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Winter Dynamics of the Greenhouse Gas Exchange in a Natural Bog

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ABSTRACT

Northern peatlands are important in the context of the climate change. Since they comprise huge amounts of soil organic carbon and are found where the most significant greenhouse warming is predicted, they have the potential to exert major feedback effects on the global warming.

Studies of the greenhouse gas exchange in northern peatlands have mainly focused on the growing season when the soil is thawed. But recently, attention has been drawn to the importance of winter processes in the estimations of global greenhouse gas budgets.

In this study, fluxes of CO₂, CH₄ and N₂O in a natural, nutrient-poor peatland (ombrotrophic bog) in southern Sweden were measured from February to April using a closed chamber technique. Mean fluxes during this time for CO₂ and CH₄ were 68.6 ± 9.9 (mean \pm SEM) and 0.70 ± 0.06 mg m⁻² h⁻¹, respectively. Fluxes were significantly higher when the soil was thawed as compared to when it was frozen. Fluxes of CO₂ and CH₄ also correlated strongly with temperature, and revealed high temperature sensitivities around 0 °C.

Fluxes of N₂O showed an interesting trend. During the time when soil was frozen, a net uptake (-0.013 ± 0.003 mg m⁻² h⁻¹) was detected. Matching the moment in time when soil thawed, the mire turned from being a sink to a source (0.020 ± 0.003 mg m⁻² h⁻¹) of atmospheric N₂O. This delicate development can be ascribed to the theory that during the time when soil was frozen, N₂O was the sole electron acceptor available for denitrifiers. When the soil thawed, nutrients derived from frost-killed soil organisms became available for the surviving microbial population, which allowed N₂O production. More research is needed to quantify the N₂O exchange in different mire sub-types, and to evaluate whether northern peatlands should be included in global N₂O budgets.

This study concludes that winter processes are important, and should be taken into consideration in global greenhouse gas budgets. Temperature and freeze-thaw cycles are important factors regulating winter dynamics. The temperature sensitivity of the mire ecosystem is high at these low temperatures, which indicates that northern peatlands can act to enhance the climate change.

SAMMANFATTNING

Torvområden på det norra halvklotet är av stor vikt i forskningen kring klimatförändringen. Eftersom de håller stora mängder organiskt kol i marken, och återfinns där den mest signifikanta uppvärmningen förväntas, har de potential att utgöra en stark feedbackeffekt på den globala uppvärmningen.

Forskningen kring växthusgasutbytet mellan mark och atmosfär i torv-områden har huvudsakligen fokuserat på växtsäsongen. Men på senare tid har växthusgasutbytet under vintertid ådragit sig ett ökat intresse, då det kan vara av stor betydelse för den årliga växthusgasbalansen.

I detta examensarbete har utbytet av CO₂, CH₄ och N₂O studerats i en naturlig, näringsfattig myr (mosse) i södra Sverige från februari till april med hjälp av en portabel gasanalysator kopplad till aluminiumkammare. I medel var utsläppet av CO₂ $68,6 \pm 9,9 \text{ mg m}^{-2} \text{ h}^{-1}$ (medelvärde \pm SEM) och CH₄ $0,70 \pm 0,06 \text{ mg m}^{-2} \text{ h}^{-1}$. Utsläppen då marken var frusen var statistiskt sett lägre än då marken hade töat. Utsläppen av CO₂ och CH₄ korrelerade också starkt med temperatur, och uppvisade hög temperaturkänslighet kring 0 °C.

Utbytet av N₂O uppvisade en intressant trend. Då marken var frusen, uppmättes ett nettoupptag ($-0,013 \pm 0,003 \text{ mg m}^{-2} \text{ h}^{-1}$) av myren. Då marken började töa, blev myren istället en källa ($0,020 \pm 0,003 \text{ mg m}^{-2} \text{ h}^{-1}$) för N₂O. Denna utveckling kan förklaras med att under den tid då marken var frusen, var N₂O den enda tillgängliga elektronacceptorn i denitrifikationskedjan. När den frusna marken töade, frigjordes näringsämnen från markorganismer som frusit ihjäl för den överlevande mikrobiella populationen, vilket möjliggjorde produktion av N₂O. Det behövs ytterligare forskning för att kvantifiera utbytet av N₂O i olika myrtyper, samt för att undersöka huruvida torvområden bör inkluderas i en global N₂O budget.

Slutsatserna av denna studie är att växthusgasutbytet under vintertid är viktigt, och bör tas hänsyn till i en global växthusgasbudget. Temperatur och frys-tö cykler är faktorer som är viktiga för vinterdynamiken. Temperaturkänsligheten är hög för myren vid låga temperaturer, vilket kan vara en indikation på att torvområden kan förstärka klimatförändringen.

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INTRODUCTION

Northern peatlands and wet tundra regions are of great importance in the context of the climate change. They hold a huge amount of organic carbon in the soils, almost one-third of the world total (Post et al. 1982), and are also found where the most significant greenhouse warming is predicted (IPCC 2001). Altered carbon balances in these ecosystems can cause feedback effects that may further enhance the climate change (Joabsson et al. 1999).

Peatlands accumulate carbon when the vegetation sequesters more carbon from the atmosphere than is lost by decomposition, leaching or fire (Huttunen et al. 2003). Therefore, these ecosystems are in their natural state sinks for the important greenhouse gas carbon dioxide, CO₂. But due to the prevalent water-logged, anaerobic conditions that are favorable for methanogenesis, they are also significant sources of methane, CH₄ (Christensen et al. 2003). Natural peatlands do in general show negligible atmospheric exchange with nitrous oxide, N₂O (Martikainen et al. 1993).

Production and consumption of these atmospheric trace gases are the result of biological processes such as photosynthesis, aerobic respiration and decomposition (CO₂), methanogenesis and methanotrophy (CH₄), and nitrification and denitrification (N₂O). These processes are to a large extent sensitive to changes in climatic parameters, such as temperature and precipitation. When peatlands are subjected to climate change, a wide array of possible feedback effects is to be expected (Öquist 2001).

Most studies concerning the exchange of CO₂, CH₄ and N₂O in peatlands have focused on the growing season when the soil is thawed. But recently, attention has been drawn to the importance of winter processes in the calculations of global greenhouse gas budgets (Christensen et al. 1999). Microbial activity has been proved to occur at sub-zero temperatures (e.g. Dorland & Beauchamp 1991; Clein & Schimel 1995). This can occur at greater depths where temperatures are above zero, or at unfrozen microsites in the soil. Winter emissions from wetland and tundra regions have also been found to significantly contribute to annual greenhouse gas budgets (e.g. Melloh & Crill 1996; Alm et al. 1999).

Freeze-thaw cycles are of particular interest, since peaks in greenhouse gas emissions have been reported in connection with these events (e.g. Friborg et al. 1997; Papen & Butterbach-Bahl 1999). However, the mechanisms regulating winter emissions remain unclear. The ice and snow layers act as physical barriers, preventing exchange of gaseous compounds between soil and atmosphere. Gases produced in deeper soil will be restrained from escaping to the atmosphere, and the oxygen diffusion into the soil will also be limited, which regulates the aerobic respiration. Thaw events will remove this barrier and release entrapped gases.

Freeze-thaw events also have the potential to induce a transient increase in microbial activity. During the frost period, a large amount of the soil microbial biomass will die off. This will result in an easily degradable carbon and nitrogen source for surviving microbes. When the soil thaws and microbial activity

increases as a response to warmer temperatures, the additional nutrient source will boost the greenhouse gas production (Schimel & Clein 1996; Papen & Butterbach-Bahl 1999; Teepe et al. 2001).

The aim of the study is to explore the winter dynamics of greenhouse gas fluxes. I hypothesize that frozen soil on the mire will restrain greenhouse gas exchange, while microbial activity will continue, albeit at a lower rate. When the soil thaws, there will be a release of physically entrapped gases. A transient increase in biological greenhouse gas production is also expected as a response to soil thaw, due to the increased nutrient and substrate availability derived from frost-killed soil microbes. The temperature sensitivity of the mire system at these low temperatures is likely high, and global warming can therefore exert a significant impact on the wintertime greenhouse gas emissions.

To address these hypotheses I measured fluxes of CO₂, CH₄ and N₂O in a natural, ombrotrophic mire in southern Sweden. Flux measurements from February to April were performed using a closed chamber technique. The exchange of trace gases will be compared to environmental variables, and the temperature sensitivity of the system will be evaluated.

BACKGROUND

The Greenhouse Effect

The energy that drives the climate system of the Earth is incoming solar radiation. In average, 342 W m^{-2} reaches the Earth each year, and about 31 % is immediately reflected back by the atmosphere and surface (Kiel & Trenberth 1997). The remainder is absorbed, and will eventually be lost to space as thermal infrared radiation. However, if the atmosphere would not contain the so-called greenhouse gases absorbing outgoing long-wave radiation, life on Earth as we know it would not be possible since the mean global temperature would be approximately $-19 \text{ }^\circ\text{C}$ (IPCC 2001).

The atmospheric content of greenhouse gases, primarily water vapor ($\text{H}_2\text{O}_{(\text{g})}$), carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O) raises the mean global temperature to about $14 \text{ }^\circ\text{C}$. These gases absorb energy in the infrared spectra, reemit it in all directions, and thus trap the thermal radiation and keep the Earth's surface warmer. This greenhouse effect is natural.

The Climate Change

Any changes in the factors regulating incoming solar and outgoing thermal radiation will affect the net radiation, and thus warm or cool the Earth's surface. These changes can either be induced by natural or anthropogenic causes. Examples of natural causes are changes in solar radiation due to alterations in Earth's orbit around the sun, or increased amount of particles in the atmosphere due to volcanic eruptions.

Anthropogenic causes primarily include combustion of fossil fuels and land-use changes, which release huge amounts of CO_2 to the atmosphere. Also other radiatively active compounds such as CH_4 and N_2O are increasing; due to industrial and agricultural activities. The accumulation of these gases in the atmosphere increases the entrapment of thermal radiation, and is therefore called the enhanced greenhouse effect.

The response of the climate system to the enhanced greenhouse effect is complex due to feedback mechanisms and non-linear responses. A feedback mechanism can either intensify (positive feedback) or dampen (negative feedback) the original effect (IPCC 2001). An example of a positive feedback is increased atmospheric CO_2 concentrations resulting in raised temperatures, which will intensify the decomposition processes in soils and thus further increase CO_2 emissions to the atmosphere.

