



Synthesizing greenhouse gas fluxes across nine European peatlands and shrublands – responses to climatic and environmental changes

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Abstract. In this study, we compare annual fluxes of methane (CH₄), nitrous oxide (N₂O) and soil respiratory carbon dioxide (CO₂) measured at nine European peatlands ($n = 4$) and shrublands ($n = 5$). The sites range from northern Sweden to Spain, covering a span in mean annual air temperature from 0 to 16 °C, and in annual precipitation from 300 to 1300 mm yr⁻¹. The effects of climate change, including temperature increase and prolonged drought, were tested at five shrubland sites. At one peatland site, the long-term (> 30 yr) effect of drainage was assessed, while increased nitrogen deposition was investigated at three peatland sites.

The shrublands were generally sinks for atmospheric CH₄, whereas the peatlands were CH₄ sources, with fluxes ranging

from -519 to +6890 mg CH₄-C m⁻² yr⁻¹ across the studied ecosystems. At the peatland sites, annual CH₄ emission increased with mean annual air temperature, while a negative relationship was found between net CH₄ uptake and the soil carbon stock at the shrubland sites. Annual N₂O fluxes were generally small ranging from -14 to 42 mg N₂O-N m⁻² yr⁻¹. Highest N₂O emission occurred at the sites that had highest nitrate (NO₃⁻) concentration in the soil water. Furthermore, experimentally increased NO₃⁻ deposition led to increased N₂O efflux, whereas prolonged drought and long-term drainage reduced the N₂O efflux. Soil CO₂ emissions in control plots ranged from 310 to 732 g CO₂-C m⁻² yr⁻¹. Drought and long-term drainage

generally reduced the soil CO₂ efflux, except at a hydric shrubland where drought tended to increase soil respiration.

In terms of fractional importance of each greenhouse gas to the total numerical global warming response, the change in CO₂ efflux dominated the response in all treatments (ranging 71–96%), except for NO₃⁻ addition where 89% was due to change in CH₄ emissions. Thus, in European peatlands and shrublands the effect on global warming induced by the investigated anthropogenic disturbances will be dominated by variations in soil CO₂ fluxes.

1 Introduction

Shrublands are natural or semi-natural nutrient poor ecosystems, characterized by patches of low stature vascular vegetation alternating with bryophytes or bare soil. Commonly, the shrublands on poorly drained, deep organic soils (> 30 cm) are called peatlands (Lai, 2009) while shrublands on mineral soils, which are typically excessively drained, are called shrublands *sensu stricto* (Beier et al., 2009). These ecosystem types make up approximately 7% of the European land area (EEA, 2006; Montanarella et al., 2006) and may contribute valued ecosystem services, such as biodiversity, habitat provision, recreation, water purification and carbon (C) sequestration (Wessel et al., 2004; Kimmel and Mander, 2010). For instance, northern peatlands were estimated to sequester 0.07 Gt C yr⁻¹, which over time has accumulated, resulting in deep organic soil profiles that constitute a major store of terrestrial C (Gorham, 1991; Clymo et al., 1998). Peatlands and shrublands are sensitive to disturbances such as climate change and management, and the responses to these anthropogenic disturbances are therefore important for the overall European greenhouse gas (GHG) budget and other ecosystem services.

In Europe, peatlands are most abundant under the subarctic and temperate climates of the Nordic countries, where Finland and Sweden together account for 65% of the European area of peat soils (Montanarella et al., 2006). The geographical distribution of shrublands in Europe includes the heather-moorlands on the British Isles, dry *Calluna* heaths along the Atlantic coastlines from northern Norway to northern Portugal, and finally maquis ecosystems under the Mediterranean climate in southern Europe (Beier et al., 2009).

Peatlands and shrublands share some common properties concerning vegetation and nutrient status, but they also differ fundamentally, especially in terms of hydrology, with related differences in soil structure, thermal properties and redox state. Such differences may lead to deviation in their respective drivers of GHG fluxes. Methane (CH₄) fluxes between soil and atmosphere represent the balance between CH₄ production and CH₄ oxidation. Peatlands are generally net CH₄ sources, where CH₄ efflux is controlled by water table depth,

temperature and availability and quality of carbon substrates (Christensen et al., 2003; Lai, 2009). Presence and composition of vascular vegetation can also affect the CH₄ flux dynamics, both through root exudation of labile C substrates for CH₄ production (Ström et al., 2003), and by providing gas conduits, which may influence CH₄ production, oxidation and transport processes (Joabsson et al., 1999). In contrast, dry *Calluna* heaths and Mediterranean shrublands are usually CH₄ sinks, where CH₄ uptake most often correlates positively with temperature and negatively with soil water content (Castaldi and Fierro, 2005; Carter et al., 2011). The latter is due to the slower gas diffusion in water than in air, which causes soil water to limit CH₄ diffusion towards the zone of methanotrophic activity (Dunfield, 2007), mainly located in the upper 20 cm soil layer (e.g. Roslev et al., 1997).

Peatlands and shrublands also differ in the key drivers of nitrous oxide (N₂O) fluxes, which may involve at least two microbial processes, nitrification and denitrification, occurring under aerobic and anaerobic soil conditions, respectively (Baggs, 2011). Generally, the rates of these processes increase with nitrogen (N) availability. In a shallow peatland in Scotland, a spatial analysis revealed a negative correlation between N₂O emissions and soil pH, possibly an indirect result of limited soil N availability for the microbes at locations with higher pH values (Dinsmore et al., 2009), where the vegetation constitutes a stronger N sink. The temporal N₂O dynamics were primarily controlled by soil temperature with an apparent switch from consumption to production at about 8 °C (Dinsmore et al., 2009). Fluxes of N₂O in shrublands have only been investigated in a few studies, and knowledge of key drivers specific for this ecosystem type is sparse (e.g. Curtis et al., 2006; Carter et al., 2011). In four British moorlands, Curtis et al. (2006) detected either very low or no N₂O emission. Incubation of soil cores, however, demonstrated that N₂O efflux could be induced by warming and N addition. In a Danish *Calluna* heath, both soil moisture and temperature stimulated N₂O emissions (Carter et al., 2011).

Soil respiratory CO₂ emission originates from decomposition of soil organic matter and from plant root respiration. Together with gross ecosystem photosynthesis, soil respiratory CO₂ emission is the dominant flux of carbon between terrestrial ecosystems and the atmosphere (Schlesinger and Andrews, 2000), and changes in soil respiration in response to climate treatments is an important indicator for ecosystems' feedback to climate change. Soil CO₂ effluxes from peatlands typically correlate positively with both temperature and water table depth (Smith et al., 2003; Danevčič et al., 2010). Similarly for shrublands, soil CO₂ emissions were shown to be strongly controlled by temperature in an analysis based on two years of data from four European heathlands (Emmett et al., 2004).

The relative contribution to global warming of the three greenhouse gases CH₄, N₂O and soil respiratory CO₂ may vary between peatlands and shrublands. For instance, annual

GHG budgets for a minerotrophic fen in Finland and a shallow peatland in Scotland showed that N₂O fluxes were generally of minor importance, whereas CH₄ emissions and net ecosystem CO₂ exchange exerted the greatest impact on the ecosystem's contribution to global warming (Drewer et al., 2010). For comparison, in an old *Kunzea ericoides* shrubland in New Zealand, GHG emissions were dominated by CO₂ release from the soil while pronounced CH₄ uptake more than counteracted N₂O emissions on a CO₂-equivalent basis (Price et al., 2010). Similar studies for European shrublands are currently lacking.

In future, the exchange of GHGs between ecosystems and the atmosphere may be affected by climate change, including increasing temperatures and increased duration and frequency of summer droughts; the latter expected in western and southern Europe (IPCC, 2007a). For instance, Emmett et al. (2004) reported 0–19% increases in soil CO₂ effluxes in response to 0.5–2°C warming across four of the five shrublands described in this study. Furthermore, Carter et al. (2011) found a 20% increase in CH₄ uptake rates under elevated temperature in a dry temperate heathland (DK-Bra in this study). Emissions of N₂O from this site were reduced and stimulated by drought and elevated temperature, respectively, but only when these treatments were combined with elevated atmospheric CO₂ concentrations (Carter et al., 2011).

In addition to climate change, the hydrology of peatlands is affected by other anthropogenic disturbances, such as extensive drainage operations to enable forestry, agriculture or peat harvesting. Drainage of peatland was particularly widespread in the northern temperate zone before the 1980s (Kimmel and Mander, 2010), leading to elevated CO₂ effluxes (von Arnold et al., 2005) and to decreased CH₄ emissions (Roulet and Moore, 1995), although emissions of CH₄ can be significant from drainage ditches in nutrient-rich fens (Minkinen and Laine, 2006). By contrast, N₂O emissions from ombrotrophic bogs are relatively insensitive to changes in the water table, as the efflux is probably limited mainly by slow N transformation rates caused by low pH and nutrient availability (Martikainen et al., 1993).

