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Carbon Balance of the Arctic Wetlands in Europe

Doctoral dissertation

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ABSTRACT

Anthropogenic emissions increase the atmospheric greenhouse gas concentrations inducing climatic change. Predicted climatic warming is expected to result in changes in arctic wetland ecosystems. Changes in ecosystem structure and function will likely have important implications for direct feedbacks to global biogeochemical cycles. Arctic ecosystems presently store a large amount of soil carbon and there is a risk that a significant amount of this carbon will be released to the atmosphere with climate warming. Areas of discontinuous and continuous permafrost are especially vulnerable to the effects of warming.

Carbon gas exchange was studied in various wetland ecosystems in Kaamanen (sub-arctic), Kevo (arctic) and Lek Vorkuta (tundra) areas. Carbon dioxide (CO₂) and methane (CH₄) fluxes over a range of terrestrial and aquatic ecosystems were measured using static chamber techniques. The gas flux measurements and environmental parameters allowed fluxes to be extrapolated for growing season and annual carbon balances. A geographic information system (GIS) was used to upscale the fluxes to an areal balance first for the Lek Vorkuta catchment and further over the East European tundra. Carbon gas flux balances from years with different weather patterns were used to predict the possible consequences of variation in temperature and precipitation on ecosystem carbon dynamics.

In water saturated terrestrial ecosystems carbon accumulates as peat when C assimilation in photosynthesis exceeds the losses by respiration and decomposition. In general, wet *Sphagnum* sp. and *Carex* sp. dominated flarks and lawns were net sinks for carbon dioxide and net sources of methane. The source strength of CH₄ was coupled with water table level. On drier shrub dominated hummocks the CO₂ circulation was high and the ecosystem C sink/source strength depended on the soil respiration. All palsas were sources of atmospheric carbon. In addition, the degradation of palsas supplied nutrients to the waterlogged palsa margin areas promoting decomposition and CH₄ emissions. The net ecosystem production in a fertile thermokarst lake margin showed zero-balance despite of the high biomass and photosynthesis potential. A whole thermokarst lake, and also a arctic river, were constant sources of carbon to the atmosphere.

East European tundra lost approximately 8.1 Tg carbon during the summer 2001 when temperature was 1.6 °C higher than the long-term mean. In a warm summer the active layer thickness is greater increasing the decomposition in active soil layer. Wet terrestrial tundra ecosystems have a high potential to shift from sink to source under changing climate conditions. In drier tundra ecosystems, the rate of organic matter decomposition and CO₂ efflux will increase with rising soil temperature. The short term changes in ecosystem carbon exchange balance are reflecting the variations in temperature and moisture regimes while long-term changes in carbon balance are affected by changes in vegetation characteristics and permafrost level. An important finding is that even in the present climatic conditions the East European tundra is vulnerable to carbon loss to the atmosphere, further accelerating the global warming.

Universal Decimal Classification: 574.4, 504.7

CAB Thesaurus: climatic change; carbon cycle; greenhouse gases; carbon dioxide; methane; wetlands; arctic regions; tundra; geographical information systems

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We learn from the history. Since our ancestors fell from the trees the growth of human population was up to the communication and social skills as much as hunting skills. The communication engendered questions and answers. At some point human nature became inquisitive. Yet, the knowledge or excess information can not guarantee right conclusions and decisions.

Science, elegantly defined as “the field of study which attempts to describe and understand the nature of the universe in whole or part”, is an arrow's head of the previous knowledge. One of the major principles of science is to question the prevailing knowledge. The critics and suggestion of options are often needed to point out the “right” way.

Alongside with this thesis I have tumbled the first steps in research. Two excellent supervising scientists, Professor Pertti J. Martikainen and Dosent Jukka Alm, have patiently responded my questions, guided me through the misinterpretations and widened my view of life. They also pointed out the essence of good question in solving problems. You run out of superlatives with these two gentlemen.

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I have discovered that the fieldwork is like a leap to the history. We started the field season in 1998 in Russia with hands down and thumbs up. Unfortunately, the mighty customs of Russia confiscated our equipment due to our ignorance of Russian law! At the timing of the episode, we exercised the communication skills with our Russian field personnel from Komi Science Centre, Syktyvkar and other TUNDRA personnel. Especially warm memories gave the time in stony island in Kosju River near Ural Mountains. The predators were present in a form of excess mosquito's. Yet the craftsmen and moviemakers made the time enjoyable.

I have excellent memories from all the field seasons. Despite of the various episodes of misfortune, I owe humble gratitude to my Russian and Finnish colleagues at the field. Enthusiastic field worker, botanist PhD V. Elsakov was my soul mate sharing all the ups and downs in Russian customs. Ms. T. Kodjanova was the chef of chefs. Someday, Ms. I. Alatalo, Ms. A.-L. Lohila and Mr. T. Turrek may be asked to recall their memories from the field studies; I hope they have many.

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Dedicated to Mirjami Haasiosalo

Kuopio May 2003

TERMS AND ABBREVIATIONS

Aapa: A mire complex with minerotrophic central parts, occurring in the middle or northern boreal region. A pronounced surface pattern of wet flarks and hummocky strings oriented along the contours are common.

Acrotelm: At least temporarily aerated (may extend below WT) surface layer of peat.

Arctic: The regions north of the Arctic Circle. Arctic Circle is the imaginary circle round the earth, parallel to the equator, at latitude 66° 32' N.

Catotelm: Permanently saturated and anoxic layer of peat underlying the acrotelm.

GIS: Geographical Information System. Satellite image based map information.

MAT: Mean annual temperature.

Minerotrophic: Receives nutrients from groundwater via lateral or vertical water flow. Mineral status: described with subclasses eutrophic, mesotrophic and oligotrophic from rich to poor, respectively.

MWT: Mean water table during the summer.

NEE: Net ecosystem exchange, instantaneous CO₂ balance.

NEP: Net ecosystem production, modelled ($P_G - R_{TOT}$) over time.

Ombrotrophic: Receive nutrients only from precipitation i.e. rain or snow.

Palsa Plateau or Peat Plateau: Large palsa surface extending hundreds of meters in diameter.

Palsa: is a peat mound with permanent ice core and a possible height of several meters (1 - 3 meters).

PAR: photosynthetically active radiation. [$\mu\text{mol m}^{-2} \text{s}^{-1}$]

Peat: organic deposit of terrestrial origin in wetlands.

Peatland (mire): Peat forming terrestrial ecosystem, term includes ombrotrophic bogs and minerotrophic fens.

P_G: Gross photosynthesis.

R_{TOT}: Total respiration.

Sub-arctic: Intermediate ecotone between boreal and arctic.

Thermokarst: Meltdown and thermal erosion of permafrost: a pond is formed at the edge of palsa where peat erodes.

Tundra: Treeless arctic region usually with patterned surfaces with underlying discontinuous or continuous permafrost.

Wetland: General classification for high water table or shallow open water ecosystems.

WT: Water table.

1 Gg = 10⁹ g = 1000 t

1 Tg = 10¹² g = 1 Mt

1 Pg = 10¹⁵ g = 1 Gt

1 Mha = 10⁶ ha = 10⁴ km²

LIST OF ORIGINAL PUBLICATIONS

The following articles are referred by their roman numerals in the text:

- I. Heikkinen, J. E. P., M. Maljanen, M. Aurela, K. J. Hargreaves, and P. J. Martikainen, Carbon dioxide and methane dynamics in a sub-arctic peatland in northern Finland, *Polar Research*, 21(1), 49-62, 2002.
- II. Nykänen, H., J. E. P. Heikkinen, L. Pirinen, K. Tiilikainen and P. J. Martikainen, Annual CO₂ exchange and CH₄ fluxes on a subarctic palsamire during climatically different years, *Global Biogeochemical Cycles*, 17(1), 1018, doi:10.1029/2002GB001861, 2003.
- III. Heikkinen, J. E. P., V. Elsakov, and P. J. Martikainen., Carbon dioxide and methane dynamics and annual carbon balance in tundra wetland in north east Europe, Russia, *Global Biogeochemical Cycles*, 16(4), 1115 doi:10.1029/2002GB001930, 2002.
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- V. Heikkinen J. E. P., T. Virtanen, P. Kuhry, K. Mikkola and P. J. Martikainen. The carbon balance of the East European tundra is highly sensitive to global warming. Submitted.

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PREFACE

The large majority of scientific experts, recognizing that scientific uncertainties exist, believe that human-induced climate change is inevitable [IPCC, 2001]. Indeed, during the last few years, many parts of the world have suffered major heat waves, floods, droughts and fires leading to significant economic losses and loss of life. In addition, there is evidence that precipitation patterns are changing, that sea level is rising, that glaciers are retreating world-wide, that Arctic sea ice is thinning, and that the incidence of extreme weather events is increasing in some parts of the world [IPCC, 2001]. While individual events cannot be directly linked to human-induced climate change, the frequency and magnitude of these types of events are predicted to increase in a warmer world. The climatic effects of global warming are expected to be most pronounced in the Arctic [IPCC, 2001]. However, there are regional differences among the recent trends in climate observations [Maxwell, 1997]. In Canadian high latitudes the trend of annual temperature is towards warming and in continental Russia the trend is opposite [IPCC, 2001].

The Earth's surface temperature of 20th century is clearly warmer than any other century during the last thousand years [IPCC, 2001]. The Earth has warmed by between 0.4 and 0.8 degree centigrade over the last century, with land areas warming more than the oceans, and with the last two decades being the hottest of the century. The change in Earth surface temperatures is primarily considered to be due to the combustion of fossil fuels (coal, oil and gas), deforestation and agricultural activities. Since the beginning of the pre-industrial era around 1750, the atmospheric concentrations of carbon dioxide has grown nearly by 30% [IPCC, 2001] and methane by more than a factor of two [Dlugokency

et al. 1998]. The current atmospheric carbon dioxide concentration, 365 ppm, increases at the rate of 1.5 ppm yr⁻¹ mainly due to the anthropogenic emissions. Atmospheric methane concentration (1800 ppb) continues to increase at the rate of 9 ppb yr⁻¹ despite the overall rate of increase has slowed [Dlugokency *et al.*, 1998; IPCC, 2001; Khalil *et al.*, 1993].

Coupled physical-biogeochemical climate models that include a dynamic global vegetation model assume that mixing ratio of atmospheric carbon dioxide (CO₂) will be from 540 to 960 ppm by 2100 [Joos *et al.*, 2001]. The most important uncertainties in global climate change predictions arise from the complexity of the Earth climatic system. The lack of knowledge of many important micro and macro scale interactions and feedback mechanisms increase the uncertainty of the predicted consequences of global warming. The present GCM's predict the climate according to the 2 x CO₂ scenarios. However, the fact that temperature is more variable both spatially and temporally than is CO₂ concentration makes the human induced warming much more difficult to distinguish against the natural background variation [Vitousek, 1994].

Changes in climate are predicted to be greatest at high latitude environments and should therefore be first identified in arctic regions. These changes are likely to impact the ecosystems and their biota and affect the feedbacks from these ecosystems to the climate. The goals of measuring and predicting climate change impact on arctic ecosystems are fraught with difficulty and uncertainty largely because there is often considerable variability in all aspects of climate change, ecosystems responses to it and the ways which we assess the impacts.

