Boreal Mire Carbon Exchange

Sensitivity to Climate Change and Anthropogenic Nitrogen and Sulfur Deposition

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Cover: "The foot-bridge to infinity". The photo is taken from the north-eastern entrance to Degerö Stormyr in middle of September 2009.
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Abstract

Boreal peatlands are important long-term sinks of atmospheric carbon and in the same time the largest natural source of methane to the atmosphere. A changing climate as well as deposition of anthropogenically derived pollutants, such as nitrogen and sulfur, has the potential to affect the processes that control the carbon exchange in peatlands. Many of the biogeochemical responses to changed environmental conditions, such as changed plant community composition, are slow and therefore long-term studies are required. In this thesis I have investigated the long-term effects of nitrogen addition, sulfur addition and greenhouse enclosures on carbon exchange by using a field manipulation experiment in a boreal minerogenic, oligotrophic mire after 10-12 years of treatment. Treatment effects on CH_4 emissions, gross primary production (GPP), ecosystem respiration (R_{eco}) and net ecosystem exchange (NEE) were estimated from 1-2 seasons of chamber flux measurements. Treatment effects on potential CH_4 production and oxidation were estimated in incubations of peat from different depth intervals. The effect of nitrogen deposition on carbon accumulation was evaluated in peat cores at different depth intervals. The long-term nitrogen additions have: shifted plant community composition from being dominated by *Sphagnum* to being dominated by sedges and dwarf shrubs; changed mire surface microtopography so that mean water table is closer to the surface in plots with high nitrogen; increased CH_4 production and emission; increased R_{eco} slightly but have not affected GPP or NEE; reduced the peat height increment, but increased both peat bulk density and carbon content, leading to an unchanged carbon accumulation. The long-term sulfur additions have not reduced CH_4 emissions, only slightly reduced CH_4 production and did not have any effect on the CO_2 carbon exchange. The greenhouse treatment, manifested in increased air and soil temperatures, reduced both CH_4 emissions and CH_4 production by approximately 30%, decreased R_{eco} slightly, but had no effect on either GPP or NEE. Many of these results oppose to earlier findings, and this suggests that long-term field manipulations are important when evaluating effects with a long time constant.

Keywords: peatland, nitrogen, sulfur, deposition, temperature, field manipulation, carbon, methane, CO_2,

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Contents

List of Publications

This thesis is based on the work described in the following papers, which are referred to by the corresponding Roman numerals in the text:

I **Eriksson T.**, Öquist M.G. and Nilsson M.B. (2010). Production and oxidation of methane in a boreal mire after a decade of increased temperature and nitrogen and sulfur deposition. *Global Change Biology 16(7) 2130-2144.* doi: 10.1111/j.1365-2486.2009.02097.x

II **Eriksson T.**, Öquist M.G. and Nilsson M.B. (2010) Effects of decadal deposition of nitrogen and sulfur, and increased temperature, on methane emissions from a boreal peatland. Accepted in *Journal of Geophysical Research-Biosciences.*

III **Eriksson T.** and Nilsson M.B. Decadal deposition of nitrogen and sulfur, and increased temperature, has only caused minor changes in carbon dioxide fluxes between the atmosphere and a boreal mire. Manuscript.

IV Nilsson, M.B. and **Eriksson, T**. Long-term increases in nitrogen deposition have not reduced carbon accumulation rates in a boreal peatland. Manuscript.

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1 Introduction

1.1 Background

Mires are ecosystems with high water table levels, and usually nutrient-poor and acidic conditions, in which rates of carbon (C) fixation are low but rates of decomposition even lower, thus C is accumulated as peat (Immirzi *et al.*, 1992). Since these conditions have persisted for thousands of years in many cases, mires store large quantities of C. About 85% of the global peatland area is located in the boreal and subarctic regions (Joosten & Clarke, 2002). Boreal mires cover only approximately 3% of the global land area, but currently store presently 270-455 Pg of C, corresponding to about 30% of the global soil C pool (Turunen *et al.*, 2002; Gorham, 1991) and 35-60% of the total atmospheric C pool (IPCC, 2007). Mires are important biologically as habitats for unique plants and animals, economically for harvestable resources such as fuel and horticultural products, and socially for aesthetic, cultural and landscape values (Charman, 2002). In addition, mires may play an important role in the context of climate change. Boreal peatlands have acted, and still act, as long-term atmospheric sinks of carbon dioxide (CO_2) and simultaneously as atmospheric sources of methane (CH_4), both of which are important greenhouse gases (Frolking & Roulet, 2007). Wetlands in the northern hemisphere add approximately 36 Tg CH_4 per year to the atmosphere, constituting 6 % of the total and 22 % of the natural sources of atmospheric CH_4 (Chen & Prinn, 2006).

Numerous variables influence CO_2 exchange and CH_4 emissions, but the most important include the water table level (Granberg *et al.*, 1997), the vegetation community composition mainly determined by the nutrient availability (Joabsson *et al.*, 1999b) the annual average temperature (Christensen *et al.*, 2003) the availability of competing electron acceptors

(Conrad, 1989). Any change in these controls may in turn affect CO_2 fluxes and CH_4 emissions. Such a change can, for example, be initiated by a changing climate or deposition of anthropogenic pollutants (Gauci *et al.*, 2004; Granberg *et al.*, 2001; Gorham, 1991).

Anthropogenic pollutants, such as chemicals containing nitrogen (N) and sulfur (S) released during industrial processes and combustion, may be transported by wind and clouds and deposited in mires as either wet or dry deposition. High deposition of N has the potential to shift the vegetation community composition (Berendse *et al.*, 2001), and thereby affect the biogeochemical processes of these ecosystems (Gunnarsson & Rydin, 2000). Sulfate (SO_4^{2-}), the oxidized form of S, may affect both plant production (Ferguson & Lee, 1979) and CH_4 processes (Gauci *et al.*, 2004). In addition to anthropogenic pollutants, climatic changes may have strong effects on the C exchange properties of peatlands, through changes in temperature (Dorrepaal *et al.*, 2009) and water balance (Bubier *et al.*, 2003).

Thus, it is of great importance to understand the long-term effects of N deposition, S deposition and temperature increases on C exchange processes in peatlands. Field manipulations are often used to evaluate these effects. However, most field studies are based on short-term (1-3 years) experiments; hence the results mostly reflect effects of changes in nutrient availability, rather than those of long-term shifts in plant community composition. Clearly, to assess the latter using field manipulations, the treatments must be at least sufficiently prolonged to induce changes in the vegetation.

1.2 Objectives

The objectives of the project this thesis is based upon were to evaluate the effects of long-term N and S deposition and increased temperature on carbon exchange and storage in a boreal minerotrophic mire. An experimental site in northern Sweden, where N and S applications and greenhouse cover have been applied for 10-12 years to a poor fen lawn, was observed to assess effects of these treatments on CH_4 production and CH_4 oxidation potentials (Paper I), CH_4 emissions (Paper II), net CO_2 ecosystem exchange (Paper III) and finally the C accumulation of the mire (Paper IV). For convenience, the studies described in Papers I-IV are referred to as Studies I-IV, respectively, and their specific objectives were as follows:

In Study I, colleagues who participated in the project and I (hereafter we) investigated whether CH_4 production in the upper 40 cm of the peat was: (1) stimulated by the long-term N additions via increases in the density of vascular plants, (2) reduced by the long-term S deposition due to enhanced competition from sulfate-reducing bacteria and/or (3) enhanced by the greenhouse treatment as a direct effect of increased soil temperature, or if other long-term indirect effects of the treatment were more significant. In addition, we evaluated the effects of the three field treatments on CH_4 oxidation potentials.

In Study II we hypothesized: (1) that deposition of N increases CH_4 emissions by enhancing vascular plant cover, with associated increases in plant root exudation and plant-mediated transport of CH_4; (2) that deposition of S reduces CH_4 emissions by enhancing competition for available energy between sulfate-reducing bacteria and methanogens; and (3) that long-term greenhouse enclosure reduces CH_4 emissions by reducing the quality of substrates entering the anoxic zone.

In Study III we evaluated the responses of net CO_2 ecosystem exchange and the flux components gross primary production (GPP) and ecosystem respiration (R_{eco}) to the experimental treatments. We hypothesized that: (1) N deposition stimulates both GPP and R_{eco}, and leaving net ecosystem exchange (NEE) virtually unchanged; (2) S deposition slightly reduces NEE through negative effects on GPP; and (3) the greenhouse treatment stimulates both GPP and R_{eco}, leaving NEE essentially unchanged.

Finally, in Study IV, our main interest was to investigate the effects of long-term N deposition on C accumulation in the upper 40 cm of the peat. We hypothesized that N deposition decreases the height growth of the peat, but increases its bulk density and C content so overall rates of C accumulation are not substantially changed.

1.3 Mire ecology – a brief introduction

The vegetation and hydrology play key roles in C cycling of mires, which are often classified by their hydrological and nutrient status; ombrotrophic peatlands (bogs) receive water and nutrients only from precipitation, while minerotrophic peatlands (fens) also receive water and nutrients from mineral soils. Boreal mire systems often form large complexes, with some parts that could be classified as ombrotrophic and others that are minerotrophic. The plant communities are mainly controlled by the nutrient conditions and hydrology of the mire site (Lindroth *et al.*, 2007) and can be classified according to the hydrotopographical conditions, ranging from hollows, carpets and lawns in wet areas to ridges and hummocks in dry areas (Rydin & Jeglum, 2006). The vegetation in boreal peatlands is typically dominated by three groups of plants; *Sphagnum* mosses, sedges and dwarf shrubs.

Different species of *Sphagnum*, with differing adaptations to hydrological conditions, are represented in many mire plant communities. *Sphagnum* mosses are well adapted to nutrient-poor and water-logged environments by their capacity of taking up and efficiently use nutrients (Malmer *et al.*, 2003; Clymo, 1963). *Sphagnum* species are also good at maintaining a nutrient-poor, acidic and anoxic environment, which makes it difficult for vascular plants to compete for nutrients (Van Breemen, 1995). Sedges, such as *Carex spp.* and *Eriophorum vaginatum L.*, are represented in many different plant communities, but are often dominating in wet communities such as lawns, since they have the ability to transport oxygen down to the roots in aerenchymatous tissues (Armstrong *et al.*, 1991). Dwarf shrubs do not have aerenchymatous tissues and are therefore more sensitive to anoxic conditions and, therefore, is dominating in dryer communities such as hummocks (Malmer *et al.*, 1994).

