because the other measuring systems needed collars of this shape and size. Aluminium chambers (60 × 60 × 20 cm) were fitted onto the collars and four gas samples (40 mL) were taken with syringes during the 20-min measuring period. In order to compare the performance of the different chambers, the FIN site also had small chambers similar to those in the other sites on the CONTROL plots. Glass flasks were not used since the methane concentrations in the syringe samples were analyzed within 24 hours. The samples from all the sites were analyzed with a gas chromatograph using a FI detector. The gas chromatographs used were Shimadzu 14A (FIN), Packard 428 (SE), ATI UNICAM 610 (UK), HP 5710A (NL) and Perkin-Elmer F22 (CH).

[18] The depth of the water level and the air and peat temperatures were measured at the time of sampling. Methane fluxes were measured during the snow-free period (1996–1998 at the FIN, NL and SE sites, 1997–1998 at the UK site, and only during summer 1998 at the CH site) weekly at the FIN site and approximately every 3 weeks at the other sites. Methane fluxes were calculated by linear regression of the CH$_4$ concentrations over time. Only rates having $r^2 >= 0.9$ were accepted.

2.4. Vegetation Analyses

[19] Plant species composition and abundance were measured by the point-quadrat method [*Buttler*, 1992]. A homogeneous subplot (25 × 37.5 cm) was chosen on every plot. For counting, a Plexiglas plate with 150 holes was placed over the subplot. A thin pin was pushed down through the holes and contacts with the plant species were counted. At the end of the experiment (between late July and early September 1998 depending on the site), the vascular plants on the point quadrat areas were harvested. The species were separated, dried (70°C) and weighed. The amount of living belowground biomass was determined from core samples taken from the peat. The vegetation studies have been described in more detail by *Mitchell et al.* [2000], *Berendse et al.* [2001], *Heijmans et al.* [2001] and *Hoosbeek et al.* [2001]. The cover of the most abundant plant species on the different sites is shown in Table 2. The number of shoots of *Carex* and *Eriophorum* species growing in the methane measurement collars were counted on the CH, NL and UK sites.

2.5. Nutrient Analyses

[20] For the analysis of soil water chemistry, samples were taken at the beginning of the growing season in 1996 and in spring, summer and autumn in 1997. DOC, pH and major cations and anions were analyzed at the Wageningen Agricultural University according to *Buurman et al.* [1996]. The sampling method and soil water chemistry are described in more detail by *Mitchell et al.* [2000].

2.6. Statistical Treatments

[21] Factors causing differences in CH$_4$ emissions among different sites were evaluated using data from the CON-

Table 2. Cover of the Most Important Vascular Plant and Moss Species and the Total Covers of Those Plant Groups in the Different Sites[a]

	FIN	SE	UK	NL	CH
			Vascular Plants		
Total cover,%	23	40	40	13	8
Most abundant species (cover% in parentheses)	*Eriophorum vaginatum* (9)	*Eriophorum angustifolium* (18)	*Eriophorum vaginatum* (14)	*Erica tetralis* (5)	*Carex nigra* (3)
	Andromeda polifolia (7)	*Drosera rotundifolia* (6)	*Erica tetralis* (13)	*Vaccinium oxycoccos* (4)	*Eriophorum vaginatum* (3)
			Mosses		
Total cover,%	100	95	79	98	147
Most abundant species (cover% in parentheses)	*Sphagnum balticum* (63)	*Sphagnum magellanicum* (81)	*Sphagnum papillosum* (79)	*Sphagnum magellanicum* (96)	*Sphagnum fallax* (89)
	Sphagnum papillosum (35)	*Sphagnum papillosum* (10)		*Sphagnum papillosum* (1)	*Polytrichum strictum* (58)

[a]Cover percentages have been estimated by the point-intercept and classical vegetation releves methods [*Mitchell et al.*, 2000]. At the Swiss site, *Polytrichum* overtops *Sphagnum*, resulting in a total cover of over 100%.

TROL plots. Dependence of the CH_4 flux on the water table (WT) and on temperature at a depth of 15 cm (T) was calculated by multiple regression. For the UK site, the peat temperature at a depth of 15 cm was calculated as an average of measurements made at depths of 10 and 20 cm. Q_{10} values (10–20°C) of the log-transformed CH_4 emission were calculated in order to compare the temperature dependence at the different sites. CH_4 emissions corrected to a common temperature were used when testing the effect of certain physical and chemical characteristics at the different sites.

