Land-Atmosphere Exchange of CO_2, Water and Energy at a Boreal Minerotrophic Mire

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Abstract

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Boreal and sub-arctic peatlands cover a small part of the global land area (only ca 3%) but have stored considerable amounts of carbon during Holocene. The carbon stored is equivalent to ~ 20-30% of the global soil carbon pool and ~ 40-60% of the carbon currently held in the atmosphere as CO_2. Due to the enormous amounts of carbon available in the peat, great interest has been paid to whether the carbon will remain in the peatlands, or migrate to the atmosphere. The current fluxes of carbon between these ecosystems and the atmosphere are therefore considered to be important in global carbon budgets, and may be even more important in the future, if the exchange rates change in response to anticipated climatic changes.

Five years of continuous Eddy Covariance measurements on an acid, oligotrophic, minerogenic, mixed mire, Degerö Stormyr, has shown that the mire ecosystem was a stable sink for CO_2, with an uptake of 54 ± 6 $gCO_2\text{-}Cm^{-2}y^{-1}$ (±SD). Also when considering carbon effluxes such as by CH_4-C or carbon in the runoff water, the mire still remains as a stable sink of 27 ± 6 $gCm^{-2}yr^{-1}$ (±SD).

A positive water balance is a prerequisite for the development and maintenance of peatland ecosystems. The water balance is, in turn, intimately connected to the energy balance at any site since the partitioning into evapotranspiration of water directly affects the water balance. The water balance is delicately controlled by the relationship between precipitation and recharge, evapotranspiration and discharge. A high water table is required to maintain the moist environment essential for mire plant species. Both the annual water balance and the within-year variability in water balance affect the development and maintenance of mires.

By combining traditional measurements of precipitation and runoff with Eddy Covariance measurements of evapotranspiration, we could achieve an estimate of the total water balance and further analyze seasonal variations in the respective water pathways. The mire did not show any sign of water limitation within a wide range of water levels measured during the five years of the study.

Mire systems are often considered to be "wet" and are sometimes compared to lakes. Data from Degerö Stormyr shows that the opposite is more common, that the mire is house-holding with its water and that a mire surface with low water content has relatively lower evapotranspiration than many other ecosystems such as e.g. a forest ecosystem.

Therefore we conclude that regarding the water availability at Degerö Stormyr, it is at a stable equilibrium and extreme changes are needed to alter the present water regime and in turn, alter the carbon balance into a source.

Key words: CO_2, Methane, Carbon, Water, Energy, Budgets
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Contents

Appendix

Paper I-IV

This doctoral thesis is based upon the following papers, hereafter referred to by their respective Roman numerals:

I Sagerfors, J., A. Lindroth, A. Grelle, L. Klemedtsson, P. Weslien and M. Nilsson. 2006. Annual CO_2 exchange between a nutrient poor, minerotrophic, boreal mire and the atmosphere. Submitted manuscript.

II Sagerfors, J., A. Lindroth, I. Buffam, A. Grelle, L. Klemedtsson, H. Laudon and M. Nilsson. 2006. Water budget and energy partitioning of a boreal, minerogenic mire. Submitted manuscript.

III Sagerfors, J., A. Lindroth, A. Grelle, L. Klemedtsson and M. Nilsson. 2006. CO_2 dynamics at a boreal oligotrophic fen during spring and autumn. Manuscript.

IV Nilsson M., J. Sagerfors, I. Buffam, T. Eriksson, A. Grelle, L. Klemedtsson, P. Weslien, H. Laudon and A. Lindroth. 2006. Two years of complete carbon budgets for a boreal oligotrophic minerogenic mire. Submitted manuscript.

Abbreviations

R_n = Net radiation [Wm^{-2}]
R_g = Global radiation [Wm^{-2}]
H = sensible heat flux [Wm^{-2}]
LE = Latent heat flux [Wm^{-2}]
A = available energy [Wm^{-2}]
δe = saturation vapor pressure deficit at air temperature [Pa]
VPD = δe
Δ = slope of vapor pressure saturation versus temperature curve [PaK^{-1}]
γ = psychrometric ''constant'' = 66 [PaK^{-1}]
ρ = air density [gm^{-3}]
k = von Karman's constant 0.41 [-]
Re_0 = the roughness Reynolds number [-]
λE_{eq} = Priestly-Taylor equilibrium evapotranspiration [mmd^{-1}]
λE = observed evapotranspiration [mmd^{-1}]
AET = observed evapotranspiration [mmd^{-1}]
ν = air viscosity [m^2s^{-1}]
c_p = specific heat capacity of air at constant pressure [Jg^{-1}]
β = Bowen ratio (H/LE) [-]
α = Priestly – Taylor coefficient [-]
z0 = roughness length for momentum [m]
$z0_t$ = roughness length for temperature [m]
r_a = aerodynamic resistance [sm^{-1}]
r_s = surface resistance [sm^{-1}]
G_s = surface conductance [mms^{-1}]
G_c = canopy conductance [mms^{-1}]
L_v =specific heat of vaporization [J g^{-1}]
u(z)= Wind speed [ms^{-1}]
u_* = Friction velocity [sm^{-1}]

INTRODUCTION

Mires and their global importance

Boreal and sub-arctic peatlands cover a small proportion of the global land area (only ca. 3%) but store a considerable amount of carbon: 450, 390, 270-390 or 230–250 Gt according to estimates by Gorham (1991), Immirzi et al. (1992), Turunen et al. (2002) and Lappalainen (1996), respectively. These amounts are equivalent to ~ 20-30% of the global soil carbon pool (Schlesinger, 1997) (Figure 1) and ~ 40-60% of the roughly 730 Gt of carbon currently held in the atmosphere as CO_2 (IPCC, 2001). Due to the enormous amounts of carbon available in the peat, great interest has been paid to whether the carbon will remain in the peatlands, or migrate to the atmosphere. The current fluxes of carbon between these ecosystems and the atmosphere are therefore considered to be important in global carbon budgets, and may be even more important in the future, if the exchange rates change in response to anticipated climatic changes.

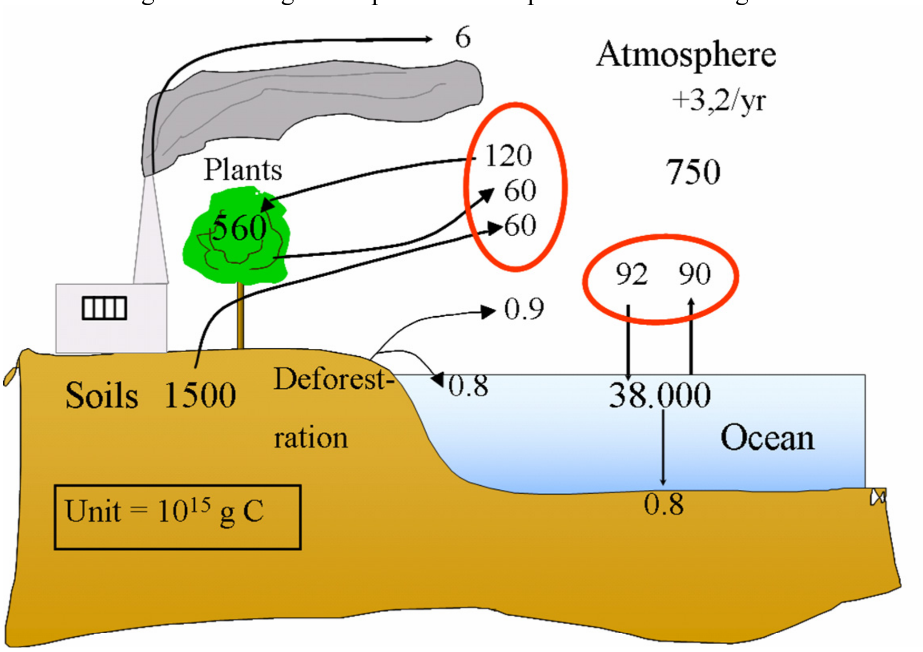


Figure 1 Global pools and fluxes of carbon and the rate of increase in the atmosphere (redrawn from (Schlesinger, 1997)).

The net exchange of carbon between a mire ecosystem and the atmosphere is determined by the balance between CO_2-fixation (photosynthesis) and the sum of autotrophic respiration (plant respiration) and heterotrophic respiration (degradation of plant material), both of which result in CO_2 emissions (Figure 2). This balance is hereafter referred to as Net Ecosystem Exchange (NEE). Since respiration is considered an efflux from the ecosystem and is assigned a positive sign, a negative value thus represents carbon uptake. Carbon may also be lost from the system as CO_2, CH_4 or organic C. Both CO_2 and CH_4 can be released directly to the atmosphere, or transported in the sub-surface water and released to the atmosphere as the water leaves the mire in open streams. The organic carbon leaves the mire as either particulate or dissolved organic carbon (POC or DOC) in the run-off water.

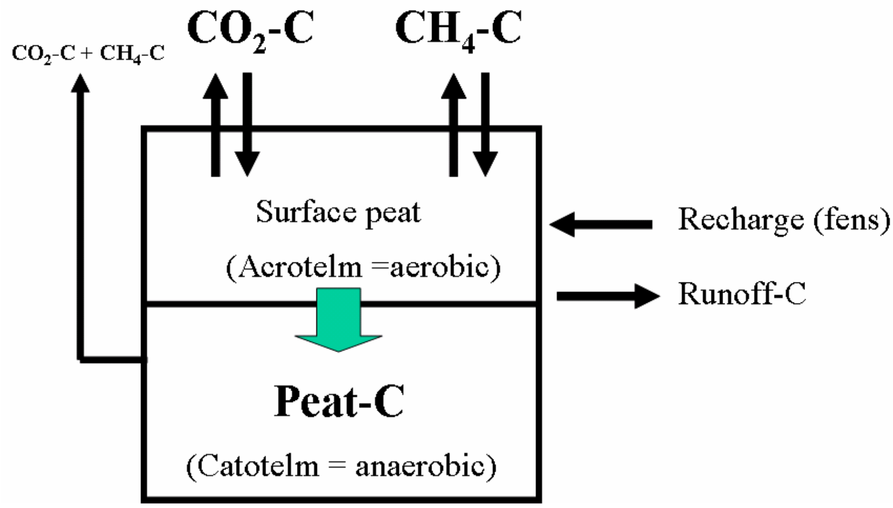


Figure 2 Major carbon pathways in a peatland. The net ecosystem exchange of carbon (NEE) between a mire ecosystem and the atmosphere is determined by the balance between CO_2-fixation (photosynthesis) and the sum of autotrophic respiration (plant respiration) and heterotrophic respiration (degradation of plant material), both of which result in CO_2 emissions.

The factors affecting both photosynthesis and degradation in the acrotelm (aerobic or temporally aerobic upper peat layer) are highly dynamic and reflect to a large extent variations in the local climate. The processes in the catotelm (permanently anaerobic lower peat layer) are much more stable, with fluxes of a lower magnitude than in the acrotelm. Both variations in incoming energy from the sun (due for instance to variations in cloud cover) and variations in water availability (due to variations in precipitation and evapotranspiration) could be assumed to be closely linked to carbon accumulation. The carbon, water and energy dynamics within and between different parts of an ecosystem, such as the fen system at Degerö Stormyr investigated in the studies underlying this thesis are, of course, inter-related in ways, and are likely to show highly specific responses to climatic variables, although different ecosystems are also likely to have a number of common features. The relationships amongst these variables are very interesting since they provide valuable information regarding the effects of climate, and possible climatic changes on the ecosystem(s) and the mechanisms involved.

Objectives

To determine the present status of the carbon, water and energy dynamics in the boreal oligotrophic fen Degerö Stormyr, to assess whether the dynamics have changed in the recent past and to predict possible changes in the future, the following features were studied

- Annual carbon exchange
- Carbon, water and energy dynamics
- Spring and autumn carbon dynamics
- Total carbon budget

The questions ultimately addressed were the following: Is Degerö Stormyr currently a sink or a source for atmospheric carbon? Is its current status stable or will it change in the future?

BACKGROUND

Carbon exchange

The rates of carbon exchange between a mire and the atmosphere are generally estimated by one of two approaches: by measuring the "apparent" rate of peat carbon accumulation from peat cores or by estimating the "true" i.e. current exchange from direct measurements of CO_2 and CH_4 fluxes at the mire surface and the losses of carbon through water exports from the mire [Paper IV]. The "peat core" approach yields estimates of apparent carbon accumulation. The estimates from peat cores are usually based on a basal ^{14}C dating, which together with the total mass over a defined area gives the average carbon accumulation rate for the entire period of mire development. To obtain an estimate of the true carbon accumulation, including the contributions of continuous CO_2 and CH_4 fluxes, this approach needs to be combined with modeling (cf. Clymo (1998)).

Long-term estimates

Estimates of long-term average rates may not provide valid estimates of current boreal mire C-exchange, especially if the rates of peat accumulation have changed during the Holocene. The global average Long term Apparent Rate of Carbon Accumulation (LARCA) has been estimated to be 29 $gCm^{-2}yr^{-1}$ (Gorham, 1991). Data derived from 1125 peat cores suggest that the average LARCA in Finnish mires during the period covered was 23 ± 12 $gCm^{-2}yr^{-1}$ (throughout the text, cited values are means ± standard deviations unless otherwise stated), ranging from 2 to 103 $gCm^{-2}yr^{-1}$ with an average in bogs of 24 $gCm^{-2}yr^{-1}$ compared to 15 $gCm^{-2}yr^{-1}$ in fens (Tolonen & Turunen, 1996).

Apparent rates of carbon accumulation seem to have fallen in recent times (the last thousand years) to 50-60% of LARCA, according to estimates based on peat cores from ecosystems in western Siberia (Turunen *et al.*, 2001), Canadian low arctic and high sub-arctic regions (Vardy *et al.*, 2000), *Sphagnum fuscum* Schimp. Klinggr. peat in western boreal Canada (Kuhry & Vitt, 1996) and "mature peat plateau phases" in the east-European Russian Arctic (Oksanen, Kuhry & Alekseeva, 2001). Thus, based on rates of apparent peat accumulation during the most recent part of the Holocene, the potential for C-accumulation in boreal mires may have decreased (Gorham, 1991; Kuhry & Vitt, 1996; Turunen*, et al.*, 2001).

Direct measurements

The direct measurements are either measurements obtained from chambers taking "snapshots" of the prevailing fluxes, or micrometeorological techniques such as "gradient flux" or "eddy covariance" which are continuous measurement techniques. Very few estimates of annual CO_2 exchange have been derived from full-year micro-meteorological measurements and even fewer from multiyear measurements. Micro-meteorological-based estimates of annual exchange are available from: an ombrotrophic mire in southeastern Canada, Mer Bleue (45°40'N, 75°50'W) (Lafleur, Roulet & Admiral, 2001; Lafleur *et al.*, 2003); a wet minerotrophic mire in northern Finland, Kaamanen (69°08'N, 27°17'E) (Aurela, Laurila & Tuovinen, 2001; Aurela, Laurila & Tuovinen, 2002; Aurela, Laurila & Tuovinen, 2004; Aurela, Tuovinen & Laurila, 1998); an ombrotrophic bog in Siberia (60°45'N, 89°23'E) (Arneth *et al.*, 2002; Schulze *et al.*, 2002); an Irish blanket bog (51°55'N, 9°55'W) (Sottocornola & Kiely, 2005); and a lowland temperate peatland (55°48.8'N, 3°14.40'W) in central Scotland (Billett *et al.*, 2004).

Direct flux measurements have suggested that boreal mires may currently act as either sinks (Alm *et al.*, 1999b; Aurela, Laurila & Tuovinen, 2002; Lafleur, Griffis & Rouse, 2001; Oechel *et al.*, 1995; Shurpali *et al.*, 1995; Whiting, 1994) or sources of atmospheric CO_2 (Alm*, et al.*, 1999b; Aurela, Laurila & Tuovinen, 2002; Carroll & Crill, 1997; Lafleur, Griffis & Rouse, 2001; Oechel*, et al.*, 1995; Shurpali*, et al.*, 1995; Whiting, 1994; Wickland *et al.*, 2001).

The estimates for the Canadian ombrotrophic mire represent net uptake rates over a 5-year period (1998-2002) varying between 9 $gCO_2\text{-}Cm^{-2}yr^{-1}$ (not significantly different from zero) to a significant uptake of 75 $gCO_2\text{-}Cm^{-2}yr^{-1}$ (Lafleur*, et al.*, 2003). The estimates for the wet minerotrophic mire in northern sub-arctic Finland yield average uptake rates over six years (1997-2002) of 22 $gCO_2\text{-}Cm^{-2}yr^{-1}$, with net ecosystem exchange (NEE) rates ranging between -4 and -53 $gCO_2\text{-}Cm^{-2}\ yr^{-1}$ (Aurela, Laurila & Tuovinen, 2004). Data on NEE from the ombrotrophic bog in Siberia for 1998-2000, which do not include the winter period and therefore yield overestimates, vary from -43 to -62 $gCO_2\text{-}Cm^{-2}yr^{-1}$ (Arneth*, et al.*, 2002; Schulze*, et al.*, 2002). The annual NEE values at the Irish blanket bog were -49 and -61 $gCO_2\text{-}Cm^{-2}yr^{-1}$ for the years 2003 and 2004 (Sottocornola & Kiely, 2005) and average uptake over a 2-year period (1996-1998) was found to be 28 (± 2.5) $gCO_2\text{-}Cm^{-2}yr^{-1}$ at the lowland temperate peatland in central Scotland (Billett*, et al.*, 2004).

Total carbon estimates

To obtain a complete mire carbon budget, i.e. "true" exchange rates, as defined above, the exchange of CO_2-C between the mire and the atmosphere has to be complemented with data on emissions of methane and discharges of carbon, resulting in current True Rates of Carbon Accumulation (TRACA). The average annual CH_4 emissions from boreal minerotrophic mires in Sweden amount to roughly 10 to 20 $gCH_4\text{-}Cm^{-2}yr^{-1}$ (Nilsson *et al.*, 2001) [Paper IV], and in Finland 10 to 30 $gCH_4\text{-}Cm^{-2}yr^{-1}$ (Huttunen *et al.*, 2003) while the average carbon losses through runoff (TOC) from catchments in Finland with high percentages of peatland (>35%) are about 4 to 9 $gCm^{-2}yr^{-1}$ (Kortelainen, Saukkonen & Mattsson, 1997). This means that a net CO_2-C uptake of < 20 $gCO_2\text{-}Cm^{-2}yr^{-1}$ in this region, e.g. the Kaamanen mire, is probably counteracted by losses through methane emissions and runoff, implying that the mires here are currently in balance. The ombrotrophic mire, Mer Bleue, in Canada generates hardly any methane emissions so the only additional carbon losses are C-exports through runoff and it varies between being a net C-sink and being in balance. Thus, despite their scarcity, the very limited full-year micro-meteorological measurements of CO_2 exchange currently available indicate that there are major variations both between mire types and between years.

LARCA vs. TRACA

In comparisons to LARCA values these results have led to conclusions by some authors that boreal and sub-arctic mires may be currently changing from sinks to sources of atmospheric carbon (Oechel*, et al.*, 1995). Similar conclusions, suggesting that peatlands that are currently in equilibrium may change to being either sources or sinks of carbon following expected climatic changes, have also been drawn from simulations (Hilbert, Roulet & Moore, 2000). Using global or close to global data sets, TRACA values have been estimated to be 23 $gCm^{-2}yr^{-1}$, equivalent to 79% of LARCA (29 $gCm^{-2}yr^{-1}$) by Gorham (1991) and 21 $gCm^{-2}yr^{-1}$ by Clymo et al. (1998) based on parameters estimated from the 1125 peat cores from Finland (Tolonen & Turunen, 1996).

Carbon and water

Although climate change and carbon are often discussed together, climatic changes will not directly affect carbon exchange; instead they may have causal effects on water and energy dynamics which in turn may affect the carbon balance. Of course, feedback mechanisms are involved that have counter-acting influences, but this implies that knowledge about water and energy dynamics are important and can help elucidate carbon dynamics (Figure 3).