1.4 Carbon processes in mires and their controls

Carbon cycling in peatland ecosystems is conceptually illustrated in Figure 1. This model includes the atmospheric CO_2 and two main pools of C in the mire (Ingram, 1978): the active C pool, often called the acrotelm, which is oxic or periodically oxic (depending on water table dynamics) and is where most of the growth and decay occurs; and the passive C pool, or catotelm, which is permanently anoxic with low rates of decomposition. This two-pool model is a simplification of the system and the boundary between the acrotelm and catotelm is much less pronounced in fens compared to ombrotrophic bogs (Ingram, 1978). The C is brought into the system by the photosynthesis of plants, here denoted as gross primary production (GPP), and introduced to the active C pool as aboveground or belowground biomass or root exudates, i.e. soluble sugars exuded from plants in a process that improves the mineralization and uptake of nutrients (Nardi *et al.*, 2000). The output of C from the system is controlled by various mineralization processes, including autotrophic respiration (R_A), heterotrophic respiration (R_H), fermentation, CH_4 production and oxidation, and/or transport of C out of the system by runoff.

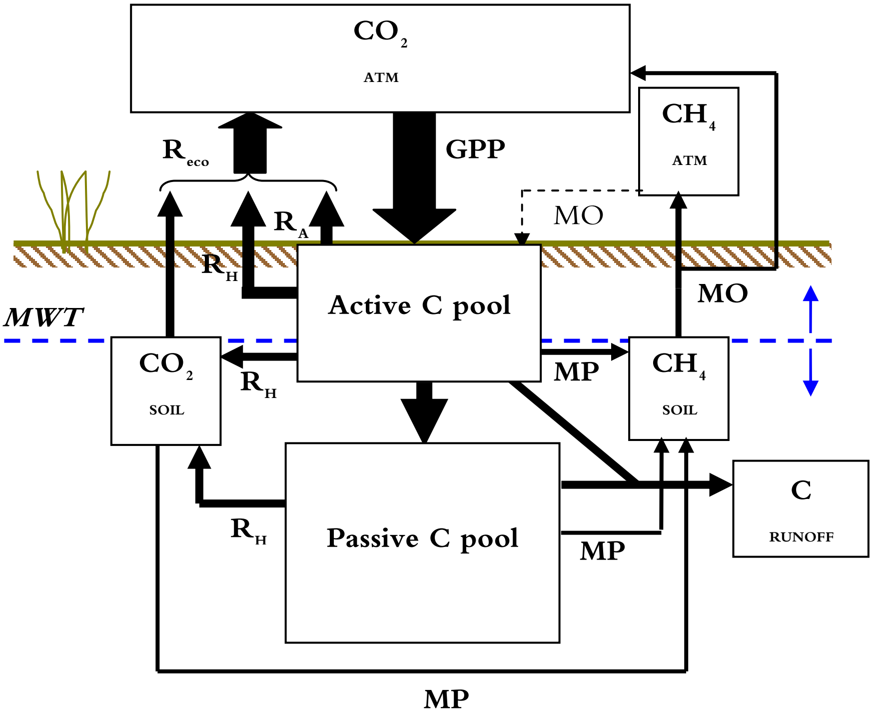

Figure 1. Conceptual model of the carbon pools and pathways in a mire ecosystem. This model includes three main pools of carbon: CO_2 in the atmosphere, the active C pool and the passive C pool. The carbon is brought into the system as gross photosynthesis (GPP). Ecosystem respiration is the sum of all CO_2 emitted from the mire and is dominated by autotrophic and heterotrophic respiration (R_A and R_H, respectively). ME and MO are the processes of CH_4 production and oxidation, respectively. The dotted line indicates the mean water table (MWT).

1.4.1 Gross primary production

The gross photosynthesis is heavily dependent on the photosynthetically active radiation (PAR), CO_2 concentration, water supply, temperature and leaf area index. The potential GPP in a particular mire site is reflected by its plant community composition, which in turn is mainly controlled by the nutrient availability and average water table depth of the site (Lindroth *et al.*, 2007; Riutta *et al.*, 2007). The photosynthetic potential varies between plant species, but vascular plants have higher light-response levels for fixation of CO_2 than mosses such as *Sphagnum* sp. (Marschall & Proctor, 2004).

Therefore, larger green area of vascular plants generally increase GPP (Riutta *et al.*, 2007) Among vascular plants, approximately 90% of the fixed C is allocated to below-ground tissues (Sjörs, 1991; Wallén, 1986).

1.4.2 Ecosystem respiration

Formally, respiration is a redox-reaction in which external electron-acceptors are used in the transformation of organic substrates to energy, biomass, CO_2 and water. However, in this thesis ecosystem respiration (R_{eco}) is defined as all processes that yield CO_2 emissions from the peat surface to the atmosphere, including both fermentation and respiratory processes. R_{eco} is almost entirely dominated by autotrophic and heterotrophic respiration. Autotrophic respiration includes respiration from the whole root system, and is controlled by the inflow of photosynthetic sugar to above and below ground respiratory systems (Högberg & Read, 2006). The size of autotrophic respiration is thus influenced by the same factors that control GPP, but in addition the nutrient status of the soil may affect the partitioning of sugars between the above and below ground systems (van Noordwijk *et al.*, 1998). Heterotrophic respiration includes respiration associated with the microbial decomposition of organic material, mostly plant litter. Decomposition rates in peatlands are generally limited by the quality of the organic material, the oxygen content which is regulated by the water level, temperature and the nutrient status of the soil (Laiho, 2006). In the absence of oxygen and other external electron acceptors, the mineralization of C cannot be linked to respiration. Instead there will be a stepwise transformation of C by different types of fermenting bacteria, from polymers to simpler molecules, such as acetate. The contribution of fermentation to the total CO_2 production depends on the water table but is relatively small. However, the role of fermenting bacteria is central to the transformation of organic matter in anaerobic systems (Fenchel *et al.*, 1998).

1.4.3 CH_4 production, oxidation and emission

The CH_4 emissions from mires are reflected by the balance between CH_4 production in the anoxic zone and CH_4 oxidation in the oxic zone. CH_4 production is the final step in the anaerobic mineralization of organic material. Two types of methanogens are responsible for the CH_4 production: H_2/CO_2 methanogens use H_2 as an electron donor and reduce CO_2 to CH_4, while acetoclastic methanogens transform acetate to CH_4 and CO_2 (Fenchel et al., 1998). The main controls on CH_4 production are substrate availability and quality, water level, and temperature. Substrates for methanogens are produced by fermentation of plant litter or plant root exudates (Joabsson *et al.*, 1999b). The methanogenic population is mainly located just below MWT, as close as possible to the plant root matrix, where their requirements for both anoxic conditions and high substrate availability are met (Sundh *et al.*, 1994). In addition, methanogenesis may be suppressed by competition from other microorganisms using other electron acceptors, such as nitrate (NO_3^-), ferric iron (Fe_3^+) and SO_4^{2-} (Conrad, 1989).

The CH_4 produced is either oxidized by methanotrophs in the oxic zone or transported to the atmosphere. The methanotrophs that oxidize CH_4 in the oxic zone are directly dependent on access to CH_4 and oxygen (King, 1994). Therefore, CH_4 oxidation is concentrated in the oxic zone close to MWT (Sundh *et al.*, 1994), or close to the roots of vascular plants (King, 1994), where the supplies of both CH_4 and oxygen are optimal. The efficiency of methanotrophs in oxidizing the produced CH_4 varies between systems, but is generally in the range 20 to 50% (Conrad, 1996).

CH_4 is emitted to the atmosphere through diffusion, ebullition or plant-mediated transport in aerenchymal tissues. In the presence of vascular plants, the plant-mediated transport seems to dominate (Greenup *et al.*, 2000; Schimel, 1995; Whiting & Chanton, 1992; Sebacher *et al.*, 1985). Sedges, such as *E. vaginatum L*, the dominating vascular plants on ombrotrophic lawn communities, are important contributors to CH_4 emissions since they both provide root exudates as potential substrates for methanogens in the anoxic zone and can function as a transport path for CH_4 to the atmosphere (Joabsson *et al.*, 1999b). Dwarf shrubs are not known to stimulate CH_4 emissions, since they do not have aerenchymal tissues and generally have more superficial roots (Malmer *et al.*, 1994). Ebullition of CH_4 may also be substantial (Glaser *et al.*, 2004; FechnerLevy & Hemond, 1996). Bubbles of CH_4 can be trapped in the root matrix, especially during periods of high CH_4 production, and released when the atmospheric pressure or water level changes (FechnerLevy & Hemond, 1996).

1.4.4 Carbon export through runoff

While the input of C through runoff to a mire is generally small, the export through runoff can be substantial. For example, in a two-year study of the C budget of Degerö Stormyr, the boreal mire that was the focus of Studies I-IV, 34%, on average, of the annual net CO_2-C uptake was found to be exported through runoff, when all C fluxes were accounted for (Nilsson *et al.*, 2008). Similarly, Roulet *et al.* (2007) found the corresponding proportion of 6-year mean NEE-C to be 37% in an ombrotrophic bog in Canada. In Studies I-IV, the runoff component could not be account for, since they focused on C exchange within the experimental plots rather than a whole mire ecosystem.

1.5 Effects of nitrogen deposition, sulfur deposition and increased temperature on mire biogeochemistry

In mires with low anthropogenic N deposition, the availability of N and other nutrients is often extremely low and *Sphagnum* mosses retain free nutrients highly effectively (Clymo, 1963). However, if rates of N deposition are high, the cover of *Sphagnum* mosses is usually reduced, due to both direct effects of unbalanced accumulation of nitrogen (Gunnarsson & Rydin, 2000) and indirect effects of competition from vascular plants (Limpens *et al.*, 2003; Malmer *et al.*, 2003). Shifts in vegetation from *Sphagnum*-dominated to vascular plant-dominated peatlands have been observed both in N gradient studies (Berendse *et al.*, 2001) and field N manipulation studies (Wiedermann *et al.*, 2007). Since vegetation composition affects the GPP of plant communities, the nature of the organic material, decomposition rates and emissions of CH_4 in peatlands, these shifts in vegetation composition may strongly influence the C balance and greenhouse gas dynamics. In addition, it has been reported that different forms of N may be inhibitory for both methanogens (Kluber & Conrad, 1998) and methanotrophs (Crill *et al.*, 1994). The deposition of N has increased successively since 1950 and increased N supply in many ecosystems. Despite international restrictions on the release of N pollutants the deposition is still high in south-western Sweden (10-20 kg ha^{-1} yr^{-1}, based on values for 2007 extracted from the website of the European Monitoring and Evaluation Programme (EMEP), http://webdab.emep.int/Unified_Model_Results/AN/).

There have only been a few observations of effects of high S deposits or supplies on mire vegetation and GPP, but high concentrations of bisulfate may be toxic to *Sphagnum* species (Ferguson & Lee, 1979). Reductions in the photosynthetic capacity of *Sphagnum* following S supplements have also been observed in a long-term manipulation experiment on a minerogenic oligotrophic mire (Granath *et al.*, 2009), although no effects of the treatment on *Sphagnum* cover or biomass were observed (Gunnarsson *et al.*, 2004). On the other hand, S deposition is considered to be a strong regulator of CH_4 emissions from mires, since sulfate-reducing bacteria (SRB) are stronger competitors for substrates than methanogens (Conrad, 1989). Reductions in CH_4 production and CH_4 emissions induced by SO_4^{2-} have been observed in both laboratory (e.g. Yavitt *et al.*, 1987) and *in situ* manipulations (e.g.