[22] On the basis of previous studies, elevated CO_2 was expected to influence methane emission particularly in warm climatic conditions [cf. *Saarnio and Silvola*, 1999; *Saarnio et al.*, 2000]. Therefore the summer time data (weeks 23–32 in 1997 and 1998) were used when testing the effects of the CO_2 and N treatments on CH_4 emission. Three covariates, soil temperature at a depth of 15 cm (T), depth of the water table (WT), and the number (CH, NL and UK sites) or biomass (FIN and SE sites) of shoots of *Carex* and *Eriphorum* species, were tested in the analysis of covariance. If any of the covariates were statistically significant, the analysis was repeated using only this (these) covariate(s). If none of the covariates were statistically significant, the effect of the treatment (CO_2 enrichment or nitrogen addition) on the CH_4 flux was tested using the t-test. In all analyses, $p < 0.05$ was used as the criterion for statistically significant effects.

3. Results
3.1. Methane Emissions in the CONTROL Plots

[23] The average CH_4 emissions (mg CH_4 m^{-2} h^{-1}) of all the CONTROL plot measurements were 6.5 (NL), 4.3 (CH), 2.8 (SE), 2.5 (FIN, large chambers) and 0.45 (UK). In all the sites the CH_4 emissions were highest in the middle of summer, although especially in the UK site the annual variation was very small (Figure 2). Typically the summer time fluxes varied between 6 and 15 mg CH_4 m^{-2} h^{-1} in the NL site, 2 and 7 in the FIN, SE and CH sites and 0.5 and 1 in the UK site.

[24] The dependence of the CH_4 fluxes on soil temperature and moisture varied considerably among the sites. In the analysis of regression, WT and T (at a depth of 15 cm) were significant variables ($p < 0.001$) only in the NL and FIN sites. r^2 was 53% for WT and 57% for T in the NL site, and 4% and 41% in the FIN site, respectively. In the multiple regression, the combined r^2 of WT and T was 68% and 50% for the NL and FIN sites, respectively. The Q_{10} values (peat temperature 10–20°C at a depth of 15 cm) calculated from linear regressions of the log-transformed CH_4 efflux of the CONTROL plots were 6.5, 3.4, 1.5 and 1.1 for the NL, FIN, SE and UK sites, respectively. In the SE and UK sites, however, temperature was not a statistically significant variable. Q_{10} was not calculated for the CH site because of the limited number of measurements with a small temperature range ($\sim$2°C).

[25] The differences in the CH_4 flux between the sites could only be partly explained by the physical and chemical characteristics of the sites. The temperature explained 68% of the variation in the flux rates among the different sites (Figure 3a). A rise in the pH tended to increase emissions and a rise in the DOC, total N and SO_4 concentrations to decrease it. In all cases, however, r^2 was low (Figures 3b–3f).

[26] The small and large chambers gave similar results with low and medium flux rates, except that variability was much higher with small chambers (Figure 4). However, at higher flux rates smaller chambers yielded higher flux rates.

3.2. Effects of the Treatments on Methane Emissions

[27] The CH_4 emissions, temperatures and water tables with their standard errors are shown in Figure 5, and the results of the analysis of covariance in Table 3. At the CH site, CH_4 fluxes from the enhanced CO_2 treatment plots ($\bar{x}$ = 6.6 mg CH_4 m^{-2} h^{-1}) were 23% higher and those from the NITROGEN treatment ($\bar{x}$ = 4.1 mg CH_4 m^{-2} h^{-1}) 43% lower than from the corresponding control plots. None of the covariates or treatment effects were statistically significant.