1. INTRODUCTION

1.1. Carbon dynamics in northern wetlands

The northern mires or peatlands, where dead organic matter accumulates as peat, are sustained by humid climate and high water table [Gorham, 1991]. In peatlands, the atmospheric CO₂ is fixed to the green plant biomass through photosynthesis during the growing season. The dead plant biomass enters the decomposition processes where part of the plant derived matter is deposited as soil organic matter in waterlogged conditions. The organic matter undergoes complex transformation processes by soil fauna and microbes in oxic acrotelm and anoxic catotelm. Oxidic decomposition returns over 90% of the fixed organic carbon back to the atmosphere as CO₂ [Clymo, 1983] and the remaining fraction of carbon descends in to the catotelm, increasing the thickness of the peat matrix because of very slow decay rate. Approximately 50% of the peat matrix is carbon [Gorham, 1991; Turunen *et al.*, 2001].

The present peatlands began to form about 14000 B.P., spreading across the landscape until 4000 B.P. [Gorham, 1991; Gorham *et al.*, 1992]. In Europe, the age of boreal peatlands are between 5000 and 9500 years while arctic peatlands are generally younger, 3000 to 5000 years old [Botch *et al.*, 1995; Tolonen *et al.*, 1996; Turunen *et al.*, 2001; Turunen *et al.*, 2002]. The estimate of area-weighted long term apparent rate of carbon accumulation for Finnish undrained boreal and subarctic mire areas is 18.5 g C m⁻² yr⁻¹ [Turunen *et al.*, 2002]. The long-term peat accumulation rates for European part of Russian polygonal mires, palsa mires, aapa mires and fens are estimated to 12, 16, 40 and 80 g C m⁻² yr⁻¹, respectively [Botch *et al.*, 1995; Turunen *et al.*, 2001]. However, the relationship of long-term carbon accumulation rate with the present carbon accumulation rate is not known. Eventually, peat accumulation is supposed to decrease with time because the ratio of photosynthesis to decomposition decreases with thickening catotelm [Clymo, 1983; Turunen *et al.*, 1999].

The arctic tundra, including upland and peat soils, covers around 560 Mha [Wookey, 2002]. The world peatlands cover approximately 500 Mha, most peatlands locating in arctic, boreal and temperate zones. Boreal and subarctic peatlands (350 Mha) contain between 270 and 370 Pg C [Gorham, 1991; Sjörs, 1981; Turunen *et al.*, 2002] which is 60% of the atmospheric carbon pool or 1/3 of the global soil organic carbon pool of 1395 Pg C [Post *et al.*, 1982]. The areal extent of Russian

tundra zone is estimated to be 235 Mha from where 23.2 Mha is located in east Europe [Zamolodchikov *et al.*, 2001]. The total peatland area of the Russia has been estimated at 165 Mha with 215 Pg peat carbon pool [Botch *et al.*, 1995]. The mismatch in these numbers suggests that only part of the tundra is defined as peatland. Uncertainties of the areal extent of peatlands, peatland definition and peatland classification suggest that these figures should be interpreted carefully.

Terrestrial ecosystems release carbon to the atmosphere mainly as CO₂ and CH₄ through faunal, oxic respiration by plants, fauna and microorganisms, and by microbial anaerobic processes. During the summer, when the photosynthetic carbon uptake exceeds the carbon losses, the northern ecosystem may become a carbon sink. Annual carbon balance is the carbon gain subtracted by the carbon losses in respiration, decomposition, weathering (mostly leaching) and occasional fire [Alm *et al.*, 1997].

Photosynthesis is a light controlled process where CO₂ is a source of carbon and light is used as energy. In general, the plant growth in arctic wetland ecosystems is not light limited [Chapin III *et al.*, 1985]. In most wetland ecosystems the light saturation point is close to the 500 μmol m⁻² s⁻¹ while on sunny days with open sky the direct maximum photosynthetically active radiation (PAR) values vary from 1500 to 1800 μmol m⁻² s⁻¹, the level of irradiation decreasing northwards [III; IV; Oechel *et al.*, 1995]. PAR has a clear diurnal cycle with early morning (hours 02-04) minimum and early afternoon (12-14) maximum [Oechel *et al.*, 1995]. In addition, rate of photosynthesis depends on the species composition and quantity of the green biomass in the ecosystem, defining the variation in seasonal cycle of gas fluxes. Bryophytes have an especially low light saturation point yet they can utilize a lower radiation intensity than shrubs or sedges [Harley *et al.*, 1989; Titus *et al.*, 2002].

Total soil CO₂ release (R_{TOT}) includes aerobic and anaerobic decomposition, root respiration and respiration of soil fauna. In northern peatlands the autotrophic and heterotrophic respiration comprise 1/3 of the CO₂ uptake in photosynthesis during the intensive growth [I; III; Bubier *et al.*, 1998]. The rate of autotrophic respiration is regulated by photosynthesis and temperature while heterotrophic respiration is controlled largely by soil temperature [Chapman *et al.*, 1998]. Root associated respiration follows the phenology of the vegetation and may account for 10-45% of the total soil CO₂ release

[Silvola *et al.*, 1996], mainly originating from the turnover of fine root litter and root exudates.

Some carbon and nutrients are lost from terrestrial ecosystems to aquatic ecosystems by leaching of dissolved and particulate organic matter. Depending on the landscape, lateral leaching is mainly due to runoff induced by snowmelt or rainfall. With a limited water storage capacity in the active layer, greater floods will occur from rainfall than snowmelt [Kane, 1997]. Nevertheless, every spring significant streamflow occurs in arctic watersheds due to the volume of water in snowpack and because snow damming produces a higher peak runoff response [Dankers, 2002; Kane, 1997]. Aquatic ecosystems are thus recognized as important sources of CO₂ and CH₄ in arctic [IV; Kling *et al.*, 1991; Kling *et al.*, 1992; Ramlal *et al.*, 1994; Zimov *et al.*, 1997].

Significant amount of the carbon fixed in the growing season is released from soils during the winter as CO₂ and CH₄ [III; Alm *et al.*, 1999; Brooks *et al.*, 1997; Dise, 1992; Fahnestock *et al.*, 1999; Lafleur *et al.*, 2001; Melloh *et al.*, 1996; Panikov *et al.*, 2000; Sommerfeld *et al.*, 1993; Zimov *et al.*, 1993]. Soil biological activity, in part, controls the production rate during the winter while gas exchange is controlled by the snowpack characteristics i.e. porosity, tortuosity and depth of snowpack [Mast *et al.*, 1998; Sommerfeld *et al.*, 1993]. Peat may also contain a large storage of gases in bubbles, allowing a steady release during the winter. There is a high temporal and spatial variation in snowpack characteristics which also affects the underlying soil processes and eventually, gas emissions [Brooks *et al.*, 1996]. The total winter C loss is controlled by the duration and timing of snow accumulation especially in ecosystems where the snow cover allowed the underlying soil to thaw [Brooks *et al.*, 1996; Brooks *et al.*, 1997; Lafleur *et al.*, 2001].

1.2. Climatic warming feedbacks on carbon fluxes in arctic wetlands

Hydrology plays an important role in Earth's climate through the water and energy fluxes and is interrelated with meteorology [Kane, 1997]. There is high annual and seasonal natural variability in precipitation as snow and rain. In arctic the land surface is covered with snow over half of the year. With thicker, longer lasting snowpacks, the albedo (reflected energy) remains high for longer periods of time reducing the energy flux to the soil. Bare upland areas with less snow cover and snowpacks with plants penetrating the surface reduce the albedo and melt first [Kane, 1997]. With no change

in snowfall, snowmelt will probably occur earlier initiating lower albedo, soil thawing and vegetation growth. However, increased winter time precipitation is likely to increase the snow cover in depressions (drifting snow), depending on the wintertime temperature cycles and winds in open areas.

One of the most important consequences of climatic warming in the northern wetlands may be winter warming and duration of snow cover. Winter warming will probably change the overwintering capability of plants, especially by promoting excessively early deacclimation, i.e. premature loss of frost hardiness and earlier growth onset leading to increased risk of frost damage in spring. The changes in season length, and temperature regimes within, may profoundly affect plant, community, and ecosystem processes in arctic, both directly and indirectly [Oberbauer *et al.*, 1998]. It has been suggested that the snow-free period may increase for one month or even more in the next century [Maxwell, 1997]. The albedo of an arctic snow cover is approximately 0.8, and while snow free albedo is 0.2 [Kane, 1997]. The increase in absorbed energy and radiant energy increases the soil warming and respiration.

Discontinuous and continuous permafrost wetlands are particularly vulnerable to climate change because biological processes are affected by the presence of permafrost and duration of the snow-free season. Changes in permafrost depth may result in increased water movement, mobilization of nutrients and subsequently higher rates of primary productivity and decomposition [Billings *et al.*, 1982; Zoltai, 1993]. In addition, in patterned peat plateau ecosystems the result of warming and water flowing may be an accelerated erosion and formation of thermokarst lakes [Billings, 1997]. And further, the watercourses may change in shape or place pronouncing the runoff and peak discharge of melt water. In discontinuous permafrost, a warmer climate may eliminate the shallow permafrost areas and result in leaching of organics directly to the groundwater [Kane, 1997].

During the summer, soil thermal properties are moisture dependent, i.e. soil moisture affects the dynamics of soil temperature, which in turn affects the soil moisture through changes in active layer thickness and drainage conditions [Waelbroeck *et al.*, 1997]. However, soil moisture is primarily determined by soil temperature over precipitation (via evapotranspiration), thus in a warming climate soils are expected to become drier [Bridgham *et al.*, 1999; Rowntree, 1997]. An increase in decomposition in soil could result in higher nutrient

availability and primary productivity, which may compensate the loss of carbon to the atmosphere [Oechel *et al.*, 1993]. In high water table ecosystems, the plant emergence is often delayed by the temporary flooding and slow heat transfer in melting process. This may reduce the potential carbon uptake and delay the growing period.

Availability of atmospheric CO₂ and nitrogen control the plant growth pattern [Billings *et al.*, 1984]. In nutrient limited soils, plants allocate the resources preferentially below ground in order to pre-empt critical deficiencies. However, on the fertile soils plant growth is functionally limited by photosynthetic carbon and thus the plant allocates the energy into leaf growth to acquire growth limiting carbon. Leaf development is crucial to plant function since the leaves control light interception, photosynthesis, water use and therefore, total plant productivity. Vegetation growth in elevated CO₂ alters plant structure through its effects on both primary and secondary meristems of shoots and roots [Pritchard *et al.*, 1999]. Despite the fact that tundra plants are well adapted to low temperatures and arid conditions, the greatest impact of climate change to vegetation and carbon gas fluxes may arise from the consequences of soil warming [Chapin III *et al.*, 1985; Kane, 1997].

1.3. Study objectives

The objectives of the research were:

- To study the carbon gas dynamics in different latitudinal and longitudinal arctic wetlands in Europe (I-IV),
- To study the environmental and climatic factors affecting the gas fluxes (I-IV),
- To construct seasonal / annual carbon balance for arctic and tundra wetlands in present climate (II-IV),
- To study the sensitivity of ecosystem carbon balance to climatic variability (II, IV),
- Upscale the present day seasonal carbon balance for Usa basin and whole European tundra (IV-V).

2. MATERIALS AND METHODS

2.1. Study sites

The climatic gradients within the study sites provided an excellent opportunity to compare carbon gas dynamics and carbon balance between different ecosystems. There is a latitudinal North-South temperature gradient between north boreal Kaamanen [I] and sub-arctic Kevo [II], while arctic Kevo and Lek Vorkuta [III, IV] form a clear East-West oceanic-continental gradient. See the articles for more detail descriptions of seasonal climate conditions [I, II and III].

In Finland, the main wetland complex types are raised bogs and aapa mires [Euroala *et al.*, 1984; Seppä, 1996]. The distinct morphological features, especially surface patterns of hummock / hollow alternation in raised bogs and strings and pools in aapa mires, can be used to separate the boreal raised bogs and north boreal aapa mires [Seppä, 1996; Sjörs, 1961]. In palsa mire zone, classified also as the sub-arctic zone, the string-pool topography disappears and palsas become dominant peatland features [Euroala *et al.*, 1984; Seppä, 1996].