Since the late 19th century, the global average surface temperature has increased with $0.4 - 0.8 \text{ }^\circ\text{C}$ (IPCC 2001). And further increases are to be expected. Due to the numerous amounts of feedback mechanisms and the interrelated components of the climate system, it is truly complicated to simulate the impacts of the climate change. By the means of numerical modeling of the climate system it is predicted that global temperature will continue to rise, with between 1.5 and $4.5 \text{ }^\circ\text{C}$ at the end of this century. It is also likely that most land areas will warm more rapidly than the global average,

particular those at northern high latitudes in the cold season (IPCC 2001). A warming trend could also lead to changes in rainfall patterns, with increased desertification in some areas, and flooding in other areas.

The Greenhouse Gases

Human activities have significantly increased the atmospheric concentration of greenhouse gases, which acts to increase the radiative forcing of the atmosphere and raise global temperatures.

Carbon Dioxide, CO₂

Measurements of trapped air bubbles in ice cores reveal historical variations in the atmospheric CO₂ concentration. During the last 420 000 years, the CO₂ concentration has oscillated between 180 ppm during glacial periods and 300 ppm during interglacial periods (Petit et al. 1999). Pre-industrial levels (~280 ppm) are found within this range, but the present-day CO₂ concentration (~370 ppm) is unprecedented during the past 420 000 years (IPCC 2001).

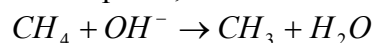
The current anthropogenic emissions of CO₂ are primarily the result of combustion of fossil fuels and cement production. These are estimated to $6.3 \pm 0.4 \text{ Pg C yr}^{-1}$ (mean \pm SD). The emissions are balanced to some extent by the net uptake of oceans ($-1.7 \pm 0.5 \text{ Pg C yr}^{-1}$) and the terrestrial biosphere ($-1.4 \pm 0.7 \text{ Pg C yr}^{-1}$), resulting in an atmospheric increase of $3.2 \pm 0.1 \text{ Pg C yr}^{-1}$ (IPCC 2001).

Methane, CH₄

Similar to CO₂, CH₄ has varied between low concentrations (320-350 ppb) at glacial periods and high concentrations (650-770 ppb) at inter-glacial periods (Petit et al. 1999). The present-day concentration of 1745 ppb dwarfs these earlier concentrations (IPCC 2001).

The atmospheric CH₄ concentration is much lower than CO₂, but its global warming potential (GWP), i.e. the relative radiative effect of CH₄ compared to CO₂, is 23 on a 100 years time horizon (IPCC 2001). Its atmospheric concentration is also increasing at a higher rate, approximately 1 % per year. The sources of CH₄ are dominated by anthropogenic activities; e.g. fossil fuel burning (19 %) and waste management (17 %). The dominant natural source is methanogenesis in wetlands (21 %) (Schlesinger 1997). The total CH₄ source strength is approximately $598 \text{ Tg CH}_4 \text{ yr}^{-1}$. Although the major sources have been identified, there are still uncertainties regarding the actual strengths, due to high variations in space and time (IPCC 2001).

The major sink of atmospheric methane is the reaction with hydroxyl radical (OH) in the atmosphere;



Together with some additional removal processes, the total sink strength equals about $576 \text{ Tg CH}_4 \text{ yr}^{-1}$. The resulting atmospheric increase would then be $22 \text{ Tg CH}_4 \text{ yr}^{-1}$ (IPCC 2001).

Nitrous Oxide, N₂O

The atmospheric concentration of N₂O is 314 ppb with an average rate of increase of 0.8 ± 0.2 ppb yr⁻¹, and its GWP is 296 on a 100 years time horizon (IPCC 2001). The global sources and sinks are not well known, but N₂O emissions from soils, the result of microbial nitrification and denitrification processes, are a major term in the budget. The increase of the atmospheric N₂O concentration is almost exponential, and is believed to be the result of increased soil nitrogen availability due to anthropogenic activities such as fertilization and increased nitrogen deposition (IPCC 2001).

The identified sink for N₂O in global budgets is photolysis in the atmosphere. The nitric oxide (NO) produced from N₂O in this process is further involved in stratospheric ozone destruction (Schlesinger 1997).

A small N₂O uptake by soils is identified (e.g. Tiedje 1988, Conrad 1996) although not directly included in global budgets. According to IPCC (2001), it is incorporated into the net emissions of N₂O from soils because it is coupled to the overall N-partitioning.

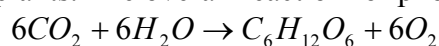
Biogeochemistry of Northern Peatlands

The concept of redox potential is important in the context of flooded soils. Redox potential is an expression for the tendency of an environment to gain or supply electrons; i.e. to oxidize or reduce a substrate (Schlesinger 1997). Presence of oxygen (O₂) results in a high redox potential, since O₂ is a strong oxidizing agent. Soil organisms obtain its energy from the oxidation of reduced materials (Paul & Clark 1989), and heterotrophic organisms use O₂ as an electron acceptor in aerobic respiration.

However, when O₂ is absent, a thermodynamically determined sequence of alternative electron acceptors in the following processes is expected as the redox potential declines (Bouwman 1990); denitrification (NO₃⁻), general fermentations (Fe³⁺, Mn⁴⁺), sulphate reduction (SO₄²⁻) and methanogenesis (CO₂). In wetland soils, O₂ is depleted rapidly with depth due to the high moisture content, creating a vertical redox gradient. Most wetland soils are dominated by CO₂ as electron acceptor, and methanogenesis is therefore the dominating metabolic pathway. The same redox gradient as in the vertical dimension is also found around vascular plant roots releasing O₂ to the rhizosphere, i.e. the area surrounding plant roots (Conrad 1996).

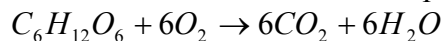
Fluxes of CO₂ in Wetlands

The assimilation of CO₂ by photosynthesis is probably the most important process on Earth. Photosynthetic active radiation (PAR) provides the energy for enzymes to reduce CO₂ and build carbohydrates that acts as building stones for living plants. The overall reaction for photosynthesis is;



Plants use about one-half of the carbon fixed in photosynthesis as an energy source for maintenance and growth in the autotrophic respiration (Schlesinger 1997). The remainder, net primary production (NPP), will sooner or later enter the soil system as dead organic matter. This extensive carbon source is then

subjected to the process of decomposition, where heterotrophic organisms (bacteria, fungi, microfauna) obtain energy through oxidation of the reduced compounds. The overall reaction for respiration is the reverse of photosynthesis;



During the decomposition process, nutrient elements are released (mineralized) and are made available for plant uptake and microbial use (immobilized).

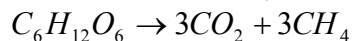
In continuously wet conditions, photosynthesis usually exceeds total respiration. Decomposition is hampered by the lack of oxygen, and dead organic matter accumulates as peat. In general, temperature, moisture and substrate quality regulate decomposition rates (Schlesinger 1997).

Kirschbaum (1994) evaluated the temperature dependence of soil organic matter decomposition. He found the highest temperature sensitivity around 0 °C; with a Q_{10} of almost 8 (i.e. an increase of 10 °C would increase decomposition by a factor of 8). Low temperatures will therefore dampen the cold season decomposition rate. On the other hand, soil freezing will act to destroy soil microbes and aggregates, resulting in increased substrate availability (Schimel & Clein 1996).

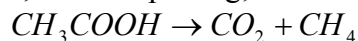
When a frozen soil thaws, substrates captured in ice will be made available for heterotrophic organisms. This can result in a CO_2 flux peak when soil temperature exceeds 0 °C. Öquist (2001) found that freeze-thaw treatments resulted in almost 100 % increase of the CO_2 production potential, explained by the release of carbon substrates and inorganic compounds. Winter CO_2 emissions from three natural bogs in Finland averaged 25 % of the annual CO_2 budget, with mean daily winter emissions of 24.4, 45.8 and 38.2 $mg\ m^{-2}\ h^{-1}$, respectively (Alm et al. 1999).

Fluxes of CH_4 in Wetlands

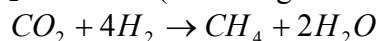
Under anaerobic conditions, dead organic matter is degraded to CO_2 and CH_4 ;



However, no single microbe can complete this reaction by its own. Instead, many different species contribute to the complete process by degrading complex organic compounds to simpler molecules. The complex organic molecules (such as cellulose, hemicellulose, lipids and proteins) are enzymatically hydrolyzed into soluble sugars and amino acids. These are taken up by bacteria and fermented to alcohols, fatty acids, H_2 and CO_2 . The alcohols and fatty acids are then oxidized to acetate and H_2 . (Conrad 1989; Öquist 2001). The actual methanogenesis mainly occurs via two metabolic pathways at low redox potential, acetate splitting;



and CO_2 reduction (Schlesinger 1997);



The net flux of CH_4 to the atmosphere is regulated by methanotrophic bacteria consuming CH_4 in the presence of O_2 . Methanotrophy in wetlands occurs in the top layers, where the available substrate (CH_4) to O_2 ratio is optimal (Dedysh 2002). The net flux is also dependent on the type of CH_4

transport. Diffusive transport exposes CH₄ for methanotrophic bacteria in the aerobic layer, while ebullition (transport by gas bubbles that are created when CH₄ production is high) causes CH₄ to pass the aerobic layer too fast for oxidation to take place (Conrad 1989). During the growth season, plant-mediated transport of gases in internal ventilation systems in vascular plant stems (aerenchyma) is of major importance for CH₄ fluxes. Oxygen may be transported to the rhizosphere, inhibiting methanogenesis and enhancing aerobic respiration and CH₄ oxidation. Methane may also escape the methanotrophic layer through the aerenchymateous tissue without being oxidized (Joabsson et al. 1999).

In wintertime, it is unlikely that ebullition and plant-mediated transport of CH₄ occurs, due to the ice layer and dormant vegetation. However, cracks in the ice as well as the unfrozen layer surrounding plant stems can create temporary diffusive transport pathways. Melloh & Crill (1996) identified a CH₄ buildup in deeper peat that began near the end of the growing season. This was explained by changed transport mechanisms, and also increased CH₄ solubility in water at low temperatures.

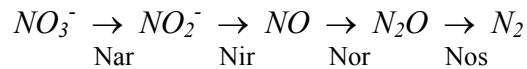
In the process of freezing, pure water will freeze first and substrates will accumulate in the unfrozen water, causing its freezing point to decrease (Papen & Butterbach-Bahl 1999). This would increase methanogenic potential, since substrate availability and quality are important factors for CH₄ emissions (Conrad 1989). However, the effect of low soil temperature during winter is also a strong regulator. Methanogenic activity usually shows high Q₁₀ values, ranging from 5 – 10, which would significantly decrease methanogenesis at low temperatures (Christensen et al. 1999). However, at sub-zero temperatures no systematic relationship with CH₄ emissions could be found at a Swedish sub-arctic mire (Friborg et al. 1997).