[28] At the FIN site, CH_4 emission from the enhanced CO_2 plots ($\bar{x}$ = 4.6 mg CH_4 m^{-2} h^{-1}), as well as from the
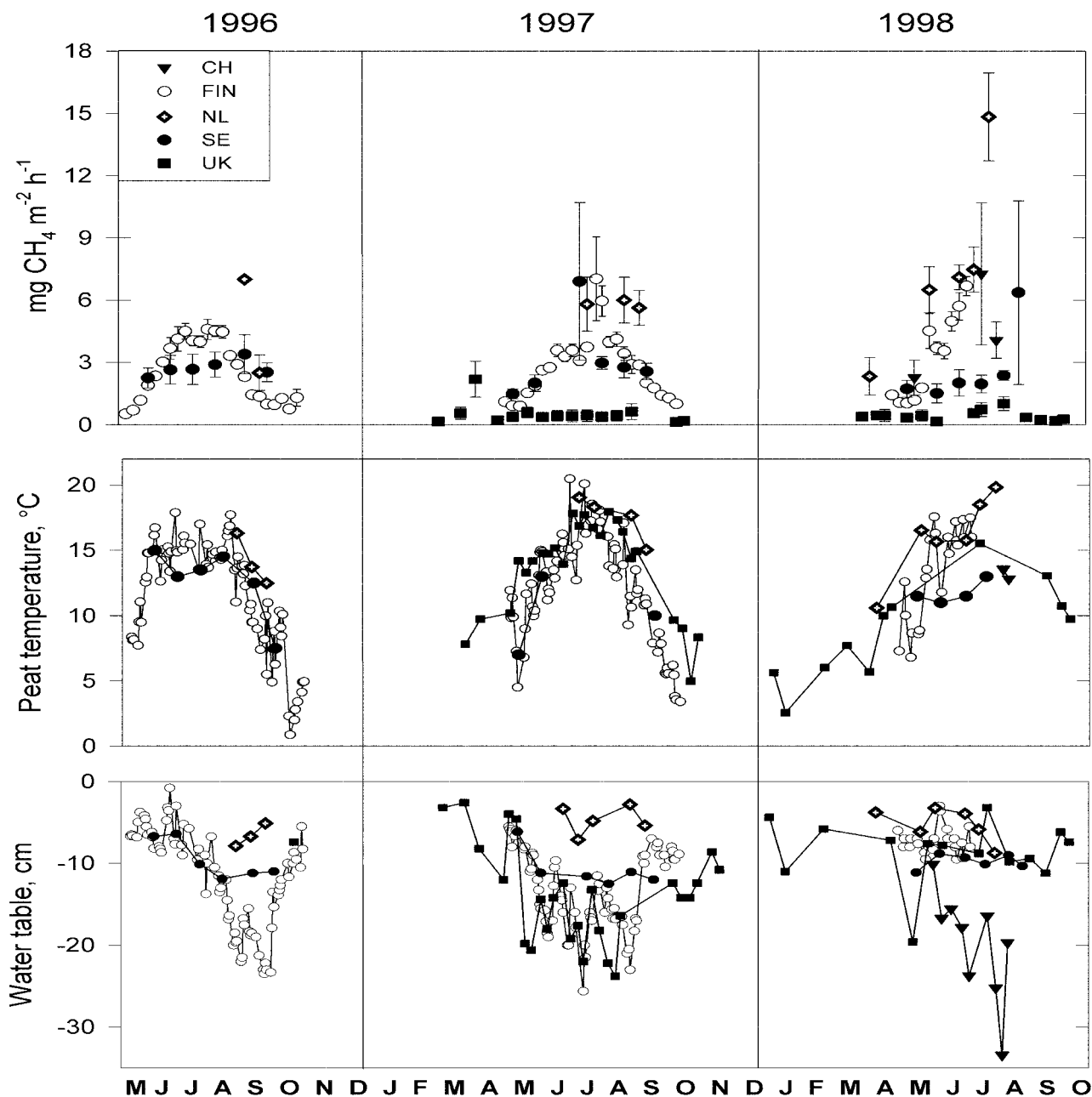
Figure 2. CH_4 fluxes, peat temperature (at a depth of 15 cm in the NL and CH sites, 10 cm in the other sites) and depth of the water table in the CONTROL plots at the different sites, calculated as weekly averages (S.E.).

NITROGEN plots ($\bar{x}$ = 3.5 mg CH_4 m^{-2} h^{-1}), were 14% (elevated CO_2) and 7% (N addition) higher than from the corresponding control plots. In the case of the CO_2 treatment, WT and T were significant covariates and the treatment effect was slightly above the 0.05 significance level (p = 0.085). In the case of the N treatment, none of the covariates and treatment effects were statistically significant.

[29] At the NL site, CH_4 emissions from the CO_2 plots ($\bar{x}$ = 11.0 mg CH_4 m^{-2} h^{-1}) were 4% lower and those from

the NITROGEN plots ($\bar{x}$ = 8.7 mg CH_4 m^{-2} h^{-1}) 28% higher than those from the corresponding controls. In the elevated CO_2 plots, the number of *Eriophorum* shoots was a significant covariate, but the treatment effect was statistically nonsignificant. In the NITROGEN plots, the treatment effect and covariates were nonsignificant.