A less well understood anthropogenic influence on GHG fluxes in peatlands and shrublands is the effect of enhanced atmospheric N deposition, originating from intensive agriculture (reduced N) and fossil fuel combustion (oxidized N). The global N pollution is unlikely to decline in the immediate future (Galloway et al., 2004; Peñuelas et al., 2012). Bragazza et al. (2006) investigated peatlands along an atmospheric N deposition gradient ranging from 2 to 20 kg N ha⁻¹ yr⁻¹ and found increased soil respiratory CO₂ emissions under higher N deposition rates. This relationship was explained by the removal of N constraints on microbial metabolism and by improved litter quality. The effects of increased N availability on CH₄ exchange are dependent on site specific properties. Some soils show inhibitory effects on CH₄ oxidation (Crill et al., 1994; Christensen et al., 1999),

while others show minor or no effects (Saarnio and Silvola, 1999). If the abundance of vascular plants increases in peatlands as a result of higher N availability, this may increase CH₄ emissions by providing gas conduits and improving litter quality (Joabsson et al., 1999; Nykänen et al., 2002). Increasing the amount of inorganic N in a soil will also enhance the potential for N₂O emissions both through nitrification and denitrification processes (Firestone and Davidson, 1989).

Experimental manipulation studies at the field scale, as well as studies along natural gradients, are valuable tools to understand how ecosystems will respond to climatic and environmental changes. While manipulation studies are well-suited to study effects of changes in specific experimentally controlled drivers, they are intrinsically constrained in time (years). Natural gradient studies are better suited to study effects on longer time scales (decades to centuries), but suffer from possible biases caused by changes in factors other than the gradient component under investigation, for example, climate. Studies based on a combination of experimental manipulations performed across multiple sites covering larger natural gradients should combine the strengths of both strategies and increase the reliability of the results.

Within the framework of the NitroEurope Integrated Project, we investigated how the soil-atmosphere exchange of the three greenhouse gases, CH₄, N₂O and CO₂, responded to simulated changes in drought, warming, drainage or nitrogen addition at nine experimental peatland and shrubland sites situated across natural gradients in precipitation and temperature. The aims of the study were (i) to identify environmental variables that correlated with GHG fluxes across the nine sites or within an ecosystem type, (ii) to evaluate whether specific variables had a direct effect on GHG fluxes and thereby could be identified as key drivers based on treatment responses at the site level, and (iii) to quantify the relative contribution of each GHG to the total global warming response for each experimental treatment.

2 Materials and methods

2.1 Study sites

The nine experimental peatland and shrubland sites included in the synthesis were all part of the NitroEurope project. The climatic conditions at the field sites ranged from subarctic conditions in northern Sweden to a Mediterranean climate in Spain, and from hydric temperate conditions in Wales to mesic temperate climates towards Estonia in the east (Fig. 1). The ecosystems represented open landscapes in these regions and included four peatlands and five shrublands (Table 1). The peatlands were all ombrotrophic bogs, while the shrublands covered heather-moorland (UK-Clo), dry *Calluna* heath (DK-Mol, DK-Bra, NL-Old) and Mediterranean garrigue shrubland (ES-Gar). Soil type and plant species

Table 1. Site characteristics.

| Ecosystem and location | Coordinates | Altitude (m) | Site code | Soil type | Dominant vegetation ^a | Experimental treatment |
|------------------------|-------------------|--------------|-----------|----------------------|---|--|
| Peatland | | | | | | |
| Männikjärve, EE | 58°52′ N 26°14′ E | 80 | EE-Män | Histosol | <i>S. fuscum</i> , <i>S. rubellum</i> , <i>Scheuchzeria palustris</i> , <i>Ledum palustre</i> , <i>Vaccinium oxycoccus</i> , <i>Chamaedaphne calyculata</i> , <i>Betula pubescens</i> , <i>Pinus sylvestris</i> | Drainage |
| Storflaket, SE | 68°20′ N 18°58′ E | 380 | SE-Sto | Histosol | <i>S. fuscum</i> , <i>S. balticum</i> , <i>E. nigrum</i> , <i>Andromeda polifolia</i> , <i>Rubus chamaemorus</i> , <i>E. vaginatum</i> | N addition (NH ₄ NO ₃) |
| Fäjemyr, SE | 56°15′ N 13°33′ E | 140 | SE-Fäj | Histosol | <i>C. vulgaris</i> , <i>Erica tetralix</i> , <i>S. magellanicum</i> , <i>S. rubellum</i> , <i>E. vaginatum</i> | N addition (NH ₄ NO ₃) |
| Whim, UK | 55°45′ N 03°16′ E | 280 | UK-Whi | Histosol | <i>C. vulgaris</i> , <i>E. vaginatum</i> , <i>S. capillifolium</i> | N addition (NH ₄ or NO ₃) |
| Shrubland | | | | | | |
| Clocaenog, UK | 53°03′ N 03°28′ W | 490 | UK-Clo | Peaty podzol | <i>C. vulgaris</i> , <i>Vaccinium myrtillus</i> , <i>E. nigrum</i> | Drought, warming |
| Mols, DK | 56°23′ N 10°29′ E | 57 | DK-Mol | Sandy podzol | <i>C. vulgaris</i> , <i>Deschampsia flexuosa</i> | Drought, warming |
| Brandbjerg, DK | 55°53′ N 11°58′ E | 9 | DK-Bra | Sandy podzol | <i>C. vulgaris</i> , <i>Deschampsia flexuosa</i> | Drought, warming |
| Oldebroek, NL | 52°24′ N 05°54′ E | 25 | NL-Old | Sandy podzol | <i>C. vulgaris</i> | Drought, warming |
| Garraf, ES | 41°19′ N 01°49′ E | 210 | ES-Gar | Petrocalcic calcisol | <i>Erica multiflora</i> , <i>Globularia alypum</i> | Drought, warming |

^a *C. vulgaris* – *Calluna vulgaris*, *E. nigrum* – *Empetrum nigrum*, *E. vaginatum* – *Eriophorum vaginatum*, *S.* – *Sphagnum*.

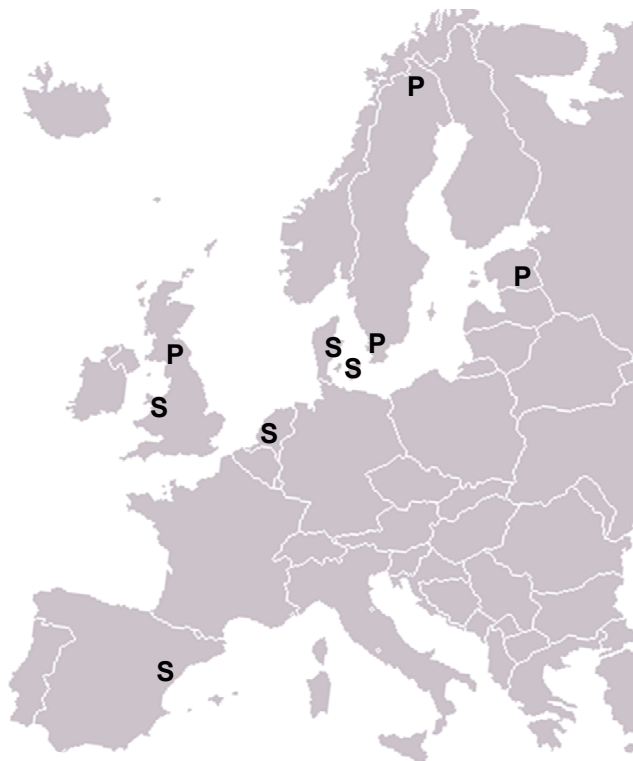


Fig. 1. Location of the nine experimental sites across Europe. Abbreviations are P for “peatland” and S for “shrubland”.

composition differed between the sites, but all sites had dwarf shrubs in common, mainly *Calluna vulgaris*, *Empetrum nigrum* or *Erica* spp. (Table 1). The experimental sites existed before the NitroEurope project started and therefore already had ongoing methodologies and procedures.

2.2 Experimental manipulations

At the Estonian peatland EE-Män, the long-term effect of drainage was studied in a part of the bog where a drainage ditch system established in the 1950s (Veber, 1974) was reconstructed in 1975 (Table 1). Substantial lowering of the water table has resulted in significantly improved tree growth (Niinemets et al., 2001; Portsmouth et al., 2005). Thus, when this study took place, *Pinus sylvestris* was 10–12 m tall in the drained part of the bog compared to 1–3 m in the non-drained part. The effect of increased nitrogen deposition was investigated at three peatland sites. At the two Swedish sites SE-Sto and SE-Fäj, fertilized plots received NH₄NO₃ three times per year, corresponding to a total input of 4 g N m⁻² yr⁻¹ (Lund et al., 2009). At the Scottish peatland UK-Whi, treatment plots were given an extra 5.6 g N m⁻² yr⁻¹ in wet deposition using an automated sprinkler system, which provided ca. 120 artificial rain events per year coupled to rainfall (Sheppard et al., 2011). Nitrogen was applied either in the reduced form as NH₄Cl or in the oxidized form as NaNO₃. The effects of temperature increase and prolonged drought were tested at the five shrubland sites using passive night-time warming and horizontal rainout curtains, respectively. The experimental

setups at these sites are described in more detail by Beier et al. (2004) and Mikkelsen et al. (2008).

