Carbon dioxide and methane dynamics in a sub-Arctic peatland in northern Finland

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We studied carbon dynamics on various surface parts of a highly patterned fen, typical in northern Finland, to examine the importance of different microsites to the areal carbon fluxes. The studies were carried out in June–September 1995 on a mesotrophic flark fen (an aapa mire) in Kaamanen (69° 08' N, 27° 17' E). Wet flarks, moist lawns and dry strings accounted for 60 %, 10 % and 30 % of the surface area, respectively. A static chamber technique was applied to measure the CH_4 exchange, the instantaneous net ecosystem exchange (NEE, transparent chamber) and the ecosystem respiration (R_{tot}, opaque chamber) in several microsites. The static chamber results were compared with those obtained by the eddy covariance technique. The mean daytime areal net ecosystem CO_2 exchange rate measurement in conditions where photosynthesis was light saturated (PAR > 400 μmol m_{-2} s_{-1}) varied during the measurement period from -59 mg CO_2-C $m^{-2}h^{-1}$ (release) to 250 (uptake). The mean CH_4 emission during the measuring period was 78 mg CH_4-C m^{-2} d^{-1} on the flarks, 68 mg on the lawn and 6.0 mg on the strings. The strings without shrubs (mainly *Betula nana*) were in general net sources of CO_2, even during the middle of the growing season, whereas the lawns, flarks and also strings growing *B. nana* showed a daytime net uptake of CO_2. Areally integrated chamber results showed lower CO_2 and higher CH_4 fluxes than predicted from the eddy covariance measurements.

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Northern peat-forming wetlands (peatlands) are considered to store 200 - 455 Pg of carbon that has accumulated during the Holocene (Post et al. 1982; Gorham 1991; Turunen 1999). The feedback mechanisms between peatland carbon dynamics and the atmosphere must be understood if one wishes to predict the consequences of global warming. This warming trend is predicted to be greatest at northern latitudes where global climate models estimate an increase in surface temperatures by 3 - 5 °C as a consequence of a doubling of the atmospheric CO_2 concentration (IPCC 1996). This kind of warming is predicted to result in changes in hydrology (Roulet et al. 1992), permafrost melting (Oechel et al. 1995), vegetation zones and plant species composition (Bubier et al. 1998; Verville et al. 1998)—all affecting the carbon dynamics.

Most of the studies of carbon dynamics in peatlands have been carried out in the boreal region. There are fewer data on the carbon dynamics of Arctic and sub-Arctic peatlands.

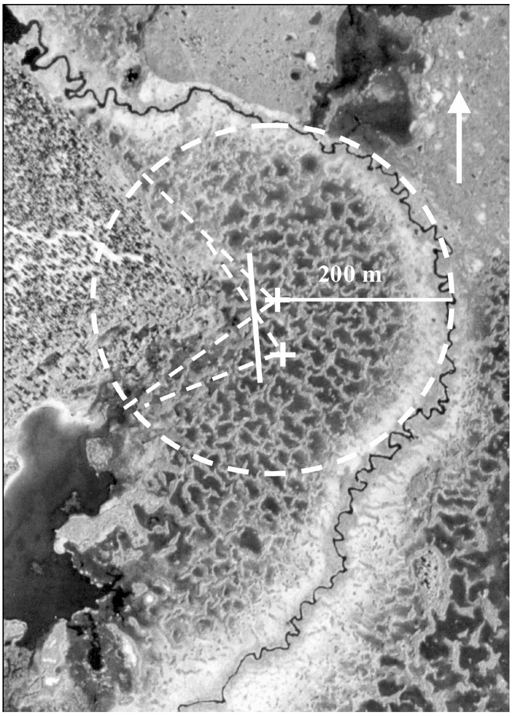

Fig 1. False colour aerial photograph. The dashed line delimits the area from which originates 80% of the eddy covariance study fluxes according to a footprint analysis. The chamber studies were arranged from a north to south direction (thick line) on the west side of the micrometeorology towers marked with + sign (CO_2 tower on the north and CH_4 tower on the south side). Darkest grey represents open water and pale/light shades are dry areas or dense vegetation. Areal distribution of wet flarks 60%, moist lawns 10% and high strings were drawn from colour analysis from the representative area.

Previous studies of biogeochemical cycles of carbon in Arctic peatlands are mainly from Alaska, Canada and, recently, from Siberia (Harriss et al. 1993; Zimov et al. 1997; Nakano et al. 2000). There are some limited data from Fennoscandia (Svensson 1980; Aurela et al. 1998, 2000; Waddington & Roulet 2000) and eastern European Russia (Slobodkin et al. 1992; Panikov 1994). The dynamics of soil and plant processes are highly dependent on temperature, hydrology and photosynthetically active solar irradiation (PAR) (King 1990). The hypothesis that an increase in the atmospheric temperature would convert the northern peat soils from a sink to a source of carbon are supported both by laboratory (Billings et al. 1982) and field experiments (Crill et al. 1988; Oechel et al. 1995; Aurela et al. 1998; Soegaard & Nordström 1999).