[30] At the SE site, CH_4 emission from the CO_2 plots ($\bar{x}$ = 3.0 mg CH_4 m^{-2} h^{-1}) was 4% higher and that from the NITROGEN plots ($\bar{x}$ = 3.4 mg CH_4 m^{-2} h^{-1}) 7% higher than that from the corresponding control plots. None of the
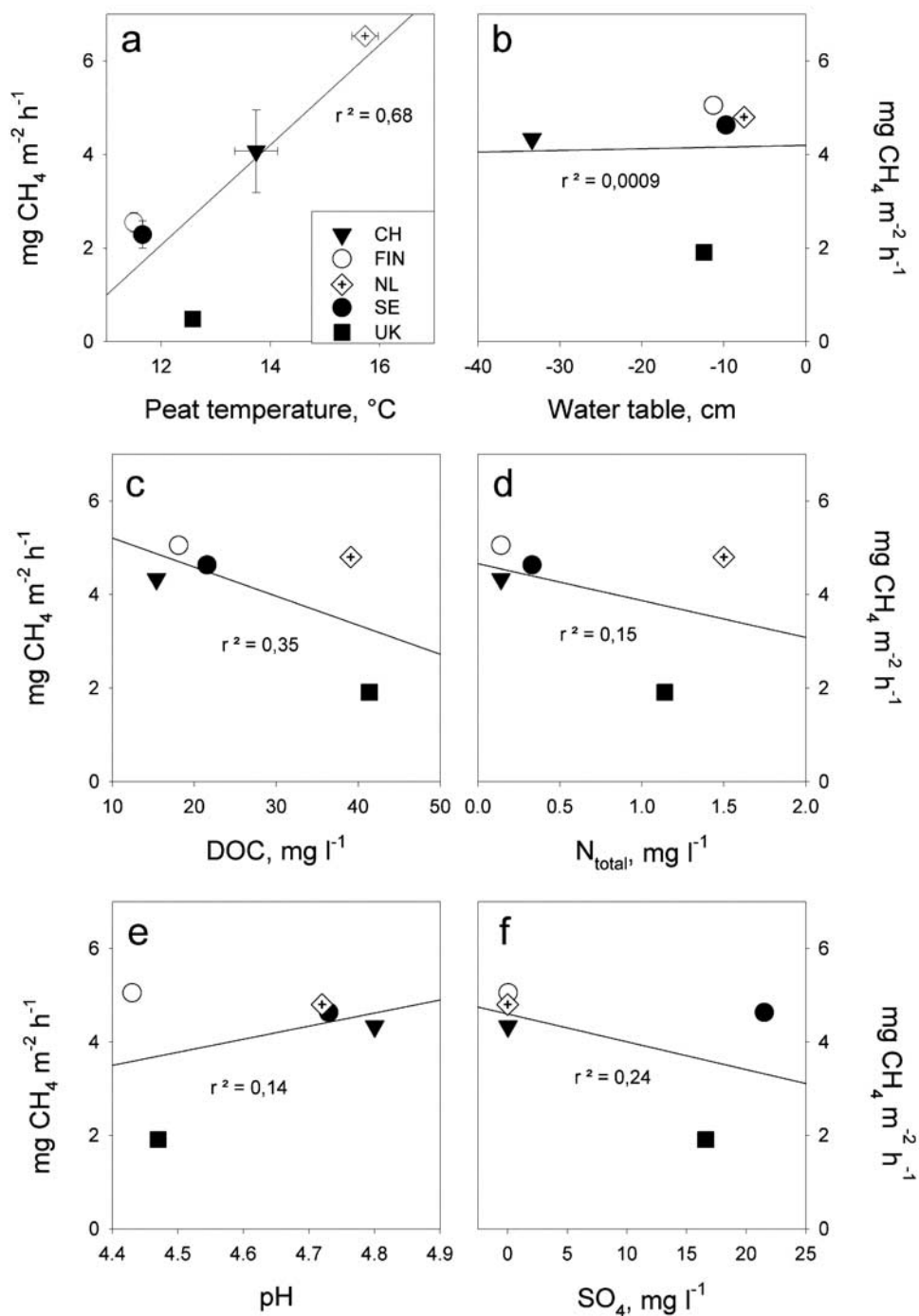
Figure 3. CH_4 fluxes of the CONTROL plots (averages of all measurements) compared with the different site characteristics. Water table depth and temperature are averages of the same data as in Figure 2. The pH, and the DOC, total N and SO_4 concentrations were measured on the soil water [*Mitchell et al.*, 2000]. CH_4 fluxes are standardized to a common reference temperature of 14°C in Figures 3b–3f.

covariates (T was not included in the test because it was not measured on a plot-specific level) or treatment effects were significant.

[31] At the UK site, CH_4 emission from the CO_2 plots ($\bar{x}$ = 0.99 mg CH_4 m^{-2} h^{-1}) was 33% lower and that from