2.3 Soil greenhouse gas flux measurements

Fluxes of CH₄, N₂O and soil respiratory CO₂ were measured monthly or twice a month using static chamber methods described by, for example, Carter et al. (2011) and Sowerby et al. (2008). The chamber design and the measurement procedure varied across the nine sites. Overall, at least five weeks before simultaneous measurement of CH₄ and N₂O fluxes started, a permanent soil collar was installed in each replicated treatment plot ($n \geq 3$) on which a chamber was placed during measurements. Three to four times during the enclosure period of 20–180 min, a sample of headspace air was collected using a syringe through a septum in the chamber. At the Spanish shrubland ES-Gar, however, only two gas samples were collected during the 15 min enclosure period to avoid adverse effects on headspace air pressure in the small chambers (volume 0.8 l) used at this site. Gas samples were stored in plastic syringes (SE-Sto), pre-evacuated vials (UK-Clo, NL-Old) or non-evacuated vials using a double-needle approach (EE-Män, UK-Whi, DK-Mol, DK-Bra, ES-Gar) before analysis for CH₄ and N₂O concentrations by gas chromatography. One exception was the Swedish site SE-Fäj, where headspace concentrations of CH₄ and N₂O were determined in the field using a photoacoustic gas analyzer (Lund et al., 2009). Previous studies showed that gas flux rates measured using a photoacoustic gas analyzer were statistically identical to flux rates based gas sampling and analysis by gas chromatography (Ambus and Robertson, 1998; Lund et al., 2009). Soil CO₂ emissions were measured within permanent collars without vegetation, i.e. where any aboveground plant growth was removed on a regular basis. However, at the two Swedish sites SE-Sto and SE-Fäj, fluxes were assessed on vegetated plots and are therefore ecosystem respiratory CO₂ emissions. Generally, an opaque chamber was placed on the collar and the build-up of CO₂ during the enclosure period was monitored by a portable infrared gas analyzer. At three out of nine sites (EE-Män, NL-Old and ES-Gar), vascular plant free patches enabled soil CO₂ emissions to be determined concurrently with CH₄ and N₂O fluxes using the same chamber and gas chromatography approach. For all three gases, the flux rates were calculated using linear regression of headspace concentration versus time, except for long enclosure periods (≥ 120 min), where CH₄ uptake was determined by fitting a first-order function.

The year of measurement deviated between sites, but was generally within the period 2006–2009. Annual cumulative fluxes were obtained by linear interpolation between measurement days. This is a common, but crude, upscaling procedure since measurements carried out at one point in time, and over a relatively short time span, will represent the whole period between two neighboring measurements, despite potentially large variation in the controlling climatic

factors during this period. A more precise method would be to model the fluxes based on more frequent measurements of key drivers such as temperature and soil moisture (e.g. Selsted et al., 2012). In the present study, we did not have sufficient measurements to build such a model for each site. At the Swedish peatlands SE-Fäj and SE-Sto, gas flux measurements were not conducted during the five and eight coldest months of the year, respectively. When calculating the annual CO₂ fluxes for these two sites, we assumed that the contribution of the winter period to annual fluxes is 9 % at SE-Fäj (Lindroth et al., 2007) and 22 % at SE-Sto (Larsen et al., 2007). These ratios were also used to estimate annual CH₄ and N₂O fluxes, assuming that CO₂ fluxes represented the general level of microbial activity; more specifically, that Q_{10} values for CO₂, CH₄ and N₂O fluxes were not substantially different. Reported Q_{10} values for CH₄ and N₂O fluxes in natural ecosystems are sparse, however, Smith (1997) compiled Q_{10} values for N₂O emissions ranging 2.8–3.1 and 1.5–5 in unfertilized grassland and short grass prairie, respectively. This is within the range of Q_{10} values often reported in literature for soil respiratory CO₂ emissions (e.g. Kim and Verma, 1992).

2.4 Precipitation, temperature and soil moisture

The meteorological measurements included precipitation and air temperature. Soil temperature probes were installed at either 5 cm depth (EE-Män, SE-Fäj, DK-Bra, ES-Gar) or 10 cm depth (UK-Whi, UK-Clo, DK-Mol, NL-Old) and data were logged at least twice a day. Volumetric soil water content was measured at least twice a week by time domain reflectometry probes installed in the top 6 cm (DK-Mol), 10 cm (SE-Sto, SE-Fäj, UK-Clo, NL-Old), 15 cm (ES-Gar) or 20 cm soil layer (DK-Bra). For UK-Whi and EE-Män, volumetric soil moisture in 0–10 cm depth was calculated from monthly or seasonal measurements of gravimetric soil water content. At the peatland sites, water table depth was measured manually in dipwells or automatically using a pressure transducer.

2.5 Nitrogen deposition and leaching

Bulk N deposition was measured with bulk deposition collectors with a minimum diameter of 10 cm. Concentrations of NH₄⁺, NO₃⁻ and total N in the sampled precipitation were determined by ion chromatography or colorimetric assays. If bulk N deposition was not assessed at the site, then total N deposition reported in the literature for this specific area was used instead. Nitrate leaching was determined from modelled water percolation combined with NO₃⁻ concentrations measured in soil water collected below the rooting zone using porous suction cups (Schmidt et al., 2004; Larsen et al., 2011). Soil water was also sampled in the upper part of the soil profile, generally just below the O-horizon, and analyzed for NH₄⁺ and NO₃⁻ concentrations (e.g. Schmidt et al., 2004).

2.6 Plant and soil analyses

Aboveground biomass C and N at the shrubland sites were determined using plant tissue C and N analyses combined with biomass estimation based on pinpoint data (Peñuelas et al., 2004; Beier et al., 2009). Briefly, pinpoint measurements were conducted by lowering a sharpened pin through the vegetation, recording species and height for each plant hit with the pin. Total plant biomass was subsequently estimated using a site specific correlation between pinpoint data and actual biomass obtained by destructive samplings outside the experimental plots (Peñuelas et al., 2004). At the Scottish peatland UK-Whi, biomass C and N were obtained by destructive harvest. Soil samples collected in the upper soil layer (i.e. generally the O-horizon) were extracted with distilled water (DK-Bra), 1 M KCl (UK-Whi, UK-Clo, DK-Mol, NL-Old) or 2 M KCl (EE-Män, ES-Gar) to measure concentrations of extractable NH_4^+ and NO_3^- by ion chromatography or colorimetric assays (e.g. Andresen et al., 2009). For upper and lower soil layers, soil pH was determined in a suspension of soil in distilled water, 0.01 M CaCl_2 or 1 M KCl. Furthermore, bulk density, total C and N contents, and microbial biomass C were measured as described by Beier et al. (2009), and C stock in the 0–10 cm soil layer was calculated.

2.7 Responsiveness

Relative responsiveness (RR, %) of CH_4 , N_2O and CO_2 fluxes to the different treatments was calculated as

$$\text{RR} = (\text{Treat} - \text{Cont}) / \text{Cont} \times 100 \quad (1)$$

where Treat is mean treatment flux across sites and Cont is mean control flux across sites (given in mg C or $\text{N m}^{-2} \text{yr}^{-1}$). Similar to Liu and Greaver (2009), we refrained from calculating relative responsiveness in cases where the flux changed direction in response to a treatment. This occurred in the N addition experiments, where N_2O fluxes changed from net uptake to emission. For each gas species and treatment, we also calculated the absolute responsiveness (AR) in CO_2 -equivalents as

$$\text{AR} = (\text{Treat} - \text{Cont}) / \text{MR} \times \text{GWP} \quad (2)$$

where molar ratio (MR) is 12/16, 28/44 and 12/44, and global warming potential (GWP) is 25, 298 and 1 for CH_4 , N_2O and CO_2 , respectively (IPCC, 2007b). To compare the relative contribution of each gas species to the total global warming response for a specific treatment, we calculated the fractional importance (FI, %) of each gas species as

$$\text{FI}_i = |\text{AR}_i| / (|\text{AR}_1| + |\text{AR}_2| + |\text{AR}_3|) \times 100 \quad (3)$$

where $|\text{AR}_1|$ to $|\text{AR}_3|$ is the numerical value of the absolute responsiveness for each of the three gases. Numerical values were used in order for the total global warming response of

all three gases to sum up to 100. To clarify, when assessing the overall response patterns across sites and treatments, we calculated RR, AR and FI for all treatments, also including treatments that did not show significant effects on flux rates in the cross-site statistical analysis described below.