Dise & Verry, 2001). Further, according to a meta-analysis by Gauci *et al.* (2004) such reductions is increase with increases in the S deposition rate up to approximately 30% at 20 kg S ha^{-1} yr^{-1}. Although S deposition rates successfully have been reduced through international agreements, purifications of the combustion of fossil fuels and shifts to renewable energy sources, some regions in Europe still have substantial inputs (up to 20 kg ha^{-1} yr^{-1}; according to data provided by EMEP, http://webdab.emep.int/Unified_Model_Results/AN/. In addition, the effects of S deposition on peatland biogeochemistry may be long lasting since reduced or organically bound S can be reoxidized to SO_4^{2-} again (Freeman *et al.*, 1994).

Temperature is considered to be a key determinant of plant and soil processes that acts both directly and indirectly. Increases in temperature may affect plant production (Chivers *et al.*, 2009; Myneni *et al.*, 1997), alter plant community composition (Wiedermann *et al.*, 2007; Weltzin *et al.*, 2003) and increase nutrient mineralization (Rustad *et al.*, 2001). Heterotrophic respiration, fermentation and the production and oxidation of CH_4 may respond directly to increased temperature, but the responses are modulated by the amount and quality of the C source (Davidson & Janssens, 2006; Ågren & Bosatta, 2002; Bergman *et al.*, 1998). Methanogens are known to have stronger temperature responses than methanotrophs (Dunfield *et al.*, 1993), thus CH_4 emissions may be stimulated by temperature increases (Bellisario *et al.*, 1999). In northern Sweden, summer temperatures is predicted to increase by 2.9 °C and summer precipitation is expected to increase 21% in the end of the 21th century (Lind & Kjellström, 2008). These predicted changes may have further indirect effects on plant and soil processes that influence the C balance of mires, including increases in the length of the growing season (Sagerfors, 2007; Myneni *et al.*, 1997) and changes in the water balance (Chivers *et al.*, 2009; Turetsky *et al.*, 2008).

2 Material and methods

2.1 Study site

The research this thesis is based upon was conducted at the site of a manipulation experiment at Degerö Stormyr (64°11’ N, 19°33’ E, altitude 270 m above sea level), a minerogenic, oligotrophic, mixed mire system located on a highland between two rivers, Vindelälven and Umeälven, 70 km northwest of Umeå, in the county of Västerbotten, Sweden. It covers an area of 6.5 km^2, in total, and consists of a system of interconnected mires divided by ridges and islands of till. The site has been utilized for scientific research since the beginning of the 20th century (Malmström, 1923) and has later been described in detail by Granberg et al. (2001). The climate is characterized as cold temperate, humid with the 30-year (1961-1990) average annual precipitation and temperature of 523 mm and +1.2°C, respectively, while the average January and July temperatures are -12.4°C and +14.8°C, respectively. Snow depth is on average 0.6 m. The growing season, defined as the period when daily mean temperatures exceeds +5°C (Ångström *et al.*, 1974), extends approximately from the beginning of May to the end of September.

The experimental site is located on a poor fen lawn with a peat depth of 4.5 m. The bottom vegetation layer is dominated by *Sphagnum balticum* (Russ) C. Jens. and *Sphagnum lindbergii* Schimp., and the field layer is dominated by the sedge *E. vaginatum L.* and the dwarf-shrubs *Andromeda polifolia* L. and *Vaccinium oxycoccos* L.

Figure 2. Aerial photograph of Degerö Stormyr view towards the southeast. The experimental site is located next to the red hut and the meteorological station is in the upper right of the photograph. (Photographer: Tomas Lundmark).

Figure 3. Photograph of the experimental site in July 2004. (Photographer: Tobias Eriksson).

2.2 Experimental design and manipulations

To investigate the long-term effects of increased temperature and deposition of N and S on C exchange processes and C storage, experimental plots that were established at Degerö Stormyr in 1994 and have been treated since 1995 were observed. The original aim of the experiment was to study the effects on CH_4 emissions (Granberg *et al.*, 2001), but more recently the plots have also been used in investigations of plant-composition changes (Wiedermann *et al.*, 2007; Gunnarsson *et al.*, 2004), plant-parasite interactions (Wiedermann *et al.*, 2007) and plant physiological responses (Granath *et al.*, 2009; Wiedermann *et al.*, 2008). The experiment has a full factorial design, in which each of the three treatments are applied at two levels; a greenhouse treatment (GH) with GH, or no GH; N deposition at ambient levels (2 kg ha^{-1} yr^{-1}) or 30 kg ha^{-1} yr^{-1}; S deposition at ambient levels (3 kg ha^{-1} yr^{-1}) or 20 kg ha^{-1} yr^{-1}. All combinations of treatments have been duplicated and, in addition, four midpoints have been included with additions of half the amounts of fertilizers applied in the high N and S treatments, hence in total there are 20 plots (Figure 4). The N and S deposition has been simulated by adding fertilizers five times, once a month between May and September. The greenhouse treatment, installed to increase air and soil temperature, was applied by enclosing plots with transparent polycarbonate frames and covering them with perforated plastic film during the snow-free period. Since this treatment not only increases air and soil temperatures within the plot, but also reduces PAR by 10-25%, reduces wind and change the humidity, we refer to it as a greenhouse treatment instead of a temperature treatment. For more details on the experimental design and setup, see Granberg *et al.,* (2001).

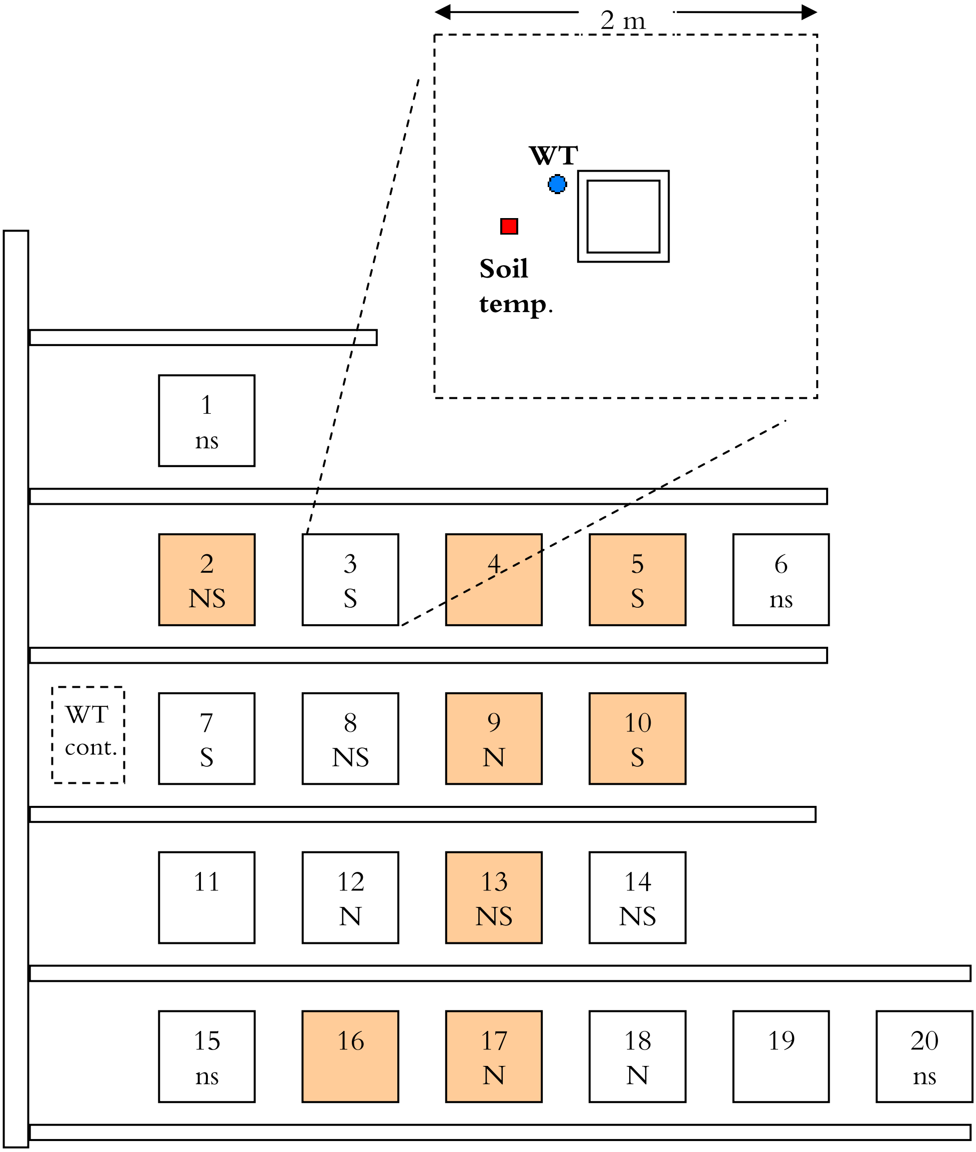

Figure 4. Experimental setup of the field manipulations at Degerö Stormyr. The high nitrogen and high sulfur treatments are represented by the letters N and S, respectively, and the greenhouse treatment is indicated by shading. Treatments have been applied in all combinations. The combination "ns" represents half the dose of both N and S. Each plot contains a steel frame in the center for gas flux measurements, a water table tube (WT) for water table measurements, and temperature probes for soil temperature measurements at 3-5 levels. WT logg = well for continuous water table measurements. Redrawn from Granberg *et al.* (2001).

2.3 Methods

2.3.1 Measurements of climatic variables

Air temperature, precipitation and snow depth were all measured at a meteorological station 100 m from the experimental site. In addition, soil temperatures at 3-5 depths down to 42 cm and water table level were measured hourly throughout the year in the plots and in an area adjacent to the plots, respectively (Figure 4).

2.3.2 Gas flux measurements (Papers II and III)

CH_4 emissionswere measured between May and October 10 times in 2005 and 5 times in 2006, using closed chambers in which gas was sampled in evacuated vials over 6 minutes. CH_4 concentrations in the sampled gas were then measured using a gas chromatograph (Perkin Elmer Autosystem, Waltham, MA, USA) equipped with an HS40 Autosampler, a HeySep Q column and a flame ionization detector. The CH_4 emission rate, i.e. the change in concentration in the chamber over time, was calculated using the slope obtained from a linear regression model. All CH_4 emission rates were transformed to obtain normal distribution.

For estimations of CO_2 flux rates, we measured CO_2 flux rates in chambers connected to an Infrared gas analyzer (IRGA), which recorded CO_2 concentrations every 1.6 seconds. In addition, PAR was measured both inside and outside the chamber. R_{eco} was estimated from dark chamber measurements. Light (transparent) chambers were used for estimating NEE under current light conditions. In order to compare GPP and NEE values of different plots the light response of every plot was characterized by incrementally shading them with 2-3 layers of netted fabric to vary the PAR reaching the vegetation. GPP was then calculated as the difference between NEE and R_{eco} at every PAR level, and GPP responses to PAR were modeled using a simple Michaelis-Menten hyperbolic function (e.g. Bubier *et al.*, 1998):

$$GPP(PAR) = \frac{V_{\max} \cdot PAR}{PAR + K}$$

where V_{max} is the rate of photosynthesis at light saturation. K is the level of PAR at which GPP is half of V_{max}, expressing the sensitivity of GPP to PAR at low radiation levels. Throughout this thesis NEE is considered to be downward flux from the atmosphere to the soil.