the NITROGEN plots ($\bar{x}$ = 0.47 mg CH_4 m^{-2} h^{-1}) 2% lower than that from the corresponding control plots. The number of *Eriophorum* shoots was a significant covariate in the N experiment (T was not included in the test because it was not measured on a plot specific level). The CO_2 effect
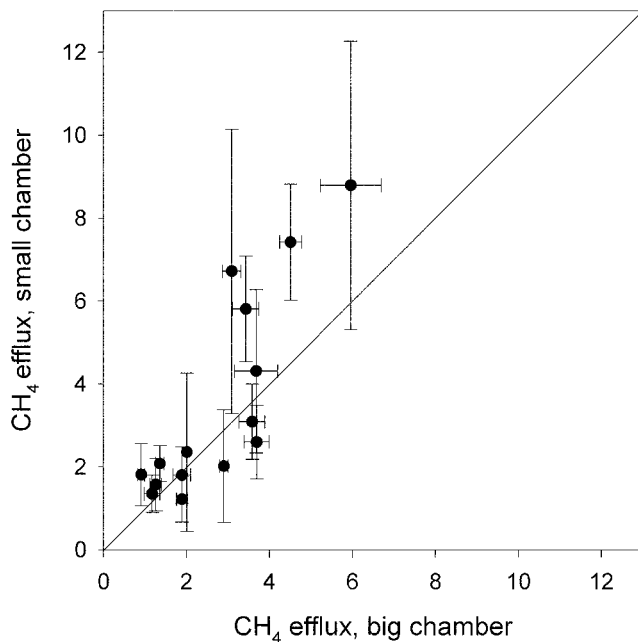
Figure 4. Comparison of the CH_4 fluxes measured simultaneously with small and large chambers in the FIN CONTROL plots.

was nonsignificant, but after the covariate correction, the treatment effect was statistically significant in the NITROGEN plots.

4. Discussion

4.1. CONTROL Plots

[32] In the FIN and SE sites, which were located in natural peatlands, the CH_4 fluxes were typical for slightly minerotrophic mires in the boreal and nemoral regions [*Bubier et al.*, 1993; *Saarnio et al.*, 1997; *Nykänen et al.*, 1998]. Because the other sites were former drained or peat-cutting areas, their CH_4 emissions are probably not fully comparable with those from natural peatlands [cf. *Nykänen et al.*, 1998; *Tuittila et al.*, 2000a]. However, they do represent the prevailing conditions in Central Europe, where most of the peatlands are more or less disturbed. Therefore our experimental design can be expected to give representative results, since both treatments were compared to control plots in corresponding conditions at every site.

[33] The Q_{10} values of the methane fluxes varied considerably among the sites. The large variation is understandable, because methane is the end product of a series of processes. Temperature and other limiting factors can exert an effect on the individual phases. Furthermore, during the growing season when the temperature varies, other changes also occur that affect CH_4 fluxes, for example, changes in the water table and the number of vascular plant shoots. In this study the other Q_{10} values fell within the range (1.3–28) presented in the review of *Segers* [1998], apart from the Q_{10} of the UK site which was exceptionally low (1.1). The UK site seemed to be very insensitive to changes in environmental conditions (Figure 2). One possible reason

for this may be the history of the site. Also *Nykänen et al.* [1998] reported that the effects of variations in the water table or temperature on CH_4 fluxes were very small in some drainage areas. Another possibility could be a high SO_4 concentration [*Bartlett et al.*, 1987]. The UK site is located very close to the coast, and most of the marine-derived sulphur deposition in coastal areas takes place during the summer and autumn [*Steudler and Peterson*, 1984]. The SE site also had a high SO_4 concentration, and the Q_{10} value at this site was rather low (1.5). The CH_4 emissions, however, were markedly higher than at the UK site.

[34] The average CH_4 flux rates of the different sites correlated rather well with the corresponding peat temperatures (Figure 3a). In contrast, differences in water table depths did not explain the differences in the CH_4 fluxes among the study sites (Figure 3b). The water table has been shown to explain quite well the CH_4 fluxes from different habitats or from individual habitats during the seasons [*Bubier et al.*, 1993; *Nykänen et al.*, 1998]. One probable explanation for the lack of correlation between water table and emission in our study is that, apart from the CH site, the range in average water table was very small (which was deliberate, and due to the criterion applied for site selection). The explanatory power of the other physical and chemical factors was also rather low. Increasing methane emissions with increasing pH have been reported by some researchers [e.g., *Dunfield et al.*, 1993; *Valentine et al.*, 1994], but not in all cases [*Moore and Knowles*, 1990].

[35] Comparison of the small and large chambers shows that the sampling method has some effect on the methane flux results. There are at least two possible reasons for the differences. If bubbling occurs during sampling as a result of movements of the collar in the peat, this will have a greater effect on the CH_4 concentration in small chambers. Another reason could also be the use of transparent (small) and opaque (large) chambers. In the transparent chambers the temperature increases more during sunshine. On the other hand, if the plants close their stomata in the opaque chambers, this may decrease gas transport through the plants. However, the role played by stomata in CH_4 emissions is not clear [cf. *Kelker and Chanton*, 1997; *Bellisario et al.*, 1999]. Anyway, the sampling method had only a small effect on the Q_{10} value. At the FIN site, Q_{10} was 3.4 with large chambers and 3.7 with small chambers.