2.8 Statistics

To assess treatment effects on GHG fluxes across the sites, two-factor analyses of variance (ANOVA) with treatment, site and their interaction as fixed effects were conducted using the PROC MIXED procedure of SAS (SAS Institute, 2003). The random effects included site and treatment \times site. The GHG flux datasets were unbalanced as the number of replicates was unequal between sites, however the MIXED procedure is used in the same way whether data are balanced or unbalanced (Littell et al., 2002). More specifically, equal weight is given to each site regardless of the number of replicates when determining treatment effects. Data were log-transformed as required to obtain normality and homogeneity of variance. Main effects and interactions with $P \leq 0.05$ were considered to be significant, and were interpreted using differences of least squares means.

3 Results

3.1 Precipitation, temperature and soil moisture

Annual precipitation during the study period ranged from 311 mm at the subarctic peatland Storflaket in Sweden (SE-Sto) to 1351 mm at the Welsh shrubland Clocaenog (UK-Clo) (Table 2). Mean annual air temperature in control plots ranged from -0.3°C at the subarctic site SE-Sto to 15.6°C at the Spanish shrubland Garraf (ES-Gar). The passive nighttime warming generally raised annual soil temperature at 5 or 10 cm depth by 0.5°C , and decreased the soil water content by 2 % vol. (Table 2). Experimental drought caused a decline in mean annual soil moisture ranging from a reduction of 1.5 % vol. at the Danish shrubland Brandbjerg (DK-Bra) to 10.2 % vol. at the wet shrubland UK-Clo. Drainage of the Estonian peatland Männikjärve (EE-Män) lowered the water table from an annual depth of 15 cm to 38 cm below soil surface. Characteristics of the upper and lower soil layers at the sites as well as data on aboveground biomass, N deposition and leaching are found in the Supplement.

3.2 CH_4 fluxes

Annual CH_4 fluxes in control plots ranged from uptake of $519 \text{ mg C m}^{-2} \text{yr}^{-1}$ at the Danish shrubland Mols (DK-Mol) to emission of $6890 \text{ mg C m}^{-2} \text{yr}^{-1}$ from the Scottish peatland Whim (UK-Whi) (Table 3). For the peatland sites, the natural gradient analysis showed a clear relationship between annual CH_4 emission and mean annual air temperature (Fig. 2). In contrast, CH_4 fluxes at the temperate shrublands

Table 2. Annual precipitation, air temperature (Air *T*), soil temperature (Soil *T*) and soil water content (Soil *W*) during the study period at the nine experimental sites depending on treatment.

| Site | Treatment | Precipitation (mm) | Air <i>T</i> (°C) | Soil <i>T</i> (°C) | Soil <i>W</i> (% vol) |
|--------|-----------|--------------------|-------------------|--------------------|-----------------------|
| EE-Män | Control | 889 | 4.3 | 5.6 | 76.7 |
| | Drainage | na | 6.0 | 5.9 | 37.2 |
| SE-Sto | Site data | 311 | -0.3 | na | 23.4 |
| SE-Fäj | Site data | 626 | 7.1 | 7.6 | 59.1 |
| UK-Whi | Site data | 1092 | 8.5 | 7.7 | 71.9 |
| UK-Clo | Control | 1351 | 7.5 | 8.1 | 45.9 |
| | Drought | 1130 | 7.7 | 7.9 | 35.7 |
| | Warming | 1127 | 7.9 | 8.1 | 43.6 |
| DK-Mol | Control | 668 | 8.7 | 9.0 | 17.6 |
| | Drought | 563 | 8.9 | 9.0 | 15.1 |
| | Warming | na | 9.7 | 9.8 | 15.3 |
| DK-Bra | Control | 714 | 10.2 | 8.9 | 16.5 |
| | Drought | na | na | 8.8 | 15.0 |
| | Warming | na | na | 9.4 | 15.0 |
| NL-Old | Control | 986 | 8.3 | 8.8 | 21.8 |
| | Drought | 792 | na | na | 17.1 |
| | Warming | 855 | 9.6 | 9.5 | 16.5 |
| ES-Gar | Control | 550 | 15.6 | 17.0 | 19.8 |
| | Drought | 397 | 15.8 | 16.8 | 17.0 |
| | Warming | 520 | 16.1 | 17.7 | 20.0 |

na: not assessed.

correlated with the carbon stock in the top 10 cm soil layer (Fig. 3). Concerning experimental manipulations, the effect of increased N input was tested at three peatland sites and overall no uniform effect was found on the CH₄ efflux ($P = 0.65$) (Table 3). At the peatland UK-Whi, though, additional deposition of oxidized N, corresponding to 5.6 g NO₃-N m⁻² yr⁻¹, resulted in an almost 300% increase of the annual CH₄ emission ($P = 0.031$). Concurrently, soil pH rose from 3.7 to 4.0 (Table S1). Permanent drainage of the Estonian peatland EE-Män reduced the CH₄ efflux substantially ($P = 0.003$), whereas no consistent effect on the CH₄ flux was observed for prolonged drought or warming at the shrubland sites ($P \geq 0.49$) (Fig. 4, Table 3).

3.3 N₂O fluxes

Annual fluxes of N₂O generally consisted of low efflux rates, although net N₂O uptake was observed in control plots at the Swedish peatland Fäjemyr (SE-Fäj) and the Scottish peatland UK-Whi (Table 3). Within each of the two ecosystem types, peatland and shrubland, the highest N₂O efflux occurred at the site with highest soil water NO₃⁻ concentration (Fig. 5). The stimulatory effect of NO₃⁻ on the N₂O efflux was supported by the N deposition experiments. More specifically, the two peatlands SE-Fäj and UK-Whi changed from N₂O sinks into N₂O sources as a result of increased NH₄NO₃ and NaNO₃ input, respectively ($P = 0.011$) (Fig. 6a). Overall, differences in volumetric soil water content across sites did not explain the variation in annual N₂O fluxes for control

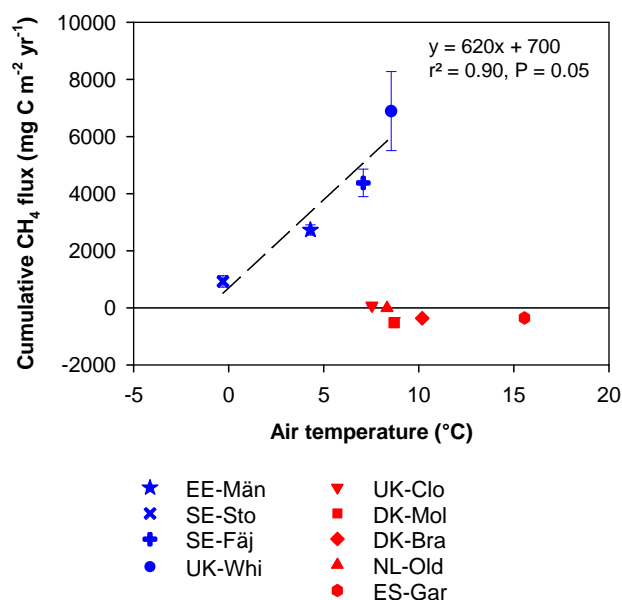


Fig. 2. Annual CH₄ flux related to mean annual air temperature in control plots at the nine sites (means \pm SE). A linear regression line was fitted to data from the four peatland sites. Site codes are described in Table 1.

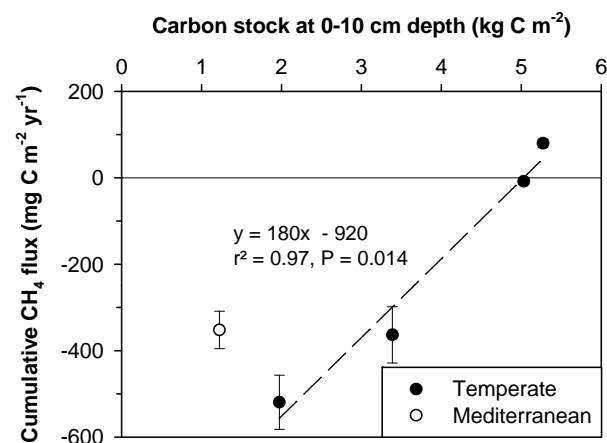


Fig. 3. Annual CH₄ flux as a function of carbon stock in the 0–10 cm soil layer at five shrubland sites (means \pm SE). A linear regression line was fitted to data from the four temperate shrubland sites.

plots (Fig. 6b). At the site level, however, reduced soil moisture caused by drainage or drought consistently reduced the N₂O efflux ($P = 0.0005$). According to differences of least squares means, this was especially pronounced for drainage at the Estonian peatland EE-Män and for drought at the Dutch shrubland Oldebroek (NL-Old) (site \times treatment; $P = 0.034$). The warming treatment had no effect on N₂O fluxes ($P = 0.47$) (Table 3).