Future changes in fluxes of CH_4 and CO_2 in response to climate change may be preferentially mediated by changes in hydrology and vegetation composition rather than by direct temperature effects on the biological processes (Moore & Knowles 1989; Silvola et al. 1996a; Nykänen et al. 1998; Verville et al. 1998). Climatic warming and drying of soil stimulates the rates of CO_2 release relatively more than the gross primary production, resulting in a net carbon loss from the ecosystem (Oechel et al. 2000). In particular, an increased soil temperature will favour methane production over methane oxidation (Nykänen et al. 1998). However, a lowering of the water table would decrease CH_4 production in the uppermost anaerobic peat profile and increase methane oxidation, thus reducing the overall methane flux. However, the water table depth does not alone predict the CH_4 release because the characteristics of vegetation are closely associated with the CH_4 emissions from peat soils (Verville et al. 1998; Bellisario et al. 1999). As a consequence, the changes occurring in vegetation in response to a changing climate will be of crucial importance for CH_4 release.

Wetlands in Finland can be divided into the southern raised bog zone and the northern aapa mire zone. The transition of these two major peatland types follows the climate, i.e. the length of the growing season and the length of the thermal summer (Seppä 1996). The surface patterns on the aapa mires, consisting of high strings and low pools, usually have an even more distinctive morphology than dry hummocks and wet hollows in bogs. The sides of the strings are steeper than hummocks (Seppä 1996). This is due to the hydrostatic pressure from open pools to the strings and a frozen peat core or ice lens in the middle of the string. The spring flood also enhances the topography of aapa mires and inhibit hummock-forming *Sphagnum* from becoming dominant on the surface (Ruuhijärvi 1982; Seppä 1996). With the short growing season, all this must reduce carbon accumulation in wet flarks and moist lawns.

We need a deeper understanding of the present CO_2 and CH_4 dynamics of flarks, lawns and strings and how they are regulated by environmental factors if we wish to predict the changes in carbon dynamics in Arctic peatlands. We studied the exchange of carbon dioxide and methane across the highly patterned surfaces of aapa mire using static chamber techniques and then compared the areally extended results to those obtained for the same area by micrometeorological eddy covariance measurements.

Materials and methods

Study site

The open mesotrophic flark fen at Kaamanen (69° 08' N, 27° 17' E, 155 m a.s.l.) is typical aapa mire with series of wet and dry surfaces (Fig. 1). The site is situated in the transition between northern aapa mire and palsa mire. The climate is affected by the close proximity of the Arctic Ocean in the north and the Scandes in the west. Humid air from low pressures in the Atlantic Ocean tends to form rain on the eastern slopes of the Scandes, resulting in lower precipitation in northern Finland (Haapasaari 1988). Eastern winds bring in continental warm air in the summer and cold Arctic air in the winter. The Utsjoki-Kevo meteorological station (69° 45' N, 27° 02' E, 107 m a.s.l.) is the nearest (68 km) long-term meteorological station to the Kaamanen fen. The station is located in the River Teno Valley, where the climate is slightly milder than in Kaamanen. At the meteorological station, the length of the growing season is approximately 120 days and the mean annual precipitation is 395 mm with 60 - 70 % of that falling as snow (Finnish Meteorological Institute 1991). Table 1 presents the monthly mean temperature and precipitation from the measurement period and the long-term averages for the period of 1961–1990.

The relative coverage of three microsite types of the fen was determined using false colour photography (Fig 1.). Approximately 60 % of the total area consisted of wet flarks, 10 % of moist lawns and 30 % of dry strings. Flarks are the flat fen surfaces with emergent vegetation between the drier lawns and high strings with shrubby vegetation. Flarks, lawn and strings are further characterized by their vegetation coverage (Table 2). The areal vegetation consists of dwarf shrubs (*Betula nana*), herbaceous species (*Eriophorum* spp., *Rubus chaemaemorus*, *Empetrum nigrum*, *Carex* spp.), mosses (*Sphagnum* spp. and *Dicranum* spp.) and lichens (*Cladina* spp. and *Cladonia* spp.). There were seven microsites in the wet flarks, two in the hummock type of lawn and 11 in the strings. The strings had two different sub-types according to the vegetation, i.e. strings without shrubs and strings with shrubs, mostly *Betula nana* (Table 1).

The average peat depth was 0.90 m (range 0.26 - 1.35 m, N = 12, s.d. = 0.36 m). A small river running across the fen tended to stabilize the water table after the spring flood (Aurela et al. 1998). Soil temperatures were measured at depths of 2, 5, 10 and 20 cm (Fluke 51 digital thermometer) during the chamber measurements. The depth of the water table relative to the vegetation surface was monitored through perforated PVC groundwater tubes (Ø 17 mm).

Static chamber measurements

Boardwalks were constructed above the vegetation to minimize disturbance to the monitored microsites. Gas fluxes were measured once each week starting from 17 June 1995 (Julian date 167). Some string sites with shrubs were sampled only occasionally in July and August. For the CO_2 and CH_4 measurements, aluminium collars (60 × 60 × 20 cm), with a groove for water sealing, were pressed into the peat, with the sleeve inserted to a depth of 15 cm, about a week before the measurements started in June 1995. Net ecosystem CO_2 exchange (NEE) and total dark respiration (R_{tot}) were measured with the 72 dm^3 temperature controlled transparent static chamber. The headspace air temperature was maintained close to the ambient temperature by an automatic cooling system (Alm et al. 1997). The system included an electronic control unit, sheet cooler and fan. For the high shrubs, a portable 72 cm