The European arctic wetlands are mainly situated in northern Scandinavia and continental part of East European Russia. Within Europe, tundra soils vary from the dry, mineral, calcareous or siliceous soils of polar deserts and semi deserts in the high-arctic of Svalbad, Greenland, Franz Joseph Land and Novaya Zemlya, to the deep acidic peat's of sub-arctic bogs of Iceland, North Fennoscandia and Northwest Russia [Heal *et al.*, 1998].

2.2. Methods

Arctic and boreal landscapes exhibit a considerable spatial heterogeneity in microtopography, water table depth, soil temperature, and plant species composition. Thus it is necessary to use various measurement approaches such as chamber and eddy covariance (EC) techniques to cover all the spatial and temporal variations within ecosystems gas fluxes. While the chamber technique is applicable to micro-scale flux measurements, the EC technique can successfully be applied to the landscape-scale measurements of net carbon flux and energy balance [Aurela *et al.*, 1998; Frolking *et al.*, 2002; Hargreaves *et al.*, 1998; Hargreaves *et al.*, 2001; Lafleur *et al.*, 2001; Lafleur *et al.*, 1997; Soegaard *et al.*, 1999; Vourlitis *et al.*, 1999]. In intercomparison studies, the chamber and the eddy covariance techniques have yielded similar carbon fluxes [Norman *et al.*, 1997].

We applied the closed (static) chamber technique [Carrol *et al.*, 1997; Crill, 1991] to measure the CO₂ and CH₄ fluxes on various functional surfaces in Kaamanen, Kevo and Lek Vorkuta [I-IV]. In terrestrial ecosystems we used aluminum collar to frame the ecosystem under study while in aquatic systems floating chambers were used. For gas sampling, a transparent chamber (CO₂) or aluminum chamber (CH₄) was placed on grooved collar and sealed with water. The CO₂ concentration change vs. time inside the chamber was measured and recorded with an infrared analyzer while for CH₄ measurements samples were collected in gas tight glass vials and transported to the laboratory for further analysis using a gas chromatography [III; IV].

A weather station recorded environmental variables such as wind speed and direction, PAR and T_{Air} and ground temperatures, at 10 minute intervals. In addition, soil temperature at different depths, water table and the depth of permafrost were manually recorded at the same time as gas flux measurements.

In order to estimate the gross photosynthesis we measured the net ecosystem exchange (NEE) with transparent chamber and subsequently, total respiration (R_{TOT}) in similar temperature and moisture conditions by blocking the light entering the chamber. The gross photosynthesis (P_G) was calculated by subtracting (R_{TOT}) from the (NEE), assuming that the plant photo-respiration equals the plant respiration under dark conditions (Eq. 1).

$$NEE = P_G - R_{TOT} \quad (1)$$

For seasonal CO₂ balance estimates, models using hourly rates of PAR, T_{AIR} and effective temperature index (ETI) were developed. Below is the formula for photosynthesis (Eq. 2) and respiration (Eq. 3) [III, IV].

$$P_G = (Q \cdot PAR) / (K + PAR) + b_1 \cdot ETI + b_2 \cdot T_{AIR} + c_1 \quad (2)$$

$$\ln R_{TOT} = b_3 \cdot T_{AIR} + b_4 \cdot ETI + c_2 \quad (3)$$

where, Q is an asymptote at the maximum P_G, K is the light intensity where 50% of the maximum P_G is reached. The b_x and c_x denote constants. The seasonal carbon balance was integrated from the hourly results (usually for 100 days) calculated for each individual collars. The regression models that were used to fill in the data between measurements were site and year specific, i.e. they can not be applied to the other surfaces or seasons [IV].

Annual or seasonal carbon balance (A) for a peatland ecosystem can be presented as follows (Eq. 4) [Alm *et al.*, 1999]:

$$A = P_G - (R_{TOT} + D + W + F) \quad (4)$$

where, P_G is the gross photosynthesis, total respiration (R_{TOT}) includes respiration of soil organisms and plants, D includes carbon gases (CO₂ + CH₄) from the anaerobic decomposition, W is weathering (DOC and DIC) and F is possible carbon loss in fire (ignored here in annual balance).

The gradient technique was used to estimate the carbon fluxes from the snowpack [II; III]. The carbon gas concentrations from 5 cm below the surface to 5 cm above the soil surface of the snowpack were measured. Gas fluxes through snow were calculated according to the Fick's first law of diffusion (Eq. 5).

$$J_g = D_g (dC_g / dz) \cdot t, \quad (5)$$

where J_g is the diffusive flux for a gas (g) along a concentration difference (dC_g) below z (cm) of snowpack with an air filled snow porosity (t). Diffusion coefficients (D_g) for CO₂ (0.139 cm² s⁻¹) and CH₄ (0.22 cm² s⁻¹) were taken from [Sommerfeld *et al.*, 1993]. The methods and formulae are described in more details in the articles [I-IV].

2.3. Estimating the areal carbon balance

Arctic ecosystems are highly heterogenous in vegetation, hydrology and soil properties [Whalen *et al.*, 1990] and it is possible that there are striking differences between any two wetland ecosystems. For example, the Skalluvaara fen in Kevo has characteristic palsa formations in hollow dominated peatland while in Kaamanen the fens are ridge-hollow or flark-lawn-string wetland ecosystems [I, II]. The surface pattern in palsa peatland is relatively stable while aapa mires consisting strings and pools are unstable due to the hydrostatic pressure from pools to strings [Seppä, 1996]. Within Lek Vorkuta study area there is more microscale variation in hydrological, vegetational and mineral characteristics [III, IV] compared to that of the Kevo study area. In addition, the presence of permafrost dominates the terrestrial ecosystems in Lek Vorkuta while ecosystems in Kevo and Kaamanen become frost free in late July [II, III].

The whole ecosystem carbon balance depends on the areal coverage of the different ecosystems and their specific unit carbon fluxes [Waddington *et al.*, 1996]. A detailed classification of vegetation with other environmental parameters (especially hydrology) and the combination of data in a GIS with a high spatial resolution improves the areal estimates of the present day carbon balance [IV; Roulet *et al.*, 1992]. For that purpose vegetation and landuse classification were produced for the Usa basin [Virtanen *et al.*, Manuscript]. Area of the Usa basin is 93 500 km² of which 48 500 km² is tundra. The classification was based on a mosaic of eight Landsat 5 TM images (pixel size 30 m). Images were georeferenced and rectified to Universal Transverse Mercator (UTM) coordinates using Russian 1:200 000 digital map data (GOSGISCENTER, Moscow) including contours and hydrological layers. The spectral signatures for different vegetation types were derived by creating representative samples with ERDAS IMAGINE's interactive seed pixel tools around ground truth points measured in the field during the summers 1998, 1999 and 2000.

In the supervised classification the maximum likelihood method was used to assign a class value

to every pixel, and the decision rules forced pixels to be classified to the spectrally most probable category. After every classification cycle, the apparent misclassifications were identified and new signatures were added to the set until the area showed no more clear discrepancies. The number of spectral classes increased up to 100 during the process. These primary classes were then combined to the 21 final classes [Virtanen *et al.*, Manuscript]. From these classes we calculated the area of the different tundra ecosystem types, e.g. Wet peaty tundra, Dry peaty tundra, Peat plateau, Dwarf shrub tundra heath, Lichen-dwarf shrub tundra heath, Willow stands, Lakes and ponds, Rivers, etc. [V]. An example of the areal classification of Lek Vorkuta region can be seen in Figure 1 and figure 2. When the present day carbon balance was calculated for the whole East European tundra, we assumed that the area proportions of the different vegetation types of the tundra was similar to that in the Usa basin. The area of East European tundra was calculated from the 1 km cell sized Global Land Cover Data produced by the University of Maryland [V; Hansen *et al.*, 2000].



Figure 1. Relative coverage of tundra in North Europe (T. Virtanen, Metla)

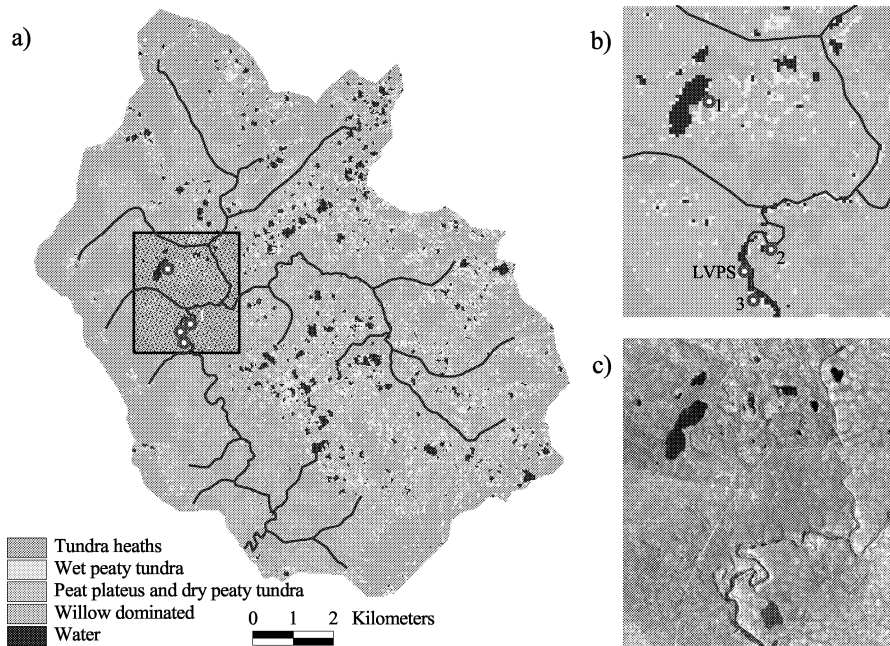


Figure 2. Lek Vorkuta catchment. See details from article IV, Fig. 1. (T. Virtanen, Metla)



Figures: Lek Vorkuta accommodation in huts and tents, tundra landscape, C flux measurements from lake river and peatlands. (Foto: J. Heikkinen)

3. RESULTS AND DISCUSSION

3.1. Recent summertime climate trends

In 1998, the weather in Kevo was drier and colder than in 1999 during the summer months from May to October. The monthly mean precipitation was 50 and 70 mm for 1998 and 1999, respectively. The monthly mean air temperature was 6.4 and 7.4 °C for summer months of 1998 and 1999 in Kevo, respectively [II; Table 1]. In Lek Vorkuta the summertime monthly mean precipitation was 44 and 63 mm in 1999 and 2001, respectively. In addition, the summer mean temperatures were on average 1.6 °C higher in 2001 than in 1999 [IV; Table 1].

Mean annual temperatures from the Khosedakhard weather station, located in the southernmost part of the Usa basin [V], shows a slight negative trend (-0.07 °C per decade for the period of record 1932-2000). Furthermore, mean annual temperatures in the warm mid-1990's were not exceptionally high compared to previous warm periods in the record. Long-term meteorological data were obtained from the Komi Republican Centre for Hydrometeorology and Environmental Monitoring, Syktyvkar, Russia [V].