Alm et al. (1999) report winter CH₄ emission of 22 % of the annual release from natural Finnish bogs (average winter flux on three bogs: 0.64, 0.78 and 0.37 mg m⁻² h⁻¹, respectively). Average winter flux rates from a temperate poor fen in New Hampshire for five winters ending in 1994/1995, was 2.3 mg m⁻² h⁻¹ for years with average snowfall and 1.0 mg m⁻² h⁻¹ for years with low snowfall (Melloh & Crill 1996). The relationship with snow was explained with limited frost penetration and higher peat temperatures. Friborg et al. (1997) also found a rapid increase in CH₄ emissions as an immediate result of surface thawing. The physical effect of snow and top soil melting, releasing accumulated CH₄, was regarded as the driving force.

Fluxes of N₂O in Wetlands

Nitrous oxide is a key component in the global nitrogen cycle, since it is an intermediate in denitrification and a by-product of nitrification (Yoshinari 1990). Nitrification rates are primarily controlled by ammonium (NH₄⁺) and oxygen availability (Firestone & Davidson 1989). Since nitrification is an aerobic process, it is likely not a significant process involved in N₂O production in wetlands. However, a drawdown of the water table can increase N₂O emissions from nitrification activity (Martikainen et al. 1993).

Denitrification is a wide term responsible for the processes in which nitrate (NO_3^-) and nitrite (NO_2^-), are reduced to nitrogen gases. Respiratory denitrifiers are basically aerobic bacteria with the alternative ability to reduce nitrogen oxides when oxygen is limiting (Tiedje 1988). The denitrification pathway of free intermediates and enzymes responsible for each step (Nar – nitrate reductase; Nir – nitrite reductase; Nor – nitric oxide reductase; Nos – nitrous oxide reductase) are shown below (Tiedje 1994).



Most denitrifiers can perform the entire pathway, but some strains lack one step, e.g. $\text{N}_2\text{O} \rightarrow \text{N}_2$. N_2O will then be the final product of denitrification. Since N_2O can be further reduced to N_2 , natural environments can act both as source and sink for atmospheric N_2O .

General requirements for denitrification are anaerobic conditions and availability of nitrogen oxides (oxidant) and organic carbon (reductant). The ratio N_2O to N_2 is increased by increasing amount of oxidant and oxygen availability, decreased amount of reductant, and decreasing pH and temperature (Firestone & Davidson 1989).

Nitrous oxide can also be both produced and consumed by the so-called DNRA (dissimilatory nitrate reduction to ammonia) bacteria (Conrad 1996). This process has not been extensively studied, but DNRA activity seems to be favored in carbon-rich, electron acceptor-poor environments with low redox potential (Tiedje 1988). Matheson (2002) found that DNRA bacteria were responsible for as much as 49 % of the nitrate removal in an unplanted riparian wetland soil.

Aerts (1997) demonstrated that natural peat soils in the Netherlands have a high potential for denitrification, but the process was severely nitrate limited. Available nitrate was quickly utilized and its re-supply (nitrification) was inhibited in the absence of oxygen. Nitrate input via precipitation is likely important in these environments.

Dorland & Beauchamp (1991) found active denitrifiers down to -2 °C, and modeling suggests denitrification activity down to as much as -13 °C. Koponen et al. (2002) studied N_2O emissions in agricultural soil cores, and found that N_2O was produced at temperatures down to -6 °C. Good conditions for denitrification were achieved at unfrozen microsites in the soil surrounded by ice, which induced anaerobiosis. Produced gases were released during thaw events, and also through ice cracks.

Papen & Butterbach-Bahl (1999) found extreme N_2O emissions in German forests during long-term frost periods and soil thawing, emissions higher than during summer-time (maximum N_2O emissions were $0.5 - 0.6 \text{ mg m}^{-2} \text{ h}^{-1}$). It was explained with high microbial nitrogen turnover rates in small unfrozen water films surrounding soil particles, with high concentrations of easily degradable substrates, derived from frost-killed microbial biomass. Furthermore, since vegetation was dormant there was no competition for nitrogen. Neither nitrate leaching nor net immobilization was observed. At the end of the

frost period, N₂O peaks were attributed to the fact that soil thawing released additional substrates captured in ice.

Alm et al. (1999) report low winter N₂O emissions from a forested bog in Finland ($< 0.1 \text{ mg m}^{-2} \text{ d}^{-1}$), while Maljanen et al. (2004) found that N₂O emissions from organic agricultural soils during winter were important in the global budget, ranging from 2 to 99 % of annual emissions.

Interactions with the Climate Change

The proposed changes in temperature and precipitation will alter ecosystem properties and thus the natural greenhouse gas balance. The response of the biosphere to climate change will further impact the atmospheric chemistry.

Since most of the processes that are regulating carbon and nitrogen exchange between northern peatlands and the atmosphere are affected by the climate, a wide range of feedback mechanisms is possible in a future climate change. Rates of photosynthesis, respiration and CH₄ emission are expected to increase with increasing temperature. Respiration is likely to increase more than photosynthesis, and thus implying a positive feedback (Gorham 1991).

Warmer temperatures will increase soil activity and release more nutrients due to enhanced mineralization. A longer growing season and more available nutrients are likely to increase CO₂ uptake by photosynthesis (Chapin et al. 1995). Trees might be expected to increase in abundance on mires; resulting in increased evapotranspiration and decreased albedo, which would increase the respiration. On the other hand, the enhanced tree growth will have a carbon assimilating effect, although transient (Moore 2001). Gorham (1991) argues that peat-accumulating ecosystems will have to move northwards as the climate becomes warmer and possibly drier in the southernmost peatland locations. One alarming possibility is that the rapidity of climate change will cause southern peatlands to be degraded faster than northern peatlands can expand northward. This will lead to a global net carbon loss from peatland soils.

Changes in hydrological patterns are hard to predict, but if evapotranspiration increases, water tables will be lowered in general (Gorham 1991; Moore 2001). Martikainen et al. (1993) estimated that drying caused by climate change equivalent to drainage by ditching 30 and 50 years ago in Finnish peatlands, would only increase N₂O emissions with 0.3-1 %. Significant feedback effect from N₂O emissions therefore seems unlikely. A lowered water table will increase the oxygen availability, hence the aerobic respiration and methane oxidation (Moore 2001). The sum effect of these processes is difficult to foresee.

METHODS AND MATERIAL

Site Description

The study site, Fäjemyren, is a natural, nutrient-poor peatland (ombrotrophic bog) located approximately 20 km northwest of Hässleholm in southern Sweden. Average temperature in February, March and April is -2.1, 0.6 and 5.0 °C, respectively (based on the years 1960-1990). Average precipitation is 38, 48 and 44 mm in the same months. The spring of 2005 was similar to the average, except for an unusually dry April, with only 7 mm of precipitation (SMHI 2005).

The main nutrient source of the bog is precipitation; average nitrogen deposition (dry and wet [NO_x + NH_x]-N deposition) in the area is 15-20 kg N ha⁻¹ yr⁻¹ for the years 1999-2002 (Persson et al. 2004). Average peat water pH at the field site measured during this campaign is 3.3.

The bog is sparsely vegetated with trees such as *Pinus silvestris* and *Betula pubescens*; and the field layer is dominated by mosses (*Sphagnum spp.*), sedges (*Eriophorum vaginatum*) and dwarf shrubs (such as *Calluna vulgaris* and *Erica tetralix*). In drier parts, trees are more abundant and other shrubs such as *Vaccinium vitis-idaea* and *Empetrum nigrum* are present.

Flux Measurements

Flux measurements of CO₂, CH₄ and N₂O were performed between the 29th of January and the 27th of April using a closed chamber technique. Six groups with four aluminum collars (60 × 60 cm, height 20 cm) each were inserted into the soil during the summer of 2004. Before measurements, aluminum chambers (62 × 62 cm, height 20 cm, total airspace 76.9 dm³) were fitted onto the preinstalled collars. The collars have grooves, which were filled with water, to provide an airtight seal. During one measurement cycle, three chambers were measured simultaneously, and each chamber was active in a predetermined time interval (300 or 600 seconds) for three to four cycles (total measurement time: 60 - 90 minutes). The experimental setup is described in *figure 1*. It should be pointed out that all flux measurements were performed during daytime, between 10:00 and 18:00. Fans were not used in the chambers.

The concentrations of CO₂, CH₄, N₂O and H₂O in the active chamber headspace were recorded continuously using a photoacoustic multigas (IR) gas analyzer (INNOVA 1312). During a measurement, a sample of air is drawn into the analysis cell. Pulsating light is sent from an infra-red light source through an optical filter, which transmits light in a defined wavelength range (i.e. the wavelength range of CO₂, CH₄, N₂O or H₂O), and this light enters the cell. If there is a gas in the cell that absorbs light of this wavelength, a pressure wave is created due to the pulsating light that is increasing and decreasing gas temperature. Microphones measure this acoustic signal, which is proportional to the gas concentration.

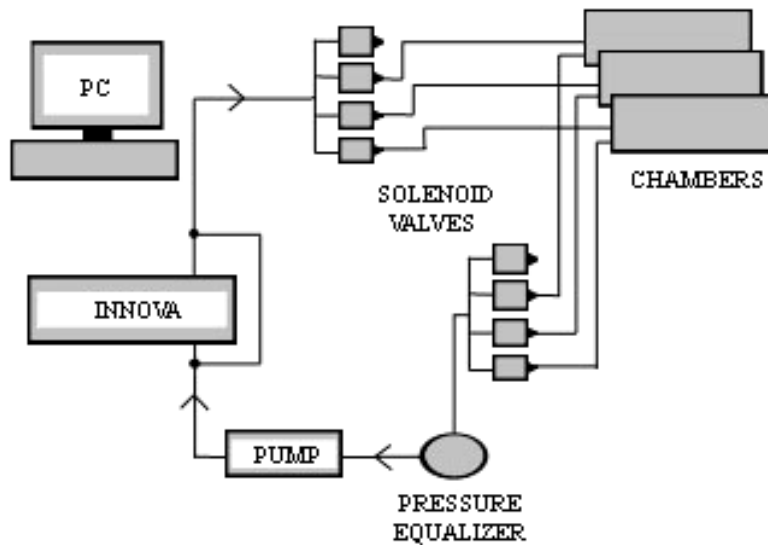


Figure 1. A schematic drawing of the flux system setup. One pair of solenoid valves (for air inlet and outlet) is active during a predetermined time interval. A pump creates internal airflow, and air is drawn from the active chamber headspace through PVC tubes. The PC controls the solenoid valves and logs data from the photoacoustic multigas (IR) gas analyzer (INNOVA 1312). A pressure equalizer assures that an equal amount of air is taken from the chamber as is returned, to avoid pressure issues.