Table 1. Monthly mean values in 1995 and the long term averages (1961–1990) of temperature and precipitation at Utsjoki-Kevo meteorological station. The long-term data are from the Finnish Meteorological Institute (1991)

	May		June		July		August		September	
	1995	1961–1990	1995	1961–1990	1995	1961–1990	1995	1961–1990	1995	1961–1990
Temp. (°C)	2.6	3.2	10.4	9.6	11.2	12.7	10.1	10.3	5.3	5.3
Precip. (mm)	16	23	105	39	48	67	79	55	18	42

high polycarbonate extension collar was used on the permanent aluminium collars. The chamber headspace CO_2 concentration was monitored with a portable infrared gas analyser LCA-2 (ADC, Analytical Development Co. Ltd., UK) equipped with a pump (100 - 150 ml/min). PAR and CO_2 readings were taken in stable irradiation conditions at 30 sec intervals over 180 sec. After NEE measurement, the transparent chamber was removed for a minute to allow stabilization of the gas concentration inside the collar. After stabilization, the chamber was reinstalled and covered with an opaque lid made of aluminium for the measurement of respiration.

Methane emission measurements were made using a static chamber technique (Crill 1991; Nykänen et al. 1995). Gas samples of 50 mL were drawn from the chamber headspace into plastic syringes (B-D Plastipak, Becton Dickinson, Dublin, Ireland) via three-way stopcocks (Connecta, Boc Ohmeda AB, Helsingborg, Sweden) through 1.5 m plastic tubing. Four samples of 50 mL were taken after incubation times of 3, 10, 15 and 20 min. Samples were injected through brombutyl rubber septa to 125 mL glass flasks containing N_2 and 10 ml of saturated NaCl solution. After sampling, the flasks were kept upside down and transported to the laboratory for analysis within one week. The methane concentration was determined using a Hewlett-Packard 5890 gas chromatograph (GC) equipped with a flame ionization detector (FID) (Nykänen et al. 1995). The CH_4 flux rates were determined by a linear regression from four headspace gas samples taken during the measuring period. Regression line parameters were estimated using the four sample points in time and the slope was accepted when r^2 exceeded 0.9. In cases of lower

Table 2. Vegetation composition by collar in mesotrophic flark fen in Kaamanen, 1995.

Water table *	1	1	1	1	1	1	1	2	2	3	3	3	3	3	4	4	4	4	4	4
Collar	12	13	15	16	18	21	22	20	24	14	17	19	23	29	25	26	27	28	30	31
Vascular species																				
Betula nana								1	10						20	50	30	30	1	1
Carex chordorrhiza	7		15		2	20	40	20												
Carex dioica						30			20											
Carex lasiocarpa	15				20	10	3	10	+											
Carex livida	3	+	+		2	1	4													
Carex rostrata	1		3		3	10	5	10	2											
Empetrum nigrum									+	7	5	10	10	20	2	3	2	5	3	7
Eriophorum angustifolium	2	7	+	3	2	1	3	3	+								+			
Rhododendron tomentosum								+	+	5	4		5	40	15	20	3	1	30	40
Molinia caerulea		20																		
Rubus chamaemorus										7	10	20	7	3	20	20	10	10		7
Salix lapponum															15					
Triehoprum cespitosum		40	20																	
Vaccinium myrtillus										1	5	1			+	1		5	2	
Vaccinium uliginosum								+	10			7		+	5	2	10	3		10
Vaccinium vitis-idaea										5	20	1		10	5	7	5	5	2	
Bryophytes and lichens																				
Campylium stellatum		50	30		1			+												
Cladina											20	7	20	7				+		5
Cladonia										+	15			+				+	2	1
Dicranum polysetum									40						40	+				
Dicranum scoparium								+		20	2		78				+	20	18	1
Hylocomium splendens								2	+						+	30	+		20	33
Mylia anomala		+										7								
Pleurozium schreberi									+	80	15	50	2	93	+	70	+	10	60	60
Scorpidium scorpioides	15		10	10	3	30	40													
Sphagnum angustifolium																	35			
Sphagnum fuscum											5	31								
Sphagnum russowii									60						60		55			
Sphagnum warnstorfii		+						50									10			
Warnstorfia procera			20		30															

* Mean water table (MWT) 1: MWT < 0, 2: 1 < MWT < 20, 3 & 4: MWT > 21 cm.

r^2, the sample points were visually inspected and accepted if no reason for discarding them could be found. The minimum detectable methane flux was estimated to be 0.5 mg m^{-2} d^{-1}. Methane emission was marked as positive and methane uptake as negative.

Daily maximum NEE (PAR > 400 µmol m^{-2} s^{-1}) was calculated by averaging the results from grouped microsites and weighting the flux with the areal coverage of the microsites derived from the false colour photograph and then compared to the 30 min interval eddy covariance flux from the daily hours of 0900 to 1700, local time. The areally weighted maximum NEE for the study area (Fig. 1) was calculated from the annual means according to the relative coverage of the microsites. Daily methane flux was calculated from areally weighted and averaged microsite fluxes. Annual methane flux was calculated from the areal mean fluxes according to the relative areal coverage.