3.4 Soil respiratory CO₂ emission

Soil CO₂ emissions ranged between 518 to 732 g C m⁻² yr⁻¹ at six of the nine sites investigated (Fig. 7a), but was considerably lower at the remaining three sites. As expected, the lowest rate was observed at the northernmost and coldest site SE-Sto (231 g C m⁻² yr⁻¹), where fluxes were only measured on vegetated plots and therefore are ecosystem-level respiratory CO₂ losses. Consequently, soil respiratory CO₂ losses should be even lower than the rate reported here. Soil respiration was also considerably lower at the temperate shrubland NL-Old (310 g C m⁻² yr⁻¹), and at the southernmost and warmest shrubland ES-Gar (390 g C m⁻² yr⁻¹), compared to the six sites with highest emissions. Across the five sites where warming was applied as treatment, the temperature rise of 0.5 °C in the soil had no effect on soil CO₂ emissions ($P = 0.83$) (Table 3). At the site level, the CO₂ efflux seemed to be more controlled by soil moisture. More specifically, prolonged drought and long-term (> 30 yr) drainage overall caused a reduction of soil CO₂ emissions ($P = 0.003$) (Fig. 7b). In particular, this was pronounced for drainage at the peatland EE-Män and drought at the dry shrubland DK-Mol, whereas drought tended to have the opposite effect at the wet shrubland UK-Clo (site × treatment; $P = 0.0086$). Increased N input at three peatland sites had no effect on annual CO₂ emissions ($P = 0.69$) (Table 3).

3.5 Responsiveness of greenhouse gas fluxes

Relative to control plots, the observed treatment response was generally higher for CH₄ and N₂O fluxes than for CO₂ fluxes (Table 4). However, when comparing the fractional importance of each GHG to the total numerical global warming response (GWR), the changes in CO₂ emissions dominated the response in all treatments (ranging 71–96 %), except for NO₃⁻ additions where 89 % of the total GWR was due to a change in CH₄ emissions. Relative to the other GHGs, the impact on GWR from changes in N₂O fluxes was generally low; only 4 % of total GWR across the shrubland sites and absent across the peatland sites. Across all treatments and gas species, anthropogenic disturbance overall reduced the shrublands' contribution to global warming, while peatlands generally showed an increased contribution for CH₄ and a reduced contribution for CO₂.

4 Discussion

In Europe, open landscapes represented by peatlands and shrublands cover about 7 % of the land area (EEA, 2006; Montanarella et al., 2006). In the current synthesis, we investigated greenhouse gases fluxes between these ecosystems and the atmosphere in order to identify factors that seemed to control cross-site variation in flux rates, either directly or indirectly. Furthermore, we assessed the effect

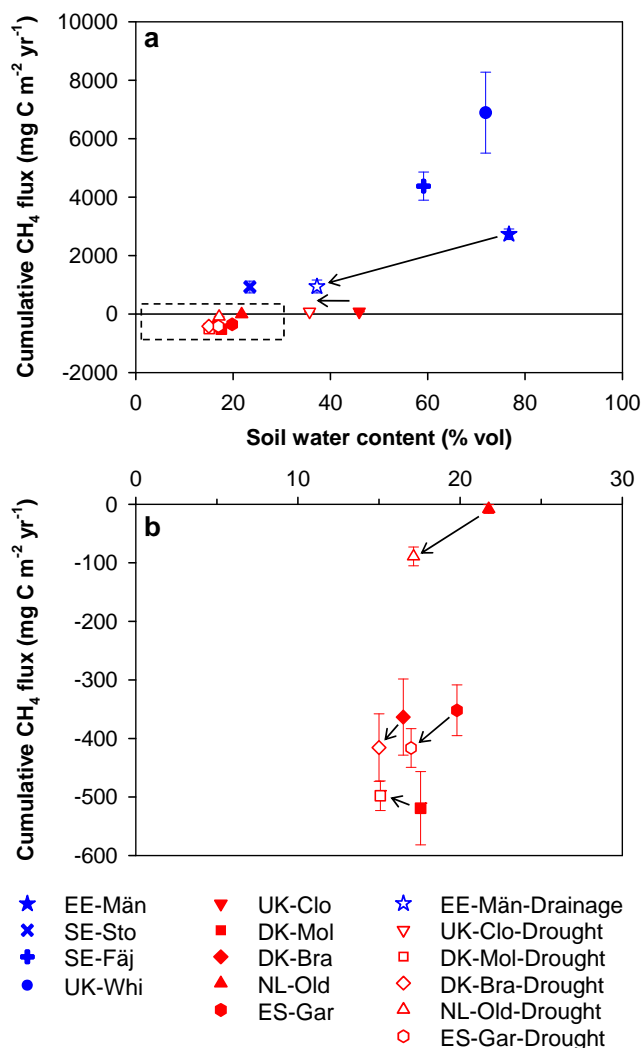


Fig. 4. Annual CH₄ flux at the nine sites related to mean annual soil water content, predominantly measured in the top 10 cm soil layer (means ± SE). Closed symbols are control plots, whereas open symbols are drained or drought treated plots. Arrows indicate direction of treatment responses. In (b), the bottom left corner of (a) has been enlarged. Site codes are described in Table 1.

on the GHG fluxes of anthropogenic disturbances, such as temperature rise and prolonged droughts caused by climate change, drainage of peatlands and increased atmospheric nitrogen deposition.

4.1 CH₄ fluxes

On a global scale, wetlands are the largest single source of CH₄ emission to the atmosphere, accounting for 100 to 231 Tg CH₄ yr⁻¹ (IPCC, 2007b), whereas aerobic soils are substantial CH₄ sinks, estimated to take up about 22 Tg CH₄ yr⁻¹ (Dutaur and Verchot, 2007). The present study illustrates these fundamental differences between

Table 3. Annual cumulative CH₄, N₂O and soil CO₂ fluxes at the nine experimental sites depending on treatment (means; SE in brackets). Number of replicated plots and year of measurement (either one or two years) are also indicated.

| Site | Treatment | Replicates | CH ₄ flux | | N ₂ O flux ^a | | Year | Soil CO ₂ emission ^b | | Year |
|--------|---------------------------------|------------|---------------------------------------|----------|---------------------------------------|--------|-----------|--|-------|-----------|
| | | | mg C m ⁻² yr ⁻¹ | (SE) | mg N m ⁻² yr ⁻¹ | (SE) | | g C m ⁻² yr ⁻¹ | (SE) | |
| EE-Män | Control | 3 | 2729 | (180) | 41.8 | (5.7) | 2008/2009 | 528 | (66) | 2008/2009 |
| | Drainage | | 943 | (222) | 4.1 | (7.9) | | 226 | (56) | |
| SE-Sto | Control | 4 | 926 | (201) | na | | 2007 | 231 | (6) | 2007 |
| | NH ₄ NO ₃ | | 551 | (110) | na | | | 265 | (39) | |
| SE-Fäj | Control | 4 | 4377 | (482) | -2.4 | (1.8) | 2007 | 522 | (179) | 2007 |
| | NH ₄ NO ₃ | | 5883 | (846) | 8.0 | (3.7) | | 585 | (51) | |
| UK-Whi | Control | 4 | 6890 | (1383) | -14.3 | (3.5) | 2007–2009 | 572 | (69) | 2006/2007 |
| | NH ₄ | | 7412 | (2590) | 5.5 | (16.6) | | 535 | (51) | |
| | NO ₃ | | 27 020 | (11 101) | 16.1 | (13.2) | | 496 | (26) | |
| UK-Clo | Control | 3 | 80 | (10) | 10.8 | (5.7) | 2007–2009 | 518 | (32) | 2006/2007 |
| | Drought | | 81 | (12) | 0.8 | (2.7) | | 633 | (12) | |
| | Warming | | 70 | (7) | 11.2 | (2.1) | | 584 | (45) | |
| DK-Mol | Control | 3 | -519 | (63) | 13.3 | (5.7) | 2006/2007 | 732 | (36) | 2003/2004 |
| | Drought | | -498 | (25) | 9.9 | (4.6) | | 513 | (18) | |
| | Warming | | -552 | (36) | 10.8 | (2.3) | | 730 | (48) | |
| DK-Bra | Control | 6 | -363 | (65) | 31.0 | (5.6) | 2006/2007 | 651 | (59) | 2006/2007 |
| | Drought | | -416 | (58) | 27.6 | (7.8) | | 600 | (34) | |
| | Warming | | -436 | (78) | 29.5 | (6.5) | | 659 | (52) | |
| NL-Old | Control | 3 | -8 | (7) | 6.9 | (5) | 1999 | 310 | (48) | 1999 |
| | Drought | | -89 | (16) | -30.4 | (10.2) | | 285 | (72) | |
| | Warming ^c | | 29 | (20) | -2.3 | (2.3) | | 330 | (45) | |
| ES-Gar | Control | 3 | -352 | (43) | na | | 2007/2008 | 390 | (30) | 2007/2008 |
| | Drought | | -416 | (33) | na | | | 298 | (19) | |
| | Warming | | -432 | (42) | na | | | 335 | (21) | |

^a Fluxes of N₂O were not assessed (na) at SE-Sto and ES-Gar.