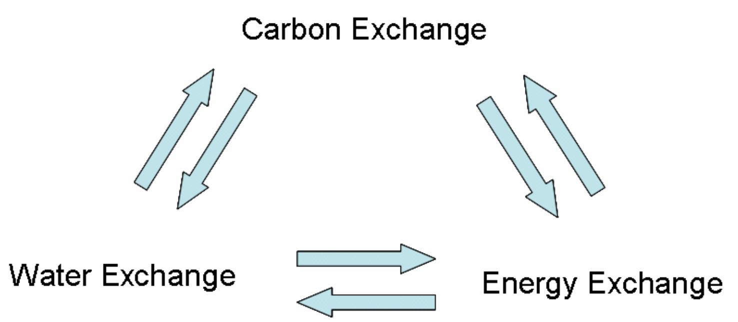


Figure 3 The carbon, water and energy exchanges are all inter-connected.

A positive water balance is a prerequisite for the development and maintenance of peatland ecosystems. The water balance is, in turn, intimately connected to the energy balance at any site (Ivanov, 1981). The water balance is inter-actively controlled by the relationships between precipitation and recharge, and between evapotranspiration and discharge. A high water table is required to maintain the moist environment essential for mire plant species. Both mire type (Belyea & Baird, 2006; Glaser *et al.*, 1997; Hilbert, Roulet & Moore, 2000; Holden, 2005; Siegel *et al.*, 1995; Yu, 2006) and the microtopography of the mire surface (Belyea & Clymo, 2001; Couwenberg, 2005; Nungesser, 2003; Rietkerk *et al.*, 2004) are largely controlled by the water balance characteristics. Both the annual water balance and the within-year variability of the water balance affect the development and maintenance of mires. *Sphagnum* mosses constitute the single most important peat-forming plant genus and differ from vascular plants in the way that they obtain water. Their lack of roots means that mosses must rely on atmospheric humidity and capillary transport from underlying layers for their water, making them sensitive to both the water table depth and the rate of evapotranspiration at the surface (Hayward & Clymo, 1982; Nordbakken, 1996; Rydin & McDonald, 1985b).

The specific water balance required to maintain a particular mire plant community could be expected to be most sensitive to changes in precipitation, recharge, evapotranspiration and discharge. Fens, which are connected to the regional groundwater, could be assumed to be more stable than bogs, which rely solely on precipitation as a source of water.

Energy and water

The radiation balance and partitioning of energy between latent and sensible heat fluxes are major determinants of regional climate and hydrology, and are, by and large, controlled by the physical structure and plant species composition of the ecosystem. Since mires represent 10-20% of the boreal landscape in Canada, Russia and Scandinavia (Paavalainen & Päivinen, 1995) and are one of the major constituents of the boreal biome, they make a notable contribution to the land surface control of the regional climate. The net radiation (R_n) absorbed by the surface is partitioned into a number of components: evaporation of water, expressed as latent heat flux (LE); warming or cooling of the air through sensible heat flux (H); and heating or cooling of the soil, manifested by the soil heat flux (G). Understanding the controls of these fluxes is essential for accurate climate modeling, and different mechanisms are likely to be involved in different mire systems, depending on the interactions between water, nutrient availability and vegetation composition in them.

Evapotranspiration (ET) is always a substantial component of the water balance in fens and bogs [Price and Maloney, 1994; Fraser et al., 2001]. Evapotranspiration plays a major role in regulating the wetness and temperature of the surface and depth to the water table, all of which are important environmental parameters affecting mire vegetation and its ability to sequester carbon (Lafleur *et al.*, 1997; Lafleur, *et al.*, 2003; Shurpali, *et al.*, 1995).

Depth to the water level

The depth from the mire surface to the water level is probably one of the key control parameters of mire ecosystems, and it varies considerably between microtopographical units within individual mires as well as between mires. The water relations of mosses and vascular plants are entirely different and, therefore, they respond differently to the water table depth. The depth to the water table also strongly affects heterotrophic aerobic respiration. It is, therefore, essential to understand the effects of variations in water and energy exchange on the water table depth.

METHODS

Measurements [Papers I, II, III, IV]

The main instrument site was a 4 m high tower located 200 m from the south-east edge of the central part of the mire Degerö Stormyr and accessed by a boardwalk. All data were collected and stored on a computer located in a hut 150 m south of the tower. The hut is on a small mire island with a sparse pine stand. Electrical power (240V AC) was available at the site. The source area of the eddy covariance measurements was an oligotrophic fen dominated by the lawn and carpet plant communities with a growing season average water table level in the carpets of 5 - 10 cm below the mire surface and 15 - 20 cm below the surface in the lawns.

The measurements used in this study were made in the center of the Degerö Stormyr during 2001-2005. The eddy covariance technique was used to measure the fluxes of heat and water vapor (Nilsson *et al.*, 2006; Sagerfors *et al.*, 2006a; 2006b). Air and soil temperatures, air humidity, radiation sensors and depth to the water level were continuously monitored. During winter the snow depth was monitored continuously. The sensors were either mounted on the same tower as the eddy covariance system or by sensors in representative plant community areas within a hundred meters from the tower.

Photosynthetic active radiation, PAR, was measured by a PAR Quantum sensor (SKP 215, Skye Instruments Ltd, Powys, UK), Global radiation by a Li 200sz sensor (LI COR, Lincoln, Nebraska, USA) and net radiation by an NR-Lite sensor (Kipp&Zonen, Delft, the Netherlands) all mounted at the top of the tower, i.e. at 4 m height. Air temperature and humidity were measured by a MP100 temperature and moisture sensor (Rotronic AG, Bassersdorf, Switzerland) inside a self-ventilated radiation shield mounted 1.8 m above the mire surface. The snow depth was measured by an SR-50 ultrasonic sensor (Campbell Scientific, Logan, Utah, USA) placed approximately 6 m from the flux tower. Water table depths and soil temperatures were monitored in a lawn plant community 100 m northeast of the flux tower. The peat and water table surfaces were measured using a float and counterweight system attached to a potentiometer (Roulet, Hardill & Comer, 1991). Soil temperatures were monitored by TO3R thermistors mounted in sealed, water-proof, stainless steel tubes (TOJO Skogsteknik, Djäkneboda, Sweden). Precipitation was measured using a tipping-bucket (ARG 100, Campbell Scientific, Logan, Utah, USA) 4 m from the tower. Data from these sensors were scanned at 30-second intervals and stored as either 30- or 60-minute mean values by data loggers (CR10X, Campbell Scientific, Logan, Utah, USA) and downloaded daily to the main computer in the hut.

Wind speed and direction were measured by a Solent 1012R2 three-dimensional sonic anemometer (Gill Instruments, England). The ecosystem roughness length, $z0_{,}$ was calculated by solving the expression:

$$\left(\frac{\overline{u}}{u_*}\right)=\frac{1}{k}\cdot\ln\left(\frac{z}{z0}\right) \tag{1}$$

for z0, where u_* and u (friction velocity and wind velocity) values were obtained from the EC-system. The above equation is true for neutral and stable stratification within the boundary layer (Salby 1996) and was solved for such conditions. The z0 value obtained was used to calculate 'footprints', i.e. the spatial distributions of the CO_2 exchange measured and the flux footprints were calculated using the footprint model FSAM by Schmid (1994). First, we verified the applicability of the parameterized version (Mini-FSAM) by comparison with FSAM-runs on a subset of data. Then, the Mini-FSAM equations were used to calculate the dimension of the elliptical flux source area for each half hour, separately for day and night, summer and winter. For each such scenario, corresponding polygon surfaces were then successively accumulated in an array in polar coordinates representing the surface around the flux tower. The resulting frequency distributions were then plotted as three dimensional colour maps and as line plots averaged over all wind directions. For winter estimates, the actual measuring height above the snow surface, updated in 30-minute-steps, was used in the model.

Eddy Covariance [Papers I, II, III, IV]

Using Eddy Covariance (EC) systems measurements of relevant fluxes can be taken continuously, day and night, year-round, even under difficult weather conditions when it would not be feasible to take manual measurements. Furthermore, such systems can provide high resolution data and avoid temporal up-scaling problems that can arise when alternative approaches such as chamber measurements or various diffusion techniques are applied. In the studies underlying this thesis an EC system was used to measure the fluxes of heat, carbon and water vapor in the mire. The methodology is based on high speed measurements (>10Hz) of the vertical movements of parcels of air combined with simultaneous measurements of other variables (e.g. temperature, or concentrations of water, CO_2, CH_4 and/or N_2O) within them. By analyzing the covariance between the vertical air movement and the other measured variables, the flux of each variable can be calculated and estimates of energy or mass transport can be obtained.

The area that can be monitored is limited by the height of the sensors, and in ideal conditions is a circle, centered on the sensors with a radius equal to 100 times the height of the sensors projected down on the measured surface (Figure 4). Within that area, the actually monitored area is determined by the wind (direction and speed) and the vegetation's "roughness" (i.e. potential to interact with the wind and thus create turbulence within the surface boundary layer). The technique used to estimate where exactly the measured fluxes originate from is denoted footprint analysis, and the area obtained is denoted the footprint area.

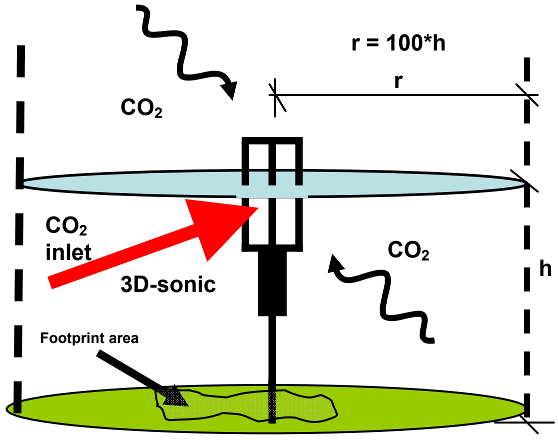


Figure 4 Schematic diagram of an Eddy Covariance system and its monitoring area.

The system consisted of a three-dimensional sonic anemometer (see 3D-sonic, figure 4) (model 1012R2 Solent, Gill Instruments, UK) and a closed-path infrared gas analyzer (IRGA model 6262, LI COR, Lincoln, Nebraska USA). The sonic anemometer was mounted on the tower at a height of 1.8 m above the mire on a 1.0 m long boom with a northerly orientation. The sonic anemometer was heated during the winter months. The signals from the sonic anemometer were connected to a computer where the fluxes were calculated in real-time, by EcoFlux software (In Situ Flux AB, Ockelbo, Sweden) and stored as 30-min averages. Fluxes directed towards the surface were recorded as negative values while upward fluxes were positive. The IRGA was mounted in an instrument box approximately 3 m south of the air intake. The air intake was less than 5 cm from the measuring volume of the sonic anemometer. The air pump was placed behind the IRGA and sucked the air through the analyzer, which was connected to the intake through a 5 m long tubing with a 4 mm inner diameter. A particle filter (Acro®50 1 µm PTFE, Pall Gelman Laboratory, Ann Arbor, Michigan, USA) was positioned between the intake and the IRGA. The H_2O concentration was calibrated retrospectively against the water vapor concentration obtained from a ventilated Rotronic sensor, (MP100, Rotronic AG, Bassersdorf, Switzerland). A typical calibration interval for H_2O was 3-4 weeks. The fluxes were calculated according to the EUROFLUX methodology (Aubinet et al., 2001). The whole Eddy Covariance system was supplied by In Situ Flux Systems AB, Ockelbo, Sweden, and delivered complete with integrated hardware and software, air conditioned system box with built-in lightning protection and power supply. The gas analyzer water vapor concentration measurements were verified against measurements of ambient water vapor measured by the Rotronic sensor. The Rotronic was in turn calibrated regularly using an aspirated psychrometer (Assman, type 761, Wilhelm Lambrecht Gmbh, Göttingen, Germany). When the water vapor measurements from the gas analyzer deviated from the Rotronic measurements, the gas analyzer values were post-processed and the fluxes corrected accordingly.

Data quality and gap filling [Papers I, II, III, IV]

The CO_2 data and sensible heat flux data were visually scrutinized to detect (and remove) obvious outliers in the CO_2 fluxes, arising for instance from failure of the measurement system or spikes without any counteracting spikes. Values of $u_*>1$ from the sonic anemometer were also discarded. The meteorological dataset was also scanned for anomalies and such values were removed.

The possibility that the fugacity of the CO_2 flux may have been affected by low u_* was also investigated. To detect any possible systematic errors in the measurements we determined the energy balance closure. Since soil heat fluxes were not measured, the energy balance was calculated on a daily basis to minimize the influence of these fluxes.

In order to integrate the annual NEE budget, missing data had to be replaced in some way. Several approaches have been used for this, but there is no generally accepted standard method (Falge *et al.*, 2001). Here we used the Mean Diurnal Variation, MDV, method (Greco & Baldocchi, 1996; Jarvis *et al.*, 1997) for gap filling, which has been previously used in attempts to estimate seasonal and annual sums in forest systems. In this method, ensemble averages are obtained from diurnal patterns of half-hourly data from days preceding and following the days with missing values. We applied this MDV approach in a "gliding" manner like a moving average. In order to replace incorrect or missing data the following protocol was used. The first choice was to use the MDV with a 15-day window spanning the period from seven days prior to the gap to seven days after it, for example, if the 10.00-10.30 measurement for day x was missing it was replaced by the average of the 10.00-10.30 values for the seven days preceding and the seven days following it.

The precision and accuracy of this ensemble average method was evaluated as follows. During periods with at least 14 consecutive days for which complete half-hourly data were available, artificial 1-, 2-, 3-, 4- and 5-day gaps were created, either sequential or separated by days for which measured data were retained. The single-day gap was repeated for all 14 of the days, while the other gaps were each repeated five times within the 14-day period. We defined a lower limit such that at least nine of the 14 values in the ensemble average had to be available in order to be used for filling a gap. If the half-hourly gaps were filled to such an extent that data (measured or filled) for more than 40 of the 48 half-hours were available for a day, it was defined as a "good day", and a sum was calculated by multiplying the average of the half-hourly (measured and filled) data by 48. If less than 40 half-hourly data were available, the second choice method was applied, in which standard moving averages were calculated from the daily sums, and 7+7-day windows were applied as in the 1st choice method. To avoid misinterpretations in the figures and the datasets, when the 2nd alternative was used an average was calculated for the entire period with missing data and the gaps were filled with that value to show that the whole day was filled. The same procedure was used regardless of the season or year.

Uncertainty in Eddy Covariance measurements [Papers I, IV]

A random error of 20% (SD) was applied on 30 min fluxes (Humphreys *et al.*, 2006; Morgenstern *et al.*, 2004), both on measured and gap filled 30 min values and the same approach was also used on the gap filled data with daily means. The total annual error (SD) was then calculated as the square root of the sum of the respective variances.

Runoff and C-export by Runoff [Papers II, IV]

Subcatchment boundary delineation for the catchment of Vargstugbäcken 3.1 km^2 (50% of the total mire catchment (6.5 km^2) was based on a 50-m grid digital elevation model (DEM) using IDRISI 14 software (Clark Labs, Worcester, MA, USA). Hourly stream discharge was calculated using measurements of stream height from water height loggers (wt-hr logger, Trutrack Inc., New Zealand) at a V-notch weir and an established height-discharge rating curve. Height measurements were not available from the stream site 45% of the time, primarily during winter when stream flow was very low, and ice and freezing temperatures made height measurements unreliable. During these periods, stream flow was predicted for the site using a calibrated ratio of flow between this site and a nearby stream (Kallkällsbäcken draining a 50 ha catchment) at which flow is measured at a V-notch weir in a heated dam house.

Uncertainty in stream water and C- export [Papers II, IV]

The precision of DOC, CO_2 and CH_4 stream water analyses were estimated to average 2%, 5% and 5%, respectively, based on replicate sample analyses. As a conservative measure 5%, 8% and 10% standard errors were used for the uncertainty in the export analyses. The higher uncertainty for CH_4 was based on its faster degassing rate and hence larger sampling error. Regarding the flow-related uncertainty the potential error was associated with two sources: stage-discharge calibration uncertainty and errors arising from water stage logger failures. The stage discharge calibration uncertainty was estimated to be less than 3% by comparing instantaneous discharge measurements and the stage-runoff relationship. Errors associated with gap filling using measurements from a nearby hydrological station (~12 km north) were estimated to be 6% by comparing specific discharges from the two stations. A total uncertainty of 10% standard error for stream water discharge was used, which is somewhat higher than the regional difference of 8% in annual discharge found by Laudon et al. (2004) from seven boreal catchments in northern Sweden. The total uncertainties in DOC, CO_2 and CH_4 export were estimated using Monte Carlo simulations, with 10 000 realizations generated from the distributions discussed above. The total uncertainties for DOC, CO_2 and CH_4 stream water export were 11%, 13% and 14%, respectively.

Stream sampling methods [Paper IV]

Stream water samples were taken frequently during the high-flow snowmelt-season (every 2-3 days) and less frequently during the rest of the year (weekly to monthly). Samples for TOC consisted of grab samples with multiple rinses of stream water, collected in acid-washed 250 ml high-density polyethylene bottles. Samples for pCO2 and CH_4 headspace gas analysis were collected in N_2-filled 60 mL glass vials sealed with bromobutyl rubber septa. For each gas sample, a 15 - mL aliquot of bubble-free stream water was injected into the glass vial and subsequently either left at ambient pH (2003 sampling season) or acidified to pH 2-3 with a drop of 30% ultrapure HCl (0.5% v/v) (2004 and 2005 sampling seasons), then stored in the cool and dark until analysis.

Sampling was undertaken at two sites along the stream Vargstugsbäcken: an upstream site at an upwelling which forms the source of the stream and drains a catchment area of 2.9 km^2, and a second site 250 m downstream (3.1 km^2 catchment) at which a permanent V-notch weir has been installed for measuring discharge. During 2003, all analytes were measured at both sites. TOC concentrations and pH were not significantly different between the two sites, and subsequently (2004-2005) TOC and pH samples were taken from the downstream site. Concentrations of CO_2 and CH_4 were always higher at the upstream than at the downstream site, due to degassing in the intervening stream length. Since the goal of this study was to measure fluxes exiting the mire complex, gas samples were subsequently taken from the upstream site.

Samples were kept cool and dark for up to a week but typically less than two days until processing. During 2003 and 2005, TOC samples were frozen until analysis without filtration. During 2004, samples were filtered through a 0.45µm MCE filter and were then frozen until they were analyzed. A comparison covering the extremes of observed flows showed that there were no measurable differences in the concentrations due to filtering. TOC was measured by combustion and analysis as CO_2 using a Shimadzu TOC-VPCH analyzer after acidification and sparging to remove inorganic carbon. Instrument precision based on replicate injections averaged 2% and was always better than 5%.

pH was measured at laboratory temperature using a Ross 8102 low-conductivity combination electrode (ThermoOrion) in the laboratory immediately after collection. Partial headspace CH_4 and CO_2 pressures were analyzed by gas chromatography using either a Varian 3800 Genesis instrument equipped with a Haysep DB column using N_2 as carrier gas, or a Perkin-Elmer Autosystem GC instrument equipped with a Haysep N column using He as carrier gas. A flame ionization detector (FID) was utilized for CH_4 analysis, while CO_2 was reduced by a methanizer and then analyzed by the FID as CH_4 (Klemedtsson *et al.*, 1997). The stream water CH_4 concentration was calculated from headspace CH_4 measurements using a value of 0.0013 $molL^{-1}$ for CH_4 solubility (Stumm & Morgan, 1996). The stream water's dissolved inorganic carbon (DIC) concentration was calculated from sample headspace pCO_2 using temperature-dependent equations for carbonate equilibria (Gelbrecht et al., 1998) and Henry's Law (Weiss, 1974), together with measured stream water pH and temperature. Stream pH ranged only from 4.3 – 5.3, well below the carbonic acid equilibrium pKa, implying that our calculations of DIC were relatively insensitive to pH.