Water vapor ($\text{H}_2\text{O}_{(g)}$), is always present in ambient air and absorbs infra-red light in a wide spectrum. This means that the presence of H_2O will create a signal in the INNOVA, which interferes with the signals of the other gases, especially of N_2O , but also of CH_4 . The INNOVA tries to compensate for this interference, but not always in a satisfactory manner. Therefore, measurements with significant CH_4 or N_2O fluxes that show similar trends as significant H_2O were excluded in this study.

Flux measurements were performed at a total of nine different collars. Boardwalks were used to minimize disturbance during the measurements. To be able to calculate fluxes, the chamber headspace volume was measured. Since vegetation biomass and microtopography differed in the collars, individual measurements were done. Each collar was divided into nine squares (20×20 cm), and in these subunits the deviation from chamber height was measured in one randomized point. The average deviation was then used as an increase or decrease of chamber height. Headspace volume was measured 31st of March and 1st of April, and no major changes in biomass were observed during this measurement campaign. Photographs of the nine collars used are provided in the *appendix*.

Snow was present during four measurement occasions: 29th and 30th of January, 23rd of February and 16th of March. Snow depth was measured, and $0.70 \text{ cm}^3 \text{ cm}^{-3}$ was used as an average of snow porosity (Alm et al. 1999). The estimated volume occupied by snow was then subtracted from chamber headspace volume. Fluxes could be underestimated on these occasions due to gas exchange in the snow. At the 17th of March, the two collars used were

flooded four centimeters, and a new headspace volume was calculated using a decreased chamber height.

Additional Measurements

The vegetation composition was investigated on the 8th and 12th of April. The collars were once again divided into nine squares, and in each square the projected coverage of different species was estimated. Vegetation indices to be used in the analyses are the *Eriophorum vaginatum* to *Sphagnum spp.* ratio, *Eriophorum vaginatum* coverage, *Sphagnum spp.* coverage and total coverage of all vegetation species. *Eriophorum vaginatum* is a vascular plant with aerenchymateous tissue that provides a transport pathway for gases between soil and atmosphere.

Soil temperature at the mire was measured approximately 200 m from the flux measurement site, starting on the 9th of February. Five thermocouples were inserted into the ground during the summer of 2004. Three thermocouples measured at a depth of 5 cm at three vegetatively and topographically different sites. At one of these sites, soil temperature was also measured at a depth of 10 and 20 cm. A Minicube datalogger stored the temperature data at a time resolution of ten minutes. In the following analyses, gas fluxes will be compared to average soil temperature at 5 cm in the three sites, and soil temperature at 20 cm, averaged over the same time period as the flux measurements.

Air temperature and precipitation data were ordered from SMHI (Swedish Meteorological and Hydrological Institute). The nearest station with high temporal resolution on temperature data was located in Hörby, approximately 50 km south of Fäjemyren. Therefore, absolute values of air temperature data are ca 0.5 – 1.0 °C overestimated, but the variation will be similar. Daily precipitation data was obtained from Osby, ca 20 km north of Fäjemyren.

Data Processing

The output data from the INNOVA, concentrations of CO₂, CH₄, N₂O and H₂O (ppm), was plotted against time (minutes) in Microsoft Excel. Only those measurements with a linear regression coefficient (r^2) that exceeded a fixed value were considered significant. The r^2 -value used was 0.9 for all gases except for N₂O, for which 0.7 was used.

The following equation was used to convert units from ppm min⁻¹ to mg m⁻² h⁻¹;

$$Flux = 60 \cdot 10^3 \cdot 10^{-6} \cdot k \cdot \frac{pV}{ART} \cdot M \quad (\text{eq. 1})$$

where k is the slope of the regression line (ppm min⁻¹); V is the chamber volume (l); p is the atmospheric pressure (atm); M is the molar weight (g mol⁻¹); A is the chamber area (m²); R is the ideal gas constant (atm l K⁻¹ mol⁻¹) and T is the temperature (K).

The temperature sensitivity of the fluxes of CO₂ and CH₄ was calculated using the Q₁₀ function (Kirschbaum 1994);

$$Q_{10} = \left(\frac{k_2}{k_1} \right)^{10/(T_2 - T_1)} \quad (\text{eq. 2})$$

where k_1 and k_2 are the calculated fluxes at the soil temperatures (5 cm) T_1 and T_2 .

To be able to evaluate the spatial variation of the fluxes in different collars, each collar flux was normalized against the mean collar flux at that specific measurement occasion;

$$\text{NormCollarFlux} = \frac{\text{CollarFlux}}{\text{MEAN}(\text{AllCollarFluxes})} \quad (\text{eq. 3})$$

This was done because all collars were not used at all measurement occasions, and some collars were used at more occasions than others.

Statistical Methods

Differences in fluxes when soil was frozen and thawed were investigated using two-tailed t-tests. Flux difference tests between collars include one-way ANOVA to evaluate if differences exist, and Tukey's HSD post hoc test to find out between which collars the differences exist. Tukey's HSD takes the Bonferroni correction into account, which compensates for multiple comparisons.

The correlation between gas fluxes and independent variables was explored by calculating Pearson's correlation coefficient and testing it for significance. Regression models were evaluated by testing the independent variable for significance.

Assumptions for these parametric tests such as equal variance and normal distribution were controlled before undertaking the tests. All statistic tests were performed in SPSS.

Calculation of N₂O Solubility in Water

An uptake of N₂O was observed in the chambers during the early season when the soil was frozen. To assess whether this uptake was of physical or biological origin, the N₂O solubility in water was evaluated. Since water with warmer temperature than ambient air was poured into the collars before measurements, it was suspected that water uptake of N₂O could be an explaining factor. The water solubility of N₂O as a function of temperature, salinity and partial pressure in the gas phase can be calculated using an equation given by Weiss & Price (1980);

$$C_{N_2O} = x' \cdot F \quad (\text{eq. 4})$$

where C_{N_2O} (nmol l⁻¹ of solution) is the equilibrium concentration of dissolved N₂O in the water phase; x' (ppb) is the mixing ratio of N₂O in the gas phase; and F (mol l⁻¹ atm⁻¹) is a solubility function. Values of F are given in a table for different temperatures and salinities. Suppose that 0.5 l of 10 °C water were poured into the collar grooves before flux measurements, and that the water temperature decreased to 0 °C. The increased amount of N₂O in this water will then be equal to 3.018 nmol, or 0.132 µg of N₂O.

Melting snow in the chambers can also cause a physical uptake. However, since aluminum chambers were used the temperature inside the chambers will not be increased due to the high reflectivity of aluminum. In case of rapid snow- and ice-melt, a physical uptake may be detectable. Physical uptake of CO₂ and CH₄ is also possible, but it will have a very small relative importance.

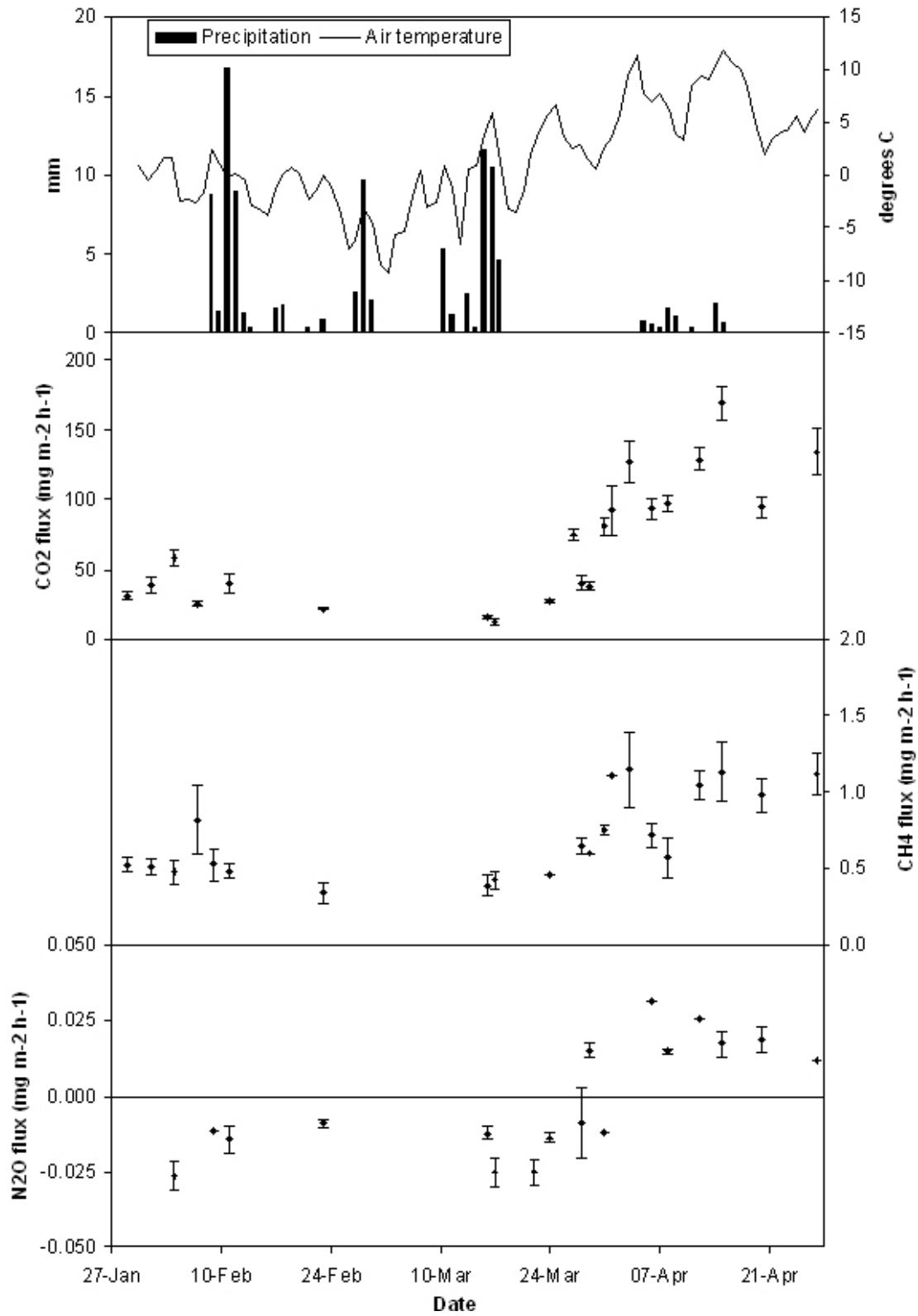


Figure 2. Daily precipitation (bars) and air temperature (line), fluxes of CO₂, CH₄ and N₂O from 29th of January to 27th of April. All flux values are in mg m⁻² h⁻¹, error bars denote SEM.