4.2. Effects of the Treatments

[36] Three of the sites had higher, and two lower CH_4 fluxes in the CO_2 plots than in their controls (AIR), but none of the differences were statistically significant. This was somewhat surprising and not in agreement with our expectations, which were based on two earlier studies showing a strong stimulation of CH_4 fluxes by elevated CO_2. Doubling of the CO_2 concentration increased methane fluxes by 80% in brackish marsh soils [*Dacey et al.*, 1994], and by 145% in cores from an ombrotrophic mire [*Hutchin et al.*, 1995]. Such effects of elevated CO_2 on methane fluxes are most probably related to the response of plants to elevated CO_2 concentrations [cf. *Hutchin et al.*, 1995; *Megonigal and Schlesinger*, 1997]. The CO_2 concentration in the soil is usually so high that an increase in the
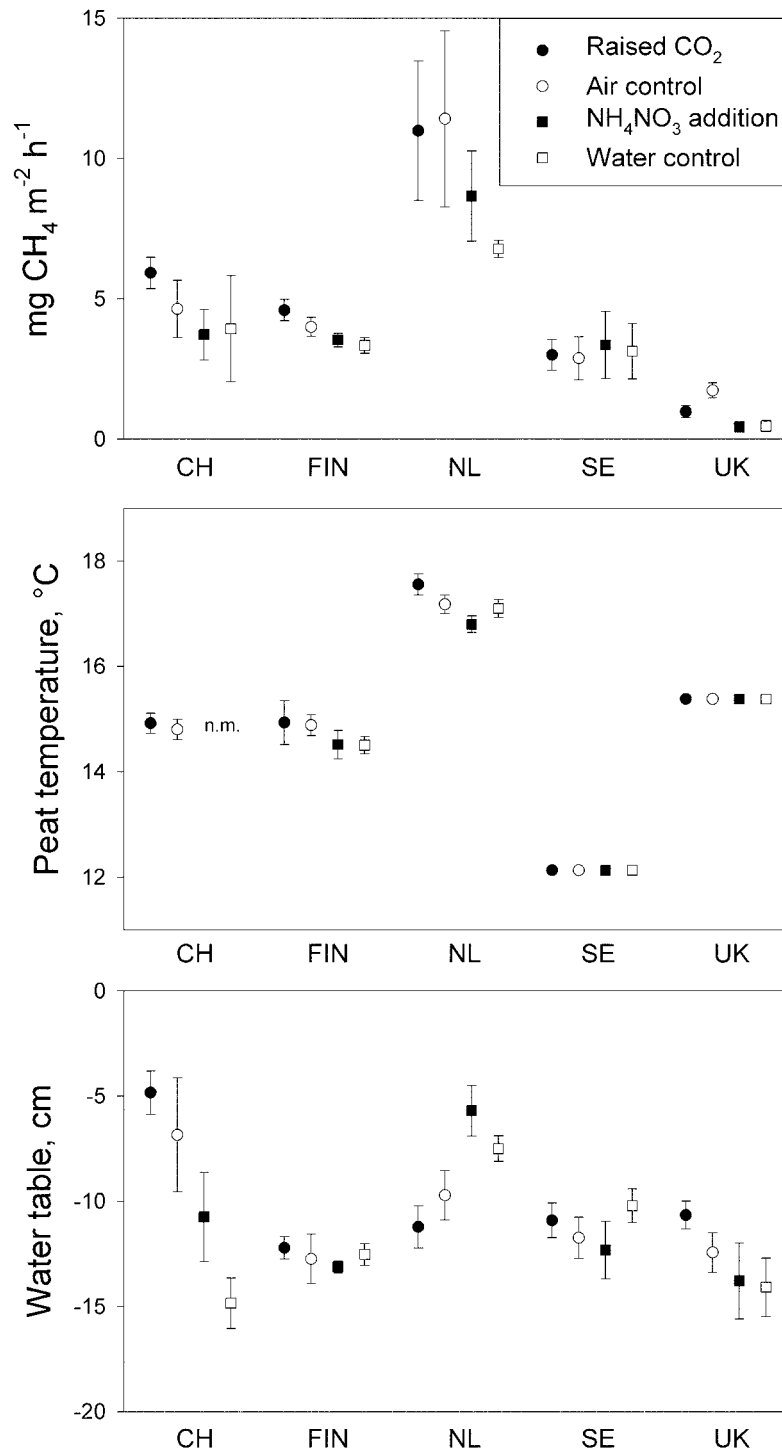
Figure 5. Average CH_4 flux, peat temperature and water table depth (mean, S.E.) in the plots with different treatments at the different sites during 15 June to 15 August in 1997 and 1998. All acceptable CH_4 results are included (compare Table 3). The temperature was measured at a depth of 10 cm, except at 15 cm in the NL and CH sites. At the SE and UK sites the temperature was measured at one point in the middle of the sites, but at the other sites in the separate plots.