Daily stream carbon exports were calculated from daily flow measurements and linearly interpolated concentrations of TOC, DIC and CH_4.

Latent heat flux and evapotranspiration [Papers II, IV]

For the annual latent heat flux (LE) budget, used to calculate the annual amount of evapotranspiration (ET), missing data were replaced by a simple regression model on daily averages where R_n was found to predict LE accurately ($r^2 = 0.85$, $p<0.05$). This was used during the vegetation period, during the remaining time gaps were filled with weekly averages.

Potential evapotranspiration [Paper II]

Actual evapotranspiration was estimated by dividing the measured latent heat flux, LE, by the latent heat of vaporization. Potential evapotranspiration was estimated by two methods: the Penman- Monteith equation (Monteith, 1965), and the Priestley-Taylor equation (Priestly & Taylor, 1972). Using the former and assuming the surface resistance (r_s) is zero, PET can be estimated as:

$$PET = \frac{A \cdot \Delta + \dfrac{\rho \cdot C_p \cdot \delta e}{r_a}}{(\Delta + \gamma) \cdot L_v} \qquad (2)$$

where:
A = available energy (= R_n) [Wm^{-2}]
Δ = slope of vapor pressure saturation versus temperature curve [PaK^{-1}]
γ = psychrometric "constant" = 66 [PaK^{-1}]
ρ = air density [gm^{-3}]
C_p = specific heat capacity of air at constant pressure [Jg^{-1}]
δe = saturation vapor pressure deficit at air temperature [Pa]
r_a = aerodynamic resistance [sm^{-1}]
L_v=specific heat of vaporization [Jg^{-1}]

The aerodynamic resistance, r_a, for transfer of heat and water vapor from the surface to the reference level was estimated as:

$$r_a = \left[\frac{u(z)}{u_*^2}\right] + \left[\frac{\ln(z0 / z0_t)}{k \cdot u_*}\right] \qquad (3)$$

where u(z) is the wind speed at the reference level measured by the sonic anemometer, u_* is the friction velocity according eddy covariance method (Aubinet *et al.*, 2000), z0 is the roughness length for wind, $z0_t$ is the roughness length for temperature and k is von Karman's constant. The first term on the right hand side of the equation is the aerodynamic resistance to momentum transfer and the second one is the so called excess resistance which considers the extra resistance due to the difference in transfer for momentum and heat/water vapor. Here, it is assumed that the resistances for heat and water vapor transfer are equal.

Since there were no measurements of temperature profiles and surface temperature it was not possible to calculate $z0_t$ directly. For a low surface and neglecting the stratification effects and following Mölder & Kellner (2002), the following approach was used:

$$\ln(z0/z0_t) = 1.58 \cdot \mathrm{Re}_0^{0.25} - 3.4 \tag{4}$$

where Re_0 is the roughness Reynolds number:

$$\mathrm{Re}_0 = z0 \cdot u_* / \nu \tag{5}$$

where ν, the viscosity of air was assumed constant and equal to its value at 15 °C. The roughness length for wind, z0 was estimated from solving equation 6 for z0:

$$u(z) = \frac{u_*}{k} \cdot \ln(z/z0) \tag{6}$$

The estimation of z0 according this equation was made during near neutral conditions ($-0.1<z/L<0.1$) (e.g., Högström, (1988)) where L is the Monin-Obukhov stability length defined as:

$$L = -\frac{\rho \cdot c_p \cdot u^3_* \cdot T_a}{k \cdot g \cdot H} \tag{7}$$

where ρ is air density, c_p is specific heat of air at constant pressure, T_a is absolute air temperature, g is acceleration due to gravity and H is the sensible heat flux.

Available energy, A, is set equal to net radiation, R_n. This is justifiable since only daily values are used and soil heat flux is normally a few percent of the net radiation at this time scale. All drivers of equation 1 were daily averages. The Priestly-Taylor evapotranspiration was estimated from the equilibrium evaporation, λE_{eq}:

$$\lambda E_{eq} = \frac{\Delta}{\Delta + \gamma}(A) \tag{8}$$

Then, the Priestly-Taylor coefficient, α, was estimated from a linear regression (forced through the origin) between actual evapotranspiration (AET) and λE_{eq} (equation 9).

$$\alpha = \frac{AET}{\lambda E_{eq}} \tag{9}$$

Surface conductance [Paper II]

Surface conductance, describes the ability of the system to transport water to the surface. The canopy conductance (G_s) was estimated by solving the Penman-Monteith equations for $1/r_s$ which equals to G_s:

$$G_s = \frac{A \cdot \gamma}{\rho \cdot C_p \cdot \delta e \cdot (1+\beta) + A \cdot (\Delta \cdot \beta - \gamma) \cdot r_a} \tag{10}$$

We calculated G_s for the daytime, 0800-1800, during precipitation-free periods, defined as times when no precipitation had occurred for at least 24 h before the measurements.

Many semi-empirical formulae have been suggested to estimate the canopy conductance of different forest ecosystems at scales from leaf to stand (Jarvis, 1976; Komatsu, 2004; Moren, 1999). Climate-driven models often include solar radiation, air temperature, air humidity and soil moisture or combinations of these variables. We decided to apply one of the simplest models, the so-called Lohammar equation (Lohammar *et al.*, 1980), which uses global radiation (R_g) and air water vapor deficit (δe) as drivers:

$$G_{Lh}\left(\delta_e, R_g\right) = \frac{R_g}{R_g + a} \cdot \frac{g_{\max}}{1 + \delta_e / b} \tag{11}$$

where a, g_{max} and b are parameters fitted to coincide with the measured G_s (equation 11).

DEGERÖ STORMYR

Site description [Papers I, II, III, IV]

The study was conducted at Degerö Stormyr, (64°11'N, 19°33'E), an acid, oligotrophic, minerogenic, mixed mire system covering 6.5 km^2 and situated in the Kulbäcksliden Experimental Forests, near Vindeln in the county of Västerbotten, Sweden. The mire area, which consists of a rather complex system of interconnected smaller mires divided by islets and ridges of glacial till, is situated on high land (270 m.a.s.l.) between two major rivers, Umeälven and Vindelälven, approximately 70 km from the Gulf of Bothnia. The depth of the peat is generally between 3-4 m, but depths up to 8 m have been measured. The deepest peat layers correspond to an age of ~8000 years. The mire catchment is predominantly drained by the small creek Vargstugbäcken. The vascular plant community of the mire unit used for the water and energy exchange studies is dominated by *Eriophorum vaginatum* L.*, Vaccinium oxycoccos* L.*, Andromeda polifolia* L.*, Rubus chamaemorus* L. with both *Carex limosa* L. and *Schezeria palustris* L. occurring more sparsely. *Carex rostrata* L. is characteristic of areas with direct minerogenic water inflow. The bottom layer of the carpets is dominated by *Sphagnum majus* Russ. C. Jens*,* and the lawns by *S. lindbergii* Schimp. and *S. balticum* Russ. C. Jens*.*, while *S. fuscum* Schimp. Klinggr. and *S. rubellum* Wils. are dominant on the hummocks.

Climate [Papers I, II, III, IV]

The climate of the site is defined as cold temperate humid, the 30-year (1961- 90)

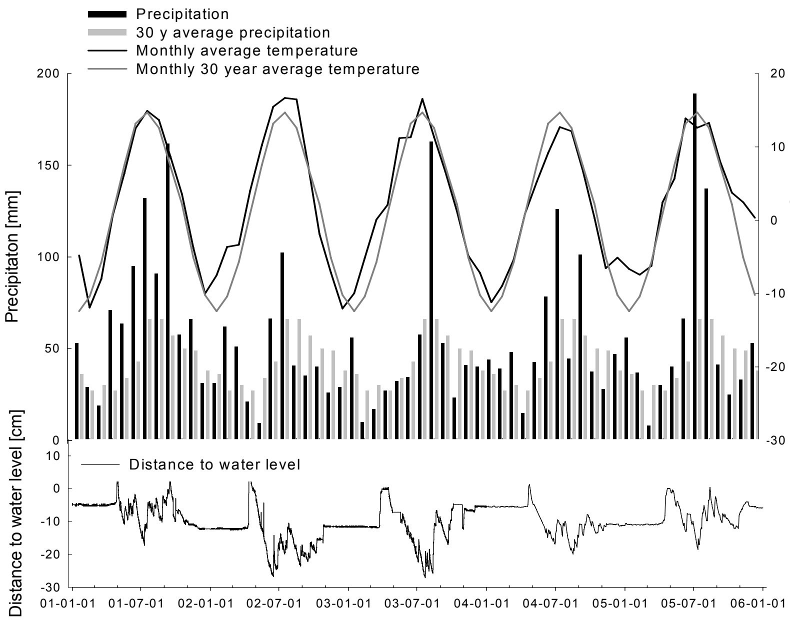


Figure 6 Air temperature and precipitation compared to 30-year averages (1960-90) and the water level relative to the peat surface.

averages for annual precipitation and temperature are 523 mm and +1.2 °C, respectively, while the mean temperatures in July and January are +14.7°C and -12.4 °C, respectively (Alexandersson, Karlström & Larsson-Mccann, 1991). The length of the growing season, defined as the period of daily mean temperature exceeding +5 °C (Moren & Perttu, 1994), was over the measuring period (2001-2005) 153 ± 15 days (Ottosson-Löfvenius, 2001; 2002; 2003; 2004; 2005; 2006). The snow cover normally reaches a depth up to 0.6 m and lasts for six months on average. The period measured covered quite a broad range concerning air temperature, precipitation and water levels (Figure 6).

Air temperatures and precipitation [Papers I, II, IV]

The monthly average air temperatures during the winter and spring periods were generally higher than the long-term averages (30-year averages, 1961-1990) (Figure 6). The monthly average air temperature during the growing season was higher during 2002 and 2003, during 2001 it was close to and during 2004 and 2005 lower than the long-term averages (Figure 1). The monthly precipitation was generally higher during late spring and summer than the 30-year average and most markedly so for 2001, 2004 and 2005. The summer and autumn of 2002 had substantially lower precipitation than the long-term average. The air temperature and precipitation patterns resulted in relatively high water tables during the soil frost-free season in 2001 and 2005, low water tables during 2002 and 2003 and intermediate levels during 2004. The annual precipitation during 2001 was 60% higher than the 30-year (1961-1990) average (860 mm versus 523 mm), it was also higher in 2004 and 2005 (651 mm and 716 mm, respectively), while the precipitation during 2002 (534 mm) and 2003 (559 mm) was close to the long-term average, although the temporal distributions deviated to some extent.

Water level [Papers I, II, IV]

The mean water level during the growing season was 7.4 ± 3.4, 17.3 ± 5.2, 14.5 ± 6.0, 11.0 ± 3.8 and 7.7 ± 4.4 cm below the vegetation surface in the years 2001, 2002, 2003, 2004 and 2005, respectively. The high precipitation and the temperatures being very close to normal during the year 2001 resulted in the water level remaining high during most of the "soil frost-free" season (Figure 3). The year 2002 began with a warmer spring and less precipitation than normal. The water table dropped to -25 cm in lawn plant communities during June compared to -12 cm in June 2001 and did not recover to the 2001 level before intense precipitation during August 2003 (Figure 6). In both 2004 and 2005 the mean water level was higher, and 2005 was almost as wet as 2001. The year with the largest variability in ground water levels was 2002, when there were eight months in which precipitation was lower than usual while temperatures were warmer than normal.

Snow cover [Papers I, IV]

No data for snow cover depth were available for the winter 2000-2001. During the winter of 2001-2002 most of the early winter snow (30 cm) melted in late December and the snow cover was maximal (55 cm) in March. In the following winter, 2002-2003, there was a continuous accumulation of snow until February, when it reached a maximum depth of 65 cm, and it remained at nearly the same depth until it thawed in April. In both 2004 and 2005 the first snow fell in late November and depths were maximal (60 and 65 cm, respectively) in late March in both years.

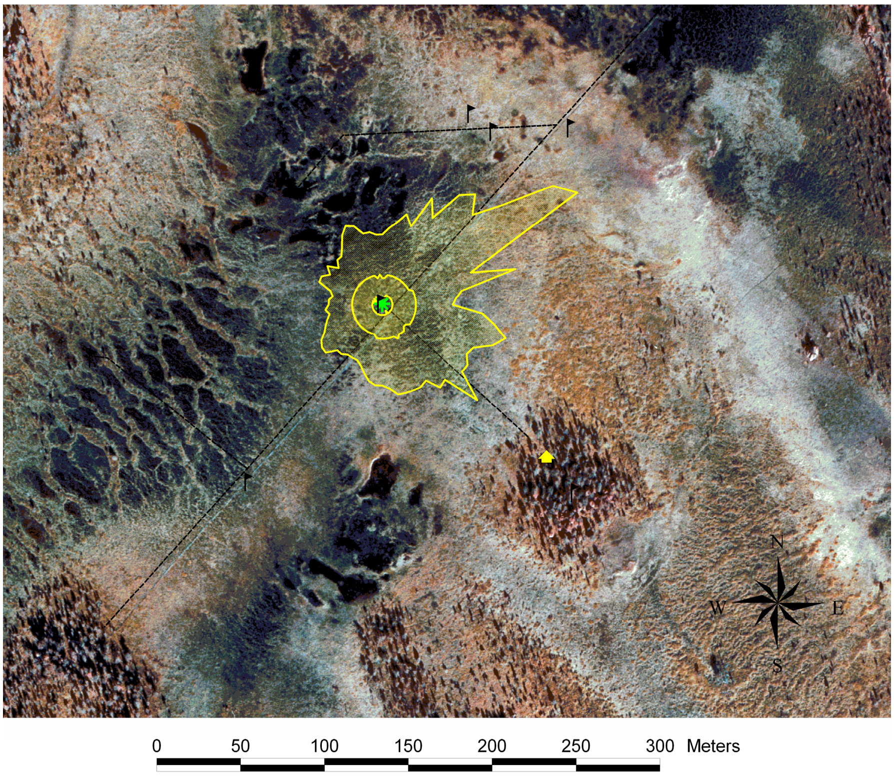


Figure 7 Aerial photograph of Degerö Stormyr. The yellow colored area inside the periphery contributes 90% of the total 30 min. measurements of the CO_2-exchange, example from daytime summer 2003 (0306-0309).The outer line represents night time footprint and the middle line daytime footprint. Footprint inside the innermost circle corresponds to 5% of the measurements. The green star shows the location of the tower. Black flags represent other experiments at the site. The yellow hut is the measuring hut.

CO_2 source area [Paper I]

The footprint area around the tower is slightly asymmetric and extends more towards the southeast during the summer and towards the south during the winter. The dominating wind direction during the summer is biased towards the ENE while in the winter the prevailing wind is from the SSE. The footprint area (95%

percentile of source distance, daytime) reached a radius of 22 m during the summer and 76 m during the winter, although the dominating area is much narrower. During wintertime the measuring height varied between 1.80 m and 1.15 m due to accumulation of snow. This means that periodically the measuring height (z_m) is much lower than during summer. The roughness, z0, was smaller during winter, only a few millimeters when snow is present compared to 2 cm during the growing season when z0 is determined by the plant community structure. The footprint varies very little diurnally (night vs. day) during the winter, but it varies substantially during the summer; a radius of about 22 m encompassing about 95% of the source distance during the daytime, which is increased to 74 m during the night time. Nighttime footprints are generally larger than during daytime. This difference is due to differences in boundary layer stability during the night and day.

The vegetation within the dominating source area during daytime in summer was very homogenous and is constituted by wet lawns and carpet plant communities (Figure 7). Also during night, most of the flux emanated from the same microtopographical units and is dominated by the same plant communities. However, the more distant flux sources towards east and south east are slightly drier dominated by “dry” lawn and hummock plant communities. Their distant location though results in most a limited contribution to the total flux and no influence from this variation in plant community composition is reflected in the half-hour average night values during the growing season. During winter time the source area extends is expanded somewhat towards south and southwest but is still dominated by lawns and carpets (Figure 7). We consider the variation in plant community composition between source directions to be minor and assume that the entire source area represents the same mire type. All budget calculations were therefore based on the entire data set without any partitioning according to wind direction.

Annual Net Ecosystem Exchange (NEE) [Papers I, III, IV]

All years showed similar seasonal patterns and the mire acted as a net sink with respect to the net ecosystem exchange (NEE) during the five measured years (Figure 8), with an average uptake of 54 ± 6 gCO_2-$Cm^{-2}yr^{-1}$ (±SD). The net carbon uptakes during 2001 and 2005 were 48 ± 1.1 and 48 ± 1.6 gCO_2-$Cm^{-2}yr^{-1}$ respectively, approximately 15 - 20% lower than the uptake during 2002, 2003 and 2004 when NEE was 61 ± 1.4, 56 ± 2.1, and 55 ± 1.9 gCO_2-$Cm^{-2}yr^{-1}$, respectively. Based on our definition of the growing season (1:st day in the period when 7-day average daily fluxes indicated stable uptake), as a period of net uptake, its length was 124 days in 2001 (May 07 – September 07), 132 days in 2002 (May 01 – September 09), 146 days in 2003 (April 26 – September 18), 130 days in 2004 (May 5 – September 25) and 148 days in 2005 (April 26 – September 21).

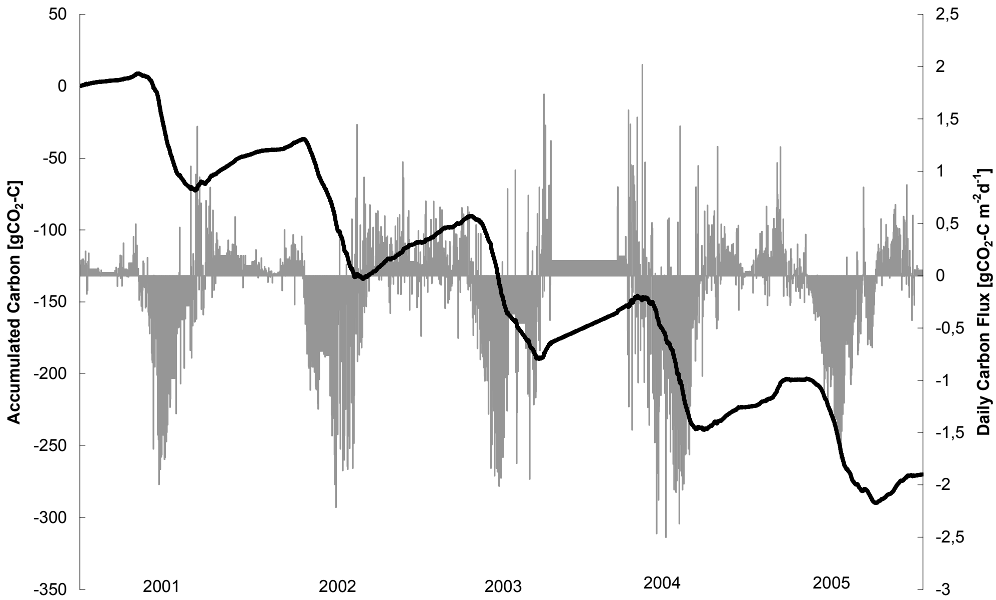


Figure 8 Daily carbon fluxes over the five study years, measured by the Eddy Covariance technique. Grey bars, daily sums; black line, accumulated curve.

Growing season vs. Non-growing season [Papers I, IV]

The total uptake during the net uptake period amounted to 81, 97, 99, 92 and 87 gCO_2-Cm^{-2} in 2001-2005, respectively. The non-growing season efflux was on average 38 ± 2 gCO_2-Cm^{-2} (±SE), with between-year variations of smaller magnitude compared to those in the growing season. The annual NEE, as a proportion of the growing season sink term, was relatively constant: 59, 63, 57, 61, and 55% for 2001-2005, respectively, thus the non-growing season efflux amounted to 41 ± 1 % (±SE) of the growing season NEE.

A significant relationship between WL and annual NEE was also found, NEE increasing as WL decreased (Figure 9).