^b Data for SE-Sto and SE-Fäj is ecosystem respiratory CO₂ emission.

^c At NL-Old, the warming treatment started in May 1999.

Table 4. Relative responsiveness to treatments compared to controls (%), absolute responsiveness (CO₂-equivalents), and fractional importance of each greenhouse gas to the total numerical global warming response (in brackets, %) for soil CH₄, N₂O and CO₂ fluxes across all sites.

| Treatment ^a | Relative responsiveness (%) | | | Absolute responsiveness (CO ₂ -eq) | | |
|---------------------------------------|-----------------------------|-------------------------------|-----------------|---|------------------|-----------------|
| | CH ₄ | N ₂ O ^b | CO ₂ | CH ₄ | N ₂ O | CO ₂ |
| Drainage | -65 | -90 | -57 | -74 (6) | -18 (2) | -1107 (92) |
| N addition, including NH ₄ | 14 | na | 5 | 23 (22) | 7 (7) | 73 (71) |
| N addition, including NO ₃ | 174 | na | 2 | 295 (89) | 10 (3) | 25 (8) |
| Drought | -15 | -87 | -11 | -1 (1) | -6 (3) | -201 (96) |
| Warming | -14 | -21 | 1 | -1 (4) | -1 (5) | 27 (91) |
| Peatlands all treatments | 124 | 0.4 | -9 | 193 (56) | 0 (0) | -153 (44) |
| Shrublands all treatments | -14 | -54 | -5 | -1 (2) | -4 (4) | -87 (94) |

^a Responsiveness is reported for the treatments “warming” and “N addition, including NH₄” although cross-site statistical analyses showed no significant effects on any of the gas species.

^b na: not assessed due to change in flux direction.

ecosystem types depending on water table depth with peatlands as CH₄ sources and shrublands generally as CH₄ sinks. The CH₄ emission from peatlands correlated positively with temperature when analyzed across the four sites. Although our natural gradient analyses could be biased by differences

in measurement years and methods, the results are in line with Christensen et al. (2003) who compared CH₄ fluxes measured during the growing season at five northern wetlands covering Greenland, Iceland, Scandinavia and Siberia. They estimated that soil temperature explained 84 % of the

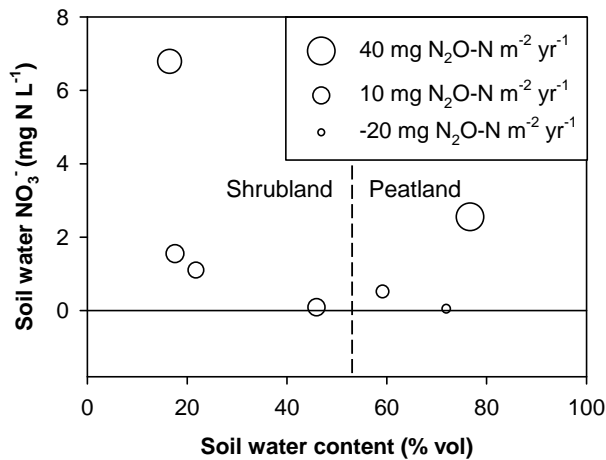


Fig. 5. Size of annual N₂O flux plotted against mean annual soil water content and nitrate concentration in soil water. Data derive from control plots at seven sites that are divided into shrublands and peatlands by the dashed line.

variability in mean seasonal CH₄ emissions, and suggested that availability of organic acids in peat water accounted for the remaining 16 % of the CH₄ fluxes variability across the sites. The stimulating effect of increased temperature on net CH₄ emissions from peatlands can be explained by basic CH₄ biochemistry as processes related to CH₄ production are more temperature dependent than those associated with methane oxidation (Dunfield et al., 1993). However, the simple temperature relationship of CH₄ emissions may also include other interrelated factors, most importantly plant productivity affecting substrate quality and quantity, but also plant aerenchyma development allowing CH₄ produced in the soil to be released into the atmosphere (Joabsson et al., 1999). Based on the current dataset, we are not able to distinguish whether temperature affected the CH₄ efflux directly or indirectly, and most likely several of the temperature-related mechanisms above acted simultaneously. Nevertheless, our natural gradient analysis suggests that temperature could be used as a common indicator when estimating the magnitude of CH₄ emissions from peatlands across wide regional scales. Furthermore, the analysis reveals that CH₄ emissions from peatlands may rise in the future as a result of the predicted temperature increases caused by climate change.

In a global analysis of CH₄ uptake by aerobic soils, Dutaur and Verchot (2007) found that soil texture strongly controlled CH₄ uptake with coarse textured soils consuming more CH₄ than other texture classes. All temperate shrublands in our study had a sandy mineral soil layer, while the soils differed in the properties of the organic layer, which consisted of peat at the heather-moorland (UK-Clo) and of mor humus at the dry *Calluna* heaths (DK-Mol, DK-Bra, NL-Old). Net CH₄ uptake at the four temperate shrublands correlated negatively with the carbon stock in the upper 10 cm soil layer, suggesting a switch from net CH₄ uptake to net CH₄ emission

as soils become enriched in organic matter. To our knowledge, such a relationship has only been reported in very few studies. For instance, Singh et al. (1997) showed that CH₄ uptake in dry tropical forest soils correlated with both carbon and nitrogen content of the soils; two variables which increased in parallel. Within soil types, the content of organic matter and soil water often correlate, either because organic matter increases the water holding capacity (Hudson, 1994) or because high soil moisture hinders aerobic decomposition (Jungkunst and Fiedler, 2007). In line with this, the two sites with the highest carbon stock of the four temperate shrublands (i.e. UK-Clo and NL-Old) also had the highest soil moisture (Table 2). Consequently, the apparent carbon control on net CH₄ exchange could be indirect via an effect on soil moisture, which limits CH₄ diffusion towards the zone of methanotrophic activity (King, 1997; Dunfield, 2007). Singh et al. (1997), however, suggested a more direct control mechanism, where reduced net uptake of CH₄ in carbon-rich soils was due to decreased O₂ content in the soil atmosphere, resulting from higher decomposition rates. In our study, though, we found no relationship between carbon stock and soil respiratory CO₂ emission at the four temperate shrubland sites. Potentially, organic matter stimulated methanogenesis by acting as a substrate for the process, leading to lower net CH₄ uptake in the carbon-rich soils in our study. Most likely, the correlation between soil organic C and CH₄ uptake was caused by a combination of these indirect and direct mechanisms, and we suggest that future studies aim at investigating this relationship in more details.

Previous studies of N additions to wetlands reported both positive and negative responses in net CH₄ emissions, and the mechanisms involved are still under debate (Bodelier, 2011). In the present study, NaNO₃ addition at the Scottish bog UK-Whi increased the CH₄ efflux by almost 300 %, whereas NH₄Cl or NH₄NO₃ additions had no overall effect. At the Scottish bog, the addition of NaNO₃ raised pH in peat water from 3.7 to 4.0 (Table S1) and increased the availability of dissolved organic carbon (DOC), possibly because the slightly higher pH enhanced the solubility of organic compounds in the soil (Evans et al., 2008). In contrast, NH₄Cl addition had no effect on pH or DOC. For comparison, Murakami et al. (2005) raised the pH of four tropical acid peat soils by ca. 2 pH units and observed a vast increase in the CH₄ production potential. The authors suggested that this was due to increased substrate supply for methanogenic microorganisms derived from decomposed organic matter such as organic acids from peat humus. A similar mechanism could explain the enhanced CH₄ efflux in response to NaNO₃ addition at the Scottish bog UK-Whi.