3.2. Carbon balance in the northern ecosystems

3.2.1. Carbon gas exchange in tundra landscape

The **wet peaty tundra** with water table within 5 cm of the peat surface was a carbon sink (106 - 110 g m⁻² season⁻¹) during the summer. Despite of the CO₂ uptake the relative CH₄ release from these ecosystems promote the climate forcing due to CH₄'s 28 times higher Global Warming Potential (GWP) over CO₂ in 100 year time horizon [Jain *et al.*, 2000]. The CH₄ emissions (up to 13.6 g m⁻² season⁻¹) account 12% of the summer carbon balance on these surfaces [IV]. The wet peaty tundra surfaces cover 13% of the Lek Vorkuta catchment and depending on the moisture conditions and NEP these ecosystems may increase the CH₄ source strength [IV].

Dry peaty tundra was mainly hummocks where the water table was lower than 20 cm from the surface. Areal coverage of dry peaty tundra was 8% of the Usa basin. Total respiration exceeded the carbon uptake in photosynthesis and resulted significant carbon loss of 123 g m⁻² in summer 2001. In concomitant warm summers hummocky ecosystems are highly vulnerable to a loss of the most of the labile carbon to the atmosphere. Eventually, this may alter the abundance of the present species and carbon balance. The wet peaty

tundra and dry peaty tundra was reclassified as peaty tundra soils when estimating the areal carbon balance in Lek Vorkuta catchment [IV].

Tundra heaths and **willow dominated shrubland** cover 47% and 24% of the Lek Vorkuta area, respectively [IV]. Due to the warm and dry summer in 2001 the respiration rate exceeded the photosynthesis and tundra heath ecosystems were carbon source (91 g m⁻² summer⁻¹) to the atmosphere. While we had no direct gas exchange measurements from the willow dominated stands we assumed zero carbon balance for willow ecosystems [IV; See Table 5]. This estimate was based on the facts that long-term peat accumulation in willow soils was low (thin peat) and the annual development of willow biomass was merely in leaves. In addition, the methane emissions are low or close to zero from these dry ecosystems [III; IV].

Aquatic ecosystems are important in tundra carbon balance since some of the terrestrial carbon is eventually transported to the ponds, lakes and rivers [IV; Dean *et al.*, 1998; Kling *et al.*, 1991]. In Lek Vorkuta catchment the areal coverage of lakes and rivers were 3.3% and 0.3%, respectively [IV]. The aquatic ecosystems, were supersaturated with gases, and therefore were constant source of CO₂ and CH₄ to the atmosphere. Methane release rate was highest in the thermokarst lake with peat sediments (2.4 g CH₄-C m⁻² summer⁻¹), while the river mainly released CO₂ (33 g CO₂-C m⁻² summer⁻¹) [IV]. Zimov *et al.*, [1997] suggest that 75% of the annual CH₄ release from north Siberian lakes occurs in winter, with annual release of 5 g CH₄-C m⁻² yr⁻¹. The importance of areal coverage of peat sediment tundra lakes and ponds are pronounced due to the higher climatic forcing potential resulting from CH₄ emissions. The summertime carbon emissions from the Lek Vorkuta river was at the same level with the emissions from Lichen dominated peat plateau surfaces (Table 1). Thermokarst lake and river carbon effluxes were constantly lower compared to the fluxes from any terrestrial ecosystem in this study.

Lake margins contribute a substantial amount of carbon to the lakes [Zimov *et al.*, 1997]. The lake and river margins have a high ecosystem production potential due to the diverse vegetation and constant nutrient supply via water. However, the vegetation growth in margin areas is delayed by the spring floods and limited to some extent by the fluctuating water or erosion caused by waves from the lake [IV]. In lake margin, both photosynthesis and respiration were higher compared to that of the

other tundra surfaces, e.g. 325 and -325 g CO₂-C m⁻² summer⁻¹, respectively.

The lake margin ecosystem NEP was close to zero or releasing the CO₂ to the atmosphere. The studies from littoral zones of two boreal lakes in Finland support our conclusion that the margin areas are a carbon source to the atmosphere [Juutinen *et al.*, 2001; Juutinen *et al.*, 2003; T. Larmola Univ. of Joensuu, pers. comm.]. It seems that the allochthonous carbon from terrestrial ecosystems is supporting the carbon turnover in lake margins. This emphasizes the thermokarst erosion in tundra landscapes in carbon cycling.

Palsa plateau ecosystems are very sensitive with respect to warming and vegetation change [IV]. In palsa plateau the permafrost conditions maintain the carbon stock until the surface cracks and the insulation fails. In concomitant warm years the carbon loss may increase the active layer inducing cracks and erosion of permafrost and eventually collapse the peat plateau [Bubier *et al.*, 1995a; Zoltai, 1993]. At the present stage of palsa formation in Lek Vorkuta the cracks were present in various widths. In open palsa the vegetation is sparse dominated by lichen while in cracks the vegetation is diverse consisting various shrubs and *Sphagnum* species. However, the palsa surface vegetation merely circulate the atmospheric CO₂ sustaining the vegetation growth and carbon allocation to the roots. In these ecosystems the vegetation plays a major role in carbon circulation while the seasonal or annual carbon balance seems to depend on the rate of aerobic decay in peat [IV]. The *Sphagnum* and *Lichen* dominated palsa surfaces in tundra released 28 and 34 g C m⁻² summer⁻¹, respectively [IV].

3.2.2. Carbon gas exchange in boreal and arctic wetlands

The summertime and annual fluxes from Lek Vorkuta, Kevo and Kaamanen are compared to fluxes from temperate wetland ecosystems (Sallie's fen), boreal ecosystems (Salmisuo fen, Ahvensalo bog, Thompson, Barrow and Stor-Åmyran) and high arctic ecosystems (Zackenberglund) in Table 1. The intercomparison of the carbon balances was difficult due to the differences in ecosystem classifications. However, when the data is separated to the high water table surfaces and low water table surfaces, the wet ecosystems frequently have positive carbon balance while drier ecosystems

have negative balance [Waddington *et al.*, 1996]. There seems to be no latitudinal or longitudinal relationship of the reported seasonal CO₂ fluxes. In Table 1, the highest short-term sink activity during summer can be found from Zackenberg 1997 summer results which is the coldest ecosystem with respect to mean annual temperature. For peatlands there are only a few summertime and annual carbon flux studies reporting both CO₂ and CH₄ fluxes for the carbon balance (Eq. 4; Table 1). When accounting all the losses to the annual carbon balance some ecosystems showing a weak sink may be in fact close to the equilibrium or even release carbon.

The seasonal carbon balance estimates for Kevo show that wet surfaces (T1 and T2) gain carbon 91.5 and 75 g C m⁻², palsa margin (T3) gain 162 and 77 g C m⁻², and palsa top (T4) gain 73 and 40 g C m⁻² in 1998 and 1999, respectively [II]. In wet surfaces and palsa margin the wetter summer climate in 1999 resulted lower net ecosystem production due to the lower photosynthesis [II]. There was no significant variation in respiration between the years. The wet conditions in 1999 increased the CH₄ emissions. Especially, the palsa margin CH₄ emission increased from 13 to 23 g C m⁻² (Table 1) [II]. It has been found that warm and wet conditions during the summer increase the carbon sink activity in wet ecosystems [IV; Griffis *et al.*, 2000]. However, the excess soil moisture may reduce the photosynthesis potential and carbon allocation. The July and August temperatures in Kevo were slightly lower in 1999 than in 1998 suggesting that the CH₄ flux from the wet ecosystems and palsa margin was primarily controlled by the high water table and anoxic conditions [II].

In sparse vegetated **palsa** top at Kevo, the annual carbon balance varied from -52 to -18 g C m⁻² [II]. At Kevo palsa site the photosynthesis was similar between years while the total respiration was controlled by temperature and soil moisture. Overall, palsa inactive core is merely storing carbon in permafrost conditions and active surface is circulating carbon and releasing nutrients to the surrounding habitats [II]. The palsa degradation increases the CO₂ efflux and organic carbon transport to the margin areas and directly to the aquatic system.

In Lek Vorkuta the interannual comparison was made in both ends of the hydrological gradient i.e. in **intermediate flarks** (wet) and in **hummocks** (dry). In wet flarks the photosynthesis increased approximately by 66% in a warmer and wetter year mainly because more green biomass emerged below the water table and participated to the carbon fluxes [IV]. The respiration rate increase only 16% while CH₄ emissions nearly tripled (Table 1). The annual balance of wet intermediate flark ecosystem showed 200% increase in C uptake in warmer and drier year in 2001 assuming equal losses in winter and leaching (Table 1).

In drier hummocks in Lek Vorkuta the photosynthesis potential was similar between 1999 and 2001 due to the little or no change in perennial vegetation (shrubs, lichens and mosses). In 1999, the carbon balance in hummock ecosystems was in equilibrium [III]. However, in the warmer year of 2001 the total respiration increased by 70% and turned the ecosystem to a carbon source of 146 g m⁻² [IV]. In most cases, the hummock vegetation is standing on the top of dry thin organic peat material (carbon stock only 14 kg m⁻²). It is obvious that in hummocks the carbon stock is sensitive to the aerobic decay mainly controlled by the temperature. In hummocks, the available fresh carbon is limited due to the low seasonal C accumulation, presence of permafrost and peat physical and chemical characteristics [III; IV].

Increase in summer air temperature may turn large dry areas into a carbon source to the atmosphere due to the increase in soil respiration [Billings *et al.*, 1983; Jones *et al.*, 1998; Oechel *et al.*, 1993; Oechel *et al.*, 1995; Oechel *et al.*, 1998]. In addition, in wetter ecosystems the increase in methane emissions have a high contribution to the climatic forcing through the higher GWP [Jain *et al.*, 2000]. In some conditions all the wetland ecosystems induce a negative climatic forcing (Table 2). However, the interannual variation in carbon fluxes is high [II; IV; Frolking *et al.*, 1994; Granberg *et al.*, 2001; Griffis *et al.*, 2000].

3.2.3. Areal carbon balance in East European tundra

The Lek Vorkuta catchment (114 km²) was estimated to have lost 4.1 Gg C during the summer 2001 [IV]. This areal carbon balance, ignoring the willow stands, is presumably an underestimate of the true annual areal balance. Estimating that willow stands were having a similar carbon balance than that of tundra heaths (-91 g C m⁻² summer⁻¹; carbon stock in soil is 1.7 times higher in willow stands) the additional release would be 2.5 Gg C summer⁻¹ from Lek Vorkuta catchment [IV]. The wintertime emissions from wet and dry surfaces were estimated to be between 24% and 2% of the seasonal NEP, respectively [III]. Additional carbon loss during winter accounted for 0.55 Gg C in Lek Vorkuta catchment. The total annual carbon loss in Lek Vorkuta catchment could be 74% higher than the summer estimate. However, this can not be applied to the annual loss from the East European tundra because the coverage of willow stands is an order of magnitude higher in Lek Vorkuta catchment than in tundra landscapes in East European tundra.

The coarse areal classification and limited monitoring data [Botch *et al.*, 1995; Zamolodchikov *et al.*, 2001] is one reason why the previous areal carbon balance estimates from east European tundra have varied from a net source to equilibrium. Botch *et al.* [1995] suggested that the present carbon loss from former Soviet Union peatlands (165 Mha) is approximately 70 Tg C yr⁻¹. We calculated that East European continental tundra (20.5 Mha; Figure 1) lost 8.1 Tg of carbon in summer 2001 when the monthly mean air temperatures were 1.6 °C warmer than the long-term mean air temperatures [IV-V]. The estimate was based on up-scaling (GIS) carbon gas exchange fluxes from all relevant ecosystem types determined in Lek Vorkuta catchment [IV-V].

Table 1. Comparison of reported carbon fluxes (g C m^{-2}) on seasonal and annual scale from various microsites in boreal and arctic peatlands. In this study, the summer methane flux is included in NEP estimate. The positive values represent a gain to the peatland and negative values represent a carbon loss from the wetland. MAT = mean annual temperature, MWT = mean water table, N = number of microsites, W = weathering (DOC + DIC).