2.3.3 Peat incubations (Papers I and II)

In order to investigate treatment effects on rates of CH_4 production and CH_4 oxidation potentials, a peat incubation experiment was performed in 2007. Peat cores from all experimental plots were collected and transported to the laboratory. The peat cores (43 cm long) were divided into five sections after removal of the photosynthetic active part (3 cm) from the top. Then, samples from all plots and all levels were incubated to determine their CH_4 production or CH_4 oxidation potentials.

Peat samples for determining CH_4 production were incubated in bottles with: (1) glucose, to obtain potential CH_4 production rates with no substrate limitations; (2) no additions, estimate CH_4 production rates at ambient substrate availability; and (3) additions of SO_4^{2-} to assess CH_4 production with competition from SRB, and hence, the potential inhibition of the SRB community. The aerobic atmosphere in the incubation bottles was replaced with N_2, and the bottles were shaken on a rotary shaker for an hour prior to gas sampling. Headspace gas samples (1 ml) were taken each day for five days and analyzed using a gas chromatograph with the same settings as in Study I (see section 2.3.2). Thereafter, CH_4 production rates were determined by linear regression.

CH_4 oxidation potentials in each section of cores from the plots were determined by aerobic incubations of the peat together with additions of CH_4 (~1500ppm in headspace; (Moore & Dalva, 1997; Sundh *et al.*, 1994). Incubation mixtures were constantly shaken on a rotary shaker and their headspace gas was sampled every third hour for 15 hours. Rates of CH_4 oxidation potentials were determined in the same way as for CH_4 production rates. For more details of the sampling and incubation procedure, see Paper I.

In Study I the incubations were used to evaluate both the field treatment effects and the effects of the laboratory amendments, while in Study II we used the incubations to evaluate the vertical distribution of CH_4 production and CH_4 oxidation potentials.

2.3.4 Peat density, height growth and C contents (Paper IV)

In Study IV, effects of the field treatments on the C stores in the peat profile down to 43 cm were evaluated. For this purpose, reliable estimates of the peat density, its C content, and increments in peat height are needed. Therefore, 43-cm peat cores were carefully sampled in 2007 to avoid compaction. Peat density was estimated from measurements of peat volume and dry weight every 4 cm along each core. Dried and milled samples were analyzed for C content. The height growth of the mire surface since the start of the experiment was estimated using two reference points in each plot: (1)) the uppermost probe for measuring peat temperature in each plot was installed at the start of the experiment 2 cm from the peat surface, and in 2005 the distance from the surface to the uppermost probes was re-measured; (2) the cables for the probes were placed on the peat surface at the start of the experiment, and in 2007 the distances from the surface to the cables were measured; (3) water levels were measured in each plot during 2005 and 2006, and the MWT in each plot was used as a height reference. The effects of N and S additions, and the greenhouse treatment, were evaluated on the increments of peat height and (at each investigated depth) its bulk density, C concentration and C content. The accumulation rates of C were evaluated by calculating the cumulative C content for each of the depth intervals 0-8, 0-16, 0-24, 0-32 and 0-40 cm. All evaluations were preceded by adjustments for treatment effects on height growth of peat. For more details, see Paper IV.

2.4 Statistical approach

The same statistical approach was applied in all of the studies to evaluate treatment effects on specific components of the C balance. The factorial design of the experiment made it possible to evaluate both main effects (GH, N and S) and interactions (GH×N, GH×S and S×N) in multiple linear regression (MLR) models.

In Papers II and III, we also included sedge cover (SC) and MWT as covariates in the models. Both of these variables influence CH_4 processes and CO_2 flux components, thus their effects may mask treatment effects if they are not considered. However, in the field manipulation experiment the variations in SC and MWT emanate from both random differences due to natural small-scale variations and responses to the experimental manipulations. In order to distinguish these two sources of variation, SC and MWT were used as response variables in separate models that included all treatments (main effects and two-way interactions of GH, S and N), as follows:

$$SC = \beta_0 + \beta_1 GH + \beta_2 S + \beta_3 N + \beta_4 GHxS + \beta_5 GHxN + \beta_6 SxN + \varepsilon_{SC}$$

and

$$MWT = \beta_0 + \beta_1 GH + \beta_2 S + \beta_3 N + \beta_4 GHxS + \beta_5 GHxN + \beta_6 SxN + \varepsilon_{MWT}$$

where β is the parameter for each factor and ε_{SC} and ε_{MWT} are the residuals of each model. The residuals represent the unexplained variance, i.e. the variation in sedge cover and microtopography, respectively, that is not related to the experimental treatments. These residuals were then included as covariates in the CH_4 emission models in Paper II and the GPP, NEE and R_{eco} models in Paper III.

In Studies II and III, all coefficients, including the main effects, interactions and covariates, were retained in the MLR models even if they were not significant. The coefficient for a certain term could then be compared between measurement times, thereby allowing seasonal trends to be studied.

In Studies I and IV, the MLR models were reduced to only include significant ($p<0.05$) or close to significant ($p<0.10$) coefficients, since no seasonal trends were to be examined.

3 Results and discussion

3.1 Treatment effects on vegetation and microtopography (Papers I-IV)

Observations at the experimental site showed that, after 11 years, N additions of 30 kg ha^{-1} yr^{-1} had resulted in *Sphagnum* cover declining from 100% to 16% and *E. vaginatum L.* cover increasing from 37% to 65% in the field layer (Figure 5). Changes in vegetation cover following N additions have been reported in a number of studies (e.g. Breeuwer *et al.*, 2009; Bubier *et al.*, 2003; Berendse *et al.*, 2001), and at N-treated plots at Degerö Stormyr successive changes in vegetation have been observed towards higher densities of vascular plants and lower densities of *Sphagnum* after 1-3 years (Granberg *et al.*, 2001), after four years (Gunnarsson *et al.*, 2004) and after eight years (Wiedermann *et al.*, 2007). Our results corroborate these trends in vegetation community composition associated with N applications, which correspond well with observed changes in plant community composition and ecophysiology in areas that have received high anthropogenic N depositions (12 kg ha^{-1} yr^{-1}) for more than 30 years (Wiedermann *et al.*, 2008).

In addition, N deposition has changed the microtopography of the peatland surface, e.g. the distance from the surface to the mean water table is now 4.6 cm shorter, on average, in plots with high N deposition (Figure 5). This effect on microtopography most likely emanates from the change in peat litter composition and increased decomposition (Bohlin *et al.*, 1989). The changes in both vegetation community composition and microtopography have the potential to affect CO_2 and CH_4 exchange processes and carbon storage.

In addition to effects from N, there are also significant effects on the cover of sedges both from S and GH treatments; the positive effect of N additions on sedge cover is reduced in combination with S additions and slightly stimulated in combination with the GH treatment (Figure 5).

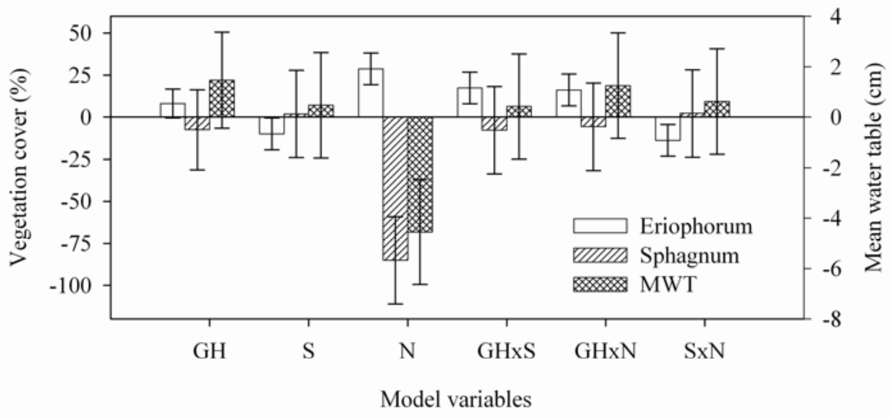

Figure 5. Modeled effects of greenhouse cover, and nitrogen and sulfur deposition, on vegetation cover and the distance to the mean water table at Degerö Stormyr in 2006. The bars for *E. vaginatum* and *Sphagnum* cover represent changes in percent cover compared to untreated plots. The model variables GH, S, N, GH×S, GH×N and S×N represent the greenhouse treatment, the sulfur treatment, the nitrogen treatment and their two-way interactions, respectively. Proportions of explained variance (and significance) of the models for the cover of *Eriophorum*, *Sphagnum* and MWT, respectively, were 0.88 ($p<0.001$), 0.80 ($p<0.001$) and 0.68 ($p<0.01$). The error bars represent 95 % confidence intervals. Error bars which do not overlap the zero line indicate that the coefficient is significant ($p<0.05$).

3.2 Treatment effects on production, oxidation and emissions of CH_4 (Papers I and II)

In Studies I and II we investigated the effects of greenhouse cover and deposition of N and S on production and oxidation of CH_4 and on CH_4 emissions, respectively. From measurements of CH_4 emission rates taken during two growing seasons (on 10 occasions in 2005 and five in 2006), we detected significant effects of the treatments. In addition, the effects of treatments on CH_4 emissions corresponded well with their effects on CH_4 production. Despite >10 years of treatment only minor effects were found on CH_4 oxidation potentials.