Eddy covariance measurements

The eddy covariance (EC) method offers a means to obtain continuous measurements of the areally integrated fluxes of various constituents. Such data permit a valuable comparison when upscaling areally more detailed chamber data. Carbon dioxide and methane fluxes were measured at the Kaamanen fen during the period from mid-August to mid-September 1995 by using two different EC-systems. The CO_2 measurements were performed on a mast 5 m above the mean flark surface. The instrumentation included a SWS-211 three-axis sonic anemometer (Applied Technologies Inc.) and a LI-6262 CO_2/H_2O analyser (Li-Cor Inc.). The measurement system and the EC-data used in this comparison have been presented in more detail by Aurela et al. (1998).

Methane fluxes were measured using a fast response tuneable diode laser spectrometer (TDL) sampling air from a mast near the CO_2 mast. The diode laser was tuned to a methane absorption line at 3.314 µm. Methane concentration was transmitted as an analogue signal to a Solent Model 1012RA sonic anemometer. The digital output from the anemometer was logged at 21 Hz and sensible heat and methane fluxes were averaged over 10 min periods. Finally, 24 h average values were used for comparison between chamber and eddy covariance CH_4 fluxes. Technical details of the eddy covariance system can be found in Fowler et al. (1995), Hargreaves & Fowler (1998) and Hargreaves et al. (2001).

Data analysis

The estimate of gross photosynthesis (P_G) was calculated by subtracting ecosystem respiration (R_{tot}) from the net ecosystem exchange (NEE) assuming that the plant dark respiration was on the same order of magnitude as the reduction of CO_2 uptake in photorespiration (Eq. 1). Carbon dioxide uptake was marked positive and carbon emission to the atmosphere as negative.

$$\mathrm{NEE} = P_G - R_{tot} \qquad (1)$$

A rectangular hyperbola describes the relationship between P_G vs. PAR where P_G levels off at PAR over 500 µmol m^{-2} s^{-1} (Oechel et al. 1995). We report here NEE and P_G at PAR over 400 µmol m^{-2} s^{-1}, i.e. close to the light saturation of photosynthesis. This allows us to compare the values from two methods without the effect of diurnal cycle on NEE.

Mean water table (WT) was used to group the microsites in statistical analysis (Table 2). Statistical analysis was performed with the SPSS for windows statistical package (SPSS Inc.). One-way analysis of variance (ANOVA) was used to compare the means of gas fluxes and environmental variables between microsites. Correlation coefficients and regression statistics for each pair of variables are based in all the cases with valid data on P_G and R_{tot} regression line estimation. Pearson correlation and linear regression analyses were applied to infer relationships between gas fluxes and environmental parameters.

Results

The rapid snowmelt in 1995 flooded the flarks and lawns and the flooding disappeared when the ground frost on the surface peat melted. Flarks were partly submerged and floating throughout the season while lawns emerged from under the water in early July. The water table remained relatively stable during the period from early July to mid-September, 1995. At the beginning of the study period, the daily average air temperatures exceeded 6 °C and the soil temperature in strings at a depth of 20 cm was about 4 °C. At the same time, the pools were warmer than the lawns at a depth of 20 cm. The soil heat capacity post-

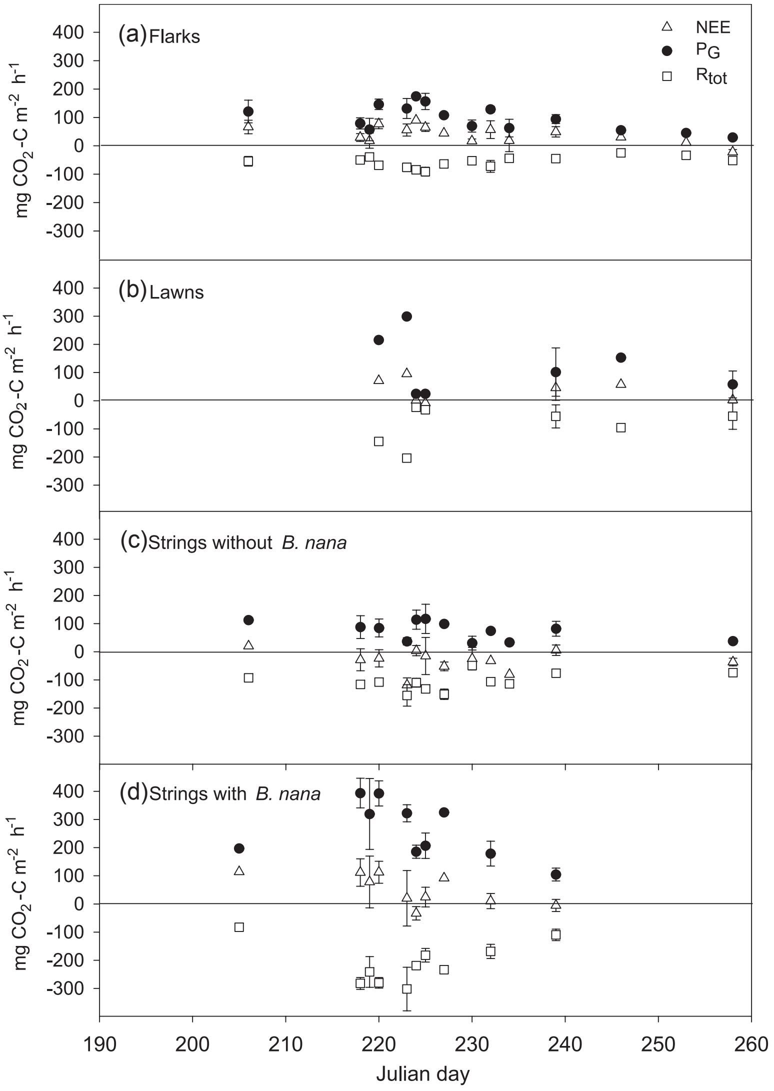

Fig 2. Net ecosystem exchange (white triangles), gross photosynthesis (filled circles) and total respiration (white squares) in (a) lawns, (b) flarks, (c) strings without *Betula nana* and (d) strings with *B. nana*. Error bars indicate standard error of mean (N=2 to 7 per day). The CO_2 uptake is marked as positive and CO_2 emission to the atmosphere as negative.