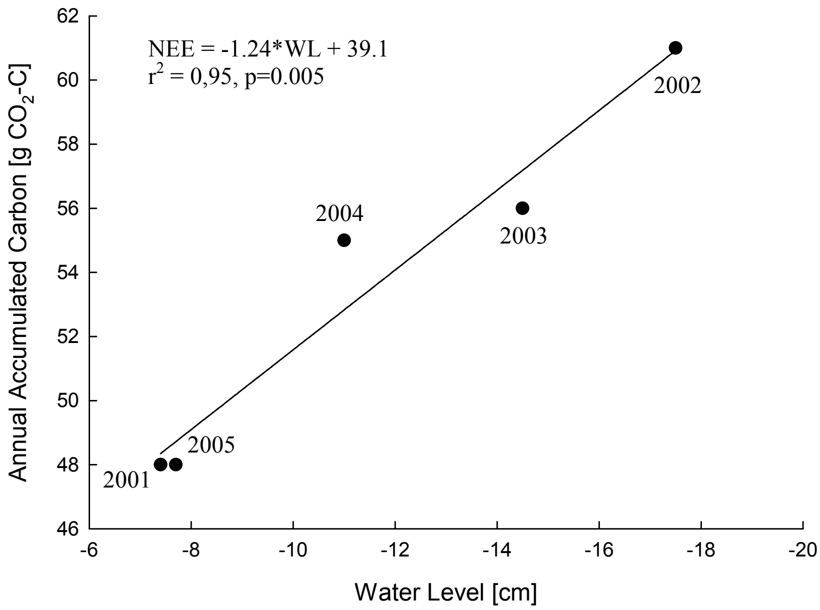


Figure 9 Relationship between annual accumulated NEE and the mean growing season water level.

Within-year variations [Papers I, IV]

When the temporal variations of the annual NEE curves were examined more closely, it was seen that a large part of the variation in annual carbon fluxes could be related to emissions during spring, both in amplitude and in the date when net accumulation began (Figure 10). The same pattern was seen during autumn, but less pronounced. The slopes of the lines during summer were fairly similar between the years, indicating that inter-year variations in flux amplitude were minor.

Daily NEE [Paper I]

The daily average uptake over the growing seasons of 2001, 2002 and 2003 was 0.65 ± 0.57, 0.73 ± 0.61 and 0.68 ± 0.62 $gCO_2\text{-}Cm^{-2}d^{-1}$, respectively. The daily average net uptake for the month with the highest uptake was: 1.10 ± 0.33 (July 2001), 1.11 ± 0.63 (July 2002) and 1.22 ± 0.55 (June 2003) $gCO_2\text{-}Cm^{-2}d^{-1}$. The daily average efflux during the non-growing season was 0.14 ± 0.28, 0.15 ± 0.20 and 0.20 ± 0.19 $gCO_2\text{-}Cm^{-2}d^{-1}$ in the years 2001, 2002 and 2003, respectively. Since the daily averages mask diurnal patterns (Figure 11), effluxes during the night, the uptake during the day, and maximum peak NEE values are all higher than these daily averages suggest.

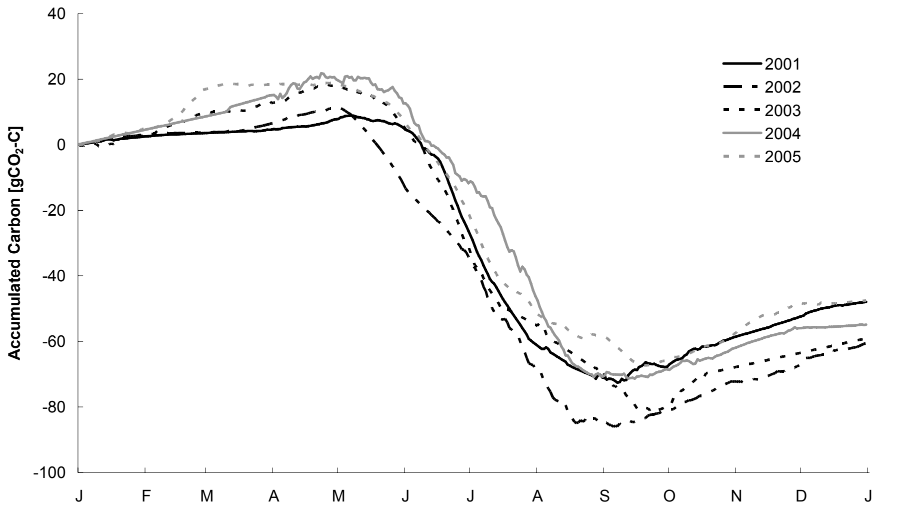


Figure 10 Comparison of temporal variations in carbon (CO_2-C) accumulation amongst the five measured years (2001-2005).

The growing season mean daily CO_2 flux represented a net uptake during each month from May to August in all three years and peaked during June or July, as described above. In 2003 net uptake also occurred during September. The night efflux was relatively independent of wind direction, indicating that although the distribution of the plant species is not completely homogenous wind variations do not significantly influence the CO_2-flux.

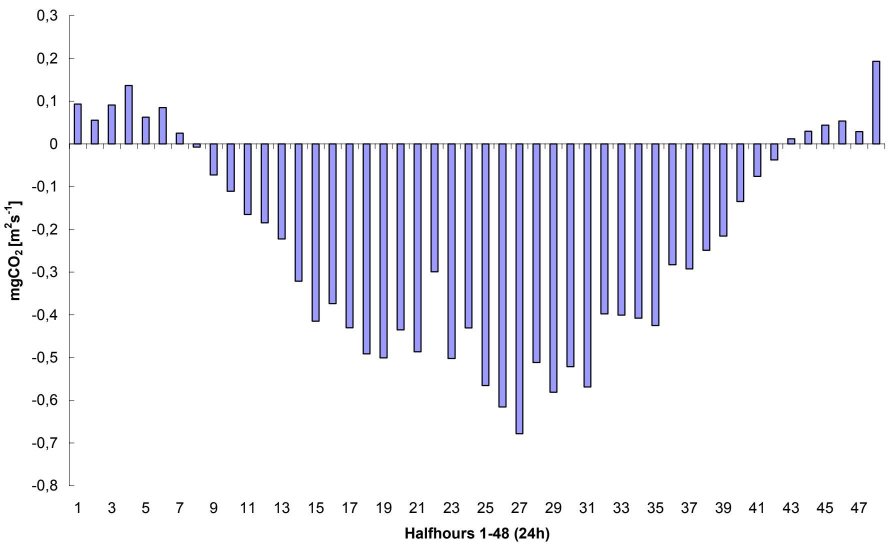


Figure 11 Example of a diurnal pattern of CO_2 flux with an efflux during the night, and uptake during the daytime (9th of June 2001).

NEE spring and autumn dynamics [Paper III]

There were several clear features of the water level (WL) dynamics during the spring; initially flooding of the area due to the snowmelt was followed by a sudden increase in the soil's permeability for water, resulting in rapid lowering of the WL.

When analyzing daily net ecosystem exchange (NEE) during the spring transition from efflux to uptake relative to the water level, it was seen that in years with late spring transitions (2001 and 2004) the date of the transition to a CO_2 sink corresponded to a water level of approximately 7 cm. In 2002 and 2005, when the transition was earlier, it corresponded to a WL of approximately 3 cm (Figure 12).

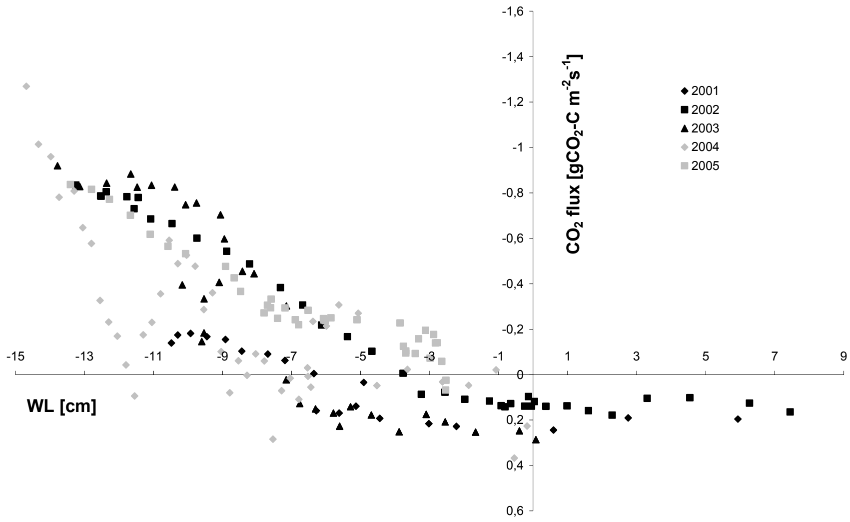


Figure 12 Daily mean CO_2 flux, (time series from right to left), relative to water level during the spring transition to net accumulation. Data points above the x-axis correspond to net uptake of CO_2. Water levels > 0 indicate flooding, daily mean CO_2 flux = 0 represents the spring transition.

The pattern differed in 2003, but if data for this year are excluded a significant correlation between WL and the spring transition appears (Figure 13), WL = 0.45*(spring transition date) – 49.3 ($r^2 = 0.99$, $p<0.005$). In the year 2003 the time course of the amplitude of fluxes of daily fluxes (Figure 12), initially resembled that of a late spring transition, but within a couple of days of the start of the transition the amplitude increased to levels more characteristic of the early spring transition fluxes. Inhibition of photosynthesis or an increase in respiration apparently occurred during the spring transition in 2003. For the spring transition, dates of snowmelt (defined as the time when all the snow had gone) and soil thaw (defined as the time when the soil becomes permeable to water and the spring flooding disappears) together with the beginning of soil heating yielded significant MLR (Multiple Linear Regression) models (Figure 14a, 14b).

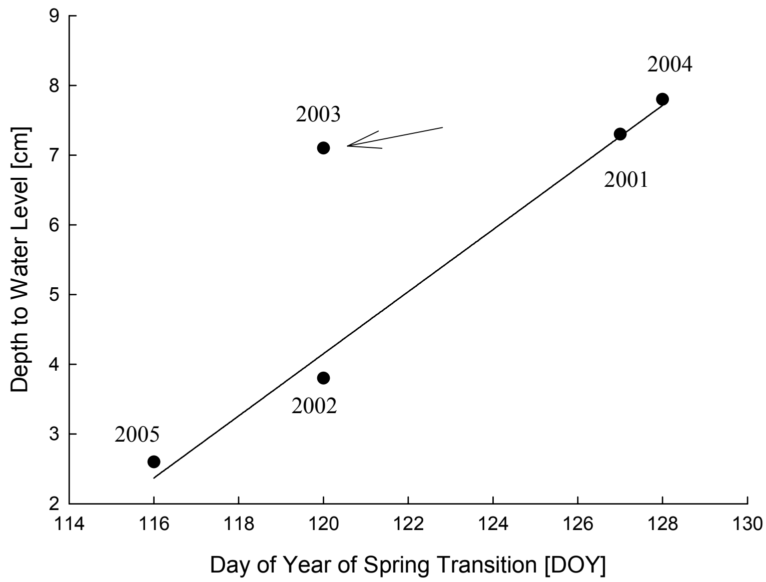


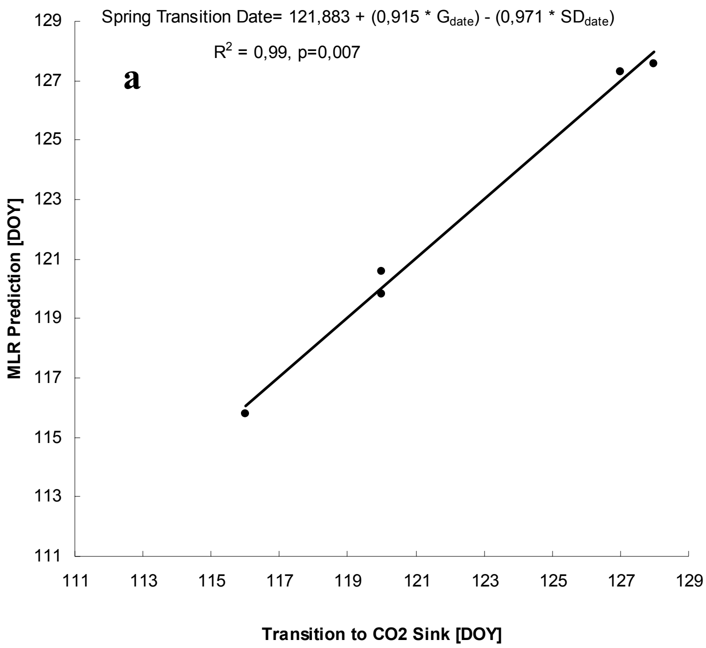
Figure 13 Dependence of the date of the spring transition on the water level, the arrow indicates the data point for the deviant year, 2003.

The beginning of soil heating was defined as the first day after the soil thaw (as defined above), when the residual (R_n- (H+LE)) which approximates the soil heat flux, decreased to approximately zero or became negative (negative value = soil heating).

Both models were significant ($r^2 = 0.99$, $p < 0.01$) and could predict the date of the spring transition (upper arrows figure 1, arrows figure 2), within ± 1 day. This also showed the close correlation between snowmelt and soil thaw which coincided with a lag of 5 ± 1 day. The spring transition seemed to be independent of soil temperature.

In autumn, by taking the average of the peat temperature at 18 cm depth 30 days prior to the date of transition to a CO_2 source provided significant predictions of the autumn transition, within ± 2 days ($r^2 = 0.99$ and $p<0.01$) (Figure 9). This shows that a faster cooling of the soil in autumn, giving a lower 30-day mean temperature, results in a prolonged accumulation period. During the observed five years the length of this period varied by 22 days.

By plotting soil temperature at 18 cm depth for specific days against the moving average for the preceding 30 days as a time series, the date of the autumn transition could be predicted from the point the time series crosses the regression line, as shown in figure 9. This could be done with a precision of ± 2 days. Using the above regressions, for spring and autumn, the length of the growing season at Degerö Stormyr could be estimated within ± 3 days.



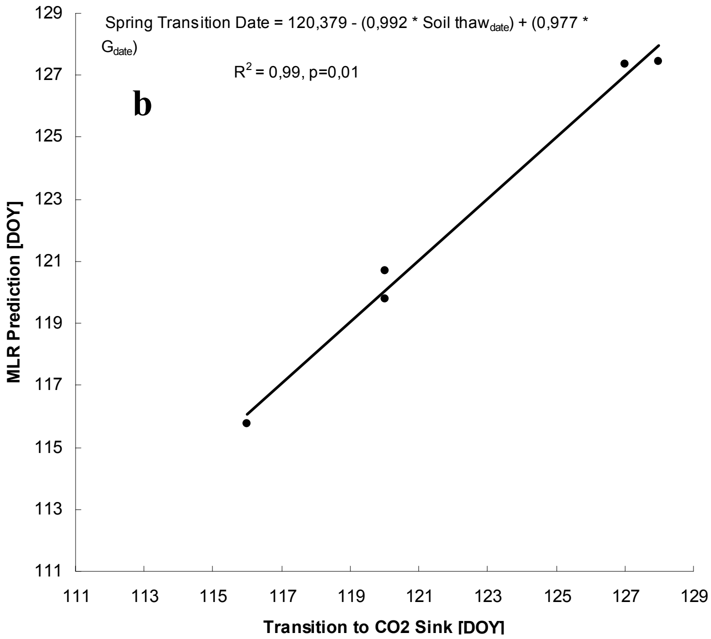


Figure 14 Plots from two MLR (Multiple Linear Regression) models for predicting the date of the transition from source to sink during the spring. DOY = day of year. (a) Soil heat flux date (G_{date}) and snow melt date (SD_{date}) predicting the spring transition. (b) Soil heat flux date (G_{date}) and soil thaw date (Soil $thaw_{date}$) predicting the transition.

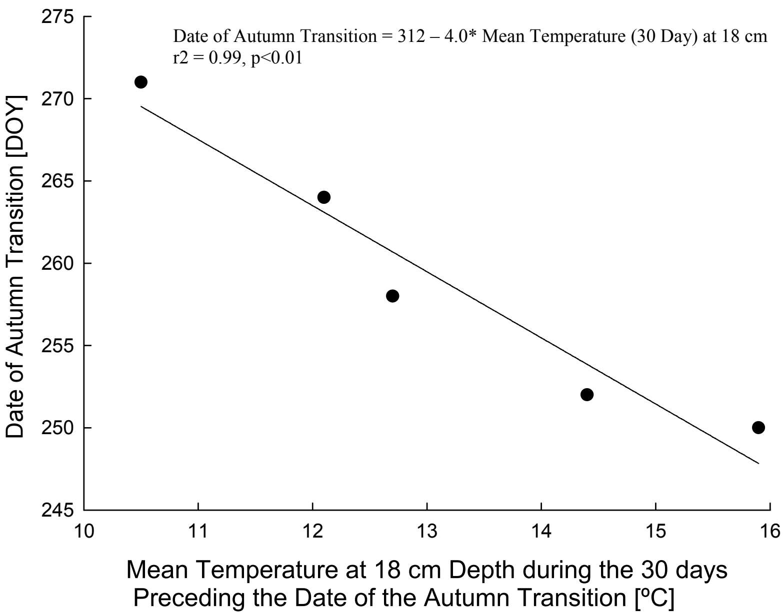


Figure 15 Correlation between peat temperature and date of the autumn transition to CO_2 source.

Total carbon budget [Paper IV]

To evaluate the importance of carbon fluxes other than the NEE (CO_2-C) measured by the eddy covariance technique, additional measurements of CH_4-C effluxes directly to the atmosphere and CH_4-C, dissolved inorganic carbon (DIC) and total organic carbon (TOC) emissions via discharge were taken in two years (2004-2005). The influence on the annual budget (Figure 16) of these carbon species was then analyzed. The largest contributor was found to be the CH_4 emissions to the atmosphere, in both years, but the summed CH_4-C, DIC and TOC discharge emissions could be almost as large as the CH_4 emissions to the atmosphere as seen in 2004. (Note that CH_4-C discharge emissions shown in figure 16 have been enlarged by a factor 10 for illustrative purposes.)

The continuous measurements also allowed the temporal variations of each of the carbon fluxes to be examined. The atmospheric fluxes were largest during late spring, summer and autumn while the amounts of TOC, DIC and CH_4 leaving the mire with water closely followed the discharge curves, resulting in large emissions during the spring flood (Figure 17).

Methane emissions were measured in both a lawn dominated plant community and a more carpet dominated plant community, together representing approximately all of the fetch area for the eddy covariance CO_2-flux measurements. During the growing season, the water table normally ranged between 10 and 20 cm below the surface in the lawn plant community, and

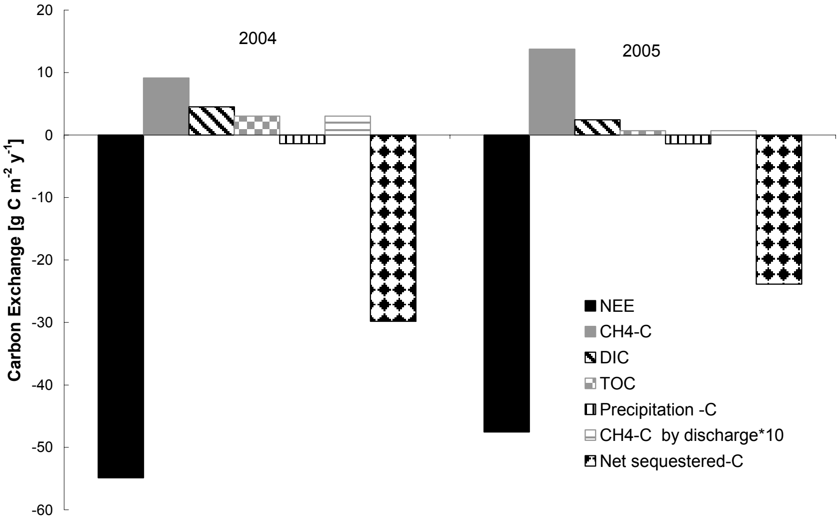


Figure 16 Contributions of measured carbon fluxes to annual carbon exchange. NEE - net ecosystem exchange, DIC - dissolved inorganic carbon, TOC - total organic carbon, Precipitation.-C – carbon input in precipitation. (Note that the CH_4-C discharge emissions have been enlarged by a factor 10 for illustrative purposes).

between 0 and 10 cm in the carpet plant community. The CH_4-flux rates were generally higher from the lawn than from the carpet, especially during 2004. The CH_4-fluxes from the carpet during the snow-free season of 2004 ranged from 2 to 6 mgCH_4-Cm^{-2}h^{-1} while the fluxes from the lawn were < 2 mgCH_4-Cm^{-2}h^{-1} most of the time. The CH_4-emissions during the snow-free season of 2005 from the two plant communities were more similar, but those from the carpet community were still higher (3 – 5 mgCH_4-Cm^{-2}h^{-1}) than those from the lawn plant community (generally 2 – 4 mgCH_4-Cm^{-2}h^{-1}). To estimate the annual flux we assumed that the flux during the season from May 25 to October 05 constituted 80% of the annual flux from the mire. The estimated total methane losses were 9 ± 1.7 gCH_4-Cm^{-2} (±SD) during 2004 and 14 ± 1.7 gCH_4-Cm^{-2} during 2005.