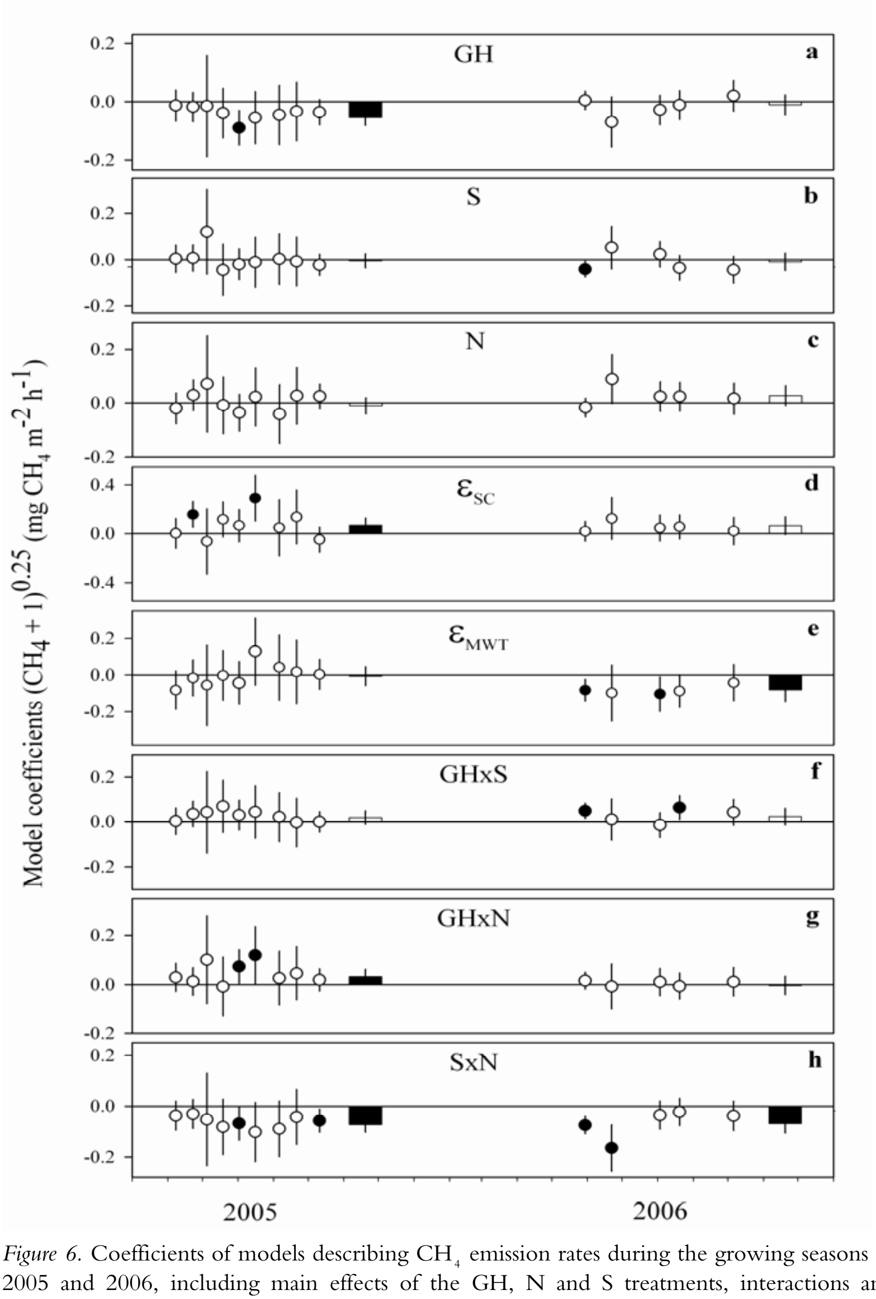

Figure 6. Coefficients of models describing CH_4 emission rates during the growing seasons of 2005 and 2006, including main effects of the GH, N and S treatments, interactions and covariates. The coefficients are centered, scaled, and presented as $(CH_4 + 1)^{0.25}$. Vertical bars represent the seasonal average CH_4 emission rates and circles represent the CH_4 emission rates on each separate measurement occasion. Error bars represent 95 % confidence intervals, and coefficients significantly ($p < 0.05$) different from zero are indicated by filled (black) circles or bars.

3.2.1 Effects of long-term nitrogen additions

My results showed that N additions over 11 years had stimulated CH_4 emission rates and, although significant effects were not observed on every single occasion, there were clear seasonal trends, manifested in significant effects on seasonal average CH_4 emissions (Figure 6c, g-h). The positive effects of N addition on CH_4 emission are opposite to those found in the same experiment after three years of the treatments (Granberg *et al.*, 2001), highlighting the importance of long-term experiments. However, the N additions did not have positive effects in combination with high S additions (Figure 7b and c).

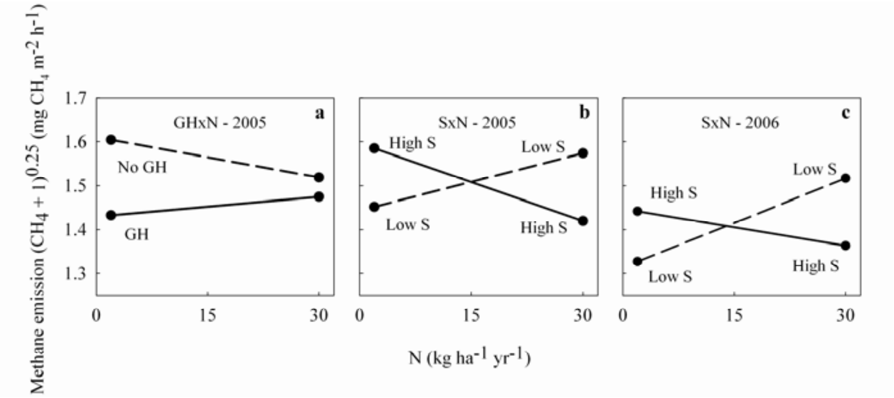

Figure 7. Effects of the significant interaction terms on CH_4 emission rates, calculated from the model coefficients. The graphs indicate the interaction effects on the seasonal average CH_4 emission rates of a) greenhouse cover and nitrogen (GH×N) in 2005, b) sulfur and nitrogen (S×N) in 2005 and c) sulfur and nitrogen (S×N) in 2006.

Similarly, the rate of CH_4 production at the level of the highest production rate ($CH4_{MAX}$) was increased by up to 35% by the N treatment ($p < 0.05$ after glucose amendment, and $p = 0.09$ without amendments; Figure 8a and b). I believe that these effects of N on both the methanogenic population and CH_4 emissions emanate from the nitrogen-induced changes in vegetation community composition and microtopography. High densities of sedges such as *E. vaginatum L.* are known to stimulate CH_4 emissions both by increasing CH_4 production by providing more potential substrates to the methanogens (Saarnio *et al.*, 2004) and by providing a transport channel for CH_4 in the aerenchymal tissues (Joabsson & Christensen, 2001; Greenup *et al.*, 2000). The change in microtopography, with higher MWT in N fertilized plots, increases the volume ratio between the anoxic and oxic zones and promotes CH_4 production on the expense of CH_4 oxidation

(Sundh *et al.*, 1994) . No effect on the CH_4 oxidation potential was detected (see Paper I). This suggests that it is insensitive to increased in sedge cover, higher MWT and stimulated CH_4 production at this site. Similarly, in a comparison of different plant communities, CH_4 oxidation was not correlated by neither MWT, CH_4 production or CH_4 emission (Sundh *et al.*, 1994)

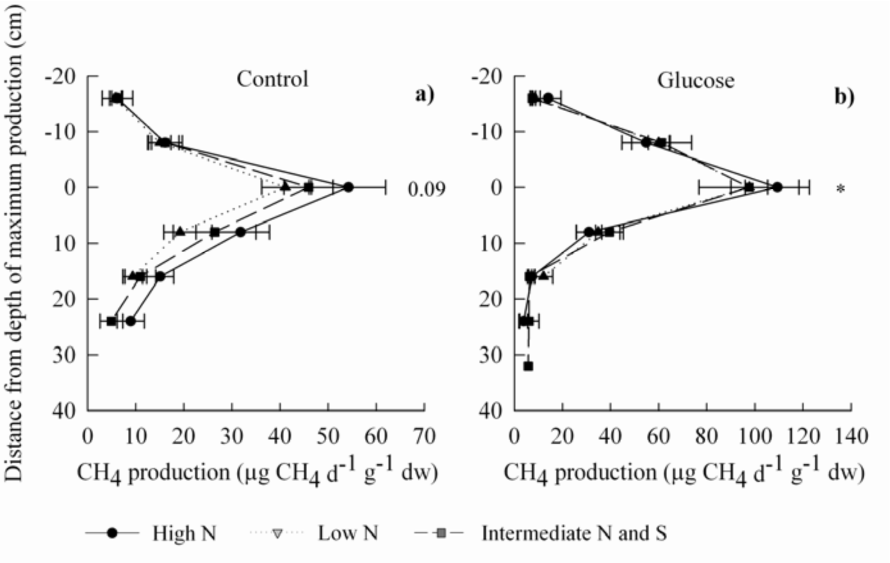

Figure 8. Effects of field additions of nitrogen on CH_4 production in the peat profile. In order to compare the average production rates between plots, the depth of maximal production rates for each peat profile was set to zero. Each graph represents the main effect (*n* = 8) of nitrogen after (a) no laboratory amendments and (b) laboratory glucose amendments. Error bars represent ± 1 standard error and the asterisks indicate the significance of the differences between the high N and the low N plots at the depth of maximal CH_4 production (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). P-values between 0.05 – 0.10 are stated in the graphs.

Other studies that have evaluated effects of experimental N additions on CH_4 emissions from mires have been mainly short-term (<3 years), and at most minor effects on vegetation cover have been observed, with effects on CH_4 emissions ranging from negative to slightly positive (Granberg *et al.*, 2001; Saarnio *et al.*, 2000; Aerts & de Caluwe, 1999; Saarnio & Silvola, 1999). A study by Nykänen *et al.* (2002) found that a Finnish bog dominated by *S. fuscum* showed a small but significant increase in CH_4 emissions after six years of N fertilization (100 kg N ha^{-1} yr^{-1}), associated with a tendency towards increased cover of *E. vaginatum L.* In a study by Keller et al. (2005) six years of fertilization (20 and 60 kg N ha^{-1} yr^{-1}) of a fen in Minnesota increased the cover of dwarf shrubs, but no effect was observed on CH_4 emissions. Due to the relatively short time-span of N additions in the abovementioned studies the observed changes are likely to represent early stages of ongoing transitions of the vegetation community composition (if the experiments continue). Our results (Papers I and II) show long-term effects of N, more similar to those observed in mires that are in a steady state with respect to community composition and plant ecophysiology after > 30 years of increased N deposition (Wiedermann *et al.*, 2008). However, the effect on CH_4 emissions depends on which components of plant communities are reduced and stimulated, respectively, by the N deposition. In mires where N additions have increased the cover of shrubs rather than sedges (Keller *et al.*, 2005) different responses in CH_4 emissions can be expected, since shrubs may interact differently with the methanogenic and methanotrophic microbial communities, compared to sedges, among other things because they have a more superficial root system (Malmer *et al.*, 1994) and no aerenchymatic tissue (Rydin & Jeglum, 2006).