Site	Lat./ Lon.	MAT °C	MWT cm	N	P_g (g m^{-2})	CO_2 Flux Summer (g m^{-2})	NEP (g m^{-2})	CH_4 flux Summer (g m^{-2})	CO_2 Flux Winter (g m^{-2})	CH_4 flux Winter (g m^{-2})	W	Annual / seasonal balance (g m^{-2})	Year	Reference / notes
Lek Vorkuta, NE Russia	67 / 63	-6.0												
Wet flark			< 0	5	68	-37	25	-6	-8	-6	-5 ^b	6	1999	III
Intermediate flark			0 - 5	5	131	-77	49	-5	-6	-1	-5 ^b	38		^a =,
Wet lawn			5 - 10	6	176	-126	45	-4	-5	-0.3	-5 ^b	35		^b = L. Arvola pers. comm
Intermediate lawn			10 - 20	6	164	-129	34	-1	-4	-0.2	-5 ^b	25		
Hummock			> 20	7	189	-187	1	-1	-4	-0.2	-5 ^b	-8		
Peat plateau fen			0 - 10	2	194	-85	109	-3				106	2001	IV
PP <i>Sphagnum</i> fen			5 - 10	2	204	-232	-28	0				-28		
Lake margin			10	2	325	-325	0	-5				-5		
PP Lichen			-	2	91	-125	-34	0				-34		
PP crack succession			-	8	133	-251	-118	0				-146		
Thin tundra soil with <i>Lichen</i>			-	3	78	-149	-72	0				-75		
TTS with shrubs			-	3	217	-308	-91	0				-120		
Bare peat			-	10	-	-28	-	-				-28		
Thermocast lake			-	1	-	-13	-	-2				-15		
Lek Vorkuta River			-	1	-	-33	-	-1				-34		
Intermediate flarks			0 - 5	3	218	-89	129	-14				125		
Hummock			> 20	2	194	-317	-123	-1				-146		
Kevo, Finland	69 / 27	-1.2												
Transect 1			4	9	151	-58	93	-8				85	1998	II
T 2			6	9	213	-104	109	-12				98		
T 3			2	3	254	-79	175	-13				162		
T 4			-	3	172	-99	73	0				73		
T 1			3	9	115	-39	76	-8				68	1999	
T 2			6	9	186	-87	99	-17				83		
T 3			4	3	182	-82	100	-23				77		
T 4			-	3	161	-120	40	0				40		
Kaamanen, Finland	69 / 27													
Flark			< 0	7	218	-132	86	-8				78	1995	I
Lawn			1 - 20	2	461	-310	153	-7				146		All fluxes
Strings without <i>B. nana</i>			> 20	5	218	-262	-45	-1				-46		integrated over 100 days
Strings with <i>B. nana</i>			> 20	6	682	-557	124	-6				118		

Site	Lat./ Lon.	MAT °C	MWT cm	N	P ₀ (g m ⁻²)	CO ₂ Flux Summer		CH ₄ flux		Annual / seasonal balance	Year	Reference / notes
						R _{net} (g m ⁻²)	NEP (g m ⁻²)	Summer (g m ⁻²)	Winter (g m ⁻²)			
Salmisuo fen, Finland	62 / 30	1.9		18							1993	Alm <i>et al.</i> , [1997]
Flark			0-7	3	225	-110	135	-15	-55	-8	35	
Eriophorum lawn			0-13	3	300	-140	160	-22	-55	-8	73	
Carex lawn			0-6	6	317	-164	153	-30	-75	-8	34	
Hummock			6-35	6	314	-206	108	-11	-55	-8	32	
Whole mire					302	-149	153	-20	-55	-8	68	
Ahvensalo bog, Finland	62 / 30	2.0		26							1994	Alm <i>et al.</i> , [1999a]
Hollow			0-10		188	-198	-10	-14	-30	-1	-62	
<i>S. ang.</i> lawn			3-12		235	-194	41	-7	-30	-1	-4	
<i>S. fuscum</i> lawn			10-20		209	-255	-46	-2	-30	-1	-86	
Hummock			> 25		171	-288	-117	-1	-30	-1	-157	
Whole mire					205	-255	50	-1	-30	-1	-90	
Thompson, Canada	55 / 98	-3.9									1996	NEP; Bubier <i>et al.</i> , [1999]
Rich fen			9				13	-5*			1994	CH ₄ ; Bubier <i>et al.</i> , [1995]
Intermediate fen			-3				31	-19*				*(mean x 120 days x 12/16)
Poor fen			11				65	-10*				
Collapse bog			11				3	-5*				
Barrow, Alaska											1992	Oechel <i>et al.</i> , [1995]
High center			13	3	43.1	-56.9	-13.8					
Ice wedge			7	2	69.3	-65.3	4.0					
Low center			16	3	75.0	-78.5	-3.5					
Moist meadow			9	3	92.0	-92.5	-0.5					
Wet meadow			6	2	105	-111	-6.0					
Sallie's fen, New Hampshire	43 / 71	8.2			281	-134	116	-16			1994	Carrol and Crill [1997]
Stor-Åmyran, Sweden	63 / 20										1992	Waddington and Roulet, [2000]
Intermediate lawn			3	5	117	-101	16	-4.8			1992	
Intermediate lawn			0	5	220	-202	18	-4.5			1993	
Intermediate ridge			30	5	210	-191	19	-0.2			1992	
Intermediate ridge			22	5	302	-278	24	-0.1			1993	
Zackenberglund, Greenland	74 / 21	-10.3									1997	Christensen <i>et al.</i> , [2000]
Cassiope heath			-		253	-230	23	0			23	Pers. comm., T.R. Christensen
Hummocky fen			4.8		457	-268	189	-6			183	
Continuous fen			-1.7		324	-217	107	-9			98	
Grassland			2.4		532	-331	200	-3			197	
Salix snowbed			16.1		404	-373	31	0			31	
Area integrated			3.7		382	-285	96	-2			94	

3.3. Mechanisms of change of the carbon balance

3.3.1. Abiotic factors

Length of the growing season, i.e. when daily mean temperature exceeds 5 °C, in the arctic is between 80 to 100 days while the average snow free season is between 120 and 155 days [II; III]. The spring time solar radiation between years is expected to be constant the timing of vegetation growth depends on the snow cover during the late winter and atmospheric temperature trends [Wookey, 2002]. The growing season 2001 in Lek Vorkuta was only 10 days longer than in 1999 despite of the early snowmelt and high temperature difference in mean monthly temperatures in May (mean air temperature -6.1 and +1.0 °C in 1999 and 2001, respectively) [IV]. The initiation of vegetation growth requires a warm period to thaw the top peat layers and thus the high temperature variation early spring in 2001 may have postponed the vegetation growth. The timing and magnitude of temperature and precipitation variation in the growing season are important for the season carbon balance [Waddington *et al.*, 2000].

All the northern terrestrial wetland ecosystems experience frequent spring time floods. The duration of flooding depend on the soil characteristics, frost depth and evapotranspiration. The floods were most pronounced in Kaamanen where the flooding was caused by the excess water running in a stream nearby. In Kaamanen, the flood delayed the emergence of vegetation in wet flarks [I]. In Kevo and Lek Vorkuta sites the lateral runoff from upland soils flooded the palsas margin and depressions delaying their vegetation growth [II, III]. In tundra landscape the flooding was short lived mainly due the shallow snow coverage in upland ecosystems and fast lateral runoff on top of the permafrost [III]. The short residence time of the surface water during high discharge events have been found to decrease the CH₄ fluxes [Crill *et al.*, 1988].

However, it is possible that the melting permafrost in tundra forms macropores where the excess water is stored increasing the soil moisture. Soil moisture has an overwhelming influence on soil development, patterns of plant communities and ecosystem processes [Bubier *et al.*, 1995a; Hodkinson *et al.*, 1999; Turetsky *et al.*, 2002]. Especially, persistent differences of few centimeters

in water table depth can influence the microscale plant community composition and function [Walker, 2000]. In addition, thawing permafrost may lead to a relatively large scale erosion, slumping, and death of plants through mechanical disturbance or flooding [Callaghan *et al.*, 1997]. It is possible that dry ecosystems will be more sensitive to water availability than to temperature change and increase in precipitation could produce dramatic effects on litter decay rates, nutrient mineralization and eventually CO₂ fluxes (Table 2).

3.3.2. Biotic factors

During the growing season the vegetation growth follow the cumulative effective temperature index curve [III]. Some species grew to their maximum within 30 days (*Betula nana*, *Rubus chamaemorus*, *Carex aquatilis*) while some grew until the first frost or senescence starts (mainly bryophytes) [III]. The vegetation growth pattern is a result of decadal adjustment to local climate. The rapid growth to the maximum extent guarantees the reproduction and survival [Callaghan *et al.*, 1997]. However, extreme weather events (frost, snow) during the intensive growing phase may cause severe damage on higher vascular plants limiting the growth and colonization favoring the early flowering species or close the surface growing populations [Callaghan *et al.*, 1997; Chapin III *et al.*, 1996]. In addition, cold episodes during the intense growth phase reduce the soil respiration and methane efflux [I; IV]. The time period preceding permanent frost in top soil or snow cover has great importance in decomposition of the plant and transport of carbon and nutrients. The allocation of the fresh organic matter consequently affects the microbial processes in the following winter or summer.

Arctic summer comes to the end when the precipitation comes frequent, solar radiation diminishes and air temperatures drop frequently close to zero during night time [IV]. The senescence of vegetation starts after the growth reaches the maximum or physical damage destroys the plant function [I; III]. Any disturbance in plant function resulting cell death diminishes the photosynthesis potential. Very quickly the carbon uptake becomes zero and respiration releases the fixed CO₂ back to the atmosphere. When modeling carbon balance the P_G value was forced to zero after the ETI reached maximum value (=1).

The arctic vegetation has several functional differences depending on the plant physiology. The growth of vascular shrubs (*Betula* sp., *Salix* sp., *Ledum* sp., *Empetrum* sp. and *Vaccinium* sp.) is highly limited by the lack of nutrients, erosion and shelter in open dry areas [III]. However, the carbon uptake rate is high during the intensive growing season due to the high green biomass in leaves [I]. Graminoids i.e. grasses and sedges (especially *Carex* sp. and *Eriophorum* sp.) grow habitats with high water table where the thermal microclimate is protecting the growth against episodes of extreme cold and warm [Harley *et al.*, 1989]. In addition, the aerenchymatous tissue of vascular species act as gas conduit for CH₄ efflux and O₂ influx to the roots zone [Joabsson *et al.*, 1999].

Bryophytes, especially mosses *Sphagnum* sp., have a good tolerance in changes of environmental moisture conditions [Bubier *et al.*, 1995a; Titus *et al.*, 2002]. In water saturated ecosystems the mosses often form a sponge type floating mat where the uppermost part is active in gas exchange, also seen in our study sites [I-IV]. Drying increases the activity of carbon exchange until the water becomes limiting factor inducing a stress factor [Griffis *et al.*, 2000]. The high and stable water table is the primary reason for low carbon turnover in wet moss dominated ecosystems [I]. In saturated ecosystems the moss mat was sparse compared to drier surfaces. There the CH₄ emission is promoted with increasing abundance of vascular sedges [II; Bubier *et al.*, 1995a; Joabsson *et al.*, 1999].