The discharge (Q) from the mire catchment amounted to 369 mm during 2004 and 343 mm during 2005. The C-export through runoff at Degerö Stormyr mainly occurred during snowmelt and rain episodes, mirroring the discharge patterns (Figure 17). The average (±SD) TOC, DIC and CH_4-C levels in the runoff water during 2004 and 2005 were 24 ± 3.9, 12 ± 5.3 and 1 ± 1.2 mgL^{-1}, respectively. In 2004, 92% of the run-off C was exported during 37% of the year when the specific discharge was at episodic levels (exceeding 0.55 mm day^{-1}), and in 2005 the corresponding figures were 88% and 37%, respectively. Furthermore, 96% and 94% of the annual run-off C was lost, in 2004 and 2005, respectively, during 52% and 48% of the year when the specific discharge exceeded 0.27 mm day^{-1}. The period of high flow (>0.55 mm d^{-1}) in spring, which constituted 12% and 15% of the year in 2004 and 2005, respectively, accounted for 38% and 40% of the annual C-discharge in these years. The total C-exports via run-off amounted to 15 ± 1.2 and 11 ± 1.0 gCm^{-2} in 2004 and 2005, respectively, and the major component was

TOC (9.8 ± 1.1 gCm^{-2} in 2004, 8.2 ± 0.9 gCm^{-2} in 2005), but CO_2 also made a significant contribution in both years (4.5 ± 0.6 and 2.4 ± 0.3 gCm^{-2}, respectively), while the amount of carbon lost as methane was negligible in both years (0.3 ± 0.04 and 0.07 ± 0.01 gCm^{-2}, respectively).

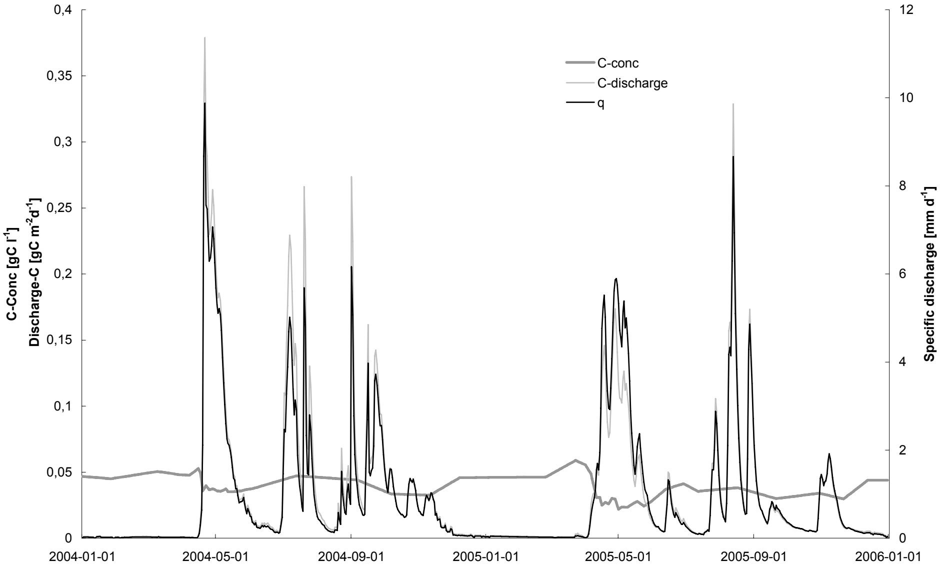


Figure 17 Water discharge, carbon concentrations and carbon transport via discharge, 2004-2005.

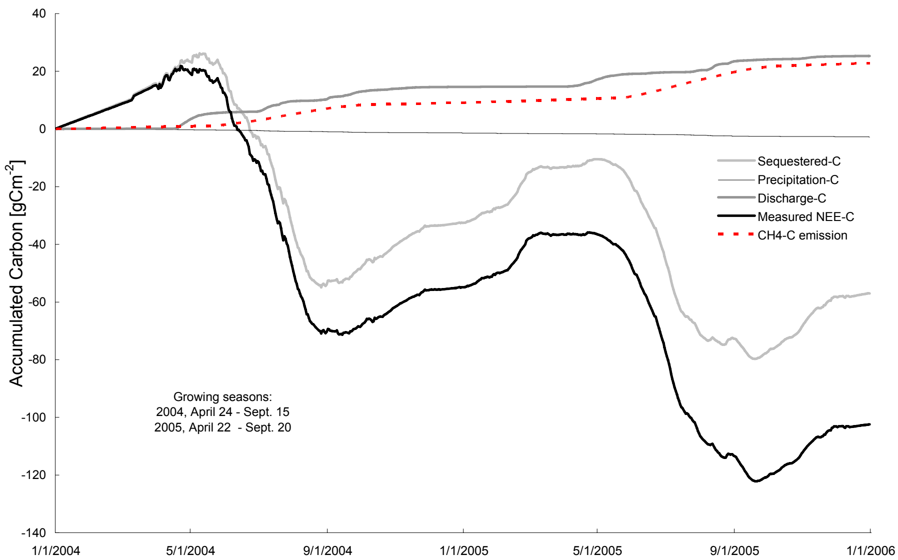


Figure 18 Carbon budget for the hydrological years 2004 and 2005.

The carbon losses through run-off and methane emissions were equivalent to 20% and 16% of annual net CO_2-C uptake (NEE) in 2004, and the corresponding figures for 2005 were 27% and 29%. Thus, the NEE figures for 2004 and 2005 should be reduced by 36% (to -31 $gCm^{-2}yr^{-1}$) and 56% (to -24 $gCm^{-2}yr^{-1}$) for 2004 and 2005, respectively to obtain estimates of the "true" rates of carbon accumulation, corresponding to 34% (2004) and 27% (2005) of the growing season NEE.

The cumulative accumulation for the total carbon exchange was thus calculated (Figure 18) and it was seen that the major change in the budget generally occurred during the period from the beginning of May to the end of September.

Energy and Water [Paper II]

During the peak of the growing season (July) the net radiation typically reached maximum values around 400-500 Wm^{-2}. Latent heat fluxes (evaporation of water) typically reached maxima of 300 Wm^{-2} while sensible heat fluxes (heating or cooling of air) were slightly lower, with maximum values just below 200 Wm^{-2}. During the winter, latent heat fluxes were small, more or less insignificant components of the energy partitioning, while sensible heat fluxes were more closely connected to net radiation. The sensible heat flux showed rather large variations during the winter, which may be related to the thawing and freezing of the snow pack with the subsequent consumption and release of energy.

The partitioning between H and LE is represented by the coefficient of the slope of the regression between daily means of these two variables (daylight values, Rg>5 Wm^{-2}), 1st of May to 31st of August, Figure 19a, Table I). The β (H/LE) values in the years 2002-2005, were all similar (0.36, 0.38, 0.34 and 0.37, respectively), but β was significantly lower in 2001 (0.24).

The relationship between LE and R_n was estimated as the coefficient of the slope of the regression of plotted daily means (Figure 19b, Table I) based on measured data from the 1st of May to the 31st of August. The average proportions of the daily net radiation (R_n) during this season that was used for evapotranspiration (LE), were 57, 62, 46, 46 and 67 % for the years 2001 – 2005, respectively. Years when higher proportions of the energy partitioned to LE coincide with seasons either with "normal" air temperature, high precipitation and high water table level (2001 and 2005) or seasons when evaporation was high despite the water table level being quite low due to high air temperatures (resulting in high vapor pressure deficits) as in year 2002. The mean 5-year ratio between actual evapotranspiration (AET) and potential evapotranspiration (PET) was 75 ± 1% (±SE) (Figure 19c).

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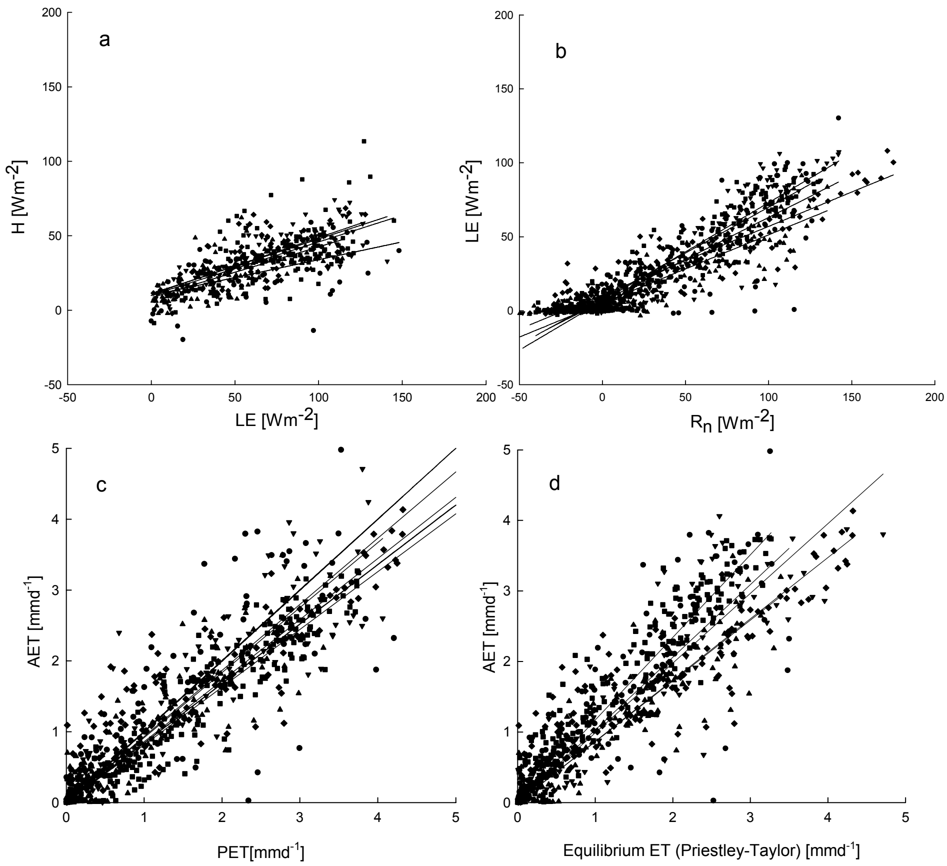

Figure 19 (a) Daily averages (for daily average of R_g> 5 [Wm^{-2}]) of sensible heat (H) versus latent energy (LE), 1 May– 31 August, 2001-2005. (b) LE vs. R_n. Daily averages, 1 May– 31 August, 2001-2005.(c) AET vs. PET. Daily sums, full year data 2001-2005. (d) AET vs. Equilibrium ET (Priestley-Taylor), the slope corresponds to the P-T coefficient α. Circles 2001, squares 2002, diamonds 2003, upward triangles 2004 and downward triangles 2005.

The mean 5-year ratio between actual evapotranspiration (AET) and potential evapotranspiration (PET) was 75 ± 1% (±SE) (Figure 19c).

The variation, between years, ranged between 69 and 85%. During the two years with higher WL, 2001 and 2005, the actual evapotranspiration (AET) constituted 84% and 85%, respectively, of PET whereas the AET during the three other years averaged 70 ± 2% (±SE) of PET (Figure 19c, Table I). The Priestley-Taylor coefficient (α) describes the relationship between observed evapotranspiration λE and an equilibrium evapotranspiration rate λE_{eq} (Priestley & Taylor, 1972). The average annual α-value was 0.99 ± 0.01 (±SE), ranging from 0.86 (2004) to 1.17 (2002) (Figure 19d, Table I).

Table I *Energy and evapotranspiration regressions, 2001-2005.*

	a[a]	**SE**[b]	**b**[a]	**r^2**[c]	**p**[c]
	β[d]				
2001	0.24	0.04	10.0	0.29	<0.001
2002	0.36	0.05	10.0	0.34	<0.001
2003	0.38	0.05	10.7	0.49	<0.001
2004	0.34	0.03	8.4	0.49	<0.001
2005	0.37	0.03	11.2	0.60	<0.001
	LE/R_n[e]				
2001	57	3	6.6	0.82	<0.001
2002	62	1	8.0	0.89	<0.001
2003	46	1	10.7	0.85	<0.001
2004	46	2	5.2	0.82	<0.001
2005	67	2	6.6	0.88	<0.001
	AET/PET[f]				
2001	84	3	0[i]	0.82	<0.001
2002	73	2	0[i]	0.89	<0.001
2003	69	2	0[i]	0.85	<0.001
2004	69	2	0[i]	0.82	<0.001
2005	85	3	0[i]	0.88	<0.001
	α[g]				
2001	1.03	0.03	0[i]	0.75	<0.001
2002	1.17	0.02	0[i]	0.92	<0.001
2003	0.87	0.02	0[i]	0.83	<0.001
2004	0.86	0.02	0[i]	0.84	<0.001
2005	0.99[h]	0.03	0[i]	0.85	<0.001

[a] Referring to the regression equation y=ax+b, a being the slope of the regression, b the intercept.
[b] Standard Error for coefficient a.
[c] r^2 and p, respectively, for the regression.
[d] Bowen ratio H/LE, being the slope of the regression between H and LE, daily mean values between 0800-1800h, 1 May-31 August.
[e] Evaporative fraction, LE/R_n being the slope of the regression between LE and R_n, daily mean values 1 May-31 August.
[f] AET/PET being the slope of the regression between AET and PET, daily mean values, full year data.
[g] Priestley-Taylor coefficient, α, being the slope of the regression between AET and the Priestley-Taylor equilibrium equation, daily mean values, full year data.
[h] Corrected for seasonally biased dataset with respect to soil heat flux.
[i] Set to zero.

Water balance [Paper II]

During the last three years (2003-2005) of the study, all of the large water fluxes were measured at Degerö Stormyr in order to compile a complete water budget. Discharge (Q) was measured in addition to precipitation (P) and evapotranspiration (ET), which were measured in all years. The water budget closure averaged 92 ± 4% (±SE) over the three years. The cumulative residual for the period was small, approximately 8% (Figure 20, Table II). The difference in precipitation and temperature between years affected the annual partitioning between Q and ET. For example, high ET during 2003 resulted in a lower Q than in 2004 and 2005 (Table II).

Table II *Water flows/fluxes 2001-2005.*

	Σ AET	Σ P	Σ q	(AET +q)/P	AET /P
		[mm]		[%]	
2001	230	869	- -	- -	26
2002	337	513	- -	- -	66
2003	304	545	170	87	56
2004	227	635	367	94	36
2005	255	648	355	94	39

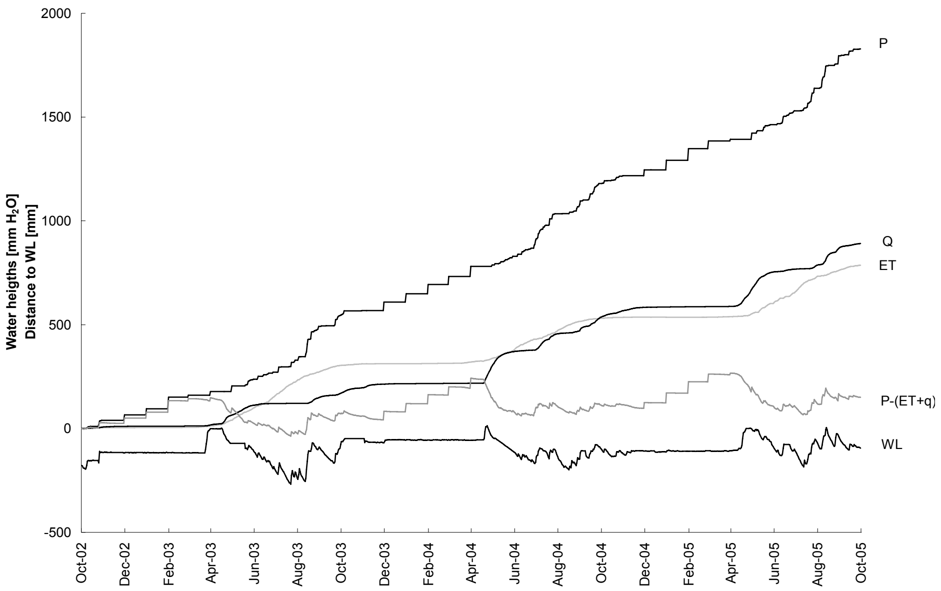

Figure 20 Accumulated water flows/fluxes recalculated as water height equivalents [mm]. Curves for P, ET, q, WL and the residual P-(ET+q) for the hydrological years 2003-2005. Note that Q and ET are shown as positive numbers although they represent losses of water from the system.

The timing and intensity of precipitation also affected the partitioning between Q and ET. Snow melt during the spring, when ET was low and the soils frozen, resulted in large prolonged episodes of flooding. Later in the spring, when soil frost was mostly melted or discontinuous, snow melt also resulted in a recharge of the mire soil storage. Precipitation during summer, when the water level was generally lower, resulted in raised WL and increased ET and hence did not substantially increase Q. During this period, ET dominated the water budget, due to high air temperature and irradiance. Rain coming during the autumn, when WL was already relatively high, increased Q (Figure 20). During autumn ET generally decreased due to lower temperatures despite increased precipitation. Depending on the height of the water table, precipitation resulted in either recharge of soil storage or increased runoff. The residual between precipitation, evapotranspiration and runoff (P-(ET+Q)) paralleled the temporal variation in WL, and except for spring flood events, a P larger than ET resulted in a closely correlated rise in WL.

Vertical water transport in the upper aerobic layer [Paper II]

The canopy conductance (G_s) reflects the capacity of the system to transport water vertically up to the plants and further away as ET. G_s generally decreased from the morning hours to the evening. During a season with high precipitation and high water table (2001) the conductance during May and September was quite high in the morning (35 mms^{-1}) and then decreased within a few hours to values between 0-15 mms^{-1}. During a more dry and warm year (2002) and during the summer months of a more wet year (2001) the G_s decreased much more gently during the day, the canopy conductance being below 10 mms^{-1} (Figure 21). This diurnal decrease indicates that the *Sphagnum* plants dried out during the daytime as reflected in the decreasing G_s, but recharged during the night time.