poned the effect of air temperature and solar heat on ground temperatures. The monthly air temperatures in 1995 slightly differed from the 30-year long-term average in 1961–1990 (Finnish Meteorological Institute 1991), with a warmer June and colder July (Table 1). The thermal growing season—the time when daily average temperature exceeds 5° C—started at Utsjoki-Kevo meteorological station on 19 May in 1995; the long-term average in 1980–1996 was 8 May (Heino 1995). The growing season ended in the early September and the length of this growing season, 80 days, was shorter than the average of 92 days (Heino 1995).

There were over 50 different species in the study area, common in northern aapa mires in Finland. The individual species in each monitored plot with abundance over 5% of the surface coverage are summarized in Table 2. Sedge (*Carex spp.*) communities as well as the *Scorpidium scorpioides* and *Eriophorum angustifolium* indicated the wet habitats. There were several indicator species on dry surfaces, e.g. *Empetrum nicrum*, *Rhododendron tomentosum*, *Rubus chamaemorus*, *Vaccinium* spp. and *Pleurozium schreberi* (Table 2). *Betula nana* was the

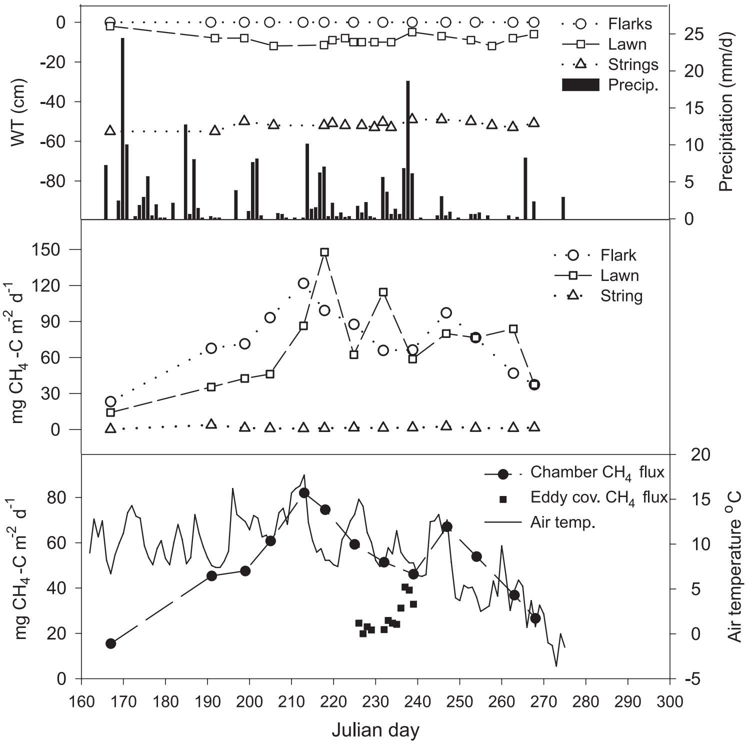

Fig 3. (a) Water table dynamics on representatively selected plots in flarks, lawns and strings and daily precipitation in Kevo meteorological station. (b) The daily average methane emissions in flarks (open circles), lawns (quadrants) and strings (triangles). (c) Area compensated methane emissions from chamber studies (filled circles), eddy covariance CH_4 emissions (small quadrants) and air temperature (thin line).

dominant shrub (coverage 20 %) on the strings; most individuals were about 0.5 m high. It must be noted that the abundance of *B. nana* increased from the open centre towards the forest. The vegetation in the lawn was similar to that in the wet flarks.

Carbon dioxide

The strings with *Empetrum nigrum*, *Rubus chamaemorus* and *Rhododendron tomentosum* as the dominant vascular plants were sources for CO_2 during the growing season. The strings with *Betula nana* as well as the lawns and the flarks mostly showed a daytime net uptake of CO_2 (Fig. 2). During the daytime hours (0900h–1700h, PAR > 400 µmol m^{-2} s^{-1}), the rate of NEE varied within the microsites in the measuring period from 273 mg CO_2-C m^{-2} h^{-1} (maximum net uptake) to -332 (maximum net emission). There was a high daily variation in the daytime maximum NEE values depending on the stage of the growing season, ground temperatures and microsite vegetation. The variation was

Table 3. Mean net ecosystem CO_2-C exchange (NEE) (PAR > 400 µmol m^{-2} s^{-1}), total respiration (R_{tot}) and gross photosynthesis (P_G) measured with the static chamber technique from different surfaces 17.7–20.9 1995. The CO_2 uptake is marked as positive and the CO_2 release as negative.