RESULTS

Figure 2 shows air temperature and precipitation during the measurement campaign, together with fluxes of CO₂, CH₄ and N₂O. The reason why there is only one flux measurement between the 11th of February and the 16th of March is that during this time the snow-cover on the mire exceeded chamber height. Removal of snow from the collars was considered to cause too much disturbance.

The issue of H₂O interference on the significant gas fluxes resulted in an exclusion of 35 % of the N₂O fluxes (24 out of 68) and 2 % of the CH₄ fluxes (2 out of 83). The overall result was not affected by the exclusion.

CO₂ Production

Since dark chambers were used in the flux measurements, photosynthesis was inhibited. The CO₂ flux is thus the result of aerobic and anaerobic decomposition, and respiration from soil animals and plants. Mean CO₂ production on Fäjemyren from 29th of January to 27th of April was 68.6 ± 9.9 mg m⁻² h⁻¹ (mean \pm SEM). Fluxes were significantly lower when soil was frozen (48.2 ± 8.4 mg m⁻² h⁻¹), compared to when soil was thawed (119.7 ± 12.5 mg m⁻² h⁻¹, $p = 0.002$).

The average CO₂ production correlates well with air temperature ($r^2 = 0.67$, $p < 0.001$, see figure 3) and soil temperature ($r^2 = 0.62$, $p < 0.001$, see figure 4). The air temperature model overestimates the CO₂ production when soil temperatures are low. By analogy, the soil temperature model underestimates the CO₂ production at low soil temperatures when air temperatures are high.

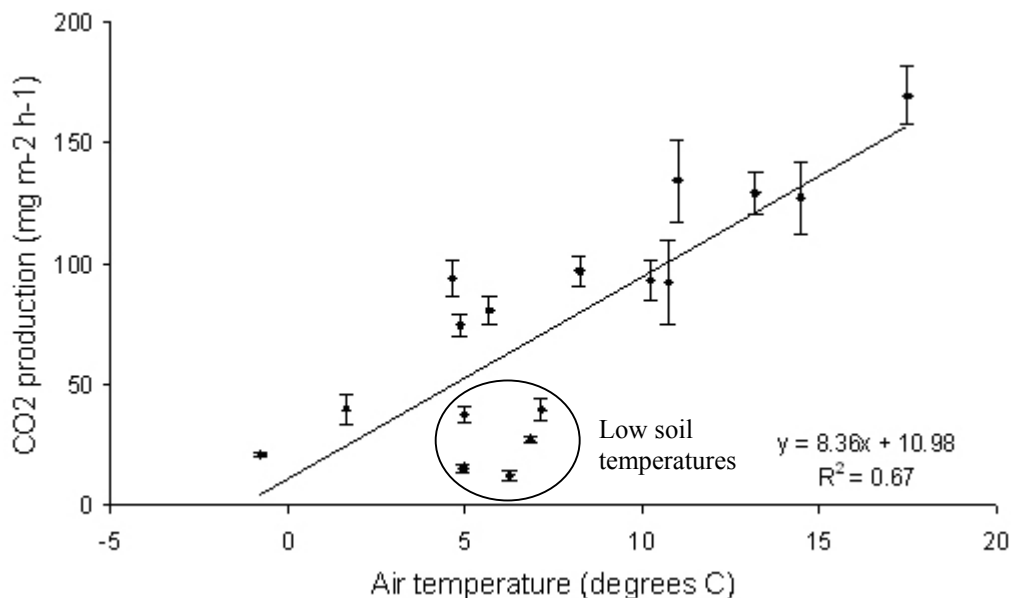


Figure 3. Average CO₂ production versus air temperature from 9th of February to 27th of April. Error bars denote SEM.

Snow was prevalent at only two measurement occasions when additional environmental variables were measured, namely 23rd of February (snow depth:

16 cm) and 16th of March (18 cm). Removing these occasions from the temperature models does not exert any major changes.

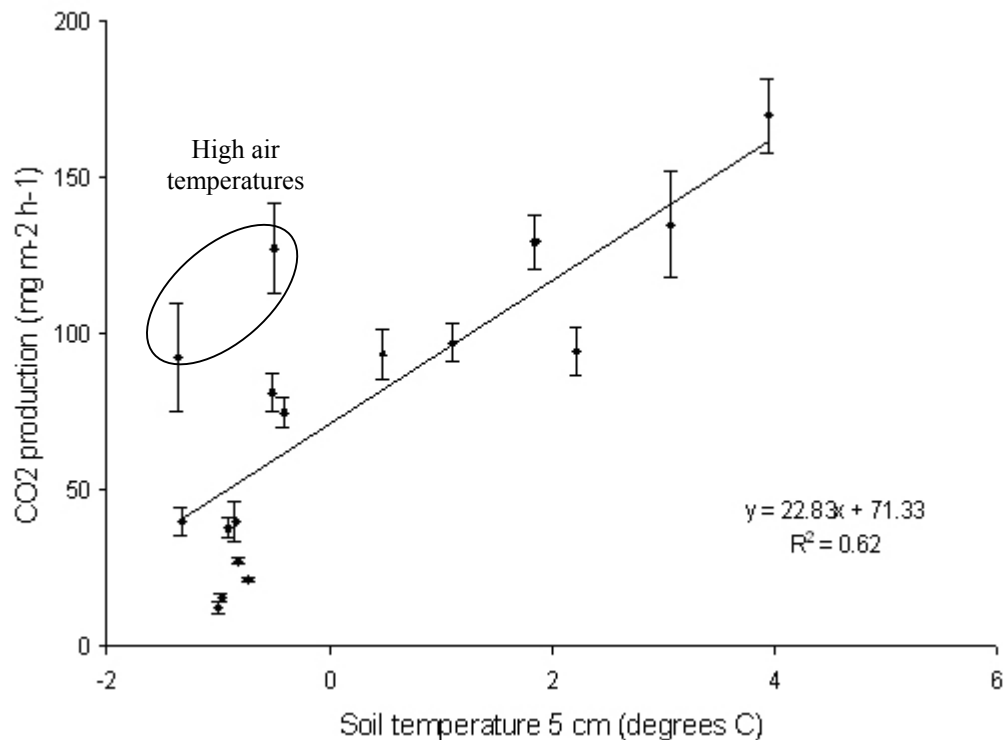


Figure 4. Average CO₂ production versus soil temperature at 5 cm from 9th of February to 27th of April. Error bars denote SEM.

The temperature sensitivity (Q_{10}) of the overall CO₂ production is 16.9. It was calculated by comparing mean CO₂ production when soil was frozen and when soil was thawed, see *table 1*. The theoretical soil temperature range for this Q_{10} is -4.37 °C to 5.63 °C (mean 0.63 °C). Relative temperature sensitivity between frozen and thawed soil could not be calculated, since the temperature ranges for which CO₂ production was measured was too small, and resulted in false values.

Table 1. Temperature sensitivity (Q_{10}) calculation for the CO₂ production.

	Frozen soil ^a	Thawed soil ^b	
Mean soil temperature at 5 cm (°C)	-0.85	2.11	
Mean CO ₂ production (mg m ⁻² h ⁻¹)	51.8	119.7	$Q_{10} = 16.9$

^a Data from 9th of February to 6th of April.

^b Data from 8th of April to 27th of April.

When the soil was frozen, CO₂ production was lower and the best predictor during this period is air temperature ($r^2 = 0.55$, $p = 0.006$). Also when the soil in the collars was completely thawed (from 6th of April), the production shows a high correlation with air temperature ($r^2 = 0.90$, $p = 0.014$). Soil temperature at 20 cm does not exert any correlation with CO₂ production.

The spatial variation of the normalized CO₂ production among the collars most frequently used (collar nr 1, 2, 3, 9, 11 and 12) is visualized in *figure 5*. The deviation from 1.0 indicates the deviation of the individual collar from mean CO₂ production. The production in collar nr 12 was significantly higher than in collar nr 1, 9 and 11 ($p < 0.05$). No clear relationship with the vegetation indices in *table 2* can be found.

Table 2. Vegetation indices in the most frequently used collars.

Collar nr	1	2	3	9	11	12
<i>Eriophorum vaginatum</i> to <i>Sphagnum spp.</i> ratio	0.34	0.33	0.14	0.27	0.11	0.39
<i>Eriophorum vaginatum</i> coverage	0.26	0.33	0.14	0.23	0.11	0.18
<i>Sphagnum spp.</i> coverage	0.76	0.98	1.00	0.83	1.00	0.45
Total coverage	1.29	1.50	1.42	1.31	1.20	0.83

The spatial variation among the collars was also examined when soil was frozen and when soil was thawed, which did not deviate from the overall pattern in *figure 5*. When the soil was thawed, a negative correlation can be found between the CO₂ production and total coverage ($p = 0.035$). Since there is no valid explanation for this relationship, it is considered to be due to randomness.

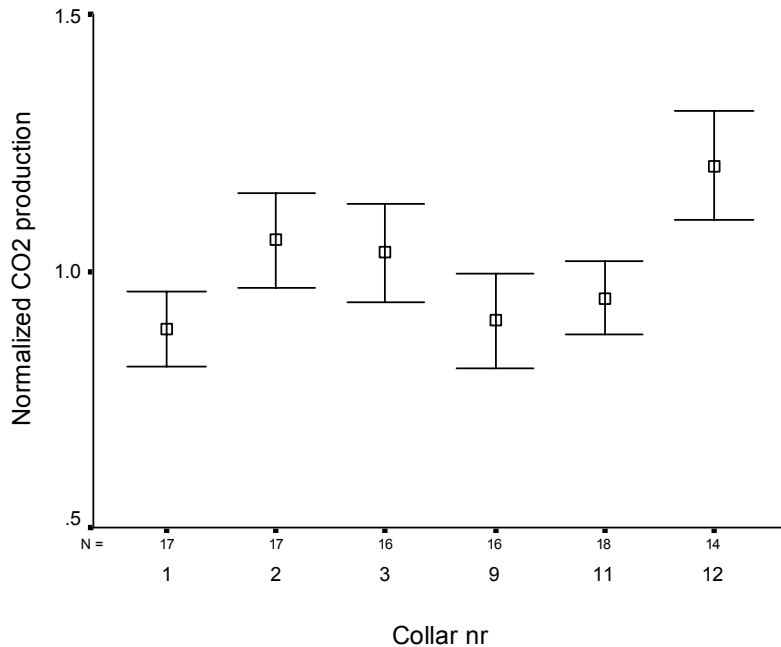


Figure 5. Normalized CO₂ production in the six most frequently used collars during the whole measurement campaign. Error bars denote 2 SEM.