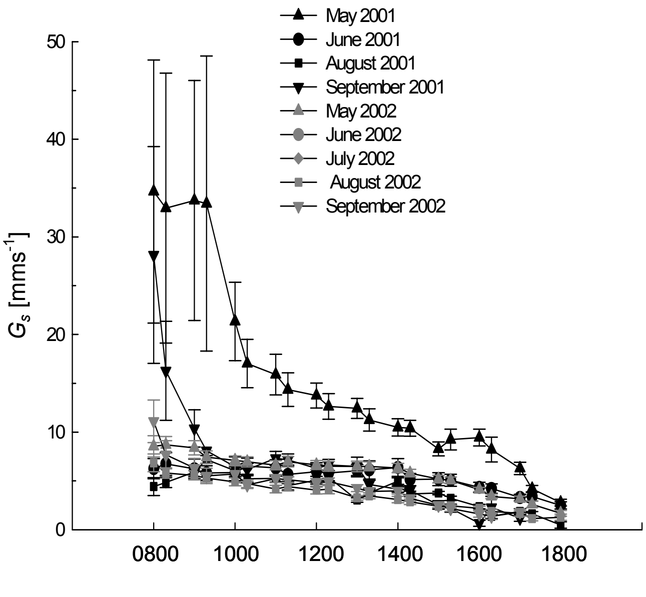

Figure 21 Monthly averages on half hour data (0800-1800 hours) for canopy conductance G_s in: 2001, a wet year, and 2002, a warm and dry year. Data missing for July 2001.

These results show that there is sufficient vertical water transport to maintain canopy conductance within a broad range of water levels, although reductions in conductance were seen at very low water levels.

Fitting the parameters in equation 10 to measured G_s and comparing with parameters derived from measurements over a forest ecosystem (Figure 22) suggesting that G_s for the mire is more driven by global radiation (R_g) than a forest with it's stomatal regulation is. The largest differences occurred at low vapor pressure deficits (VPD:s) and high R_g.

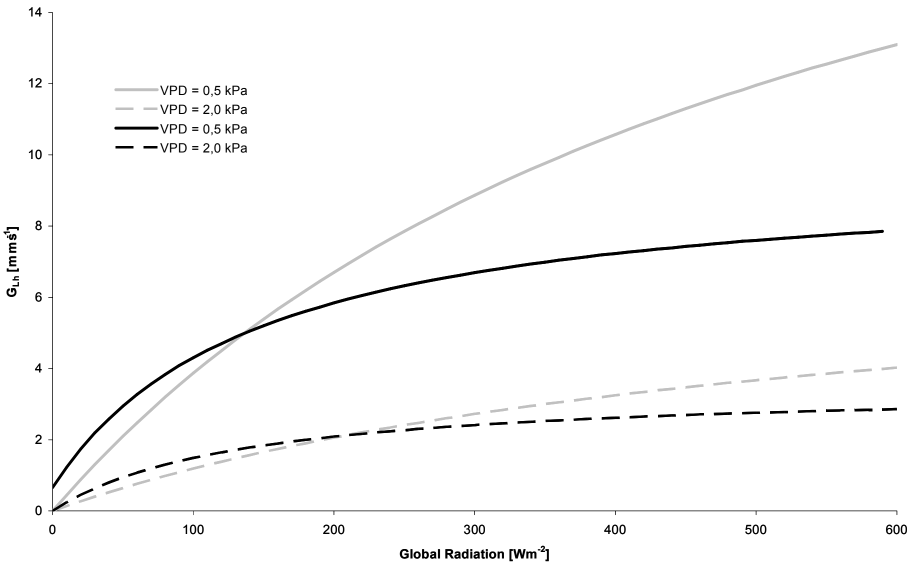

Figure 22 Comparison between Degerö Stormyr and a forest system for canopy conductance using the Lohammar equation (Lohammar*, et al.*, 1980) G_{Lh}. Forest system parameters from Lindroth (1985). Grey lines: Degerö site, Black lines: Forest system. Model fixed for two different vapor pressure deficit (VPD) levels.

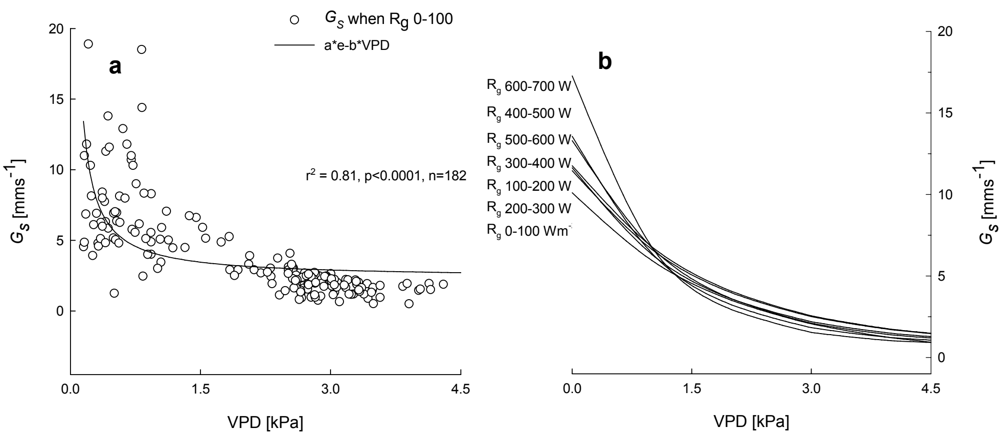

Figure 23 **(a)** An exponential decay curve fitted to data for $0<R_g<100$ Wm^{-2}. **(b)** As in figure a, but for different ranges of R_g. Figure showing surface conductance response on global radiation for different VPD.

By fitting an exponential decay curve to the surface conductance, binned for different R_g levels, it was seen that G_s only showed an increasing response at low VPD:s (< 1 kPa) and at higher levels the response was insignificant (Figure 23).

A significant decrease in G_s was observed at lower water levels (<10cm) but still at 20-25 cm WL the surface conductance reached 4 mms^{-1} (Figure 24), quite enough to keep the mire growing efficiently.

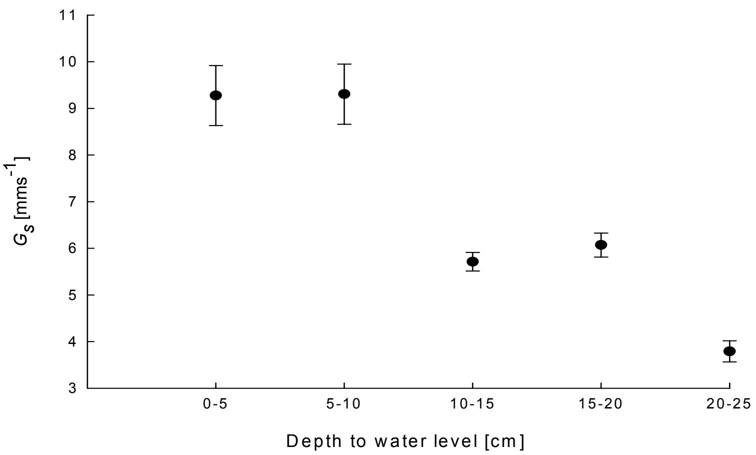

Figure 24 Surface conductance, G_s, (binned) for different water level intervals. Data from May 1 to August 31, 2001-2005. Error bars equals 95% confidence intervals.

z0, r_a and r_s

The roughness length on the mire showed a seasonal pattern with low values during winter due to the smooth snow surface, *ca.* 5 mm, increasing to a maximum around midsummer reaching *ca.* 30 mm (Figure 25).

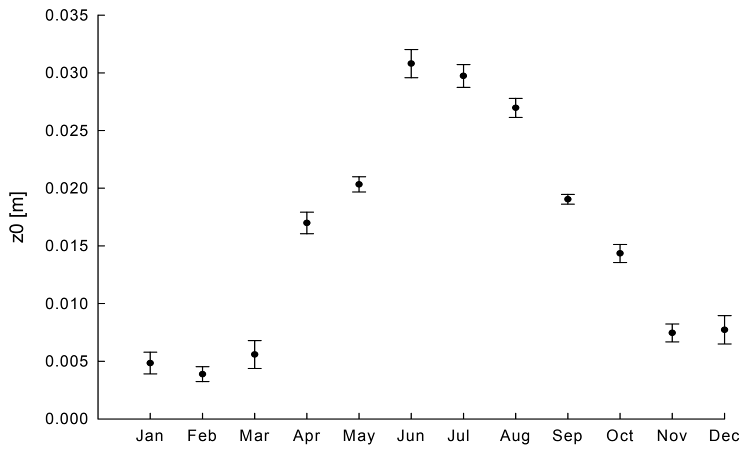

Figure 25 Annual variations of the roughness length (z0) illustrated by monthly averages (±SE). Figure showing the year of 2002.

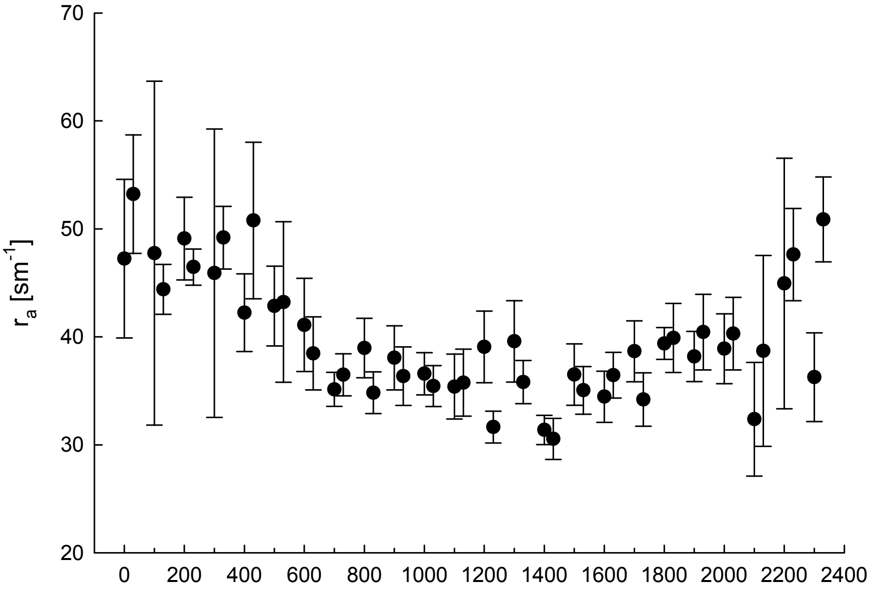

Figure 26 Half hourly ensemble averages, 17 May - 13 July year 2002 (±SE) showing a diurnal pattern of the aerodynamic resistance r_a.

The aerodynamic resistance r_a showed a diurnal pattern higher during night and lower during the day (Figure 26). The "excess" aerodynamic resistance (the second term of equation 3) was of minor importance for this mire system and added generally less than 5% to r_a. Except for a very few extremely wet occasions, r_a was larger than r_s, indicating that r_s was the dominant resistance.

DEGERÖ STORMYR IN A GLOBAL PERSPECTIVE

Eddy Covariance measurements [Papers I, II, III, IV]

The assumption made in the context of energy balance closure that available energy, A, equals net radiation on a diurnal basis will result in a slight overestimate of A in spring/early summer and an underestimate in late summer/autumn. If we assume that the positive and negative biases are evenly distributed over a year, then we argue that the regression lines are approximately correct, albeit with additional scatter caused by this effect. The resulting energy balance of 96%, with a minimal offset of only 3 [Wm^{-2}] (Figure 27), indicates that this assumption is valid and that the energy balance closure is satisfactory. The energy closure at a bog in southern Canada has been found to be 93% (Lafleur, Griffis & Rouse, 2001) and the mean energy closure at twenty-two Fluxnet sites to be 80% (Wilson *et al.*, 2002), suggesting that the energy closure in this study was quite sufficient.

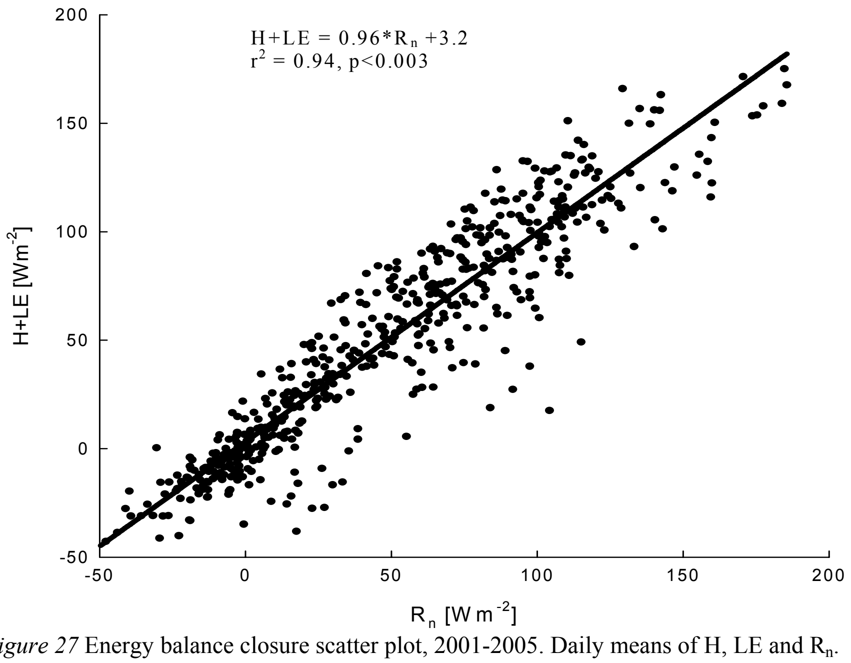

Figure 27 Energy balance closure scatter plot, 2001-2005. Daily means of H, LE and R_n.

In a S*phagnum* mire in central Sweden the daily mean soil heat fluxes were found to be 11.0 Wm^{-2}, 11.3 Wm^{-2} and 6.6 Wm^{-2} for hollows in May, June and July, respectively, by Kellner (2001). The values were slightly lower for ridges, but we consider hollows to be most representative of the microtopographical structures that dominate at Degerö Stormyr. The mean (2001-2003) net radiation values in May, June and July in this study were 80, 87 and 92 Wm^{-2}, respectively. Thus, if we assume that the soil heat fluxes presented by Kellner (2001) are also representative for Degerö Stormyr, 14, 13 and 7% of net radiation was dissipated in soil heat fluxes. However, our small offset of 3 Wm^{-2} indicates that our energy balance closure was negligible biased by the soil heat flux.

The need for u_* filtering was evaluated and deemed to be unnecessary. Sottocornola and Kiely (2005) came to the same conclusion for a blanket bog in Ireland, as did Lafleur et al. (2003) for Mer Bleue. Possible reasons for the large variance at night and the low u_* values are that the mire is surrounded by upland forests and some internal circulation may be created by temperature differences between the two surfaces. Forests normally have much higher respiration rates than mires and it is possible that parcels of air with different composition from that of the internal boundary layer of the mire may affect the flux measurements under stable conditions. Further support for the conclusion that there was no need for u_* filtering is provided by the fact that the relationship between the night-time fluxes and temperature was similar for both high and low u_* conditions (data not shown).

Losses of data from Degerö Stormyr due to spurious measurements (e.g., measurements obtained in heavy rain or frost) normally accounted for less than 5% of the total data points. Power failure and computer hang-ups typically accounted for an additional 10%, which together with a few larger system failures resulted in the overall proportion of missing data being between 20-35% of the annual total. This is comparable to, or lower than, reported proportions in other EC system-based mire studies, for instance 33-44% of the data were missing in the study of the ombrotrophic mire Mer Bleu by Lafleur*, et al* (2003), 49% in the study of the wet minerogenic mire Kaamanen in Finland by Aurela, Laurila & Tuovinen (2002), and 43-51% in the study of a blanket bog in Ireland by Sottocornola & Kiely (2005).

Gap filling [Paper I]

There have been several suggestions regarding the best method for filling gaps. The ideal ways of filling gaps often differ between seasons, between day and night and between gaps of differing sizes. Growing-season gaps are often filled using some kind of model parameterization of daytime and night time fluxes (Aurela, Laurila & Tuovinen, 2001; Lafleur*, et al.*, 2003), while winter effluxes are estimated by averages, e.g. weekly averages, and < 2h gaps by linear interpolation (Aurela, Laurila & Tuovinen, 2001; Lafleur, Roulet & Admiral, 2001). Since the variations in half-hourly rates of CO_2-fluxes at mire ecosystems seem to be less dynamic than those of various other ecosystems, e.g. forest ecosystems, because of the low light saturation limits of *Sphagnum* species (see, for instance, Letts et al., (2005) other methods for replacing missing data could also be considered. Since species growing on the mire have low light saturation limits, the fluxes are not as sensitive to daytime variations in incoming radiation, i.e. cloud cover, as the CO_2-fluxes in forest systems. Most of the diurnal variation in CO_2-fluxes is related to the diurnal variation of irradiance and variation of higher frequency is of less importance.

Since there is no generally accepted gap-filling method (Falge*, et al.*, 2001) and parameterization appeared to be highly seasonally dependent in our dataset, the

MDV method was chosen. The accuracy and precision of the MDV approach used were as high as those of more complex approaches, e.g. various parameterizations (Lafleur, Griffis & Rouse, 2001), nonlinear regression models (Aubinet*, et al.*, 2000; Sottocornola & Kiely, 2005) or neural networks (Papale & Valentini, 2003), and was therefore considered the best choice. The same approach was used for filling gaps during both day and night in both summer and winter. The moving average window of 14 days applied was found to be an acceptable compromise, being large enough to minimize the effects of large flux values that occasionally occur, and short enough to avoid seasonal changes affecting the flux estimates. In our estimated budget for the five years considered, less than 25% of the estimated carbon fluxes emanate from gap-filled data.

Annual and seasonal NEE [Papers I, IV]

The oligotrophic minerotrophic mire, Degerö Stormyr, appeared to be a significant CO_2-C sink, the annual flux being significantly different from zero. The five-year average annual NEE at Degerö Stormyr was -54 ± 6 $gCO_2\text{-}Cm^{-2}yr^{-1}$, similar to the annual average of -56 ± 31 $gCO_2\text{-}Cm^{-2}yr^{-1}$ (1998-2002) recorded at the bog Mer Bleu, Canada (Lafleur*, et al.*, 2003), but higher than at the wet minerotrophic mire Kaamanen in northern Finland, -22 ± 20 $gCO_2\text{-}Cm^{-2}yr^{-1}$ during 1997-2002 (Aurela, Laurila & Tuovinen, 2004). The annual NEE during the years 1998-2000 at an ombrotrophic bog in Siberia was estimated to be in the range -43 to -62 $gCO_2\text{-}Cm^{-2}$ by Schulze et al. (2002), but these estimates were not based on full-year data since some of the winter months were not included, so they overestimate the annual net uptake. A blanket bog in Ireland reportedly had net uptake rates of 49 and 61 $gCO_2\text{-}Cm^{-2}yr^{-1}$, during 2003 and 2004, respectively (Sottocornola & Kiely, 2005). The annual cumulated growing season net uptake was lower than at Mer Bleue in Canada, being 76 $gCO_2\text{-}Cm^{-2}yr^{-1}$ (Lafleur*, et al.*, 2003), but between-year variation was lower. The growing season net uptake at the Finnish mire Kaamanen was 188 $gCO_2\text{-}Cm^{-2}$ (Aurela, Laurila & Tuovinen, 2004), which was higher than at Degerö.

Mer Bleue is an ombrotrophic bog in a location with a warmer climate than Degerö Stormyr, the mean annual temperature being +5.8°C (1961-1990) (Lafleur*, et al.*, 2003), compared to +1.2°C at Degerö Stormyr (1961-1990) (Alexandersson, Karlström & Larsson-Mccann, 1991). The long-term average precipitation at these sites is also higher; 910 mm (1961-1990) (Lafleur*, et al.*, 2003) and 523 mm (1961-1990), respectively (Alexandersson, Karlström & Larsson-Mccann, 1991). The Finnish wet minerotrophic mire Kaamanen is situated at higher latitude (69°N) than Degerö Stormyr (64°N) in a location with a more continental climate and much lower annual precipitation, 395 mm (Heikkinen *et al.*, 2002), and shorter growing season (due to the latitudinal difference).