At the Swedish peatland sites SE-Fäj and SE-Sto, addition of NH₄NO₃ had no significant effects on the CH₄ flux. Although insignificant, the opposing effects of N addition on CH₄ fluxes at SE-Fäj (increased efflux) and SE-Sto (decreased efflux), illustrates the importance of peatland type and site specific properties, such as plant composition and

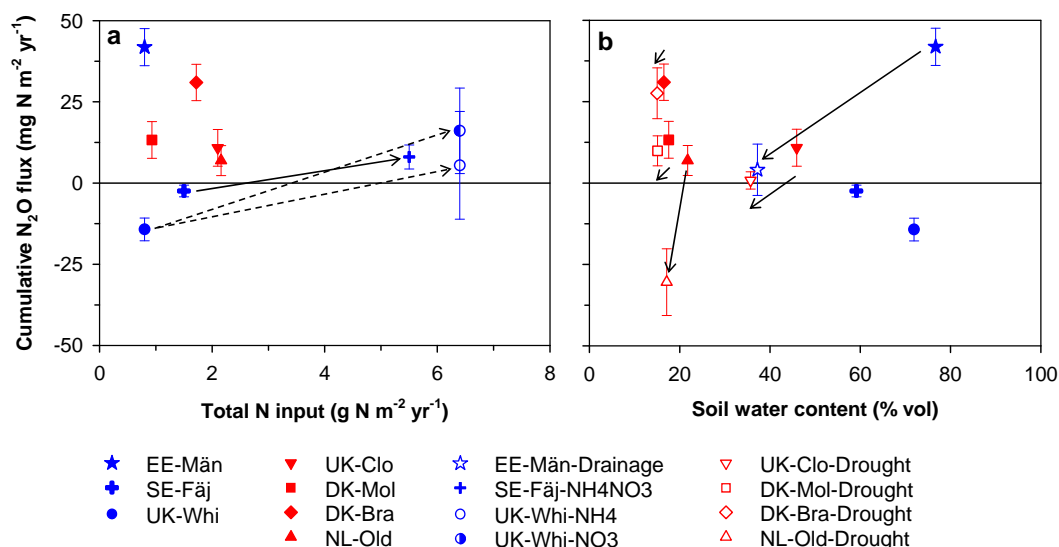


Fig. 6. Annual N₂O flux at seven sites related to atmospheric N deposition (a) and mean annual soil water content, predominantly measured in the top 10 cm soil layer (b) (means ± SE). In addition to data for control plots, results are presented for plots that were exposed to either increased N input (a) or drainage and drought (b). Arrows indicate direction of treatment responses. Site codes are described in Table 1.

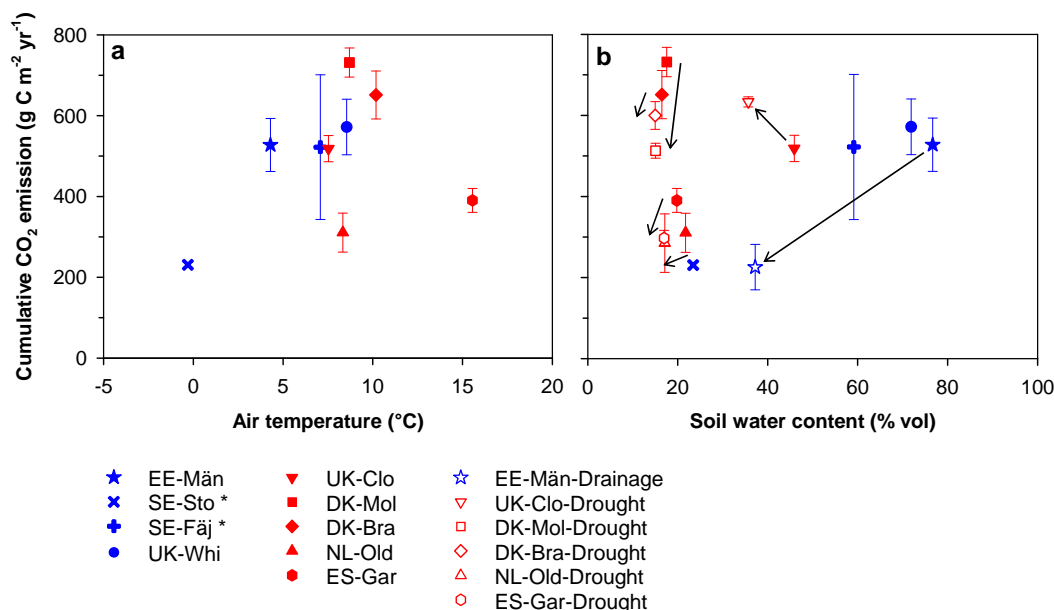


Fig. 7. Annual soil respiratory CO₂ emission in control plots at the nine sites related to mean annual air temperature (a) and mean annual soil water content, predominantly measured in the top 10 cm soil layer (b) (means ± SE). In (b), data for drained or drought treated plots are also presented with arrows indicating direction of treatment responses. * Data for SE-Sto and SE-Fäj is ecosystem respiratory CO₂ emission. Site codes are described in Table 1.

productivity, pH, substrate quality and general hydrology, for the effects of increased nutrient availability on peatland CH₄ fluxes (Keller et al., 2006).

4.2 N₂O fluxes

Latest advances in knowledge suggest that three separate processes contribute to N₂O emissions from soils. These are

nitrification, denitrification and dissimilatory nitrate reduction to ammonium (DNRA), which are thought to be important sources of N₂O in oxic, sub-oxic and anoxic microsites of the rhizosphere, respectively (Baggs, 2011). At individual field sites, daily N₂O emission rates are typically reported to increase with soil moisture in the range from 50 to 90 % water filled pore space (WFPS) (Smith et al., 2003). This

relationship is probably caused by the associated decrease in O_2 diffusion within the soil, leading to larger anaerobic microsites and thereby increased N_2O production via denitrification (Smith et al., 2003) and possibly also DNRA. However, when soil moisture exceeds 90 % WFPS, N_2O emissions may decline as N_2 is the final product of denitrification in most waterlogged soils (Davidson, 1991), although pH may also influence the N_2O/N_2 loss ratio of denitrification (Šimek and Cooper, 2002).

In the present study, the lack of relationship between N_2O emission and volumetric soil moisture across sites was possibly because N_2O production is controlled by gas diffusivity, which is poorly reflected by volumetric soil moisture when comparing soils that differ in total porosity. At the site level, however, net N_2O emissions declined consistently in response to reduced soil moisture caused by drought treatment, supporting previous results from drought experiments in a spruce forest (Goldberg and Gebauer, 2009). Furthermore, N_2O emissions from the Estonia peatland EE-Män declined due to long-term drainage, which is in contrast to results from previous drainage experiments in ombrotrophic bogs (Martikainen et al., 1993; Regina et al., 1996). Apparently, increased tree growth at the drained area reduced the availability of soil nitrate (Table S1), which in combination with lower soil moisture caused the decline in N_2O emissions.

Analysed across sites, the shrubland and peatland with highest NO_3^- concentration in soil water also had the highest annual N_2O emission within each ecosystem type, which illustrates that N_2O production in these nutrient poor ecosystems was limited by N availability. This was supported by data at the site level, where N additions ($< 60 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) that included nitrate led to increased N_2O efflux from two peatlands, suggesting that denitrification or DNRA were involved in N_2O production in these ecosystems, and that the processes were stimulated by increased substrate availability.

4.3 Soil respiratory CO_2 emission

Annual soil respiratory CO_2 emissions (R_s) ranged from 231 to $732 \text{ g C m}^{-2} \text{ yr}^{-1}$ in control plots across the nine sites. The highest fluxes were observed at the temperate sites with annual temperatures ranging 8–10 °C, where ecosystem C turnover was less likely to be inhibited by either low temperatures (i.e. SE-Sto) or low summer soil moisture, resulting from low precipitation combined with high temperatures (i.e. ES-Gar). For comparison, Hibbard et al. (2005) reported R_s rates of $427\text{--}1805 \text{ g C m}^{-2} \text{ yr}^{-1}$ across evergreen temperate forests, $509\text{--}867 \text{ g C m}^{-2} \text{ yr}^{-1}$ in temperate/Mediterranean broadleaved forests and $181\text{--}488 \text{ g C m}^{-2} \text{ yr}^{-1}$ in temperate/Mediterranean woodlands and savannas. The low fluxes at ES-Gar and NL-Old may be biased by the method applied, where headspace CO_2 concentrations were determined by gas chromatography to-

gether with CH_4 and N_2O . This implied longer enclosure periods, i.e. 15 or 60 min compared to 1–5 min when measured directly in the field using an infrared gas analyzer. Longer enclosure periods may lead to non-linear development of headspace CO_2 concentrations over time, and subsequently to underestimation of flux rates if calculations are based on linear regression (Heinemeyer and McNamara, 2011). However, EE-Män had the fourth highest CO_2 flux among the nine sites and here fluxes were also determined using the gas chromatography method. Furthermore, Beier et al. (2009) estimated annual soil respiration at ES-Gar to be $440 \text{ g C m}^{-2} \text{ yr}^{-1}$ based on other data with shorter enclosure periods (4 min), which still is lower than our estimates for six of the temperate sites. The low flux at the Dutch shrubland NL-Old could be due to the vegetation which, unlike the other sites, is a *Calluna* monoculture (Table 1). Van Vuuren and van der Eerden (1992) found that *Calluna* litter had a lower decomposition rate compared to litter of *Deschampsia flexuosa* and *Molinia caerulea*, which coincided with a double concentration of recalcitrant carbon compounds, indicated by the Klason lignin content. The low CO_2 efflux at NL-Old could therefore result from a lower quality of the soil C pool compared to the other sites. Thus, our results indicate a pattern across the sites where soil respiration increased with temperature, but that the increase was offset in the warmest ecosystem due to low soil moisture, resulting from low precipitation combined with high temperatures. At the site level, however, warming treatment had no overall effect on soil respiratory CO_2 losses, which may be due to the relatively mild temperature increase achieved with the passive warming technique of 0.5 °C in the soil.