CH₄ Fluxes

During the whole study period, Fäjemyren was a source of CH₄. Mean emission was $0.70 \pm 0.06 \text{ mg m}^{-2} \text{ h}^{-1}$. Emissions were significantly higher when soil was thawed ($0.93 \pm 0.09 \text{ mg m}^{-2} \text{ h}^{-1}$), as compared to when soil was frozen ($0.61 \pm 0.06 \text{ mg m}^{-2} \text{ h}^{-1}$, $p = 0.014$).

The fraction of CH₄ fluxes that failed the $r^2 = 0.9$ criterion during each measurement occasion is visualized in *figure 6*, and show a peak around the time when soil was thawing. Spring thaw began the 16th of March, and all snow in the collars was melted the 22nd of March. At the 27th of March, it was observed that the topsoil was thawed in parts of the collars. The soil in the collars was completely thawed at the 6th of April. The CH₄ fluxes that failed the $r^2 = 0.9$ criterion, did not show higher fluxes than previous or following CH₄ fluxes. Even an uptake of CH₄ was observed in some of the insignificant fluxes during this time period.

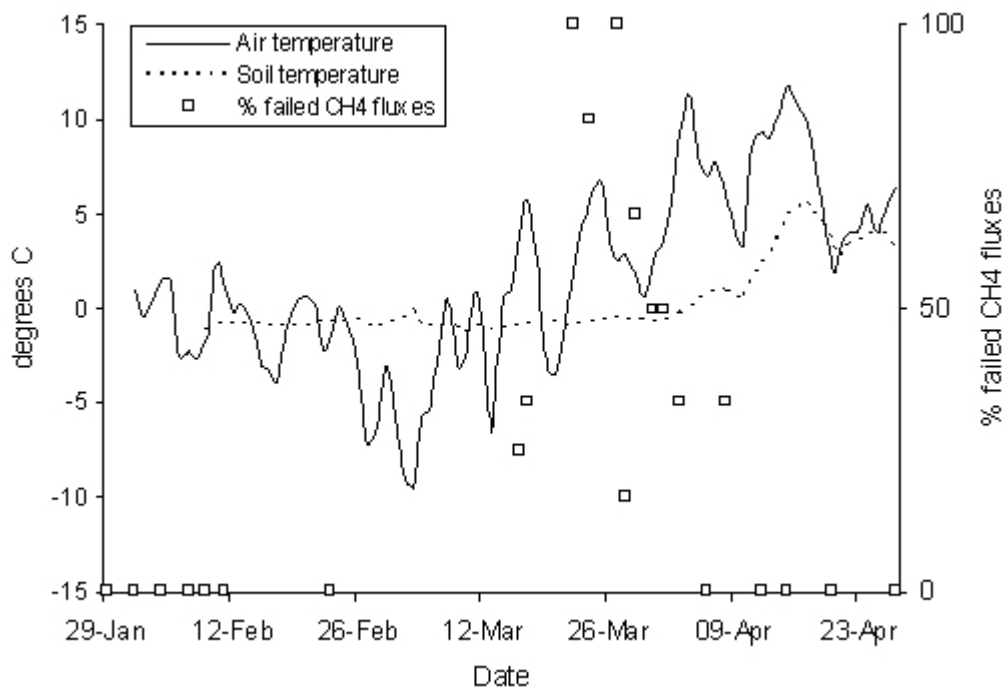


Figure 6. Percentage of failed CH₄ fluxes (squares), i.e. CH₄ fluxes that failed the $r^2 = 0.9$ criterion, daily average soil temperature at 5 cm (dotted line) and daily average air temperature (solid line).

As is the case with the CO₂ production, the average CH₄ fluxes show significant correlation with both air temperature ($r^2 = 0.63$, $p < 0.001$) and soil temperature at 5 cm ($r^2 = 0.38$, $p = 0.009$). For the period when the top soil was frozen, air temperature is the only significant predictor of the CH₄ fluxes ($r^2 = 0.69$, $p = 0.002$), although soil temperature at 20 cm is close to significance ($r^2 = 0.28$, $p = 0.095$).

The correlation between CO₂ production and CH₄ fluxes is high. It can be seen in *figure 7* that the CO₂ production increases more rapidly than the CH₄ flux. The temperature sensitivity for CH₄ is also lower; when comparing mean CH₄ fluxes at frozen and thawed soil, the Q₁₀ is 3.58 (theoretical soil temperature range -4.42 to 5.58 °C, mean 0.58 °C, see *table 3*).

Table 3. Temperature sensitivity (Q_{10}) calculation for the CH_4 fluxes.

	Frozen soil ^a	Thawed soil ^b	
Mean soil temperature at 5 cm (°C)	-0.96	2.11	
Mean CH_4 flux (mg m ⁻² h ⁻¹)	0.63	0.93	$Q_{10} = 3.58$

^a Data from 9th of February to 6th of April.

^b Data from 8th of April to 27th of April.

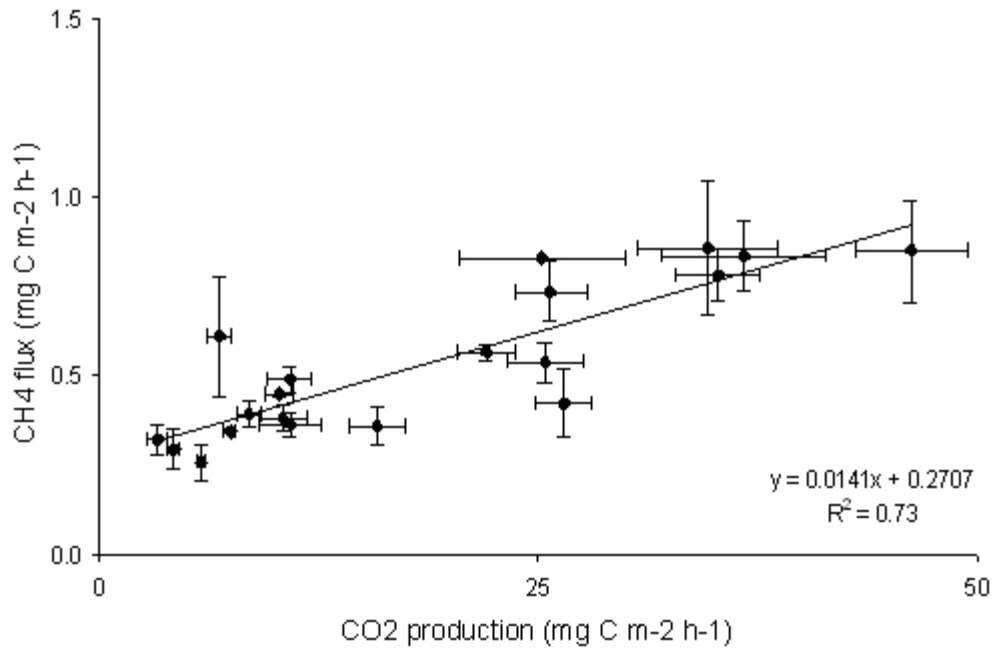


Figure 7. CH_4 flux versus CO_2 production for the whole measurement campaign. Error bars denote SEM.

The spatial variation of CH_4 fluxes among the collars during the whole measurement campaign is shown in *figure 8*. No significant relationship with vegetation indices provided in *table 2* can be found. Collar nr 3, which differs significantly from collar nr 11 and 12 ($p < 0.05$), shows the lowest CH_4 fluxes. Collar nr 3 is also one of the chambers with the lowest coverage of *Eriophorum vaginatum*. A comparison between vegetation indices and the normalized CH_4 fluxes when soil was thawed do not reveal any correlations.

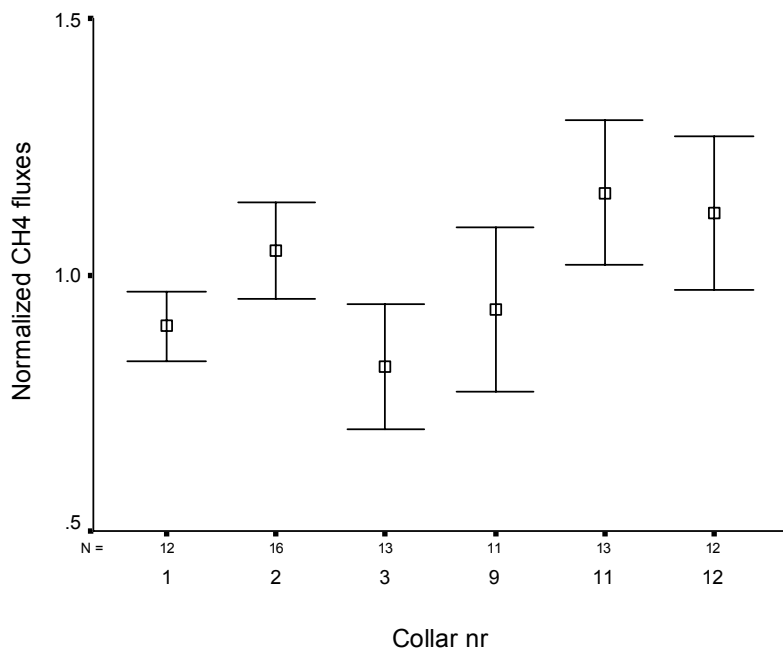


Figure 8. Normalized CH₄ fluxes in the most frequently used collars during the whole measurement campaign. Error bars denote 2 SEM.

N₂O Fluxes

The N₂O fluxes during the season show an interesting trend (*figure 2*). N₂O is consumed during the period when the topsoil was frozen. Matching the moment in time when soil thawed, Fäjemyren turned from being a sink to a source. There is a significant difference between winter uptake ($-0.013 \pm 0.003 \text{ mg m}^{-2} \text{ h}^{-1}$) and spring release ($0.020 \pm 0.003 \text{ mg m}^{-2} \text{ h}^{-1}$, $p = 0.005$), see *figure 9*.

A comparison between the average N₂O uptake and the calculated physical uptake by collar water ($0.132 \mu\text{g N}_2\text{O}$), demonstrates that approximately 1 % of the average uptake can be explained by a physical uptake. For melting snow and ice to account for the average uptake; snow and ice in the collar must turn into more than 16 l of water during the measurement cycles.

Similar to the previous gases, the N₂O fluxes correlate significantly with soil temperature at 5 cm ($r^2 = 0.47$, $p = 0.003$) and air temperature ($r^2 = 0.39$, $p = 0.01$). Improved correlation with soil temperature at 5 cm is achieved when using a quadratic model ($r^2 = 0.56$, see *figure 10*), where the N₂O fluxes tend to show an optimum curve with soil temperature.