Estimates of the annual CO_2 exchange at mires based on chamber measurements give similar or slightly higher values than available eddy covariance-based estimates. Estimates of annual NEE from a large palsa mire, Vaisejäggi, with similar vegetation to that at Degerö Stormyr were -39.6 $gCO_2\text{-}Cm^{-2}$ (1998) and -38 $gCO_2\text{-}Cm^{-2}$ (1999) with 1999 being a very wet year (Nykänen *et al.*, 2003). The winter estimates were based on snow profile measurements. In contrast, the annual NEE from the Finnish ombrotrophic Ahvensalo bog in Ilomantsi (65°N), represented a net loss of 82 gCO_2-$Cm^{-2}yr^{-1}$ during a year (1994) with an exceptionally dry summer (Alm et al. 1999b). In central Scotland, the net uptake across a lowland temperate peatland was found to be 28 (±2.5) gCO_2-Cm^{-2} over a 2-year period (1996-1998) (Billett*, et al.*, 2004). With few exceptions most estimates of average mire annual NEE values range between -20 and -60 gCO_2-$Cm^{-2}yr^{-1}$, and the average NEE from the oligotrophic minerogenic mire Degerö Stormyr is in the higher range of those values.

The wintertime or non-growing season efflux was low and more or less constant, but as stressed earlier by various authors, including Aurela et al. (2002) and Lafleur et al. (2001), it is the length of the season that makes the low winter time efflux a significant term in the annual budget. Prolongation of the non-growing season by one or two weeks affects the annual budget more indirectly than directly by shortening the growing season (when net uptake fluxes are tenfold higher than the winter effluxes) to a corresponding extent. At Degerö Stormyr the wintertime efflux is equivalent to 40 % of the growing season uptake. The effluxes during the winters of 2001-2002, 2002-2003, 2003-2004 and 2004-2005 were 36, 43, 37 and 38 gCO_2-Cm^{-2}, respectively; comparable to the 32.5-36.0 reported at Mer Bleue (Lafleur*, et al.*, 2003) and 41g at an ombrotrophic bog at Ahvensalo (Alm *et al.*, 1999a).

Despite the strong correlation of NEE to WL (Figure 9) found, the variation in NEE is probably mostly due to abiotic factors reflecting the weather conditions that prevailed during the growing seasons. The most important factor here could be assumed to be variations in incoming PAR, which is closely related to the photosynthetic activity, due to variations in cloudiness and associated changes in precipitation, evapotranspiration and (hence) the WL.

This finding somewhat contradicts the more or less accepted belief that a lowering of the WL increases the respiration rates and decreases NEE. However, at this oligotrophic fen the increases in photosynthesis due to increased energy inputs were stronger than the respiratory responses, and thus the NEE increased instead. The strong photosynthetic responses were probably due to the fact that there were no detectable water limitations during the study period.

The canopy conductance was quite insensitive (Figure 15) to changes in WL and was sufficient under all conditions to transport enough water to support the photosynthetic activity. This finding has been corroborated by modeling based on data from Degerö Stormyr (Yurova *et al.*, Submitted).

Daily NEE [Paper I]

Daily average fluxes for the growing season for 2001-2003 were -0.65 ± 0.57, -0.73 ± 0.61 and -0.68 ± 0.62 gCO_2-$Cm^{-2}d^{-1}$, respectively. Mean uptake rates were typically 1 gCO_2-$Cm^{-2}d^{-1}$ in June and July, but only half of this level in May and August. The daily maximum net uptake reached 1.8 gCO_2-$Cm^{-2}d^{-1}$ (95% percentile) while the daily maximal net release was 0.35 gCO_2-$Cm^{-2}d^{-1}$ (95% percentile) and occurred during the autumn. The average uptake rate at Mer Bleue during the net sink period is reportedly 0.81 gCO_2-Cm^{-2} d^{-1} (Lafleur, Roulet & Admiral, 2001), slightly higher than at Degerö Stormyr. During the summer (June to September 1998) mean daily NEE flux values varied considerably, from losses of 1.3 gCO_2-$Cm^{-2}d^{-1}$ to a maximum uptake of 2.3 gCO_2-$Cm^{-2}d^{-1}$. The mean daily fluxes from late fall and the snow-covered periods (November 5 to April 6, 1998-1999), were fairly constant, with effluxes of 0.3 gCO_2-$Cm^{-2}d^{-1}$ (Lafleur, Roulet & Admiral, 2001). The highest monthly daily average CO_2 net uptake at the minerotrophic mire Kaamanen in northern Finland was about -1.6 gCO_2-$Cm^{-2}d^{-1}$ and occurred in July, while the highest daily effluxes, about 1.1 gCO_2-$Cm^{-2}d^{-1}$, were observed in early June and August (1997). The daily NEE values in April were about 0.6 gCO_2-$Cm^{-2}d^{-1}$ (Aurela, Laurila & Tuovinen, 2001) and maximum daily NEE values of about -2.4 gCO_2-$Cm^{-2}d^{-1}$ were observed in July, while the highest daily respiration rates of about 0.68 gCO_2-$Cm^{-2}d^{-1}$ were observed just before and just after the sink period (1998) (Aurela, Laurila & Tuovinen, 2002). Compared to Degerö Stormyr, the Kaamanen and Mer Bleue mires both appear to have higher daily uptake rates. Mer Bleue also has a higher annual uptake than Degerö Stormyr, but Kaamanen has a lower annual net uptake, most likely due to the shorter growing season at the latter.

The maximum daytime uptake rates during the growing period at Degerö Stormyr were typically -0.10 $mgCO_2m^{-2}s^{-1}$ (95% percentile) and the night time maximum respiration rate was typically close to 0.07 $mgCO_2m^{-2}s^{-1}$ (95% percentile). Corresponding values at the bog Mer Bleue in southern Canada were -0.45 and 0.20 mg CO_2 $m^{-2}s^{-1}$, respectively (Lafleur, *et al.*, 2003). At an open peatland in north central Minnesota the peak uptake varied from 0.15 to 0.24 $mgCO_2m^{-2}s^{-1}$ (Shurpali, *et al.*, 1995), while the measured maximum net uptake rates from a minerotrophic wetland near Thompson, Manitoba, Canada, were 0.55 $mgCO_2m^{-2}s^{-1}$ at midsummer in 1994 and 1995 (Joiner *et al.*, 1999).

The highest downward flux densities found at Kaamanen were about 0.25 $mgCO_2m^{-2}s^{-1}$ and occurred at the end of July, while the highest respiration rates of 0.15 $mgCO_2m^{-2}$ s^{-1} were observed later in August (Aurela, Laurila & Tuovinen, 2001). Aurela et al. (2002) further report typical daytime peak values of about -0.20 $mgCO_2m^{-2}s^{-1}$ in July and a typical nighttime respiration rate in summer of 0.10 $mgCO_2m^{-2}s^{-1}$. Degerö Stormyr shows the same pattern with peak uptake in July and peak respiration rates in August/September, i.e. during early autumn, as also reported by Aurela et al. (1998). Relative to the compared mire sites, both the maximal daytime uptake and the night time release at the minerogenic Degerö Stormyr were relatively high. The relatively high net CO_2 effluxes during the autumn probably result from both autotrophic respiration in the large plant biomass and the combined effects of relatively high soil temperatures (which promote high rates of heterotrophic respiration) and low levels of PAR (which only allow low rates of photosynthesis).

Spring and autumn dynamics [Paper III]

The development of systems allowing continuous measurements to be taken and recorded using the eddy covariance technique have made it possible to analyze events involved in carbon dynamics at far greater temporal resolution than previously was possible. However, very few studies have analyzed spring (Aurela, Laurila & Tuovinen, 2004) and autumn variations and their influence on carbon budgets of ecosystems, and this study is the first to attempt to isolate the causal factors determining transitions of a fen to a CO_2 sink in spring and to a CO_2 source in autumn.

Although our data also support the importance of snowmelt (Aurela, Laurila & Tuovinen, 2004) we found strong correlations between soil thaw and the subsequent drop in the water level. We suggest that maintenance of a high water level (WL), and thus high water content in the *Sphagnum* during early spring, suppresses photosynthetic activity by limiting access to CO_2 (Silvola, 1990; Tuittila, Vasander & Laine, 2004; Williams & Flanagan, 1996) and this may be the cause of the delay in the transition to net accumulation of carbon in the spring that is associated with high water levels. The *Sphagnums* photosynthesize most efficiend at fresh weight/dry weight ratio of approximately 7 (Williams & Flanagan, 1996). The reduction in the supply of CO_2 is due to the lower solubility and slower transport of CO_2 in water than in a gaseous environment. This was also observed in a study concerning net ecosystem exchange (NEE) versus water level using data from Degerö Stormyr, where very high water levels were found to be associated with reductions in NEE (Yurova*, et al.*, Submitted). The cited study included modeling (of Degerö data) showing that the decrease observed in NEE is due to reductions in photosynthetic rates. This explains the observation that a delayed transition to a sink in spring corresponds to a lower WL. Thus, in order to compensate for the increased respiration induced by the higher soil temperature later in the spring, there have to be increases in the depth of the photosynthetic active layer, which corresponds to the aerated zone provided by a lower WL. Our data show that for a mid-May shift at least 7 cm is needed compared to a WL of 3 cm if the spring transition is approximately a week earlier, and the correlation between WL and the spring transition was significant (when data for 2003 are excluded). The deviant year 2003 exhibited a different pre-soil thaw history that might have interfered with the pattern observed in 2001, 2002, 2004 and 2005, with a lower NEE around the time of the spring transition as a result, but "recovered" soon after. As pointed out above, a greater "photosynthetic depth" was needed for photosynthesis to balance respiration, which in turn indicates that at least the top 7 cm of the peat layer is photosynthetically active or at least that a larger part of the peat profile photosynthesize more efficient.

Considering the importance of the water level the findings that the best predictors were the dates of snowmelt, soil thaw and start of soil heating were consistent with expectations. Snow (which melts and floods the mire), soil frost (which reduce the water percolating through the peat), and soil heating (which occurs when the soil has finished thawing), all influence the time when water can pass through the peat, leaving an aerobic zone that was found to be essential for a net accumulation of carbon. The start of soil heat flux has also been seen to correlate well with the date at which the daily mean air temperature begins to exceed +5°C (Moren & Perttu, 1994; Odin & Ottosson-Löfvenius, 1996), which defines the start of the vegetation season (meteorological definition).

Factors that affect both the amount of snow and (especially) the soil frost depth are the most important regulators of the spring transition since deep soil frost results in a thick ice core, which will of course delay the permeabilization of the soil and the spring transition. Large amounts of snow during early winter will insulate the peat and thus reduce its cooling and the development of soil frost, while late snow in spring will delay soil thawing.

During autumn the balance between photosynthesis and respiration was more straightforward. It was observed that cooling of the peat surface reduces respiration more than photosynthesis and the net accumulation period was therefore prolonged. These findings suggest that respiration responds more rapidly to temperature changes not only during spring (Aurela, Laurila & Tuovinen, 2004; Bubier *et al.*, 2003) but also during autumn. However, the net accumulation fluxes are smaller during autumn than the spring fluxes due to the lower amounts of incoming solar radiation.

The spring transition was more strongly associated with the ecosystem variables of the fen (e.g. the thawing of the frozen ice core and draining of the flooded surface) than in the autumn, when the temperature during the late growing season played a more important role and there was a more generally temperature-dependent relationship between respiration and photosynthesis, as in most ecosystems.

Both of the prediction models developed for the spring transitions and the one for the autumn transition are compatible with the points raised in the discussion above. The very good predictions they provide for the length of the growing season, which has been shown to be an important determinant of annual carbon budgets (Aurela, Laurila & Tuovinen, 2004; Sagerfors*, et al.*, 2006b), suggest they could be important tools for estimating the annual carbon exchange of peatlands.

Energy partitioning [Paper II]

The Bowen ratio, β, H/LE, was similar over the years 2002-2005, with a $\beta = 0.36 \pm 0.06$ for the five years. It was slightly lower in 2001, due to precipitation being more abundant and more evenly distributed over the growing season than in the other years. A higher water level means higher soil moisture, which leads to more energy being used for soil heating (data not shown) with a corresponding reduction in the sensible heat flux (H) as reflected in the lower β. The Bowen ratio at the oligotrophic fen Degerö Stormyr seems to be lower than reported values from other mires. The Bowen ratio at an open bog, Stormossen, central Sweden, reportedly decreased over the vegetation season from 0.9 to 0.6 in the years 1996 and 1997 [Kellner (2001), indicating that the mire surface was essentially drier there, and Lloyd et al. (2001) reported β-values for July at three different peatlands: an Arctic fen in Zackenberg valley, East Greenland, and two

Finish mires, an Aapa mire, Kaamanen, and a Palsa mire, Skalluvaara, of 0.87, 0.67 and 0.56, respectively. All being larger than Degerö, although these values might be biased towards a higher value when based on July data only, this if assuming dryer and warmer conditions during July compared to the rest of the growing season.

The LE/R_n ratio, also called the evaporative fraction, describes the energy partitioning to LE from R_n. The years 2001 and 2005, with high water levels, and the year 2002 with high evaporative forcing (increased VPD), yielded ratios of 0.6 - 0.66, which were higher than values for the years 2003-2004 (0.46 in both cases). The precipitation and temperatures during these years were close to the 30-year averages. The evaporative fraction at the bog Stormossen was relatively stable, 0.6 ± 0.05 during two growing seasons (June to September, 1996, May to September, 1997). For comparison, evaporative fractions during July of 0.36, 0.51 and 0.64 have been reported for Zackenberg valley, Kaamanen, and Skalluvaara, and vary somewhat between peatlands (Lloyd*, et al.*, 2001). The LE/R_n ratio at mires is controlled by both the amount of available water and a latitudinal component, reflecting the differences in evaporative forcing. Based on the limited number of studies cited above, the evaporation from bogs seems to be lower than from fens.

z0, r_a, and r_s

The seasonal variation of the roughness length z0, is quite obvious regarding the very smooth surface during the snow period compared to the vegetation during growing season. The intermediate values during spring and autumn should not be interpreted as vegetation growth but more reflecting the patchiness of vegetation, snow and/or open water at the mire surface. This variation of z0 must be considered in models were surface parameters are used to estimate the aerodynamic resistance. The fact that $r_s > r_a$, means that it is the surface resistance that mainly determines the water transport to the atmosphere. Even though it is easy to regard a mire as something wet more like a lake, the surface resistance is in the same order as in a forest ecosystem, when the peat surface gets drier, even larger.

Surface conductance [Paper II]

The surface conductance at Degerö Stormyr normally varied between 2-10 mms^{-1}, with lower values during the summer and in the afternoon. Maximum values were as high as 35 mms^{-1} during morning hours in spring or autumn under conditions with a high water table. The pronounced diurnal pattern is similar to that found in forests (Grelle, Lindroth & Molder, 1999; Lindroth, 1985). However, even if the diurnal variations in surface conductance are similar for forests and open mire ecosystems, the controls differ. In the forest ecosystem, stomatal conductance constitutes the major component of the surface conductance, while the contribution of stomatal conductance in a mire depends on the proportion of vascular plants within the vegetation. Although there is a small physiological contribution to the G_s at Degerö Stormyr, the dominant process is capillary transport of water. The surface conductance, G_s, was partly dependent on the WL but was relatively constant for water tables ranging between 0-10 cm, thereafter decreasing with water level. These observations are supported by the fact that the fetch area is dominated by the lawn plant community comprising *Sphagnum* species for which conditions are optimal when the water table is in the range 10-20 cm (Hayward & Clymo, 1982; Rydin & McDonald, 1985a; Rydin & McDonald, 1985b; Yurova*, et al.*, Submitted). *Sphagnum* mosses do not have the ability to transport water inside their stems, instead they rely on capillary forces determined by leaf form, the organization of the leaves on the branch and the organization of the branches on the stem (Hayward & Clymo, 1982). When the water table is lower than 20 cm, the lawn-dominating mosses are replaced by hummock-growing mosses, which have stronger capillary forces. A water table close to the mire surface allows carpet-inhabiting *Sphagnum* species to become established, which have poorly developed capillary forces (Hayward & Clymo, 1982).

The surface conductance was strongly controlled by the vapor pressure deficit (Figure 23). For surface conductance values binned according global radiation, the regressions explained 65 – 81 % of the variations (Figure 23). It was only at very low vapor pressure deficits that radiation had any effect on the surface conductance. This behavior demonstrates nicely the importance of the air humidity in controlling the evaporation from this mire system. Also in forests, the air humidity is an important controlling factor but for a different reason, namely through the sensitivity of stomata to vapor pressure deficit.

Mean reported values (for days 180 - 240) of canopy conductance from comparable ecosystems are all in the same range as those we found for Degerö Stormyr: 13 mms^{-1} in 1997 and 8 mms^{-1} in 1996 for the Artic fen in Zackenberg valley, East Greenland; 6 mms^{-1} for an Aapa mire, Kaamanen, Finland; and 7 mms^{-1} for a Palsa mire, Skalluvaara, Finland (Lloyd*, et al.*, 2001). The total range for the three mires over the same time period was 5 - 20 mms^{-1}. For comparison, recorded canopy conductance values in coniferous forest systems include: 5 - 20 mms^{-1} in a Scots pine forest system (Jädraås, Sweden) during August (Lindroth, 1985); up to 12 mms^{-1} in July for a Norway spruce/Scots pine stand (Norunda, Sweden) (Grelle, Lindroth & Molder, 1999); and 7 mms^{-1} for 50-year-old and 4 mms^{-1} for 100-year-old Norway spruce/Scots pine stands (Cienciala *et al.*, 1997).

Evapotranspiration [Paper II]

The mean AET to PET ratio was 76% ± 6% (±SE) over the five years, but it deviated considerably from this figure in two of the years. The higher AET to PET ratios, of approximately 85%, during 2001 and 2005, coincided with generally higher water levels than in the other years, in which the ratios were approximately 70%. More homogenous ratios have been found for the Canadian bog Mer Bleue, which is dominated by shrub vegetation, and a five-year average ratio of 52%, also obtained using the Penman-Monteith equation (Lafleur *et al.*, 2005a). This is quite a substantial difference, probably related to the fact that more water is available for evapotranspiration in a fen than in a bog.

Evapotranspiration rates at Degerö Stormyr were about 2-3 mmd^{-1} with peak values in most years of 4 mm d^{-1}, but occasionally higher peaks of 5-6 mmd^{-1} during the wet years 2001 and 2005. This is similar to measurements at the bog Mer Bleue, showing maximum average ET rates in June and July (5-year mean, 1998-2002) of 2.2-3.3 mmd^{-1} and maximum values of 4-5 mmd^{-1} (Lafleur*, et al.*, 2005a). Shimoyama et al. (2003) recorded ET values up to 4.2 mmd^{-1} from a west Siberian continental bog. Slightly lower ET values, but in the same range, have been recorded at a Canadian grassland near Lethbridge, Alta, (Wever, Flanagan & Carlson, 2002), where a maximum ET rate of 3 mmd^{-1} appears to be common, but rates up to 4.5 mmd^{-1} were detected during a significantly wetter then normal year.

The Priestley-Taylor (P-T) coefficient follows the same pattern as the ratio LE/R_n, which is to be expected since R_n is the single driving variable. The Penman-Monteith equation (giving PET) showed 2002 to be slightly different from the other years, because the vapor pressure deficit (δe) is included in the Pennman-Monteith equation but not in the P-T equation. A high δe increases PET, as also observed by Shimoyama et al. (2003), and for years such as 2002 when δe gave higher than normal evaporative forcing, the ET is overestimated by P-T. This can be seen, for example, by comparing the mean δe (May–August, 30 min values) for 2002 (0.67) to the mean δe for the other years (0.44 ± 0.08). The value for 2002 was significantly larger (>+2*SD). The Priestley-Taylor values at Degerö Stormyr varied between 0.86 and 1.17 for the five growing seasons (1 May–31 August) and were in the same range as the July median values reported for a number of other sites: 0.76 for the Arctic fen in Zackenberg valley, 0.82 for Kaamanen, and 0.99 for Skalluvaara (Lloyd*, et al.*, 2001). Corresponding values for a Canadian grassland were 0.6 (1999-2000) or less, but under very wet conditions (1998) values around 0.9 were reached (Wever, Flanagan & Carlson, 2002). Here the latitudinal trend is clear; ET increases as latitude decreases.