The prolonged drought or drainage manipulations showed stronger effects on soil respiration rates than both warming and N additions. Reduced soil moisture due to drought or drainage generally decreased soil respiration rates at the dry shrublands and the wet, long-term drained peatland EE-Män, but increased soil respiration rates at the wet shrubland UK-Clo. As drainage most often leads to increased CO_2 emissions in hydromorphic soils, at least in the short-term (Jungkunst and Fiedler, 2007; Danevčič et al., 2010; Maljanen et al., 2010), our results highlight how results may differ depending on the time since the experimental treatments were initiated. The drainage treatment at EE-Män started more than 30 yr ago. Currently, the easy degradable fractions of the peat at EE-Män have already been decomposed and carbon cycling in the ecosystem has reached a new balance. In contrast, the drought treatment at UK-Clo has only been running for eight years, thus it is likely that the long-term effect may differ from the current short-term effect. Furthermore, the different response directions to prolonged drought between the sites show how important the initial conditions are for the strength and directions of the response to the treatment.

4.4 Experimental manipulations

The quantitative effect on GHG fluxes of an experimental treatment is to a certain extent controlled by the magnitude of the treatment effects on environmental drivers. The question is whether our experimental manipulations have caused realistic changes in these drivers, which enable us to predict changes in GHG fluxes in future? On an annual basis, the prolonged drought treatment at the shrubland sites reduced moisture in the top soil by 10–20 %, which is a consistent decline when taking into account that the drought treatment was only carried out for about two months per year. In contrast, the warming treatment generally raised annual soil temperature at the sites by 0.5 °C. For comparison, annual mean soil temperatures in control plots at the Welsh shrubland UK-Clo varied between 7.0 and 8.7 °C during the years 2000–2007 (data not shown). Thus, the overall warming effect of 0.5 °C was less than the interannual variability at the site level. Furthermore, surface temperatures in Europe are projected to increase 2–5 °C during this century, depending on which scenario is used (IPCC, 2007a). In conclusion, the lack of experimental warming effect on any of the three GHGs in our study could relate to an insufficient temperature increase obtained by the passive night-time warming treatment.

By contrast, drainage about 30 yr ago of the Estonian peatland EE-Män has more than doubled the size of the oxic zone by lowering the water table from an annual depth of 15 cm to 38 cm below soil surface. As a result, the emission of all three GHGs had dropped dramatically after 30 yr of treatment. Furthermore, annual N deposition was raised from 0.2, 1.5 and 0.8 g N m⁻² to 4.2, 5.5 and 6.4 g N m⁻² at the peatlands in northern (SE-Sto) and southern Sweden (SE-Fäj) as well as Scotland (UK-Whi), respectively. It is unlikely that total inorganic N deposition in these regions of Europe will reach such high levels in future (Galloway et al., 2004). However, global warming will lead to increased soil mineralization rates, releasing more inorganic N and other nutrients for plant uptake (Rustad et al., 2001; Mack et al., 2004). Also, large regions of South Asia are projected to receive more than 5 g N m⁻² yr⁻¹ by 2050. Apart from the CH₄ response to NaNO₃ addition at the Scottish peatland UK-Whi, responses in GHGs fluxes to these relatively high N application rates were minor, illustrating resilience in the peatland ecosystems towards increased N deposition in the short term. However, in the longer term, changes in peatland plant composition and structure may occur, affecting the exchange of greenhouse gases. For instance, a warmer and drier climate with increased nutrient turnover will inflict competitive disadvantages for *Sphagnum* mosses, as they are adapted to cold, wet and nutrient-poor conditions (Clymo, 1984), and possibly stimulate growth of vascular plants.

4.5 Responsiveness

We observed some clear and interesting patterns in the responses of the three GHG fluxes across the nine investigated ecosystems. First of all, the observed responses to the manipulations of climate and atmospheric N deposition were stronger in relative terms for CH₄ and N₂O fluxes than for soil CO₂ emissions. However, when comparing the fractional importance of each GHG to the total global warming response, then the observed changes in soil CO₂ efflux dominated the response for the drainage, drought and warming treatments, where at least 91 % of the global warming response was caused by changes in soil CO₂ fluxes. The N addition treatments in peatlands that included NO₃⁻ differed from this overall pattern by the dominance of a change in CH₄ emissions (89 % of global warming response) compared to changes in the other gas species. This profound effect therefore also partly explains why responses in CH₄ fluxes played a slightly more dominant role across the four peatlands (56 % of the global warming response) compared to soil CO₂ emissions (44 % of global warming response) and N₂O fluxes, which did not contribute significantly. In contrast, across the five shrublands including both drought and warming treatments, the response in soil CO₂ emissions dominated (94 % of global warming response) by far over responses in CH₄ fluxes (2 % of global warming response) and N₂O fluxes (4 % of global warming response).

Based on 109 different studies on effects of N addition on ecosystem GHG budgets, Liu and Greaver (2009) reported an overall increase in the terrestrial CO₂ sink, but also that this was largely offset (53–76 %) by stimulated CH₄ and N₂O emissions. When adding up the absolute treatment responses for the three GHGs in our study, the N addition experiments led to a substantial positive climate forcing response. However, this was caused by a strong increase in CH₄ emissions, whereas Liu and Greaver (2009) found that N₂O was the primary contributor to global warming across the studies in their review. Warming effects were very small and not significant in the overall cross-site ANOVA. By contrast, the drought and drainage treatments led to a uniformly negative climate forcing response. Again, it must be emphasized that the response for the drained peatland in this study is the long-term response and it is likely that a substantial amount of carbon was lost from the ecosystem in the years immediately after drainage. But at least across the five shrubland ecosystems, the drought treatment showed a clear pattern of negative feedback to climate change.

In general, we recognize that the nine sites included in this study span differences in soil types, plant species, pre-treatment conditions and present climate, and that the experimental treatments differed between sites. For this reason, generalized conclusions based on the mean responsiveness presented here should be drawn with caution. Especially, we lack information on responses in net primary production, and it is likely that the absolute responsiveness of net ecosystem

CO₂ fluxes would differ from that of soil CO₂ emissions alone. Finally, none of the nine experiments included interactive effects with other climate drivers, which have previously been shown to be important for the combined response to multiple changes (Larsen et al., 2011).

5 Conclusions

With respect to environmental variables that seemed to influence the magnitude of GHG fluxes across the nine sites, temperature was identified as a main driver of CH₄ emissions across the peatland sites. In contrast, net CH₄ uptake at the temperate shrublands sites correlated negatively with the soil carbon stock, either due to an indirect effect via soil moisture or because soil carbon acted as a source for methanogenesis. Nitrate availability seemed to be a driver of N₂O emissions at both peatland and shrubland sites, as the highest N₂O efflux within each ecosystem type occurred at the site, which had the highest NO₃⁻ concentrations in soil water. Soil respiratory CO₂ emission showed maximum annual values at the temperate sites with mean annual temperature of 8–10 °C. Outside this range, in each end of our temperature gradient, soil respiration was either limited by low temperatures at the subarctic site SE-Sto or by low summer soil moisture at the Mediterranean site ES-Gar.

In terms of total climate forcing response, prolonged drought and long-term (> 30 yr) drainage consistently reduced the soils' contribution to global warming. However, substantial amounts of CO₂ were presumably lost from the drained peatland immediately after drainage. Furthermore, N addition to peatlands caused a considerable increase in the global warming contribution from these soils, primarily due to the response of CH₄ emissions to NaNO₃ addition at one site. Finally, experimental warming had no effect on any of the three GHGs, which could be explained by a modest temperature increase of 0.5 °C imposed by the passive night-time warming treatment. When comparing the fractional importance of each GHG to the total numerical global warming response, then the change in CO₂ efflux dominated the response in all treatments, except for NO₃⁻ addition where change in CH₄ emissions accounted for the major part. Therefore, within the applied range of water, temperature and nutrient manipulations, soil CO₂ emission plays a dominant role with respect to ecosystems' effect on global warming.

Supplementary material related to this article is available online at: <http://www.biogeosciences.net/9/3739/2012/bg-9-3739-2012-supplement.pdf>.

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