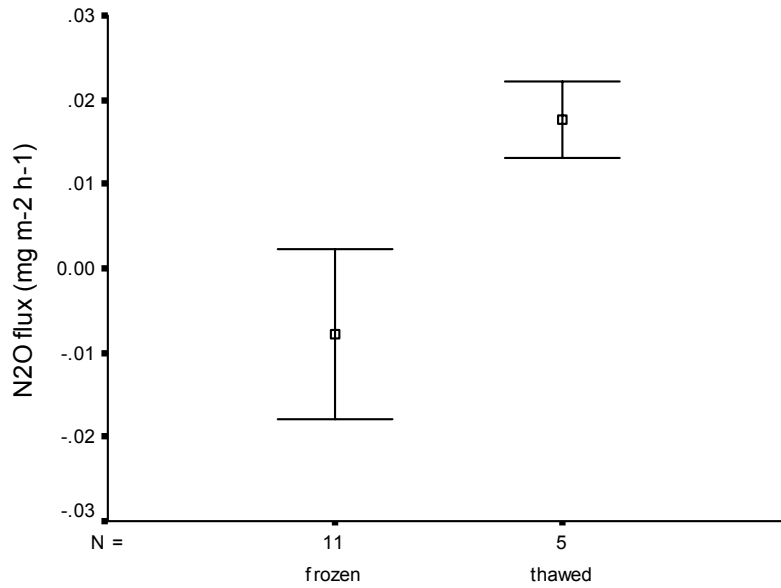


Figure 9. Comparison between N₂O fluxes when soil was frozen and thawed. Error bars denote 2 SEM.

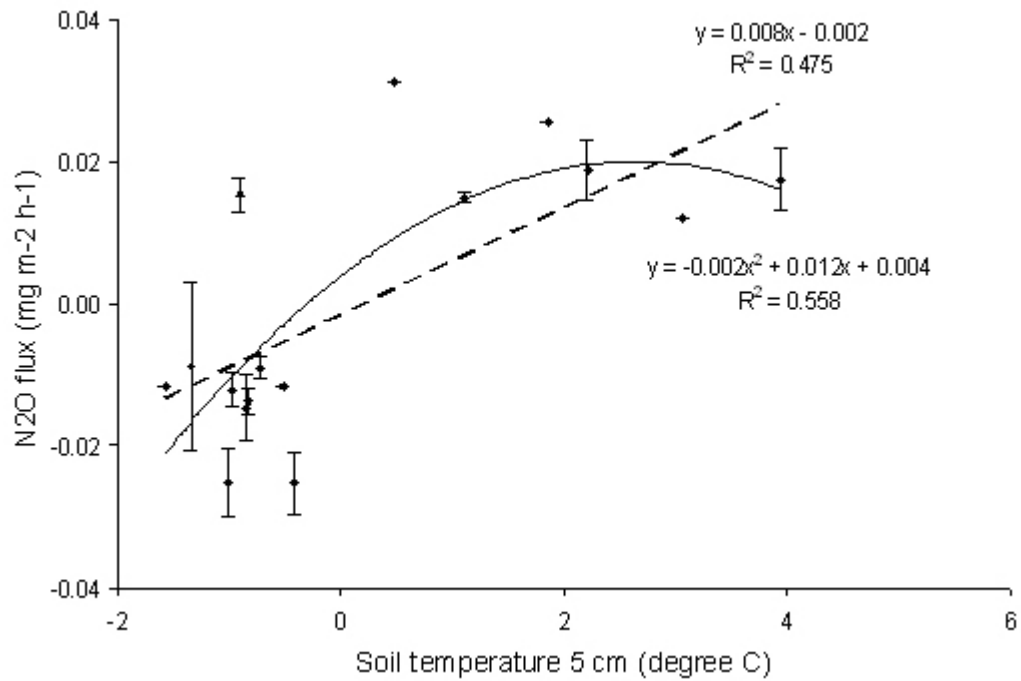


Figure 10. Average N₂O flux versus soil temperature at 5 cm for the 9th of February to the 27th of April. Error bars denote SEM.

DISCUSSION

CO₂ and CH₄ Fluxes

Both the CO₂ and CH₄ fluxes show significant emissions throughout the measurement campaign, an evidence for the hypothesis that microbial activity proceeds even though the topsoil is frozen. The mean CO₂ production on Fäjemyren ($68.6 \pm 9.9 \text{ mg m}^{-2} \text{ h}^{-1}$) is somewhat higher than the fluxes reported by Alm et al. (1999) in Finnish bogs. But since they measured winter fluxes, the mean flux when soil was frozen in this study ($48.2 \pm 8.4 \text{ mg m}^{-2} \text{ h}^{-1}$) is more appropriate to compare with, and is also in the similar range.

The mean CH₄ emission when soil was frozen ($0.61 \pm 0.06 \text{ mg m}^{-2} \text{ h}^{-1}$) in this report is also comparable with the CH₄ fluxes reported by Alm et al. The winter emissions from a temperate poor fen in New Hampshire are higher (Melloh & Crill 1996), which can be ascribed to higher pH and nutrient availability. The correlation between CO₂ production and CH₄ flux is high (*figure 7*). This can be expected since they are both decomposition pathways, regulated by similar parameters such as temperature and substrate availability and quality.

Temperature Sensitivity

The best model for predicting fluxes of CO₂ and CH₄ is air temperature. Soil temperature at 5 cm is also a strong predictor, but when the top soil was frozen, the variance in soil temperature could not explain the variance in the CO₂ and CH₄ fluxes. Soil temperature at 20 cm was not a significant variable in predicting CO₂ fluxes, but for the CH₄ fluxes, it was close to significance when soil was frozen. This can be explained by the fact that aerobic respiration occurs in the top layers to which oxygen can penetrate. Methanogenesis on the other hand, is more likely to occur in deeper layers, where redox potential is lower.

The temperature sensitivity of the Fäjemyren ecosystem is high at these cold temperatures, especially for the CO₂ production. The Q₁₀ for the CO₂ production reported in this study (16.9) is higher than those reported by Kirschbaum (1994). Clein & Schimel (1995) also found very high Q₁₀ for respiration in tundra soils, from 5.2 to 23.4 in the -2 to 5 °C range. The Q₁₀ for the CH₄ emissions on the other hand, is lower than what is generally found (Christensen et al. 1999). One explanation for this is that the water table quickly sunk when the soil thawed, because of low precipitation. This might have suppressed methanogenesis since high water table is an important regulator of CH₄ fluxes when soil is thawed (e.g. Bubier & Moore 1994, Joabsson et al. 1999), but enhanced CO₂ production since more oxygen became available in the soil. More oxygen in the soil will also increase the CH₄ oxidation.

Small changes in temperature can cause considerable effects on the greenhouse gas balance on northern peatlands. The predicted temperature increase of several degrees at the end of this century may actually double the winter-time CO₂ and CH₄ emissions on this mire, judging solely from the regression models with temperature. In the widely cited global soil carbon model by Post et al. (1982), it is apparent that soil carbon density decreases with increasing

temperature, for any particular level of precipitation. The effects of the climate change on mires will likely be more sophisticated though; the hydrology on the mire will be affected as a response to changed precipitation and evaporation patterns, as well as the nutrient availability and the competitive balance.

In recent studies, the need for distinguishing between different carbon pools in the soil is pointed out. The high temperature sensitivity in this study could primarily be caused by respiration from recently fixed carbon, i.e. plant respiration and decomposition of fresh litter derived from the last growing season. Grogan et al. (2001) found that respiration derived from recently fixed carbon in plants, fresh litter and rhizosphere exudates dominated the winter flux in sub-arctic heath tundra. Decomposition of bulk soil organic matter was low, and relatively insensitive to temperature. Melillo et al. (2002) documented changes in a decade-long soil warming experiment in a mid-latitude hardwood forest. Soil warming resulted in increased decomposition rates, but the response was transient because of the limited size of the labile soil carbon pool.

If the high temperature sensitivity for the CO₂ production in this study is mainly associated with respiration from recently fixed carbon, a feedback effect on global warming in winter is likely transient. In modeling purposes of the climate change, it is therefore of importance to make a distinction between different soil carbon pools. When studying the temperature sensitivity of an ecosystem, it is also important that other factors such as the water table level or the nutrient availability are held at constant.

Spatial Variation

No significant relationship between CO₂ and CH₄ fluxes and vegetation indices were found. Vascular plants, here represented by *Eriophorum vaginatum* is known to have a positive effect on CH₄ emissions during the growing season (e.g. Joabsson et al. 1999; Nykänen et al. 2002; Ström et al. 2003), but no clear relationship could be found in this study.

The conclusion one can draw from the lack of relationship between gas fluxes and vegetation indices is that vegetation composition is not an important factor regulating winter-time greenhouse gas exchange between soil and atmosphere on a small scale. This is not surprising since vegetation is dormant during winter. Other factors such as temperature, substrate availability and quality, microtopography or bacterial population density and diversity can be of larger importance. The lack of relationship is also an indication that plant respiration was less important than microbial respiration.

The effect of snow-cover on the greenhouse gas fluxes is hard to evaluate, since snow was prevalent at only two measurement occasions when additional environmental variables were measured. An insulating snow-pack acts to limit frost penetration (higher soil temperatures) and restrict gas exchange (Melloh & Crill 1996). Removing these events from the regression models did not exert any major changes, which indicates that even though collars were snow-covered, the fluxes did not deviate from overall pattern.

Freeze-thaw Cycles

No significant release of entrapped gases was measured during this campaign. An increased fraction of CH₄ fluxes that failed the $r^2 = 0.9$ criterion was observed though (*figure 6*), matching the moment in time when soil was thawing. Some physical release of entrapped CH₄ bubbles is possible, but the fluxes that were insignificant did not exceed earlier fluxes. At a couple of times, the insignificant fluxes did actually show an uptake of atmospheric CH₄. This rather abrupt change in physical character of the CH₄ fluxes can be attributed to changes caused by soil thaw. Increased oxygen diffusivity and higher temperatures in the top layers are important factors for methanotrophic activity (Dedysh 2002). Thawing in the top soil layers might have caused the methanotrophic community to increase CH₄ oxidation to a rate which occasionally exceeded methanogenesis. When the increased soil temperature reached the deeper layers where the methanogenesis takes place, net CH₄ exchange once again turned into emissions to the atmosphere. This suggestion is in agreement with a report by Clein & Schimel (1995), who found a shift from CH₄ oxidation to CH₄ production at sub-zero temperatures, explained by the ice layer inducing anaerobiosis.