atmospheric concentration from 360 to 560 is hardly likely to have any direct effects on methanogenic bacteria [cf. *Wang and Adachi*, 1999]. In our study, elevated CO_2 concentration had only a small effect on the plants. Under elevated CO_2 the *Sphagnum* biomass production increased slightly in the FIN and NL sites, but it decreased in the CH and SE sites. None of these differences were statistically significant [*Berendse et al.*, 2001]. Similarly, the above-

Table 3. Results of the Analysis of Covariance[a]

	CO$_2$	Air	Water Table	Peat Temperature	Shoots/Biomass	Treatment (p-Value)
CH	6.58	5.36	n.s.	n.i.	n.s.	n.s. (0.32)
FIN	4.52[b]	4.05[b]	0.017	0.029	n.s.	n.s. (0.09)
NL	11.15[b]	11.25[b]	n.s.	n.s.	0.021	n.s. 0.97)
SE	3.00	2.88	n.s.	n.i.	n.s.	n.s. (0.65)
UK	0.99	1.48	n.s.	n.i.	n.s.	n.s. (0.12)
	Nitrogen	**Control**	**Water Table**	**Peat Temperature**	**Shoots/Biomass**	**Treatment (p-Value)**
CH	4.12	7.27	n.s.	n.i.	n.s.	n.s. (0.45)
FIN	3.53	3.31	n.s.	n.s.	n.s.	n.s. (0.12)
NL	8.67	6.78	n.s.	n.s.	n.s.	n.s. (0.32)
SE	3.35	3.13	n.s.	n.i.	n.s.	n.s. (0.77)
UK	0.35[b]	0.60[b]	n.s.	n.i.	<0.0005	0.04

[a]The analysis includes only those CH$_4$ results for which concurrent WT and T data (if included) were available (cf. Figure 5). Abbreviations: n.s. = nonsignificant, n.i. = not included.
[b]Covariance-corrected mean of the CH$_4$ flux.

ground biomass of the vascular plants on the CO$_2$ plots was higher than that on the AIR plots in the CH, FIN and NL sites, but lower in the other sites (nonsignificant [*Berendse et al.*, 2001]). The belowground biomass of the plants was, however, significantly higher (10–20%) in the CO$_2$ plots than in the AIR plots at the end of the experiment [*Berendse et al.*, 2001]. An increased ratio of belowground to aboveground biomass is a typical phenomenon under elevated CO$_2$ concentrations [cf. *Eamus and Jarvis*, 1989]. Theoretically this should be reflected in the CH$_4$ emission, but a treatment period of three growing seasons may have been too short to cause any significant effects.

[37] When *Saarnio et al.* [1998] studied peat cores in growth chambers at an elevated CO$_2$ concentration in conditions typical of boreal mires, the increase in methane emission was also smaller than that found in previous studies. The reason for the different results was assumed to be the difference in temperatures [*Saarnio et al.*, 1998]. In the experiment of *Saarnio et al.* [1998], the effect of CO$_2$ increased when the temperature was kept unnaturally high at the end of the growth experiment. In our study the different sites were therefore compared using the summer data of 1997 and 1998 (Figure 5), when any effect would have been the most obvious. The CH$_4$ emissions in the FIN site support the assumption concerning the role of temperature; the increase in CH$_4$ emission caused by elevated CO$_2$ was highest in the middle of summer [*Saarnio et al.*, 2000]. However, the results of this experiment do not in general support this assumption. A small increase occurred at the cooler sites (CH, FIN, SE,), while at the warmest site (NL) the CO$_2$ plots had lower CH$_4$ emissions than their controls (Figure 5).

[38] Like the CO$_2$ treatment, the N treatment had no clear effects on CH$_4$ emissions. In the UK site the NITROGEN and CONTROL plots had almost the same CH$_4$ emission rates, but the covariate-corrected emissions were significantly lower in the NITROGEN plots. Theoretically, increased nitrogen supply can have various effects on CH$_4$ emissions. A possible direct negative effect is decreased methane production due to suppression by nitrate. Another possibility is inhibition of methane oxidation by the nitrogen compounds [*Steudler et al.*, 1989; *Adamsen and King*, 1993; *Crill et al.*, 1994], leading to higher emissions.