		NEE (mg C m^{-2} h^{-1})			R_{tot} (mg C m^{-2} h^{-1})			P_G (mg C m^{-2} h^{-1})		
	N	mean	s.e.	range	mean	s.e.	range	mean	s.e.	range
Flark	50	35.9	6.2	-52.3 - 132.4	-55	3.8	-130 to -8.7	90.9	8.6	6.1 - 263
Lawn	5	63.7	16.5	3.7 - 95.5	-129	20.9	-204 to -96.0	192	32.5	106 - 299
Strings without *B. nana*	32	-18.7	9.0	-143 -62.9	-109	7.8	-236 to -40.0	90.7	11.6	0 - 299
Strings with *B. nana*	31	51.8	20.6	-168 to -332	-232	14.9	-434 to -76.1	284	27.1	14.7 - 697
F		6.40			73.9			31.8		
p		.000	.000	.000						

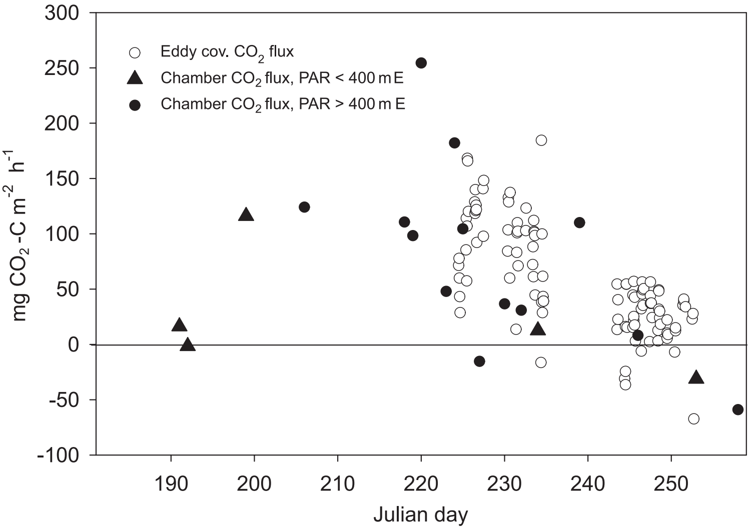

Fig 4. The area compensated NEE marked with filled circles (PAR > 400 µmol m^{-2} s^{-1}) and filled triangles (PAR < 400 µmol m^{-2} s^{-1}) is compared to eddy covariance data (daylight hours 0900–1700) open circles.

highest during the emergence of vegetation and declined towards the senescence. The lawns and strings with shrubs had the highest mean net uptake of CO_2. The seasonal mean P_G was 91 mg CO_2-C m^{-2} h^{-1} at the flarks and strings without *B. nana*. The respiration in strings with *B. nana* was double compared to the strings without shrubs (Table 3).

There were only small changes in the water table during the growing season (Fig. 3a). Therefore, no significant correlation could be observed between the dynamics of water table (WT) the respiration or NEE within any of the microsite types (Table 4). Peat surface temperature correlated with respiration rate in flarks and strings without shrubs, but not in lawns and strings with shrubs (Table 4). The higher above ground plant biomass in the two latter microsites probably explains the lack of correlation between soil temperature and respiration because the rate of plant dark respiration is not closely associated with soil temperature. The slope of the R_{tot} and P_G regression line was $\beta = -0.35$ to -0.40 ($r^2 = 0.25$ to 0.57) in all microsites except in lawns where the available data limited the analysis. The strongest correlation between photosynthesis and soil temperature was found in flarks and lawns (Table 4). The bryophytes and sedges in the wet microsites were more closely linked with the hydrology and peat-water temperature

Table 4. Pearson correlation coefficients between respiration (R_{tot}). net ecosystem exchange (NEE). gross photosynthesis (P_G). soil temperature ($T_{2\,cm}$. $T_{5\,cm}$. $T_{10\,cm}$ and $T_{20\,cm}$) and water table (WT) for different surfaces in 17.7–20.9 1995.

	Flarks (N = 50)			Lawns (N = 5)			Strings without *B. nana* (N = 32)			Strings with *B. nana* (n = 31)		
	R_{tot}	NEE	P_G	R_{tot}	NEE	P_G	R_{tot}	NEE	P_G	R_{tot}	NEE	P_G
R_{tot}	1.00			1.00			1.00			1.00		
NEE	-0.44[a]	1.00		-0.50	1.00		0.06	1.00		-0.15	1.00	
P_G	-0.76[a]	0.92[a]	1.00	-0.90[a]	0.83	1.00	-0.63[a]	-0.74[a]	1.00	-0.66[a]	0.84[a]	1.00
$T_{2\,cm}$	-0.40[a]	0.44[a]	0.49[a]	-0.79	0.63	0.83	-0.41[b]	-0.05	0.24	-0.06	-0.04	0.00
$T_{5\,cm}$	-0.37[a]	0.35[a]	0.41[a]	-0.70	0.89[b]	0.90[b]	-0.31	-0.16	0.09	-0.14	0.04	0.11
$T_{10\,cm}$	-0.28[b]	0.38[a]	0.39[a]	-0.49	0.96[a]	0.80	-0.26	-0.23	-0.01	0.05	-0.01	-0.03
$T_{20\,cm}$	-0.23	0.38[a]	0.38[a]	-0.29	0.81	0.59	-0.07	-0.13	-0.05	0.03	0.02	0.00
WT	0.17	-0.12	-0.16	-0.08	-0.81	-0.36	-0.08	0.30	0.28	-0.23	0.05	0.16

R_{tot} is always positive.
NEE is positive if CO_2 uptake, negative if CO_2 release.
P_G is always positive.