The long frost period did probably result in a dieback in the microbial biomass. However, a boost in CO₂ and CH₄ emissions as a response to increased nutrient and substrate availability could not be confirmed. The greenhouse gas emissions do indisputably increase after the soil thaw, but the cause is more likely increased temperatures. Bubier et al. (2002) suggests that the extent of prior freezing is related to the rate of release after thaw. Colder and longer frost period may kill more of the microbial population, so that there are fewer survivors when soil thaws, which results in lower thaw emissions.

It cannot be excluded that there were some release of entrapped greenhouse gases. This can have occurred during nighttime or a day when no flux measurements were performed. Another explanation for the absence of physical release of greenhouse gases in response to soil thaw can be attributed to the method used when measuring fluxes. The collars reached 10 – 20 cm down into the soil, and did in most cases reach through the ice cover at the top of the soil. The thickness of the ice cover did not exceed 10 cm during this measurement campaign. A thin layer between the soil inside the collars and the collar walls was observed. This might have provided a big pathway for gases entrapped beneath the ice layer to escape to the atmosphere. The relative importance of this pathway compared to unfrozen layers surrounding plant stems or ice cracks is probably large. If this is the case, it is apparent that the measured trace gas fluxes are the direct result of psychrophilic (cold-adapted) microbial activity in and beneath the frozen soil.

N₂O Fluxes

The recorded N₂O uptake of the peat soil during winter ($-0.013 \pm 0.003 \text{ mg m}^{-2} \text{ h}^{-1}$) seems to be of biological origin. A physical uptake by collar water could not explain the measured uptake. One could argue that melting snow and ice could cause a detectable uptake in the collars. Melting snow was only prevalent at the

16th and 17th of March. Melting soil ice can have occurred in some additional occasions, but it is unreasonable to expect such a rapid ice-melt in an area of 0.36 m². Since aluminum chambers were used, soil temperature will not increase in the collars. Aluminum chambers are more likely to decrease soil temperature, since solar radiation is effectively reflected away.

One reasonable explanation for the N₂O uptake is that since Fäjemyren is severely nitrate limited, it gains nutrients only from precipitation and pH is very low (pH 3.3), N₂O can have served as the sole electron acceptor for psychrophilic denitrifiers in the frozen soil. However, many studies have found that low pH leads to an inhibition of N₂O reductase (Firestone & Davidson 1989; Christensen et al. 1990; Aerts 1997). On the other hand, there are studies stressing the importance of microbial adaptation to the local environment. Cavigelli & Robertson (2000) report different responses to environmental regulators (pH, oxygen availability) by native denitrifying communities from two geomorphologically similar soils. Parkin et al. (1985) found that an acid-tolerant denitrifying population had been selected in an agricultural soil that had a 20-year past history of low pH. Therefore, the possibility exists that an acidophilic denitrifying population adapted to the environment of Fäjemyren, is capable of reducing N₂O even at low pH. As noted earlier, N₂O can also be consumed by DNRA (dissimilatory nitrate reduction to ammonia) bacteria (Conrad 1996), and this explanation cannot be excluded.

Nitrous oxide uptake by soils has been found in other studies. Butterbach-Bahl et al. (1998) report a net uptake of 0.5 µg m⁻² h⁻¹ in an acidic spruce forest ecosystem (pH 2.7-3.2) in Ireland with low atmospheric N input (5-6 kg N ha⁻¹ yr⁻¹). A net uptake recorded over a 2-year period averaging 7.4 µg m⁻² h⁻¹ was also reported in a deciduous forest (pH 3.8) in Belgium (Goossens et al. 2001). The explanation for the uptake in these studies is that N₂O was the only electron acceptor left for denitrification. The mean N₂O uptake reported in this study (13 µg m⁻² h⁻¹) is somewhat higher, but the emissions are not included and it is not averaged over a whole year.

Fäjemyren turned from being a sink to a source of atmospheric N₂O when the soil thawed. It can be ascribed to the fact that additional nutrients captured in, or above, the ice became available. The ice and snow layers may have prevented nitrogen from dry and wet deposition to reach the anaerobic layers where denitrifiers are present. The long period with frozen soil (more than two months) did also probably cause a big dieback of microbial biomass. When the soil thawed, nutrients from dead microbes became available for surviving microbes to grow on. Now denitrifiers can have gained access to fresh nitrogen substrates and N₂O production became possible. Since vegetation growth was still limited, competition for nutrients was probably low. The process of N₂O reduction recorded during the frozen season might have continued, but in that case it was exceeded by the production of N₂O.

April was an unusually dry month with only 7 mm of precipitation. This resulted in water tables that were lower than normal. Water tables in the end of April ranged from 9 to 15 cm below ground in the collars. A drawdown of the water table increases oxygen diffusion into the ground and the potential for

nitrification (Martikainen et al. 1993), in which N_2O is a by-product. If nitrifying bacteria were present at the mire, they can to some extent have been responsible for the recorded N_2O emissions.

Further measurements of the N_2O fluxes at the mire are needed to assess whether the N_2O production is transient. If the emissions are due to increased nutrient availability caused by soil thaw, it is reasonable to believe that the mire will once again turn into a sink for atmospheric N_2O , when the extra nutrient pool is exhausted. Slight evidence for a transient effect can also be found in *figure 10*, where the N_2O flux tend to show an optimum curve with temperature (higher soil temperatures were found late in the measurement season).

The global N_2O sources and sinks are not fully understood, and global N_2O budgets are often unbalanced. As Butterbach-Bahl et al. (1998) point out; seasonal changes between periods of net emission and net uptake of N_2O between soil and atmosphere have not been considered in the estimation of the source strength of soils. This implies that the N_2O budget is even more out of balance. In more recent budgets (e.g. Mosier et al. 1998) focus has been on the source strength of agricultural soils, which are better understood than natural soils. Northern peatlands soils are currently not included in the budgets reviewed in IPCC (2001).

Northern peatlands may be of importance for N_2O budgets in the predicted global warming. It has been proposed that in a warmer and drier climate, water tables will be lowered which could increase nitrification activity in wetland soils. However, Martikainen et al. (1993) did not find any support for significant feedback effects of N_2O emissions as a result of lower water tables in Finnish peatlands.

In this study, freeze-thaw cycles seem to be an important regulator of the N_2O exchange between peatlands and atmosphere. Freeze-thaw cycles have in several cases proved to be of major importance in annual N_2O budgets (e.g. Papen & Butterbach-Bahl 1999). The effect of global warming on freeze-thaw cycles can cause both positive and negative feedback effects. In more southerly regions normal winter freezing might not occur in the future, while in other regions long winter frost periods could be replaced by several freeze-thaw events (Smith 1997).

This study does not propose any major guidelines of how northern peatlands are to be included in N_2O budgets, since both emissions and uptakes were recorded. But it stresses the need for continuous N_2O measurements in different wetland sub-types. Northern peatlands can have the potential to exert a significant effect on global N_2O budgets, and in a future climate change this effect might be strengthened.

Conclusions

This report concludes that significant greenhouse gas exchange in a natural, nutrient-poor peatland (ombrotrophic bog) occurs throughout the winter season. The importance of the winter fluxes in the context of annual budgets, require flux measurements during a whole year. Freeze-thaw cycles and temperature are

strong factors regulating the winter dynamics at the mire; and the predicted climate change is likely to cause severe disturbances to the ecosystem.

The global sources and sinks of atmospheric N₂O are not quantified in a satisfactory manner. Northern peatland soils are currently not included in global budgets, but this study demonstrates that these soils can act both as sources and sinks for N₂O. More research is obviously needed to evaluate the total effect of the N₂O exchange between peatland soils and the atmosphere.

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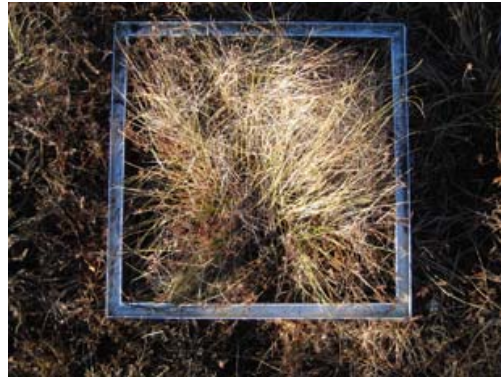
APPENDIX

Collar Photographs

Photographs taken the 31st of March. No major changes in biomass were observed during the measurement campaign. Collar nr 1, 2, 3, 9, 11 and 12 were most frequently used, while collar nr 5, 6 and 7 were used at only two measurement occasions. Vegetation species that are visible in these photographs are mainly *Eriophorum vaginatum* and *Sphagnum spp.*



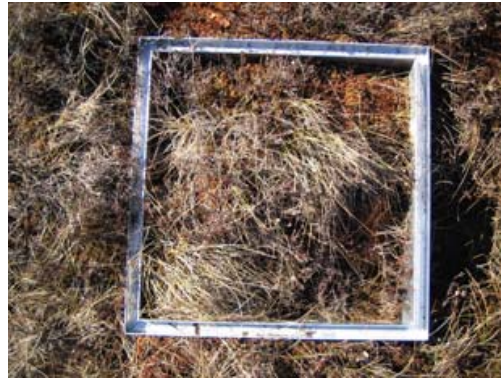
Photograph 1. Collar nr 1



Photograph 2. Collar nr 2



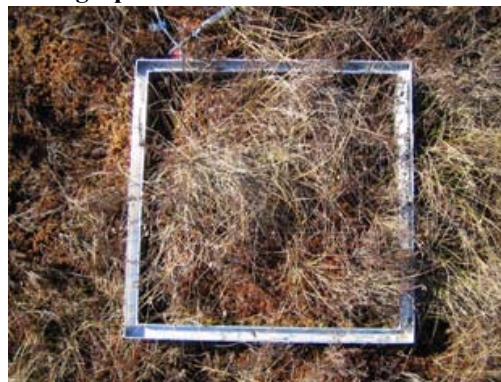
Photograph 3. Collar nr 3



Photograph 4. Collar nr 5



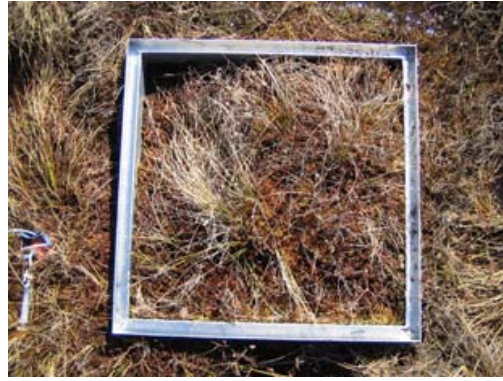
Photograph 5 Collar nr 6



Photograph 6. Collar nr 7



Photograph 7. Collar nr 9



Photograph 8. Collar nr 11



Photograph 9. Collar nr 12

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