In drier ecosystems the carbon accumulation process is limited by the absence of anoxic conditions. Lichens (*Cladonia* sp. and *Cladina* sp.) were characteristic on these dry nutrient limited acidic peat surfaces in arctic. In most ecosystems, the fresh organic carbon is transported to the roots zone in a form of carbohydrates and litter [Domisch *et al.*, 1998]. However, the thin organic peat layer with low carbon storage and relative old age of peat suggest that presently the carbon is circulating at the vegetation [IV]. From higher hummocks the dead biomass were often transported to the depressions by the wind [III]. In palsa peatland erosion and rainwater transport organic C and nutrients from the top of palsa to the palsa margin [II].

3.4. Climate-related responses in carbon gas fluxes

Despite of the high temporal and spatial variations the reported CH₄ and CO₂ fluxes from boreal ecosystems were higher than fluxes from arctic ecosystems (Table 1). In addition, the CO₂ and CH₄ fluxes were highly interrelated to ecosystem properties [I-IV]. Spatial variation in methane emissions can be connected to plant species composition, microtopography, nutrient status, substrate concentration, soil chemical characteristics and microbial characteristics [Bosse *et al.*, 2001; Bubier *et al.*, 1993; Christensen *et al.*, 1995; Christensen *et al.*, 2000; Oechel *et al.*, 1997; Oechel *et al.*, 2000; Saarnio *et al.*, 1997; Whalen *et al.*, 1990; Whiting *et al.*, 1991; Whiting, 1994]. The CH₄ flux was highest in terrestrial water saturated surfaces where a distinct relationship between water table and CH₄ flux was found [I; III; Bubier *et al.*, 1993]. In Lek Vorkuta tundra ecosystems the relation between mean log CH₄ flux and mean water table was steeper than that of others reported for northern wetland ecosystems suggesting that the high and stable water table ecosystems promote significantly to the atmospheric CH₄ (see III; Figure 8). In addition, there was no relation between fluctuating water table during the summer and CH₄ emission [I; Hargreaves *et al.*, 2001]. Small drop in water table was not able to compensate the temperature induced increase in methane emission from wet tundra ecosystems [IV]. However, when a drop in water table is high enough the increase in oxic layer increase the CH₄ oxidation and reduction in methanogenic activity reducing the overall CH₄ flux [Nykänen *et al.*, 1998].

The seasonality in CH₄ fluxes from wet ecosystems seems to coincide with the seasonal dynamics of different vegetation and ETI [III]. There is a close relationship between the number of vascular species and CH₄ flux in wet ecosystems [III; Bubier, 1995; Saarnio *et al.*, 1997]. In addition, the bryophytes are good predictors of CH₄ flux because the water table level and vegetation are interrelated [Bubier, 1995; Bubier *et al.*, 1995b; Bubier *et al.*, 1995a; Saarnio *et al.*, 1997]. In dry hummocks the low CH₄ emissions may result from reduced methanogenic microbial populations [Moosavi *et al.*, 1996]. In drier ecosystems, the absence of deep rooted aquatic vascular plants suppress the supply of fresh substrates for soil microbes [Saarnio *et al.*, 1997]. The substrate availability is an important factor controlling the CH₄ fluxes [Conrad, 1996].

Table 2. A tentative scenarios of ecosystem level responses of changes in temperature and moisture conditions during the growing season in arctic wetlands in Europe. The response is marked with + = increasing; +/- No effect; - = decreasing; ? = unclear.

Ecosystems		Warmer, wetter	Warmer, drier	Colder, wetter	Colder, drier
Flark (wet)	Permafrost table	-	-	+	+
	Water table	+	-	+	-
	Biomass	+	+	-	+
	Decomposition	+	+	+	-
	CO ₂ efflux	-	+	-	-
	CH ₄ efflux	+	-	+	-
Lawn (moist)	Permafrost table	-	-	+	+
	Water table	+	-	+	-
	Biomass	+/-	+	-	+
	Decomposition	+	+	+/-	-
	CO ₂ efflux	-	+	-	-
	CH ₄ efflux	+	-	+	-
Hummock (dry)	Permafrost table	-	-	+	+
	Water table	+/-	+/-	+/-	+/-
	Biomass	+	+/-	-	-
	Decomposition	+	+	-	-
	CO ₂ efflux	+/-	+	-	-
	CH ₄ efflux	+	-	+	-
Heaths and Willows	Permafrost table	-	-	?	+
	Water table	+/-	+/-	+/-	+/-
	Biomass	+/-	+/-	+/-	+/-
	Decomposition	+	+	-	-
	CO ₂ efflux	+/-	+	+/-	-
	CH ₄ efflux	+	?	+	-
Palsas	Permafrost table	-	-	+	+
	Water table	+/-	+/-	+/-	+/-
	Biomass	+	+/-	+/-	+/-
	Decomposition	+	+	+/-	-
	CO ₂ efflux	+	+	+/-	-
	CH ₄ efflux	+	+/-	+/-	-
Lake margins	Permafrost table	?	?	?	?
	Water table	+	-	+/-	-
	Biomass	+	-	-	+
	Decomposition	+	+	-	+/-
	CO ₂ efflux	-	+	-	-
	CH ₄ efflux	+	-	+/-	-
Lakes and Rivers	Permafrost table	?	?	?	?
	Water table	+	-	+	-
	Biomass	?	?	?	?
	Decomposition	?	?	?	?
	CO ₂ efflux	+	+	+/-	-
	CH ₄ efflux	+	-	-	-

When the preconditions of CH₄ production, i.e. anoxic conditions, carbon and nutrient source are met the temperature has found to be the key driving force for the CH₄ emissions [Christensen *et al.*, 2002]. During the growing season the correlation between soil temperature and CH₄ flux increases in deeper soils [I; Saarnio *et al.*, 1997]. When present the permafrost has a fundamental effect on reducing the soil temperature by radiating the cold and reducing the microbial activity in deeper layers of peat [III]. In a short-term climatic warming the permafrost table will drop increasing the active layer and carbon loss from the drier ecosystems.

Whiting and Chanton [1993] reported a positive correlation between CH₄ emission and NEP and suggested that the NEP is a master variable integrating many factors which control CH₄ emission in vegetated wetlands. They also suggested that NEP is a stronger CH₄ flux controlling variable than biomass [Whiting *et al.*, 1993]. Despite of the intercorrelation between NEP and CH₄ flux regulating factors we suggest that in high water table ecosystems, prevailing anoxic conditions, the CH₄ flux and NEP were linked by the number of vascular stems [II]. There is an obvious relationship between Q_{\max} (also a measure of P_G potential) and number of vascular stems. The number of vascular plants controls the P_G potential and the gas conduits important for the CH₄ emission. However, the summertime CH₄ flux had no linear correlation with the number of vascular plants in wetter transects T1 and T2 in Kevo [II; Figure 8d]. Instead, the CH₄ flux from saturated ecosystems reach the maximum when the number of vascular stems were somewhere between 100 and 300. The stems also transport the oxygen to the roots zone increasing the oxidation reducing the overall CH₄ flux [Joabsson *et al.* 1999].

The ecosystem CO₂ fluxes were primarily controlled by the PAR and vegetation phenology. Highest P_G potential was found from shrub dominated ecosystems and lake margin ecosystem

with dense vascular vegetation. However, in these ecosystems the respiration was also higher resulting zero or negative NEP [IV]. Thus the NEP vs. CH₄ flux relationship [Whiting *et al.*, 1993] can only be applied on selected water saturated ecosystems. In changing climate, the carbon gas flux response to the combined temperature and moisture effects will vary among ecosystems. Predicting the possible long-term consequences on individual ecosystems may be premature and subject to great bias.

We measured the winter time emissions only once in Kevo and Lek Vorkuta. In tundra landscape, the snow distribution is largely controlled by wind and mesotopographic features and has a wide variety of ecosystem influences, including effects on soil moisture, soil chemistry, growing season length and soil temperatures [Alm *et al.*, 1999; Brooks *et al.*, 1997; Dise, 1992; Grogan *et al.*, 1999; Melloh *et al.*, 1996; Sommerfeld *et al.*, 1996; West *et al.*, 1999]. The wintertime production of CO₂ and CH₄ were different between microsites due to the frost conditions. Especially, the Lek Vorkuta ecosystems were frozen throughout the winter (lakes through the bottom) while palsa margin in Kevo remained unfrozen below the snowpack. Brooks *et al.* [1997] suggested that majority of the CO₂ fluxes during the winter originates from the thin organic layer at the soil surface and vegetation were inactive in gas transport. In tundra, the cold weather cools the surface layers generating the frost. In the beginning, the frost penetration is slow and many microbial processes continue until the whole layer above the permafrost is frozen. The biotic activity in temperatures below zero is only possible in the presence of liquid water phase [Zimov *et al.*, 1993]. Depending on the moisture content some of the carbon gases are trapped to the frozen layer and some may be released through the channels that frost has created.

4. CONCLUSIONS

Northern wetland ecosystems are strongly coupled to the global climatic systems through the radiatively important carbon gas fluxes. The response of the physical properties of northern wetlands and the soil organisms to the global change will determine the magnitude, direction and distribution of carbon flux, i.e. impact and feedbacks. North East European wetland ecosystems have been storing carbon since the Holocene. However, carbon dynamics in northern wetlands are very sensitive in seasonal and annual climatic variations.

In a warmer climate the net carbon uptake can be overwhelmed by the carbon losses via respiration in dry upland ecosystems. In wetter climatic conditions the wet and moist ecosystems increase

their methane production and emissions. If the climatic change results in drier conditions, the wet ecosystems are likely to adapt with intermediate moisture conditions, where primary production increase and depending on the moisture conditions, the methane fluxes follow accordingly.

It was surprising to find that, already, at the present climatic conditions, at least occasionally, the tundra wetlands could be net carbon sources to the atmosphere. In future, the short-term carbon efflux may be substantial before vegetation composition transform and adapt to the climatic conditions. It will remain open if the long term consequences of carbon loss and climatic warming include shifts in treeline, permafrost meltdown and peat degradation in a large scale finally balancing the system.