[a] Correlation is significant at the 0.01 level.
[b] Correlation is significant at the 0.05 level.

than the vegetation in dryer string microsites. In the early summer, the wet microsites were flooded and had low temperature, which limited their photosynthesis and biomass production. In addition, the shrub vegetation on strings, in contrast to the vegetation in other microsites, showed a decrease in photosynthesis already in the middle of August (Fig. 2) when the temperature was still high (Fig. 3c).

The areal NEE, based on the chamber measurements, were further compared with the daytime (0900h–1700h) eddy covariance measurements of Aurela et al. (1998) (Fig. 4). The areal NEE extrapolated from chamber results varied during the measuring period from -58.9 to 254 mg CO_2-C m^{-2} h^{-1} (Fig. 4). The eddy covariance results revealed the high variation in the daytime CO_2 fluxes, which decreased towards the autumn. The fen acted as a sink for the CO_2 from JD 192 until JD 248. Carbon sequestration (highest NEE) was strongest around mid-July (JD 220) due to a cold period that reduced the total respiration. The development in areal NEE followed the growing season pattern from spring to autumn. The areally integrated chamber results were somewhat lower than eddy covariance results when measured simultaneously during late summer (Fig. 4).

Methane

The strings with low water table showed low CH_4 emissions and frequently CH_4 uptake throughout the whole growing season (Fig. 3b). In the beginning of the growing season, the CH_4 emissions from flarks were higher than those from lawns but subsequently these two microsites exhibited similar CH_4 emissions (Fig. 3b). The growth and development of sedges in the lawns was most probably responsible for the increase in their CH_4 release during the summer. The seasonal mean methane effluxes from the flarks and lawns were similar, and they were ten times the mean from the strings (Table 4). The CH_4 flux ranged from -4.2 (uptake) to 403 mg CH_4-C m^{-2} d^{-1} (emission). The highest variation in the methane fluxes occurred in microsites where the water table was above or near the peat surface for most of the year, i.e. in flarks and lawns. In particular, the wet flarks exhibited large temporal and spatial variations (Table 5). The areally weighted mean methane emission from the fen was 55.3 mg CH_4-C m^{-2} d^{-1} for the study period.

Table 5. Mean methane fluxes from different vegetation surfaces and mean areal CH_4 flux from Kaamanen 17.6–29.9 1995 (mg CH_4-C m^{-2} d^{-1}).

	Area (%)	N	Mean flux[a]	s.e.	Min. - max.
Flarks	60	86	77.8	5.2	7.8 - 302
Lawns	10	13	68.1	10.0	14.2 - 148
Strings	30	46	6.0	1.3	-3.2 - 52.5
Areal flux	100		55.3		

[a] F = 33.8, p = 0.000.

No statistical correlation was found between CH_4 flux and water table change within flarks, lawns and strings (Table 6). Comparison of the whole data revealed the following exponential relationship to the daily CH_4 fluxes and mean water table; CH_4 flux (mg CH_4-C m^{-2} d^{-1}) = 86.7 exp(-0.0744 * WT); r^2 = 0.68, WT = 0 to 60 cm. The increase in NEE and P_G flux correlated with the increase in CH_4 flux in moist lawns while a minor correlation was found with CH_4 flux and ground temperatures. The CH_4 flux from high strings did not correlate with ground temperature, NEE and P_G flux changes (Table 6). Precipitation had only a minor effect on water tables in different surfaces (Fig. 3a). In high-water table flarks, the ground temperature explained 40 - 45 % of the variation in CH_4 flux (Table 6).

Integration of weekly emission averages over the summer season yields total methane efflux of 7.5 g CH_4-C m^{-2} (JD 150 to JD 280). The modelled eddy covariance values estimated the annual emission of 5.5 g CH_4 m^{-2} a^{-1} (Hargreaves et al. 2001). When comparing our areally averaged daily CH_4 flux to eddy covariance derived fluxes

Table 6. Pearson correlation coefficients between methane flux, net ecosystem exchange (NEE), gross photosynthesis (P_G), soil temperature ($T_{3\,cm}$. $T_{5\,cm}$. $T_{10\,cm}$ and $T_{20\,cm}$) and water table (WT) for different surfaces in Kaamanen 17.7–20.9 1995.

CH_4	Flark	Lawn	String
NEE[a]	0.14	-0.82[d]	0.17
P_G[a]	0.22	-0.67	-0.24
$T_{3\,cm}$[b]	0.43[c]	0.18	-0.08
$T_{5\,cm}$[b]	0.44[c]	0.18	-0.03
$T_{10\,cm}$[b]	0.40[c]	0.20	-0.09
$T_{20\,cm}$[b]	0.45[c]	0.26	-0.05
WT[b]	0.12	0.03	0.11

[a] N = 62, 8 and 24.

[b] N = 84, 13 and 32 for flarks, lawns and strings, respectively.

[c] Correlation is significant at the 0.01 level.

[d] Correlation is significant at the 0.05 level.

in the same peatland, we found that at the start of the simultaneous monitoring period, our chamber results were more than twice the flux estimated with eddy covariance but at the end of the period these two methods showed similar flux rates (Fig. 3c). Both fluxes showed no correlation with air temperature (JD 225-240).