3.2.2 Effects of long-term sulfur additions

The long-term S additions did not have any negative effect on CH_4 emissions, rather a positive effect at low N additions (Figure 6b and h; 7b and c). Neither was any reduction in $CH4_{MAX}$ found and a significant reduction in CH_4 production was only found higher up in the peat profile, 8 cm above $CH4_{MAX}$ (Figure 9a-c). These results were not what was hypothesized and highly unexpected since SRB have been shown to outcompete methanogens for substrates in the presence of SO_4^{2-} (e.g. Yavitt *et al.*, 1987). Indeed, in our incubation experiment (Paper II) CH_4 production was reduced after laboratory additions of SO_4^{2-} to samples representing all field treatments, by on average 55%, but not reduced more in samples from plots with long-term field S additions than in samples from plots with ambient S deposition (Figure 9c). There were tendencies, although weak, that CH_4 oxidation potentials were stimulated by the S deposition (see Paper I). Most studies, although not long-term studies, suggest that S deposition tends to decrease CH_4 emissions, to an extent that depends on the S deposition rate, reaching a 30% reduction in CH_4 emissions at 20 kg S deposition ha^{-1} yr^{-1} (Gauci *et al.*, 2004 and therein). We suggest two explanations to the contrasting effects found in our study. Firstly, reductions in CH_4 production are confined to a level just above the level of $CH4_{MAX}$, suggesting stratification in the profile in accordance with expected redox conditions; most of the SRB:s are found high in the profile, closer to the SO_4^{2-} source, while the methanogenic organisms are most abundant further down, making competition less obvious (Conrad, 1996). Secondly, the timing of the CH_4 emission measurements in relation to the application of the S additions may be important. In our field study CH_4 emissions were measured at least two weeks after the most recent addition, so most of the added SO_4^{2-} could have been reduced prior to the measurement occasion. The fact that added SO_4^{2-} has been shown to be reduced to undetectable levels within three weeks after addition to the experimental site supports this explanation (I. Bergman, unpublished data). If this is valid, the SO_4^{2-} pool was dependent on reoxidation of previously reduced S from water table fluctuations and drought events, or on mineralization of organically bound S (Blodau & Moore, 2003; Freeman *et al.*, 1994).

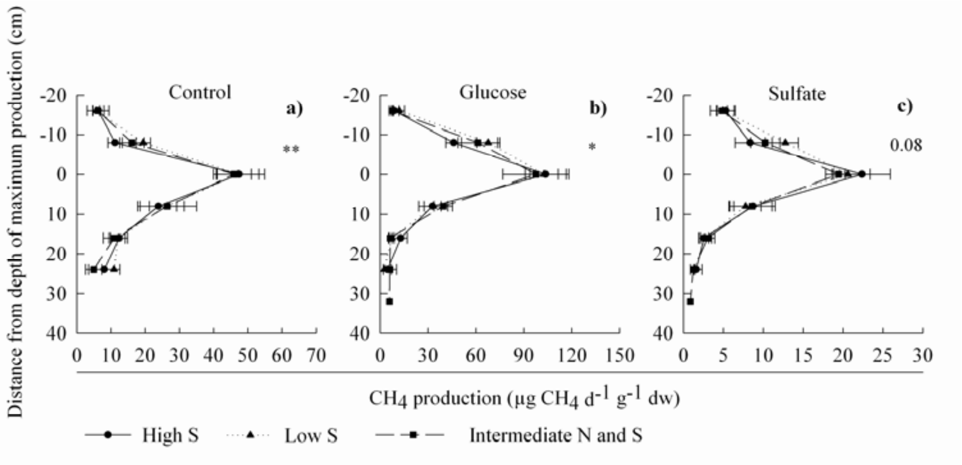

Figure 9. Effects of field additions of sulfur on CH_4 production in the peat profile. Each graph represents the main effect ($n = 8$) of sulfur after (a) no laboratory amendments and (b) laboratory glucose amendments and (c) laboratory sulfate amendments. Error bars represent ± 1 standard error and the asterisks indicate the significance of differences between the high S and the low S plots at the depth 8 cm above maximal CH_4 production (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). P-values between 0.05 – 0.10 are stated in the graphs.

3.2.3 Effects of long-term greenhouse treatment

The greenhouse treatment appeared to have reduced CH_4 emissions by 30% during 2005, but only had minor apparent effects in 2006 (Figure 6a; Paper II). In addition, $CH4_{MAX}$ was reduced by more than 30% by the GH treatment, due to both substrate limitations and differences in the potential CH_4 production (Figure 10a and b; Paper I). No effect on potential CH_4 oxidation was detected (See Paper I). The difference in apparent CH_4

emission responses to the GH treatment between the two years probably reflects the contrasting weather conditions between the years. Dry conditions in 2006 decreased the water table to below 40 cm, compared to the average of ca. 14 cm across the area in the period 2004-2006, thereby significantly reducing CH_4 emissions (Paper II). Most likely this reduction obscured possible treatment effects. Similar differences between a wet and a dry year have been observed in a temperature manipulation experiment in an Alaskan fen (Turetsky *et al.*, 2008). The negative effects found in 2005 in this study differ from reported stimulations of CH_4 emissions following short-term (2-3 years) temperature manipulations of peatlands, including: open chamber warming in an Alaskan fen (Turetsky *et al.*, 2008), infrared warming in fen and bog mesocosms in Minnesota (Updegraff *et al.*, 2001) and early stages of the greenhouse cover warming at Degerö Stormyr (Granberg *et al.*, 2001). However, there are strong indications that the positive effects found in the last two of these studies may have been transient, since no effects were found on CH_4 production (Keller *et al.*, 2004) or CH_4 emission (White *et al.*, 2008) after 5-6 years of warming in the mesocosms in Minnesota and results presented in Papers I and II suggest that both CH_4 production and CH_4 emissions declined after 10-12 years of the greenhouse treatment. The mechanism behind these reductions in CH_4 production and emission is coupled to changes in substrate quality and availability. A key factor controlling the partitioning of peat-forming organic matter into CO_2 and CH_4 **is** the degree of decomposition under oxic conditions before the material reaches the anoxic zone (Nilsson & Öquist, 2009). The organic matter in the oxic zone may decompose more rapidly in the GH plots, due to the higher temperature, and hence be more decomposed when it reaches the anoxic zone. An experimental artifact induced by the greenhouse cover that should be considered is the 10-25% reduction of PAR. In a shading experiments on peatland sites dominated by *E. vaginatum L.* and *Sphagnum* mossses, a 60% reduction in PAR reduced GPP by 25% and CH_4 production by 20% (Öquist & Svensson, 2002). Assuming that the response between PAR and CH_4 production is linear, a 10-25% reduction in PAR would account for a 3-10% reduction in CH_4 production, which is less than the reduction from greenhouse cover in this study.

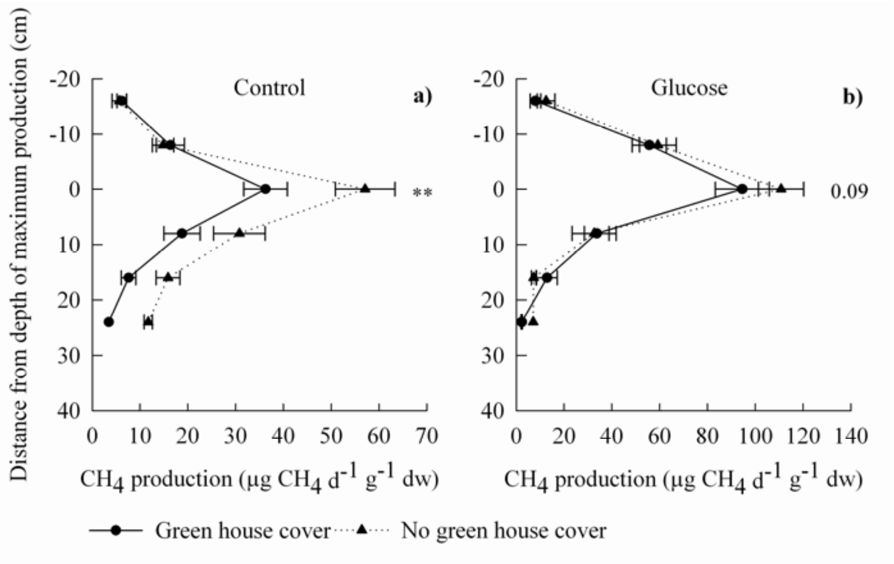

Figure 10. Effects of the greenhouse treatment (GH) on CH_4 production in the peat profile. Each graph represents the main effect (*n* = 8) of GH after (a) no laboratory amendments and (b) laboratory glucose amendment. Error bars represent ± 1 standard error and the asterisks indicate the significance of differences between plots with GH and no GH at the depth of maximal CH_4 production (⋆ $p < 0.05$; ⋆⋆ $p < 0.01$; ⋆⋆⋆ $p < 0.001$). P-values between 0.05 – 0.10 are stated in the graphs.

3.3 Treatment effects on CO_2 flux components (Paper III)

In Study III, we investigated treatment effects on each of three CO_2 flux components of the system (GPP, R_{eco} and NEE) based on R_{eco} measurements collected over two years and measurements of GPP and NEE collected over one year. The effects on GPP and NEE were evaluated at two different levels of PAR, calculated from the estimated light response functions of each plot at four different occasions.

3.3.1 Effects of long-term nitrogen additions

Significant effects of N on GPP were found only on one single date and were positive, but only in combination with low S additions (see Paper III). At high S additions no such effect was detected. Possible effects during the other measurement dates could have been masked by the extremely dry conditions in July-August in 2006. In addition, the precision of the GPP (and NEE) estimates are not as accurate as those of R_{eco}, which are based on direct measurements. Significant effects of N on R_{eco} were only detected on a few occasions, but coefficients for N were positive in R_{eco} models for most of the individual sampling occasions in both years, strongly indicating that the N treatments enhanced R_{eco} (Figure 11c) The effect on the seasonal average R_{eco} was 13% ($p = 0.09$) in 2005 and 21% ($p = 0.03$) in 2006. There were also strong indications of interactions with S, similar to patterns found when evaluating the effects of the treatments on GPP and CH_4 emission; R_{eco} was stimulated by N additions at low S additions, but less so at high S additions (Figure 11h). Our results do not reveal whether autotrophic, heterotrophic respiration (or both) has been stimulated. However, as mentioned above, litter from vascular plants is known to decompose more rapidly than *Sphagnum* litter, suggesting that the heterotrophic component has been affected. Despite the effect on R_{eco}, no effect of N deposition on NEE was detected (Paper IV). Only a few other studies have evaluated effects of field experiments with simulated N deposition on NEE and related flux components in boreal peatlands. Short-term (2-3 years) N manipulations have resulted in no significant change in NEE; in two experiments both GPP and R_{eco} were stimulated and cancelled each other out (Lund *et al.*, 2009; Saarnio *et al.*, 2003) and in one experiment neither GPP nor R_{co} was effected (Lund *et al.*, 2009). In a study by Bubier *et al.* (2007), six years of N deposition only affected GPP and NEE negatively at high N deposition (100 kg ha^{-1} yr^{-1}) in combination with high additions of phosphorous and potassium. It should be noted that none of these studies have detected dramatic changes in plant community composition.

Concerns have been raised that increased N deposition will decrease or even terminate the accumulation of C in mires (Gunnarsson *et al.*, 2008; Bragazza *et al.*, 2006; Berendse *et al.*, 2001), the mechanisms being increased decomposition induced by the shift in the plant community composition from dominance by *Sphagnum* with low decomposition rates to dominance by graminoides and dwarf shrubs (Gunnarsson *et al.*, 2008; Berendse *et al.*, 2001) that are more easily decomposed (e.g. Breeuwer *et al.*, 2008; Coulson & Butterfield, 1978) or increased decomposition as an effect of increased availability of N for microorganisms (Bragazza *et al.*, 2006). Neither the results in Paper III nor the other field investigations of C exchange described above have detected any negative effects on NEE due to N deposition. However, our results for GPP and NEE are only based on measurements taken in a single year, and measuring CO_2 exchange processes over several seasons would improve the understanding of the dynamics and the precision of estimated effects of NEE. The role of N deposition in the C accumulation is further discussed in section 3.4.