Indirect effects would most likely occur via the vegetation. For example, increased biomass production may result in more substrate being available for methanogens. On the other hand, fertilization may also decrease the root/shoot ratio of the plants [*Eamus and Jarvis*, 1989], thereby suppressing emissions. In line with this, *Granberg et al.* [2001] found that the effect of nitrogen addition on methane emission from a similar peatland to those used in this study, was negative at high sedge cover but insignificant at low sedge cover. Interestingly, the UK site that showed a negative effect of N addition had a comparatively high abundance of sedges (Table 2). However, the SE site also had a lot of sedges but no significant N effect.

[39] In our study the N treatments decreased *Sphagnum* production significantly in the CH and NL sites and nonsignificantly in the SE and UK sites, but increased it nonsignificantly in the FIN site [*Berendse et al.*, 2001]. The aboveground biomass of the vascular plants on the NITROGEN plots was higher in the FIN, UK and NL sites but lower in the other sites, but none of these differences was significant [*Heijmans et al.*, 2001; *Berendse et al.*, 2001]. However, at the end of the experiment the standing dead and litter biomass were higher in the NITROGEN plots than in the CONTROL plots at the FIN, CH, NL and SE sites [*Berendse et al.*, 2001]. In the experiment of *Aerts and de Caluwe* [1999], the addition of N increased CH$_4$ emission on a low-fertility peat soil, but there were no effects in the high-N, eutrophic peat. In the 6-year fertilization experiment carried out by *Nykänen et al.* [2002], the addition of nitrogen increased CH$_4$ emission only in the poorest *Sphagnum fuscum* site. This was concluded to be due to the secondary effect of increased coverage of *Eriophorum vaginatum* in the N-treated plots. Taken together, the results of previous studies suggest that an increased N load may result in decreased methane emissions at high sedge cover [*Granberg et al.*, 2001], in increased emissions in very nutrient poor peatlands [*Aerts and de Caluwe*, 1999; *Nykänen et al.*, 2002], but often in small and insignificant effects [*Saarnio and Silvola*, 1999; *Granberg et al.*, 2001]. On the basis of this, it is understandable that the effects of increased N on methane flux were small at most of our sites.

[40] CO$_2$ exchange (NEE and respiration) was measured only in the FIN site, where only small treatment effects were

found. [*Saarnio et al.*, 2003]. No treatment effects were found when the decomposition rates of peat samples from the FIN site were measured in the laboratory after the experiment (data not presented). However, indirect evidence for a CO_2 effect on belowground processes came from the observed increase in bacterial biomass in the living *Sphagnum* at all five sites [*Mitchell et al.*, 2003].

[41] In conclusion, an increased CO_2 and N supply for 3 years had little or no effects on the abundance of the plant species, biomass production or on the biological and biogeochemical processes of the plants and soil. This minor response of the vegetation probably explains why the treatments had no clear effects on the methane emissions. Thus it appears that elevated CO_2 concentrations do not cause fast, dramatic increases in methane emissions in boreal and nemoral peatlands. However, the methane emissions clearly depend on the temperature, moisture, nutrient status and vegetation of peatlands [e.g., *Segers*, 1998]. An increase in nutrient deposition and greenhouse gases would very probably cause changes in these regulatory factors in the long term. Longer time periods and larger changes in the vegetation are probably needed to bring about significant changes in CH_4 fluxes [cf. *Verville et al.*, 1998]. At the NL site, for instance, changes in the biomass ratio of vascular plants and mosses occurred on the NITROGEN plots in the third year especially [*Heijmans et al.*, 2001]. Thus experiments of longer duration are needed.

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A. Ekberg, Lund University, Department of Physical Geography and Ecosystem Analysis, Box 118, SE-221 00, Lund, Sweden.

J. Foot, Scottish Environmental Protection Agency, Erskine Court, Castle Business Park, Stirling, FK9 4TR, Scotland.

A. Greenup, Department of Animal and Plant Sciences, University of Sheffield, Western Bank, Sheffield, S10 2TN, UK.

M. Heijmans, Wageningen University, Nature Conservation and Plant Ecology Group, Bornsesteeg 69, 6708 PD, Wageningen, Netherlands.

E. Mitchell, Department of Biological Sciences, University of Alaska Anchorage, 3211 Providence Drive, Anchorage, AK 99508, USA.

S. Saarnio and J. Silvola, Department of Biology, University of Joensuu, P.O. Box 111, FIN-80101, Joensuu, Finland. (jouko.silvola@joensuu.fi)

I. Sundh, Department of Microbiology, SLU, P.O. Box 7025, SE-750 07 Uppsala, Sweden.

N. van Breemen, Wageningen Agricultural University, Department of Soil Science and Geology, P.O. Box 37, 6700 AA, Wageningen, Netherlands.