References

- Alm, J., Saarnio, S., Nykänen, H., Silvola, J., Martikainen, P. J. (1999) Winter CO₂, CH₄ and N₂O on some natural and drained boreal peatlands. *Biogeochemistry* **44** 163-186.
- Alm, J., Talanov, A. V., Saarnio, S., Silvola, J., Ikkonen, E., Aaltonen, H., Nykänen, H., Martikainen, P. J. (1997) Reconstruction of the carbon balance for microsites in a boreal oligotrophic pine fen, Finland. *Oecologia* **110** 423-431.
- Aurela, M., Tuovinen, J.-P., Laurila, T. (1998) Carbon dioxide exchange in a subarctic peatland ecosystem in northern Europe measured by the eddy covariance technique. *Journal of Geophysical Research* **103** 11289-11301.
- Billings, W. D. (1997) Challenges for the future: arctic and alpine ecosystems in a changing world. In: Global change and arctic terrestrial ecosystems (eds Oechel, W. C., Callaghan, T. V., Gilmanov, T., Holten, J. I., Maxwell, B., Molau, U., Sveinbjörnsson, B.), pp. 1-18. Springer-Verlag.
- Billings, W. D., Luken, J. O., Mortensen, D. A., Peterson, K. M. (1982) Arctic tundra: A source or sink for atmospheric carbon dioxide in a changing environment. *Oecologia* **53** 7-11.
- Billings, W. D., Luken, J. O., Mortensen, D. A., Peterson, K. M. (1983) Increasing atmospheric carbon dioxide: possible effects on arctic tundra. *Oecologia* **58** 286-289.
- Billings, W. D., Peterson, K. M., Luken, J. O., Mortensen, D. A. (1984) Interaction of increasing atmospheric carbon dioxide and soil nitrogen on the carbon balance of tundra microcosms. *Oecologia* **65** 26-29.
- Bosse, U., Frenzel, P. (2001) CH₄ emissions from a West Siberian mire. *Suo* **52** 99-114.
- Botch, M. S., Kobak, K. I., Vinson, T. S., Kolchugina, T. P. (1995) Carbon pools and accumulation in peatlands of the former Soviet Union. *Global Biogeochemical Cycles* **9** 37-46.
- Bridgham, S. D., Pastor, J., Updegraff, K., Malterer, T. J., Johnson, K., Harth, C., Chen, J. Q. (1999) Ecosystem control over temperature and energy flux in northern peatlands. *Ecological Applications* **9** 1345-1358.
- Brooks, P. D., Schmidt, S. K., Williams, M. W. (1997) Winter production of CO₂ and N₂O from alpine tundra: environmental controls and relationship to inter-system C and N fluxes. *Oecologia* **110** 403-413.
- Brooks, P. D., Williams, M. W., Schmidt, S. K. (1996) Microbial activity under alpine snowpacks, Niwot Ridge, Colorado. *Biogeochemistry* **32** 93-113.
- Bubier, J. L. (1995) The relationship of vegetation to methane emission and hydrochemical gradients in northern peatlands. *Journal of Ecology* **83** 403-420.
- Bubier, J. L., Crill, P. M., Moore, T. R., Savage, K., Varnier, R. K. (1998) Seasonal patterns and controls on net ecosystem CO₂ exchange in a boreal peatland complex. *Global Biogeochemical Cycles* **12** 703-714.
- Bubier, J. L., Moore, T. R., Bellisario, L. M., Comer, N. T. (1995a) Ecological controls on methane emissions from a northern peatland complex in the zone of discontinuous permafrost, Manitoba, Canada. *Global Biogeochemical Cycles* **9** 455-470.
- Bubier, J. L., Moore, T. R., Juggins, S. (1995b) Predicting methane emission from bryophyte distribution in northern Canadian peatlands. *Ecology* **76** 677-693.
- Bubier, J. L., Moore, T. R., Roulet, N. T. (1993) Methane emissions from wetlands in the midboreal region of Northern Ontario, Canada. *Ecology* **74** 2240-2254.
- Callaghan, T. V., Carlsson, B. Å. (1997) Impacts of climate change on demographic processes and population dynamics in arctic plants. In: Global change and arctic terrestrial ecosystems (eds Oechel, W. C., Callaghan, T. V., Gilmanov, T., Holten, J. I., Maxwell, B., Molau, U., Sveinbjörnsson, B.), pp. 129-152. Springer-Verlag.
- Carroll, P., Crill, P. M. (1997) Carbon balance of a temperate poor fen. *Global Biogeochemical Cycles* **11** 349-356.
- Chapin III, F. S., Shaver, G. R. (1985) Individualistic growth response of tundra plant species to environmental manipulations in the field. *Ecology* **66** 564-576.
- Chapin III, F. S., Shaver, G. R. (1996) Physiological and growth responses of arctic plants to a field experiment simulating climatic change. *Ecology* **77** 822-840.
- Chapman, S. J., Thurlow, M. (1998) Peat respiration at low temperatures. *Soil Biology & Biochemistry* **30** 1013-1021.
- Christensen, T. R., Friborg, T., Sommerkorn, M., Kaplan, J., Illeris, L., Soegaard, H., Norstroem, C., Jonasson, S. (2000) Trace gas exchange in a high-arctic valley 1. Variations in CO₂ and CH₄ flux between tundra vegetation types. *Global Biogeochemical Cycles* **14** 701-713.
- Christensen, T. R., Jonasson, S., Callaghan, T. V., Havström, M. (1995) Spatial variation in high-latitude methane flux along a transect across Siberian and European tundra environments. *Journal of Geophysical Research* **100** 21,035-21,045.
- Christensen, T. R., Lloyd, D., Svensson, B., Martikainen, P. J., Harding, R., Oskarsson, H., Friborg, T., Soegaard, H., and Panikov, N. S. (2002) Biogenic controls on trace gas fluxes in northern wetlands. IGBP Global Change NewsLetter **51**, 9-15.
- Clymo, R. S. (1983) Peat. In: Mires: Swamp, bog, fen and moor pp. 159-224. Elsevier.
- Conrad, R. (1996) Soil microorganisms as controllers of atmospheric trace gases (H₂, CO, CH₄, OCS, N₂O, NO). *Microbiological Reviews* **60** 609-640.
- Crill, P. M. (1991) Seasonal patterns of methane uptake and carbon dioxide release by a temperate woodland soil. *Global Biogeochemical Cycles* **5**(4) 319-334.
- Crill, P. M., Bartlett, K. B., Harriss, R. C., Gorham, E., Verry, E. S., Sebacher, D. I., Madzar, L., Sanner, W. (1988) Methane flux from Minnesota peatlands. *Global Biogeochemical Cycles* **2** 371-384.
- Dankers, R. (2002) Sub arctic hydrology and climate change: a case study of the Tana River basin in northern Fennoscandia. Utrecht, 1-237 pp.
- Dean, W. E., Gorham, E. (1998) Magnitude and significance of carbon burial in lakes, reservoirs, and peatlands. *Geology* **26** 535-538.

- Dise, N. B. (1992) Winter fluxes of methane from Minnesota peatlands. *Biogeochemistry* **17** 71-83.
- Dlugokency, E. J., Masarie, K. A., Lang, P. M., Tans, P. P. (1998) Continuing decline in the growth rate of the atmospheric methane burden. *Nature* **393** 447-450.
- Domisch, T., Finer, L., Karsisto, M., Laiho, R., Laine, J. (1998) Relocation of carbon from decaying litter in drained peat soils. *Soil Biology and Biochemistry* **30** 1529-1536.
- Euroala, S., Hicks, S., Kaakinen, E. (1984) Key to Finnish mire types. In: European mires (ed. Moore, P. D.), pp. 11-117. Academic Press, London.
- Fahnestock, J. T., Jones, M. H., Welker, J. M. (1999) Wintertime CO₂ efflux from arctic soils: Implications for annual carbon budgets. *Global Biogeochemical Cycles* **13** 775-779.
- Frolking, S., Roulet, N. T., Moore, T. R., Lafleur, P. M., Bubier, J. L., Crill, P. M. (2002) Modeling seasonal to annual carbon balance of Mer Bleue Bog, Ontario, Canada. *Global Biogeochemical Cycles* **16** 1-21.
- Frolking, S. E., Crill, P. M. (1994) Climate controls on temporal variability of methane flux from a poor fen in southeastern New Hampshire: Measurement and modelling. *Global Biogeochemical Cycles* **8** 385-397.
- Gorham, E. (1991) Northern peatlands: Role in the carbon cycle and probable responses to climatic warming. *Ecological Applications* **1** 182-195.
- Gorham, E., Janssens, J. A. (1992) The paleorecord of geochemistry and hydrology in northern peatlands and its relation to global change. *Suo* **43** 117-126.
- Granberg, G., Ottosson-Löfvenius, M., Grip, H., Sundh, I., Nilsson, M. (2001) Effect of climatic variability from 1980 to 1997 on simulated methane emission from a boreal mixed mire in northern Sweden. *Global Biogeochemical Cycles* **15** 977-991.
- Griffis, T. J., Rouse, W. R., Waddington, J. M. (2000) Interannual variability of net ecosystem CO₂ exchange at a subarctic fen. *Global Biogeochemical Cycles* **14** 1109-1121.
- Grogan, P., Chapin III, F. S. (1999) Arctic soil respiration: Effects of climate and vegetation depend on season. *Ecosystems* **2** 451-459.
- Hansen, M., DeFries, R., Townshend, J. R. G. and Sohlberg, R. (2000) Global land cover classification at 1km resolution using a decision tree classifier. *International Journal of Remote Sensing* **21**, 1331-1365.
- Hargreaves, K. J., Fowler, D. (1998) Quantifying the effects of water table and soil temperature on the emission of methane from peat wetland at the field scale. *Atmospheric Environment* **32** 3275-3282.
- Hargreaves, K. J., Fowler, D., Pitcairn, C. E. R., Aurela, M. (2001) Annual methane emission from Finnish mires estimated from eddy covariance campaign measurements. *Theoretical and Applied Climatology* **70** 203-213.
- Harley, P. C., Tenhunen, J. D., Murray, K. J., Beyers, J. (1989) Irradiance and temperature effects on photosynthesis of tussock tundra Sphagnum mosses from the foothills of the Philip Smith Mountains, Alaska. *Oecologia* **79** 251-259.
- Heal, O. W., Callaghan, T. V., Cornelissen, J. H. C., Körner, C., and Lee, S. E. (1998) Global change in Europe's cold regions. Brussels, European Commission. **27** 3-137.
- Hodkinson, I. D., Webb, N. R., Bale, J. S., Block, W. (1999) Hydrology, water availability and tundra ecosystem function in a changing climate: the need for a closer integration of ideas? *Global Change Biology* **5** 359-369.
- IPCC (2001) Climate Change 2001: The Scientific Basis. Contribution of working group I to the Third assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, -881 p.
- Jain, A. K., Briegleb, B. P., Minschwaner, K., Wuebbles, D. J. (2000) Radiative forcings and global warming potentials of 39 greenhouse gases. *Journal of Geophysical Research* **105** 20773-20790.
- Joabsson, A., Christensen, T. R., Wallen, B. (1999) Vascular plant controls on methane emissions from northern peatforming wetlands. *Tree* **14** 385-388.
- Jones, M. H., Fahnestock, J. T., Walker, D. A., Walker, M. D., Welker, J. M. (1998) Carbon dioxide fluxes in moist dry arctic tundra during the snow-free season: Responses to increases in summer temperature and winter snow accumulation. *Arctic and Alpine Research* **30** 373-380.
- Joos, F., Prentice, I. C., Sitch, S., Meyer, R., Hooss, G., Plattner, G.-K., Gerber, S., Hasselmann, K. (2001) Global warming feedbacks on terrestrial carbon uptake under the Intergovernmental Panel on Climate Change (IPCC) emission scenarios. *Global Biogeochemical Cycles* **15** 891-907.
- Juutinen, S., Alm, J., Iarmola, T., Huttunen, J. T., Morero, M., Saarnio, S., Martikainen, P. J., Silvola, J. (2003) Methane (CH₄) release from littoral wetlands of boreal lakes during an extended flooding period. *Global Change Biology* **9** 413-424.
- Juutinen, S., Alm, J., Martikainen, P. J., Silvola, J. (2001) Effects of spring flood and water level draw-down on methane dynamics in the littoral zone of boreal lakes. *Freshwater Biology* **46** 855-869.
- Kane, D. L. (1997) The impact of hydrologic perturbations on arctic ecosystems induced by climate change. In: Global change and arctic terrestrial ecosystems (eds. Oechel, W. C., Callaghan, T. V., Gilmanov, T., Holten, J. I., Maxwell, B., Molau, U., Sveinbjörnsson, B.), pp. 63-81. Springer-Verlag, New York.
- Khalil, M. A. K., Rasmussen, R. A., Moraes, F. (1993) Atmospheric methane at Cape Meares: analysis of a high-resolution data base and its environmental implications. *Journal of Geophysical Research* **98** 14753-14770.
- Kling, G. W., Kipphut, G. W., Miller, M. C. (1991) Arctic lakes and streams as gas conduits to the atmosphere: Implications for tundra carbon budgets. *Science* **251** 298-301.
- Kling, G. W., Kipphut, G. W., Miller, M. C. (1992) The flux of CO₂ and CH₄ from lakes and rivers in arctic Alaska. *Hydrobiologia* **240** 23-36.
- Lafleur, P. M., McCaughey, J. H., Joiner, D. W., Bartlett, P. A., Jelinski, D. E. (1997) Seasonal trends in energy, water, and carbon dioxide fluxes at a northern boreal