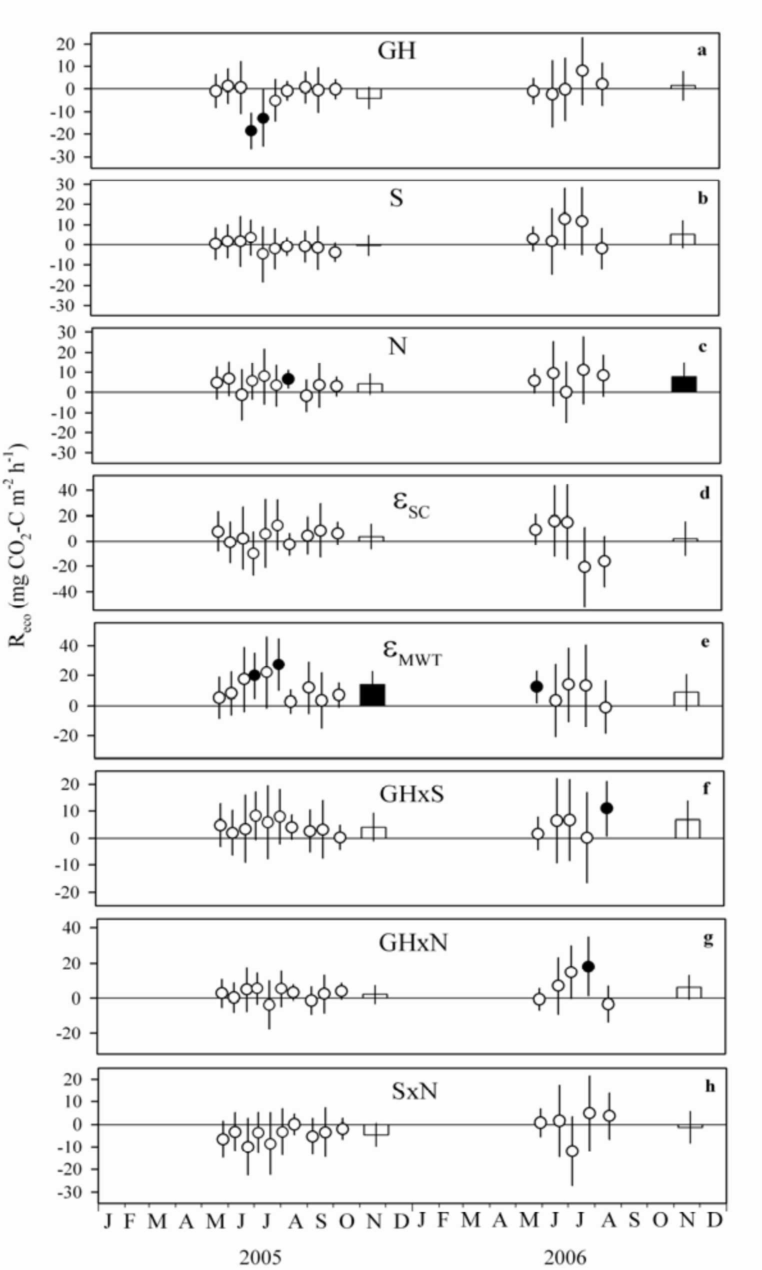

Figure 11 Coefficients of models describing R_{eco} in 2005 and 2006, including main effects of the GH, N and S treatments, interactions and covariates. The coefficients are centered and scaled. Vertical bars represent the model coefficients of seasonal average R_{eco} and circles represent the model coefficients of R_{eco} for each separate measurement occasion. Error bars represent the 95 % confidence intervals and significant coefficients ($p < 0.05$) are indicated by filled (black) circles or bars.

3.3.2 Effects of long-term sulfur additions

The S treatment only had minor effects on the CO_2 flux components (Figure 11b, f and h, and see Paper III). Although inhibition of photosynthetic potential by S deposition has been previously observed (Granath *et al.*, 2009; Ferguson & Lee, 1979), we observed no such effect on GPP. The impact of S addition on the CO_2 carbon balance is most likely small.

3.3.3 Effects of long-term greenhouse treatment

The GH treatment did not affect GPP, but a negative R_{eco} response to the GH treatment was detected in the midseason of 2005, and no apparent effect during the other parts of the season, leading to a non-significant ($p=0.09$) reduction by 12% in the seasonal average R_{eco} (Figure 11a). The pattern was not repeated in 2006, possibly because of the drought in July-August (see Paper III). The reduction in R_{eco} could possibly emanate from increases in the decomposition of labile C compounds associated with the long-term increases in temperature, and hence ultimately reductions in the quality of the C pool in the remaining soil matrix (Rustad *et al.*, 2001; Peterjohn *et al.*, 1994). In accordance with this hypothesis, a metaanalysis by Rustad *et al.* (2001) of warming experiments in a wide range of sites (including tundra, forests, peatlands and grasslands) found that generally significant stimulations in soil respiration during the first 2-3 years of warming was followed by two years of no significant effects on soil respiration, suggesting that warming treatments induce transient increases in respiration. Part of the reduction may also emanate from unintended secondary effects of the treatment; the 10-25% reductions in PAR by the greenhouse cover. Although no significant reduction in the potential GPP associated with the greenhouse treatment was observed, it is possible that this reduction in PAR could have caused a small reduction in actual GPP and belowground C allocation, thus affecting both autotrophic and heterotrophic respiration (Öquist & Svensson, 2002; Joabsson *et al.*, 1999a). However, in the study by Shaver *et al.* (1998) six years of shading (reduction in PAR by 50%) of a wet sedge tundra in Alaska increased GPP, R_{eco} as well as NEE, making the effect of the small reduction in PAR in this study difficult to predict but most likely small. Nevertheless, the overall effects on R_{eco} were minor and not manifested in any significant change in NEE (see Paper III). Similarly, although other short-term warming experiments have found positive effects on both GPP and R_{eco}, the NEE has been unaffected, in agreement with our results (Chivers *et al.*, 2009; Sullivan *et al.*, 2008; Hobbie & Chapin, 1998).

3.4 Effects of nitrogen deposition on C accumulation (Paper IV)

In Study IV we focused on the effects of N deposition on the C pool by estimating the peat growth since the start of the experiment, the bulk density, the C concentration (%) and the volume-weighted content of C (g C dm^{-3}) in the upper 40 cm of the peat profile. The peat height increment was in average 4.4 cm (±1.6 cm; ±1S.E.) lower in plots with high N additions and, similarly, 4.3 cm lower in the plots receiving intermediate N and S. On the other hand, several peat properties were significantly affected by N additions in ways that are likely to promote total C accumulation in the upper part of the peat profiles. The surface bulk density was significantly increased down to 14 cm depth by addition of N (Figure 12a), presumably due to the change in peat litter composition and in peat decomposition, which also are the controls of the changes in microtopography (Vitt *et al.*, 2009; Bohlin *et al.*, 1989). The C concentration (% C of dry mass) was increased between 4-24 cm by N additions (significantly at $p < 0.05$ at four depths and at $p = 0.07$ and $p = 0.10$, respectively, at two depths; Figure 12b) and the volume- weighted C content (g C dm^{-3}) was significantly increased between 4-12 cm from the N treatment (Figure 12c). Analysis of the effects of C accumulation, represented by the cumulated C content at increasing depth intervals, also indicated that there was a significant negative effect of N in the 0-8 cm interval, a consequence of the additional 4 cm layer generated by the increased height growth in the low N plots (Table 1). However, even in the 0-12 cm interval the higher C content at each interval had counteracted the difference in height growth thus no significant N effect was found (Table 1).

A number of studies have raised concerns that shifts in plant community composition induced by N deposition, towards greater abundance of vascular plants at the expense of *Sphagnum* mosses (Wiedermann *et al.*, 2007; Berendse *et al.*, 2001; Gunnarsson & Rydin, 2000), will enhance the decomposition of the produced litter and thus reducte C accumulation (Gunnarsson *et al.*, 2008; Gunnarsson & Rydin, 2000). The long-term experiment with N additions at Degerö does not support this view; rather we found that rates of accumulation had not been significantly affected by 12 years of N additions (Table 1). There may be several reasons for this deviation from previous expectations. Firstly, if decomposition rates alone are used to evaluate long-term effects of N deposition on rates of C accumulation in northern peatlands (Bragazza *et al.*, 2006) potential responses of GPP will be missed. Hence, effects on decomposition and GPP, net primary production (NPP) or NEE must be considered. Secondly, if decomposition rates are used to evaluate long-term C accumulation,

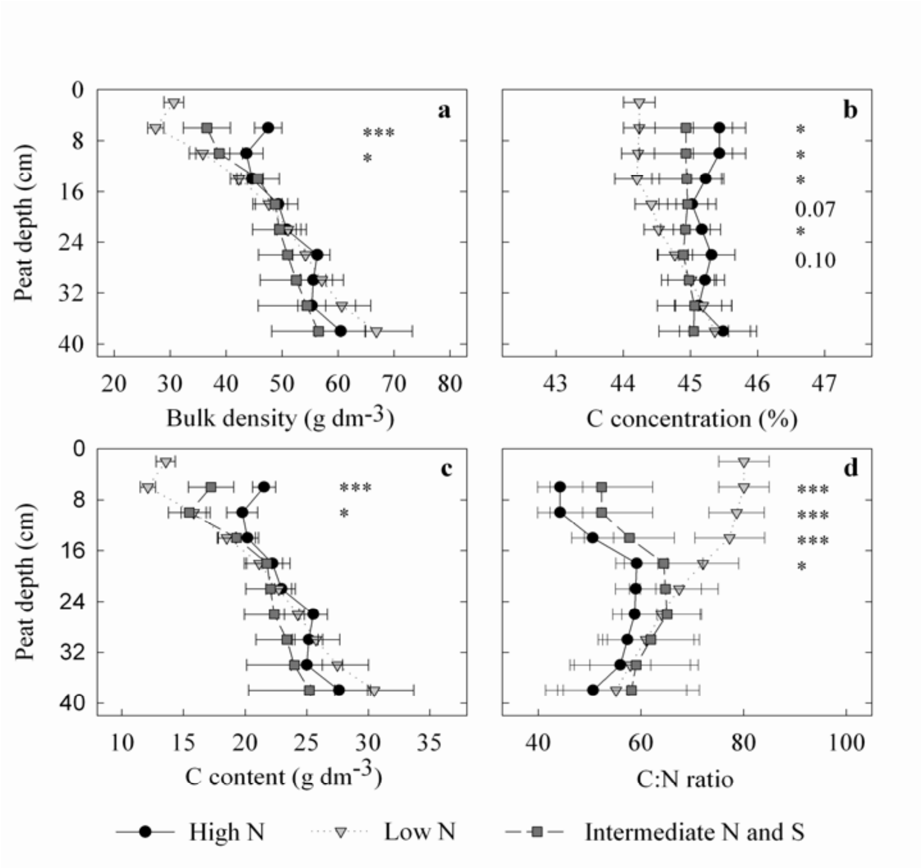

Figure 12 . Effects of nitrogen additions on the indicated peat properties. Peat depth refers to the depth below the mire surface and is adjusted for the larger height growth in the "low N" treatment. The points are positioned as midpoints in the 4-cm intervals. Error bars represent standard errors (SE) and the asterisks indicate the significance of differences between the high N and low N plots (⋆ $p < 0.05$; ⋆⋆ $p < 0.01$; ⋆⋆⋆ $p < 0.001$) and p-values between 0.05 – 0.15 are stated in the graphs.

information on long-term decomposition rates is needed. It is well known that *Sphagnum* decomposes much more slowly than graminoides initially (e.g. Breeuwer *et al.*, 2008; Coulson & Butterfield, 1978), but the decomposition rates of the common graminoid *E. vaginatum* have been shown to be close to zero after 15-25 years at a residual weight of approximately 40% (Latter *et al.*, 1998). This shows that not all graminoides are easily decomposed and Latter *et al.* (1998) stress the irrelevance of initial mire plant decomposition data for inferring long-term C accumulation properties. Thirdly, long-term experiments provide the best means to evaluate long-term effects of N deposition on C accumulation, since they allow effects of low and high N deposition rates in controlled environment to be compared.