Water balance [Paper II]

There were significant temporal variations in the relative importance of different water fluxes at Degerö Stormyr: discharge dominated in spring and autumn while ET dominated during summer, with peak fluxes after midsummer. In addition, the dynamics of the runoff from the studied peatland are dominated by the spring snow melt; the inputs from precipitation in the form of snow melt being similar to the discharge outputs. In contrast, in forested catchments in the region the snow melt period constitutes an important period of soil recharge and is followed by substantially lower spring runoff (Laudon *et al.*, 2004).

Annual mean AET for the five study years at Degerö Stormyr was 271 ± 48 mm; considerably lower than the average (1998-2002) of 476 mm recorded at the bog Mer Bleue in southern Canada (Lafleur *et al.*, 2005b). Most of the differences in AET between these systems are due to the fact that AET constitutes a higher proportion of the precipitation (AET/P) at Mer Bleue (48 - 60%), than at Degerö Stormyr (26 - 66%). The accumulated water balance closure at Degerö Stormyr amounted to more than 90% and the relatively small residual can be explained by various factors, including *inter alia*, variations in the densities of higher vascular plants and the presence of small, alternative discharge creeks.

Total carbon budget [Paper IV]

The vertical net exchange of CO_2 (NEE) during the two years it was studied were similar to the annual NEE from the same site during 2001-2003 (-48, -61 and -56 $gCm^{-2}yr^{-1}$ respectively; (Sagerfors*, et al.*, 2006b)). The average NEE for the five years was -54 ± 5.6 $gCm^{-2}yr^{-}$. Multiyear measurements of annual NEE from mire ecosystems are still scarce, but based on six years EC measurements average values of -40 ± 40 $gCm^{-2}yr^{-}$ and -22 ± 20 $gCm^{-2}yr^{-}$ have been recorded for the bog Mer Bleu, southern Canada (Roulet *et al.*, Submitted) and a subarctic fen in northern Finland (Aurela, Laurila & Tuovinen, 2004), respectively. A lowland temperate peatland in Scotland yielded a two-year average of 28 ± 25 (±SD) $gCm^{-2}yr^{-}$ (Billett*, et al.*, 2004), and annual NEE values for an Atlantic blanket bog of -49 and -61 $gCm^{-2}yr^{-}$ in two consecutive years have been reported (Sottocornola & Kiely, 2005). This comparison indicates that the five-year average annual NEE at the oligotrophic minerogenic mire Degerö Stormyr of -54 ± 6 $gCm^{-2}yr^{-1}$ is in the higher range of EC-based reported estimates of average annual NEE from mire ecosystems. The annual values for the two years used to estimate the total annual C-budget, -55 and -48 $gCm^{-2}yr^{-}$, respectively, also represent the upper range of reported annual NEE of CO_2 values from mire ecosystems.

Methane emissions [Paper IV]

The rates of methane emission from the lawn plant community in this study are close to snow-free season average rates previously obtained at the same site during 1995 – 1997 (Granberg *et al.*, 2001), the gross average over the three years being 2.2 ± 7 $mgCH_4\text{-}Cm^{-2}d^{-1}$. The estimates of the annual methane release are in the average range of rates reported from other poor minerogenic mires (Huttunen*, et al.*, 2003; Nykanen *et al.*, 1998), but somewhat higher than regional estimates for 1994 for the two regions relevant to Degerö Stormyr. After accounting for weather anomalies in 1994 the long-term averages for 1980 – 1997 were estimated to be 12 ± 5 and 8 ± 4 $gCH_4\text{-}Cm^{-2}yr^{-1}$, (average ± 95% conf. limits) in these two regions (Nilsson*, et al.*, 2001). The estimated annual methane release for 2004 and 2005 are well in accordance with these long-term averages for oligotrophic mires.

Stream losses [Paper IV]

The estimated catchment carbon losses as stream TOC from the study site are consistent with export rates reported from boreal rivers in other regions of the world, which typically range between 1 to 10 $gCm^{-2}yr^{-1}$ (see (Hope, Billett & Cresser, 1994) for a review). However, TOC losses from more Atlantic mires are reported to be considerably higher; Billet et al. (2004) reported an average TOC loss of 28 $gCm^{-2}yr^{-1}$ over a two-year period from a temperate lowland mire catchment in Scotland. Furthermore, Laudon et al. (2004) found that the annual average export of TOC in the Degerö Stormyr region, ranges between 3.9 and 8.5 $gCm^{-2}yr^{-1}$ and the export is positively correlated with the areal extent of wetlands. The largest export rates in the study by Laudon et al. (2004) from a stream draining a wetland covering 40% of the catchment, also corresponds well with the runoff exports in the form of TOC found in this study (9.8 and 8.2 $gCm^{-2}yr^{-1}$ for 2004 and 2005, respectively).

The stream export of inorganic carbon (mainly as CO_2) comprised 20% to 30% of the total stream flux of carbon. This inorganic export is in the same order as reported in other studies. For example, Billet et al. (2004) found that inorganic carbon comprised 7% of the total stream exported from a peatland in Scotland whereas Dawson et al. (2002) found it comprised 31% of the total stream carbon exported from a wetland in Wales.

The association between large discharges, hydrological episodes and large stream exports of carbon we found is a recognized feature of high latitude wetlands. In northern regions long, snow-rich winters generate snow melt episodes that often dominate the water and carbon budget (Finlay *et al.*, 2006; Laudon, Kohler & Buffam, 2004). In this study this is corroborated by the fact that 38% and 40% of the stream carbon export occurred during four weeks of snow melt in the spring.

The average NEE at Degerö Stormyr during the growing season period amounted to 89 $gCm^{-2}yr^{-2}$, before adjustments for losses through emissions and runoff, which reduce this total over the two monitored years by 27 $gCm^{-2}yr^{-2}$ (61% constituted by the CO_2 loss during the non-growing season, 18% by emissions of CH_4-C and 21% by runoff losses). However, the C-loss through methane emission and runoff-C also constitute significant components, together responsible for 39% of the net C-losses. The relative importance between NEE, methane emission and runoff-C for the annual net carbon exchange in mires are most certainly quite different between mire types. While the controls of NEE, methane emissions and runoff C-export, also differs, the impact of different weather conditions on mire net carbon exchange will therefore differ considerably between mire types

The between-year variability of NEE at the oligotrophic fen, Degerö Stormyr was quite low with a coefficient of variation (CV) of 10%. Both air temperature sums and cumulated precipitation are important climate descriptors that influence the annual NEE. The variation in both precipitation and air temperature between the years 2001 – 2005 was higher than the variation in NEE. The CV for annual precipitation was 21% (net uptake season, 28%; net loss season, 16%) and the CV for annual temperature sum was 43% (net uptake season, 13%; net loss season, 37%). The largest variations in precipitation occurred during the NEE net uptake season while the largest variations in temperature sums occurred during the NEE net loss season. The low inter-annual variation in NEE at Degerö Stormyr is in accordance with results from response surface models based on both measured and modeled data, indicating that the NEE at Degerö Stormyr is relatively insensitive to variations in water table depths between 10 - 20 cm below the surface (Yurova*, et al.*, Submitted). This is the range in depths to the water table encountered during the NEE net uptake period. As long as the between-year variation in precipitation and evapotranspiration, driven by temperature and the air humidity deficit, results in a water table depth within this range the variation in these climatic variables will have a limited impact on NEE. The inter-annual variability in NEE was found to be much higher during a six-year period at both the ombrotrophic mire Mer Bleu, southern Canada (CV, 101%; (Roulet*, et al.*, Submitted) and a mesotrophic minerogenic subarctic fen in northern Finland (CV, 92%; (Aurela, Laurila & Tuovinen, 2004) the most limited variation in NEE for the five years at Degerö Stormyr. This comparison indicates that the inter-annual variability in NEE differs quite substantially between mires.

The two years of data for methane emission and runoff-C do not allow the between-year variability in these parameters to be estimated. However, the depth to the water table is well known to be one of the master variables controlling methane emissions within a given mire (Granberg *et al.*, 1997; Granberg*, et al.*, 2001) and variability in water table depths between 10 – 20 cm (Granberg*, et al.*, 1997) have a strong effect on the annual amount of methane emitted (Granberg*, et al.*, 2001). Based on modeled annual methane emissions at Degerö Stormyr, the average 5-year inter-annual variability over 17 years expressed as CV was 25%; approximately two and half times the inter-annual variability in measured annual NEE at Degerö Stormyr. The annual water runoff also varies considerably between years and the runoff C-export is highly correlated to the water runoff. Therefore, the runoff C-export probably varies strongly between years due to variations in precipitation and evapotranspiration. Both the methane emission and the export of runoff-C will increase with a more positive water balance, while NEE will be only modestly affected within the current average range of depths to the water table. We therefore conclude that the variation in annual net C accumulation in this type of oligotrophic minerogenic mire is highly influenced by the climate variables affecting methane emission and runoff-C. The average C-losses through methane emission and water runoff over the two years amounted to 25 $gCm^{-2}yr^{-1}$. Based on data on inter-annual variability in methane emissions (Granberg*, et al.*, 2001) and water runoff from first-order stream catchments (Bishop pers. comm.) neither of the annual fluxes through methane emissions and runoff C-exports are likely to exceed more than double the values we found. This indicates that the mire is unlikely to become a significant source of atmospheric carbon, since even a reduction in the current net balance of –27 $gCm^{-2}yr^{-1}$ by a further 25 $gCm^{-2}yr^{-1}$ result in balance not different from zero but still not indicating the mire being a significant source of carbon to the atmosphere. However, it should be noted that the year 2005 was characterized by relatively high precipitation (Sagerfors *et al.*, Manuscript), resulting in a water table level of – 8 cm, which is the same depth as during 2001, and also equal to the highest water table depths modeled for the time period of 1980-1997 by Granberg*, et al* (2001).

In comparison [Paper IV]

The estimated mire net C exchange of 28 $gCm^{-2}yr^{-1}$ compares well with the global estimate of 29 $gCm^{-2}yr^{-1}$ (Gorham, 1991). Based on 1125 peat cores from Finnish mires the average long-term apparent C-accumulation was estimated to be 23 ± 12 $gCm^{-2}yr^{-1}$, with an average for minerogenic mires of 15 $gCm^{-2}yr^{-1}$ (Tolonen & Turunen, 1996). The average accumulation of peat-C in a carpet plant community (*Sphagnum majus* dominated) during the last seven hundred years at a patterned fen just seventy kilometers away was 25 $gCm^{-2}yr^{-1}$ (data from “the little ice age" when net C accumulation dropped to 10 $gCm^{-2}yr^{-1}$ excluded) (Oldfield *et al.*, 1997). Even if the estimate for net C exchange at Degerö Stormyr only covers two years it by no means indicated a decline in mire net C exchange compared to apparent long term accumulation rates for similar mire types.

Carbon stuck on the way [Paper IV]

It should be noted that loss of carbon as TOC from a mire is not equal to a loss to the atmosphere. In order to compare current mire net C exchange rates with apparent C accumulation rates in mires the runoff export of TOC should be treated in a similar way to the NEE and methane emission to the atmosphere. To assess its net effect on the mire-atmosphere exchange the runoff export of TOC should be partitioned into mineralization to CO_2 and sedimentation. Current estimates and calculations suggest that the rate of mineralization is ca. three times higher than the rate of sedimentation of the exported TOC (Algesten *et al.*, 2004; Cole et al, In press; Molot & Dillon, 1996). The longer the water turn-over time in lakes the larger is the proportion TOC respired. The estimated C-loss as TOC for the two years was 8 $gCm^{-2}yr^{-1}$. If we apply the most conservative assumption that just 50% of the TOC is mineralized to CO_2 (Algesten*, et al.*, 2004; Cole et al, In press; Molot & Dillon, 1996) the annual net mire C-uptake from the atmosphere should be increased by an additional 4 $gCm^{-2}yr^{-1}$, i.e. the current estimate of the net-C exchange at Degerö Stormyr should be increased from -27 $gCm^{-2}yr^{-1}$ to -31 $gCm^{-2}yr^{-1}$.

Global change perspectives [Papers I, II, III, IV]

Of the suggested possible outcomes of possible global climate change scenarios, such as colder/wetter, colder/drier, warmer/wetter or perhaps warmer/drier climates in the future, the last would be the most likely to have a major impact on this mire ecosystem. Although a stable equilibrium appears to exist, a decrease began in G_s was found when water levels were below 10 cm, indicating that water supply may become more limited if a lowering of the water table occurs. Furthermore, drying of the mire may not necessarily require reductions in precipitation; changes in the temporal distribution of the precipitation could also tend to dry the mire, if more fell in winter as snow, which has been shown to result in increased discharge instead of recharge of water. A colder climate would result in a longer winter, more P would be in the form of snow, and this would also result in a drought effect, although lower temperatures also reduce ET and biological activity, which would ameliorate some of the effects.

In a recent report from the Swedish Meteorological and Hydrological Institute (SMHI) (Alexandersson, 2006), the last 15 years is compared with 1961-1990 reference normals regarding precipitation and temperature, both for the country of Sweden as a whole and regions within the country. The results for the Degerö Stormyr area suggest that precipitation has increased by 5-10% and mean annual temperatures by 1.0°C. The temporal variations are even larger. Precipitation has increased by 30-40% during June-August, fallen by 10-20% during September-November, remained at 90-100% of previous levels for December-February and remained unchanged for March-May. The largest temperature changes (+2.2°C) have occurred in December-February, followed by March-May (+0.8°C), June-August (+0.6°C) and September-November (+0.4°C). The same patterns were observed in climate data from Degerö Stormyr.

If these results represent ongoing trends, they indicate that the proportions of water inputs and temperatures in the growing season are rising. Both of these increases would be more likely to increase than to reduce NEE. Higher winter temperatures result (*inter alia*) in shallower soil frost, which is associated with earlier starts of the growing season [Paper III], and thus would also tend to increase NEE. Reductions in winter precipitation would also reduce the springflood and thus carbon losses through runoff. The only carbon efflux that might increase is loss of CH_4, which has been found to increase with increases in WL (Granberg, *et al.*, 1997). However, this would be at least partly compensated by reductions in soil respiration due to associated reductions in the size of the aerobic zone. Nevertheless, after accounting for all components of the carbon balance in 2005, which can be considered as the "worst case" within the five years of the study, with a high water level (and thus high methane emissions, 14 gCH_4-Cm^{-2}), low NEE (-48 gCO_2-Cm^{-2}) and TOC losses through runoff (8gCm^{-2}), the fen still appeared to be a significant net accumulator of carbon, gaining no less than 27 gCm^{-2}.

CONCLUSIONS

Carbon

The boreal oligotrophic minerotrophic mire Degerö Stormyr constituted a substantial net sink during the measurement period 2001 – 2005, comparable to the higher annual net uptake rates among previously investigated mires. The annual CO_2 net uptake was fairly similar between years, despite large differences in weather conditions; the years 2001 and 2005 being relatively wet and 2002 being relatively dry. Although our data only span five years, the results indicate that the uptake and release processes have similar responses to changes in weather conditions, i.e. if photosynthesis decreases, the loss of C through respiration also decreases. The temporal partitioning into a non-growing season and a growing season was of major importance for the annual budgets, and approximately 40% of the carbon uptake sequestered during the growing season was lost during the non-growing season. However, the major effect of changes in the relative lengths of the growing- and non-growing seasons is the impact they have on uptake. The average net daily CO_2 uptake during the growing season is substantially higher than the average net daily CO_2 release during the non-growing season, and thus the increase in numbers of days with a net uptake is more important than the decrease in days with net release. However, the length of the growing season is not the only important factor; a one-week advance in the start of spring affects the annual budget more than an additional week in autumn.

The WL is highly correlated with the spring transition since a high water level suppresses photosynthesis and thus delays it, due to the inundation of the *Sphagnum* and consequent reductions in CO_2 availability. Thus, a high water level delays the spring transition and causes a decrease in NEE. In autumn, the peat temperature is the predominant factor and a faster cooling of the peat, earlier in the autumn, reduces respiratory rates and prolongs the period in which photosynthesis dominates, thereby extending the CO_2 accumulation period.

In order to assess the impact of possible global climatic changes on the NEE budget of ecosystems like this, we suggest that priority should be given to factors affecting the WL during the spring and/or soil temperature during the autumn.

When CO_2 exchange rates from a number of mires are compared it is evident that the non-growing season efflux rates are quite similar and the differences in annual uptake are mainly determined by the growing season accumulation. Our data show that CO_2 uptake at Degerö Stormyr increases with increases in the length of the growing season, with advances in the time when soil frost thaws and with reductions in soil frost. Reductions in soil frost may be due to either higher temperatures or to increases in the amount of snow that falls early in the winter, thus providing an insulating effect against the cold temperatures. Both higher temperatures and changes in precipitation patterns have been mentioned as possible outcomes of global warming, and thus the carbon uptake in mires like Degerö Stormyr is more likely to increase in the future.

Even when considering all relevant carbon fluxes for a complete budget, accounting for both mire-atmosphere exchange (CO_2 and CH_4) and carbon transported by runoff (TOC, DIC, CH4), this boreal oligotrophic fen appears to be a stable carbon sink

Water

Evapotranspiration plays a significant role in the water budget, often exceeding discharge during the growing season. Evapotranspiration is driven by three major factors: water availability in the mire, vapor pressure deficit in the atmosphere and the amount of radiation reaching the surface. The mire water discharge is mainly controlled by the degree of saturation of the water store and the conductivity of the saturated peat. Water transmissivity approaches zero at a depth of 15 cm from the mire surface (Granberg et al 1999). The storage capacity at the mire surface is therefore limited, resulting in episodic runoff when there is a high water table, i.e. during spring and autumn. The ability to transport water vertically to the surface of the mire vegetation is described by the canopy conductance. This was found to be relatively constant for water levels up to 10 cm. As long as the climate allows the water table to vary within this range for most of the growing season, the current mire vegetation communities will probably persist. A drier climate, forcing the water table down for substantial periods of time during the growing season, would probably lead to vegetation dominated by hummock species. Conversely, to force the mire towards a more carpet-dominated vegetation, a much more humid climate would be required, allowing the water table to remain high for longer periods. Mire water regulation is more passive, and when wet, there are generally higher levels of water losses compared to stomata-regulated ecosystems. However, the opposite also occurs, a peat surface with low water content can appear very dry and protect the mire from drying out. The greatest differences between the two types of system are seen at low VPD and high R_n. The conclusion has to be that there is no threat to this ecosystem concerning water availability.

FINAL REMARKS

The answers you all have been waiting for since the introduction are: Sink and stable, respectively.

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Myrar har tillväxt och lagrat kol inbundet i växtmaterial sedan senaste istiden. Genom den höga grundvattenyta som är karakteristisk för myrar hamnar gammalt växtmaterial snabbt under grundvattenytan. Den nedbrytning av gamla växtdelar som alltjämt fortgår reduceras markant under den syrefria miljö som då uppkommer. Kolet kvarstår och lagras i myren och bildar den torv som hittas i en myr.

Eftersom all lagring av kol härstammar från av växter fixerat kol från luftens koldioxid är det viktigt att myrens växter lever under gynnsamma förhållanden gällande vattentillgång, temperatur och vackert väder. Detta för att upprätthålla sitt aktiva kolupptagande. Många befarar att den s.k. ”växthuseffekten” skall komma att ändra klimatet så pass mycket att kolbalansen hos olika ekosystem kommer att förändras. Speciellt intressant är myren som ekosystem då den generellt innehåller mer kol än andra. Kol som potentiellt skulle kunna avges till atmosfären och bidra till en ännu mer ökad koldioxid halt i luften och därmed till en förstärkt växthuseffekt.

Våra mätningar av kol- och vattenflöden på Degerö stormyr indikerar att denna myr är ett robust system som klarar variationer i temperatur och vattentillgång på ett stabilt sätt. Den visar till och med ett ökat kolupptag vid varmare väder, trots att det innebär en sänkning av grundvattenytan och därmed en relativ minskning av vattentillgången.