- wetland. *Journal of Geophysical Research-Atmospheres* **102** 29009-29020.
- Lafleur, P. M., Roulet, N. T., Admiral, S. W. (2001) Annual cycle of CO₂ exchange at a bog peatland. *Journal of Geophysical Research* **106** 3071-3081.
- Mast, M. A., Wickland, K. P., Striegl, R. G., Clow, D. C. (1998) Winter fluxes of CO₂ and CH₄ from subalpine soils in Rocky Mountain National Park, Colorado. *Global Biogeochemical Cycles* **12** 607-620.
- Maxwell, B. (1997) Recent climate patterns in arctic. In: Global change and arctic terrestrial ecosystems (eds. Oechel, W. C., Callaghan, T. V., Gilmanov, T., Holten, J. I., Maxwell, B., Molau, U., Sveinbjörnsson, B.), pp. 21-46. Springer-Verlag.
- Melloh, R. A., Crill, P. M. (1996) Winter methane dynamics in a temperate peatland. *Global Biogeochemical Cycles* **10** 247-254.
- Moosavi, S. C., Crill, P. M., Pullman, E. R., Funk, D. W., Peterson, C. M. (1996) Controls on CH₄ flux from an Alaskan boreal wetland. *Global Biogeochemical Cycles* **10** 287-296.
- Norman, J. M., Kucharik, C. J., Gower, S. T., Baldocchi, D. D., Crill, P. M., Rayment, M., Savage, K., Striegl, R. G. (1997) A comparison of six methods for measuring soil-surface carbon dioxide fluxes. *Journal of Geophysical Research* **102** 28771-28777.
- Nykanen, H., Alm, J., Silvola, J., Tolonen, K., Martikainen, P. J. (1998) Methane fluxes on boreal peatlands of different fertility and the effect of long-term experimental lowering of the water table on flux rates. *Global Biogeochemical Cycles* **12** 53-69.
- Oberbauer, S. F., Starr, G., Pop, E. W. (1998) Effects of extended growing season and soil warming on carbon dioxide and methane exchange of tussock tundra in Alaska. *Journal of Geophysical Research* **103** 29075-29082.
- Oechel, W. C., Hastings, S. J., Vourlitis, G. L., Jenkins, M. A., Riechers, G. H., Grulke, N. E. (1993) Recent change of Arctic tundra ecosystems from a net carbon dioxide sink to a source. *Nature* **361** 520-523.
- Oechel, W. C., Vourlitis, G., Hastings, S. J. (1997) Cold season CO₂ emission from arctic soils. *Global Biogeochemical Cycles* **11** 163-172.
- Oechel, W. C., Vourlitis, G. L., Hastings, S. J., Ault, R. P., Bryant, P. (1998) The effects of water table manipulation and elevated temperature on the net CO₂ flux of wet sedge tundra ecosystems. *Global Change Biology* **4** 77-90.
- Oechel, W. C., Vourlitis, G. L., Hastings, S. J., Bochkarev, S. A. (1995) Change in arctic CO₂ flux over two decades: Effects of climate change at Barrow, Alaska. *Ecological Applications* **5** 846-855.
- Oechel, W. C., Vourlitis, G. L., Verfaillie, J. Jr., Crawford, T., Brooks, S., Dumas, E., Hope, A., Stow, D., Boynton, B., Nosov, V., Zulueta, R. C. (2000) A scaling approach for quantifying the net CO₂ flux of the Kuparuk River Basin, Alaska. *Global Change Biology* **6** 160-173.
- Panikov, N. S., Dedysh, S. N. (2000) Cold season CH₄ and CO₂ emission from boreal peat bogs (West Siberia): Winter fluxes and thaw activation dynamics. *Global Biogeochemical Cycles* **14** 1071-1080.
- Post, W. M., Emanuel, W. R., Zinke, P. J., Stangenberger, A. G. (1982) Soil carbon pools and world life zones. *Nature* **298** 156-159.
- Pritchard, S. G., Rogers, H. H., Prior, S. A., Peterson, C. M. (1999) Elevated CO₂ and plant structure: a review. *Global Change Biology* 807-837.
- Ramlal, P. S., Hesslein, R. H., Heccky, R. E., Fee, E. J., Rudd, J. W. M., Guilford, S. J. (1994) The organic carbon budget of a shallow Arctic tundra lake on the Tuktoyaktuk Peninsula, N.W.T., Canada. *Biogeochemistry* **24** 145-172.
- Roulet, N. T., Moore, T., Bubier, J. L., Lafleur, P. M. (1992) Northern fens: methane flux and climate change. *Tellus* **44** 100-105.
- Rowntree, P. R. (1997) Global and regional patterns of climate change: recent predictions for the arctic. In: Global change and arctic terrestrial ecosystems (eds. Oechel, W. C., Callaghan, T. V., Gilmanov, T., Holten, J. I., Maxwell, B., Molau, U., Sveinbjörnsson, B.), pp. 82-109. Springer-Verlag.
- Saarnio, S., Alm, J., Silvola, J., Lohila, A., Nykanen, H., and Martikainen, P. J. Seasonal variation in CH₄ emissions and production and oxidation potentials at microsites on an oligotrophic pine fen. *Oecologia* **110**, 414-422. 1997.
- Seppä, H. (1996) The morphological features of the Finnish peatlands. In: Peatlands in Finland (ed. Vasander H), pp. 27-33. Finnish Peatland Society.
- Silvola, J., Alm, J., Ahlholm, U., Nykanen, H., Martikainen, P. J. (1996) The contribution of plant roots to CO₂ fluxes from organic soils. *Biology and Fertility of Soils* **84** 219-228.
- Sjörs, H. (1961) Surface pattern in Boreal peatland. *Endeavour* 217-224.
- Sjörs, H. (1981) The zonation of northern peatlands and their importance for the carbon balance of the atmosphere. *Int.J.Ecol.Environ.Sci.* **7** 11-14.
- Soegaard, H., Norstroem, C. (1999) Carbon dioxide exchange in a high-arctic fen estimated by eddy covariance measurements and modelling. *Global Change Biology* **5** 547-562.
- Sommerfeld, R. A., Massman, W. J., Musselman, R. C., Mosier, A. R. (1996) Diffusional flux of CO₂ through snow: Spatial and temporal variability among alpine-subalpine sites. *Global Biogeochemical Cycles* **10** 473-482.
- Sommerfeld, R. A., Mosier, A. R., Musselman, R. C. (1993) CO₂, CH₄ and N₂O flux through a Wyoming snowpack and implications for global budgets. *Nature* **361** 140-142.
- Titus, J. E., Wagner, D. J. (2002) Carbon balance for two *Sphagnum* mosses: water balance resolves a physiological paradox. *Ecology* **65** 1765-1774.
- Tolonen, K., Turunen, J. (1996) Accumulation rates of carbon in mires in Finland and implications for climate change. *Holocene* **6** 171-178.
- Turetsky, M. R., Wieder, R. K., Vitt, D. H. (2002) Boreal peatland C fluxes under varying permafrost regimes. *Soil Biology & Biochemistry* **34** 907-912.

- Turunen, J., Pitkänen, A., Tahvanainen, T., Tolonen, K. (2001) Carbon accumulation in West Siberian mires, Russia. *Global Biogeochemical Cycles* **15** 285-296.
- Turunen, J., Tolonen, K., Tolvanen, S., Remes, M., Ronkainen, J., Jungner, H. (1999) Carbon accumulation in the mineral subsoil of boreal mires. *Global Biogeochemical Cycles* **13** 71-79.
- Turunen, J., Tomppo, E., Tolonen, K., Reinikainen, A. (2002) Estimating carbon accumulation rates of undrained mires in Finland - application to boreal and subarctic mires. *Holocene* **12** 79-90.
- Virtanen, T., Mikkola, K., Nikula, A. Satellite image mosaic based vegetation classification of large area with limited ground truth data: a case study in the Usa basin, Northeast European Russia. Manuscript.
- Vitousek, P. M. (1994) Beyond Global Warming: Ecology and Global Change. *Ecology* **75** 1861-1876.
- Vourlitis, G. L., Oechel, W. C. (1999) Eddy covariance measurements of CO₂ and energy fluxes of an Alaskan tussock tundra ecosystem. *Ecology* **80** 686-701.
- Waddington, J. M., Roulet, N. T. (1996) Atmosphere - wetland carbon exchanges: Scale dependency of CO₂ and CH₄ exchange on the developmental topography of a peatland. *Global Biogeochemical Cycles* **10** 233-245.
- Waddington, J. M., Roulet, N. T. (2000) Carbon balance of a boreal patterned peatland. *Global Change Biology* **6** 87-97.
- Waelbroeck, C., Monfray, P., Oechel, W. C., Hastings, S., Vourlitis, G. (1997) The impact of permafrost thawing on the carbon dynamics of tundra. *Geophysical Research Letters* **24** 229-232.
- Walker, D. A. (2000) Hierarchical subdivision of Arctic tundra based on vegetation response to climate, parent material and topography. *Global Change Biology* **6** 19-34.
- West, A. E., Brooks, P. D., Fisk, M. C., Smith, L. K., Holland, E. A., Jaeger, C. H., Babcock, S., Lai, R. S., Schmidt, S. K. (1999) Landscape patterns of CH₄ fluxes in an alpine tundra ecosystem. *Biogeochemistry* **45** 243-264.
- Whalen, S. C., Reeceburgh, W. S. (1990) A methane flux transect along the trans-Alaska pipeline haul road. *Tellus* **42B** 237-249.
- Whiting, G. J. (1994) CO₂ exchange in the Hudson Bay lowlands: community characteristics and multispectral reflectance properties. *Journal of Geophysical Research* **99** 1519-1528.
- Whiting, G. J., Chanton, J. P. (1993) Primary production control of methane emission from wetlands. *Nature* **364** 794-795.
- Whiting, G. J., Chanton, J. P., Bartlett, D. S., Happell, J. D. (1991) Relationships Between CH₄ Emission, Biomass, and CO₂ Exchange in a Subtropical Grassland. *Journal of Geophysical Research* **96** 13,067-13,071.
- Wookey, P. A. (2002) The Earth systems: biological and ecological dimensions of global environmental change. In: Encyclopedia of Global Environmental Change (eds. Mooney, H. A., Canadell, J. G.), pp. 593-602. John Wiley & Sons. Ltd.
- Zamolodchikov, D. G., Karelin, D. V. (2001) An empirical model of carbon fluxes in Russian tundra. *Global Change Biology* **7** 147-161.
- Zimov, S. A., Voropaev, Y. V., Semiletov, I. P., Davidov, S. P., Prosiannikov, S. F., Chapin III, F. S., Chapin, M. C., Trumbore, S., Tyler, S. C. (1997) North Siberian lakes: A methane source fueled by Pleistocene carbon. *Science* **277** 800-802.
- Zimov, S. A., Zimova, G. M., Daviodov, S. P., Daviodova, A. I., Voropaev, Y. V., Voropaeva, Z. V., Semiletov, I. P., Semiletova, I. V. (1993) Winter Biotic and Production of CO₂ in Siberia Soils: A Factor in the Greenhouse Effect. *Journal of Geophysical Research* **98** 5017-5023.
- Zoltai, S. C. (1993) Cyclic development of permafrost in the peatlands of northwestern Alberta, Canada. *Arctic and Alpine Research* **25** 240-246.