Table 1.

Multiple linear regression model (MLR) coefficients[a] and statistics of carbon accumulation[b] at increasing depth intervals

Depth interval	*n*[f]	Constant		GH[d,e]		N		S		Model statistics		
		Coeff[c]	*p*	Coeff	*p*	Coeff	*p*	Coeff	*p*	R^{2}[g]	R^{2} adj.	*p*
0-8 cm	20	9.06	0.00	0.70	0.06	-0.80	0.05	*n.s.*	*n.s.*	0.33	0.26	0.03
0-12 cm	20	16.05	0.00	0.91	0.12	*n.s.*	*n.s.*	*n.s.*	*n.s.*	0.13	0.08	0.12
0-16 cm	20	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*
0-20 cm	20	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*

a All model coefficients are centered and scaled (i.e. the coefficients can be compared within each model).

b Response variables are the carbon accumulation for depth interval in units of g C dm^{-2}.

c Model coefficients are included where $p < 0.15$; *n.s.*denotes coefficients with $p > 0.15$.

d GH, S and N: Model coefficients for the main effects of greenhouse cover, sulfur deposition and nitrogen deposition, respectively.

e No interaction coefficients had $p < 0.15$ and were therefore not included in the models.

f *n* = numbers of samples included in the model evaluation.

g R^2 = explained variance; R^2adj = adjusted R^2.

3.5 Methodological considerations

3.5.1 Chamber measurements

The static chamber technique is the most commonly used technique for flux measurements at experimental sites, but it has both advantages and disadvantages. It is simple, cheap, and it is easy to isolate a certain area of the ecosystem and thus study spatial variations in fluxes and compare effects of experimental treatments. It is also possible to separate the different CO_2 flux components, NEE, GPP and R_{eco}, by covering the chamber with sheets of varying transparency. The disadvantages are that the method is very laborious, time-consuming and provides poor temporal resolution. The chamber technique also introduces several sources of potential error, e.g.

increasing the temperature and moisture while reducing CO_2 concentrations inside the chamber, which may affect both CH_4 and CO_2 flux measurements (e.g. Kutzbach *et al.*, 2007; Knapp & Yavitt, 1992). CO_2 flux measurements are especially sensitive to these changes and plants respond quickly to reductions in concentrations of CO_2 and increases in temperature (Kutzbach *et al.*, 2007). To reduce these problem we used short enclosure times (30 sec-4 min and 6-7 min for CO_2 and CH_4 flux measurements, respectively). In addition, increases in temperatures were minimized by shading the CH_4 flux chambers with sun reflectors and by keeping the temperature inside the CO_2 flux chambers to within ±5°C of the outside temperature using an air-conditioning system.

3.5.2 Statistical design and data evaluation

The experiment in this thesis is conducted according to a central composite design. Basically this is a full factorial design with three factors at two levels with an additional centerpoint with treatment levels intermediate to the high and low levels of the factorial design. However, intermediate treatment levels are used for two of the factors while the third only occur at two levels. This deviation from a complete central composite design results in some covariation between the experimental factors, i.e the design is not totally orthogonal. This unbalance in the design makes it difficult to evaluate the functional response between the factors and the response, but not the effects of the factors. To evaluate the degree of orthogonality in the design we have used condition numbers where a number < 3 indicates a good design, i.e. a very low degree of colinearity between the experimental factors. The design used in this experiment had a condition number at 1.2 when the whole design was used, i.e. when there was no loss in data. When covariates were included in the models the condition number was 3.0. All orthogonal designs fulfill the prerequisites for analysis by both analysis of variance (ANOVA) and multiple linear regression (MLR) models (for more details on these designs see e.g. Box *et al.*, (1978)).

The data to be used as response variables have to fulfill the requirements of normal distribution. Only CH_4 emission rates were found to not be normally distributed and were therefore transformed using a square root transformation. The full utilization of the experimental design also requires accepted response data for all treatment combinations. All flux components have loss in data that have affected the orthogonality of the design leaving it unbalanced in the statistical evaluation and may also have increased the uncertainty in the modeled MLR parameters. The condition numbers for the models of the different responses was within the following ranges: 1.2 -

3.1 for CH4 production and oxidation models, 3.0 – 4.3 for CH4 emission models, 1.2 for all C accumulation models, 3.0 – 3.5 for Reco models, and 3.4 – 5.8 for GPP and NEE models. Clearly, the problem with non-orthogonal models was primarily a problem in the models with GPP and NEE as responses. The complexity of both measurements and data evaluation for NEE and GPP provided a data loss, in average, of 30%, which resulted in weaker models. In addition, the GPP and NEE data are products from several steps of modeling prior the MLR analysis and this increased the uncertainty of the estimated fluxes. The uncertainty in the estimated GPP and NEE could be reduced in future surveys by including more levels of PAR and replicated measurements at each level of PAR in the light-response functions.

3.6 Conclusions

- The results presented in this thesis show that long-term experiments are essential for evaluating effects of mire treatments with long effect time constants. Short-term effects are usually transient, since changes in plant community composition and ecophysiology properties, and changes in microtopography are time dependent.
- Long-term nitrogen additions have not only changed the plant community composition towards lower densities of *Sphagnum* species and higher densities of sedges and dwarf shrubs. The treatment has also changed the microtopography reducing the distance to the mean water table in nitrogen-fertilized plots. Both of these changes affect properties that play major roles in mire carbon biogeochemistry.
- Both CH_4 production and CH_4 emission are stimulated by the long-term nitrogen treatment, most likely as an effect of the increase of sedges, which promotes substrates for the methanogenic population and aerenchymatic transport of CH_4, and an effect of changed microtopography which changes the volume ratio between anoxic and oxic conditions.
- The reduction in height growth in response to long-term nitrogen deposition was compensated for by increased bulk density and carbon content, leading to no significant effects on carbon accumulation. This is in agreement with the CO_2 exchange measurements during one growing season in 2006, where no effect on the net ecosystem exchange was

- Long-term deposition of sulfate did not have a negative effect on either CH_4 production or CH_4 emission. This may be partly because sulfate deposited at the surface may stratify between populations of the sulfate-reducing bacteria and methanogens. However, the absence of negative effects may also be related to the time between application of fertilizers at this experimental site and the timing of the CH_4 flux measurements.
- The results of the greenhouse treatment suggest that the indirect effects of the treatment are much more important than the direct effects of temperature. The general view that temperature stimulates soil microbial processes was not supported by the findings of our studies. Rather the greenhouse treatment reduced CH_4 emission and CH_4 production, as well as R_{eco}, suggesting that it reduced the quality of the organic matter.

3.7 Implications

This thesis has provided insights in how long-term of deposition of nitrogen and sulfur, and increased temperature, affects CH_4 emissions, CO_2 exchange and carbon accumulation. Many of our results are not in agreement with previous observations on the same matter, and this may have many possible explanations: (1) Many studies are not based on long-term experiments and observed effects may therefore only be transitory; (2) when evaluating effects by using natural gradients in deposition rates or temperature instead of field experiments, there are a lot of factors included that cannot be controlled for and there is a risk that the observed effect represents something else than intended; (3) the responses to treatments may differ between mire ecosystems and that observed effects may be unique to that system. For example, many systems may respond strongly to N deposition, in similar ways as in this system, but the effects on carbon exchange and storage may be different due to differences in plant species composition, hydrology and peat chemistry; (4) there are though restrictions also in using long-term experiments, since the manipulations are not a perfect reflection of reality.

I believe that these results may contribute to modify the view on how environmental changes, and in particular, nitrogen deposition affects CH_4 emissions, carbon exchange and carbon accumulation. For example, we show that effects of N deposition do not necessarily decrease C accumulation in mires despite a shift to lower Sphagnum densities. Another example is that model predictions of responses in CH_4 emission to increased temperatures suggest in general an increase in CH_4 emissions from northern peatlands (Zhuang *et al.*, 2006; Walter & Heimann, 2000; Cao *et al.*, 1996). To my knowledge, the existing models do not take into account the effect of temperature on the quantity and quality of the organic matter before it reaches the anoxic zone. More information about both direct and indirect, long-term temperature effects on peat quality, net primary production and carbon allocation, for example, is needed before making more accurate predictions.

3.8 Further research

This study has also left some "Whys", that are potential questions for further research:

- In general, we still do not know enough about the direct controls on the different effects we have seen. This could be improved by combining flux measurements with; pore water measurements of sugars, organic acids and amino acids; aerobic and anaerobic incubations for decomposition rates estimates and; applying labeling experiments to study below-ground carbon allocation patterns.

- A more thorough investigation is needed to cover both intra and inter seasonal variations in treatment effects on GPP, R_{eco} and NEE, in order to be able to draw more firm conclusions CO_2 carbon exchange.

- The effects of N deposition on plant community composition and ecophysiological responses correspond well to the effects found in areas with more than 30 years of N deposition. However, plant litter in the upper 40 cm in the peat profile is still constituted by a mix of litter from different plant communities under transition. By studying an even longer-term experiment would reflect the changes in litter composition also in deeper peat layers.

- Further research on the response of CH_4 emissions and CH_4 production to the long-term S deposition is needed to investigate the mechanisms behind the effects. By measuring CH_4 emissions and tracing SO_4^{2-} transformations in the experiment in association to (before, during and after) the application of the S fertilizers to the plots, a better understanding of temporal dynamics in CH_4 emissions and interactions between methanogenic and SRB population, could be reached.

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