Discussion

Carbon dioxide dynamics in different microsites

The carbon dioxide dynamics were different in wet and dry surfaces. Photosynthesis and respiration activity in moist lawns was two times that in wet flarks (Table 2) mainly due to the difference in the height of the water table. The relative coverage of vascular species, especially *Carex* spp., was the primary controller of the NEE in the wet surfaces. In flarks the mosses formed a sponge type of floating mat where the uppermost part of *Sphagnum* spp. and *Scorpidium* spp. vegetation were active in gas exchange. The small air–plant interface in the active surface layer is the second reason for low NEE in flarks. The emergence of plants under the water increases the gas transport activity in flarks and lawns, promoting gas fluxes through the stems. In wet surfaces, the low carbon turnover (low NEE and R_{tot}) (Fig. 2) in flarks and lawns was probably promoted by the high and stabile water table. However, the change in water table had no effect on R_{tot} and NEE in flarks, lawns and strings (Table 4), where NEE is mainly regulated by the plant activity i.e. photosynthesis and respiration. It is evident that the level of water table in flarks and lawns has an indirect effect on NEE via the ground temperatures, which also controls the extent of soil respiration.

The change in the slope of the R_{tot} and P_G regression line $\beta = -0.35$ to -0.40 indicated that the sum of autotrophic and heterotrophic respiration (total respiration) corresponded to about 1/3 of the CO_2 uptake in photosynthesis. Bubier et al. (1998) found similar values for boreal peatlands. Part of soil respiration is related to the vegetation through the roots. Silvola et al. (1996b) found that root derived respiration accounted for 35 - 45 % of total soil respiration during the active growth period. The temperature dynamics (Christensen et al. 1996) with the soil moisture content can affect autotrophic and heterotrophic respiration in different microsites. Soil moisture and the heat capacity of water balances the surface temperatures and maintain the respiration level in top soil in diurnal cycles. Regression analysis revealed significant correlation between R_{tot} and surface temperature (T_{2cm}) in all microsites, except in high strings growing *B. nana* where the respiration correlated only with photosynthesis. The daytime temperature of ecosystem controls the NEE through plant respiration while the variation in the nocturnal NEE is mostly driven by the soil temperature and soil respiration (Oechel et al. 1995; Aurela et al. 1998). Oechel et al. (1995) found that efflux of CO_2 to the atmosphere from a wet sedge ecosystem was generally greatest during late night and early morning hours, while carbon accumulation was greatest during the early to mid-morning hours when light intensity was ca. 600 µmol m^{-2} s^{-1} and soil temperature was still relatively low.

The seasonal pattern of flux dynamics in different microsites is presented in Fig 2. The snow cover disappeared first from strings and several days later from the flarks. The spring flood further delayed the emergence of vegetation in flarks. Lawns and strings growing *B. nana* had almost similar NEE but the string microsites had much higher respiration. *B. nana* clearly had a major role in the carbon dynamics in strings as had the sedges in lawns. The air-filled pores in the top peat controls the heat distribution, making NEE and R_{tot} on high strings more sensitive to temperature fluctuations. The NEE values here are in line with the Waddington & Roulet (2000) study in a boreal patterned peatland in Sweden and with BOREAS studies in Manitoba and Saskatchewan (Norman et al. 1997). Towards the end of the summer, the rate of photosynthesis declined and respiration started to predominate (Fig. 2). This suggests that respiration was not coupled with photosynthesis but with heterotrophic activity via temperature.

The length of the growing season limited the growth, especially in strings where the shrub vegetation was dominant. The cold periods during the intense phase of growth resulted a higher carbon accumulation due lower respiration and methane efflux (Fig. 2). During the winter, wind erosion enhances snow accumulation from high strings to lower flarks and lawns. This results in deep frost penetration and ice formation in the strings. Ice lenses were retained in well-insulated strings until mid-August. The temperature regime in winter also affects the spring thaw in spring when open pool areas and flarks thawed before lawns. During the summer, the unfrozen active surface layer of the string was over 40 cm thick. While there is some heat transfer from lateral groundwater flow to the surface of flarks and lawns, the string margin (mostly lawns) remains under the snow until direct sunlight or air temperature melts the snow coverage. Depending on the snow cover and temperature regime, ice lenses from the one winter may occasionally be preserved until the following year. The ground temperatures near the surface follow closely the air temperature. The lag in the temperature regime depends on the peat depth and the soil moisture content. Wet flarks and lawns store heat energy to the pore water and diurnal changes in air temperature have diminishing impact on carbon fluxes with increasing depth.

Methane dynamics in different microsites

Emissions of CH_4 were highest in water-saturated surfaces where the boundary layer between the surface and air was sharp. We detected a correlation between CH_4 flux with mean water table ($r^2=0.51$) and temperature T_{20} ($r^2=0.68$). It must be noted that the small water table fluctuation in flarks, lawns and strings resulted no relationship between CH_4 flux and water table (Table 5). The CH_4 emission increased transiently due to lowering of water table via the release of CH_4 stored in pore water (Nykänen et al. 1998). However, the increased oxidation zone later decreased the CH_4 emission. Methane emissions are related to the anaerobic processes in soil and subsequently to the oxidizing microbial processes occurring in the upper soil horizon (Christensen et al. 1996). In fact, over 90% of the CH_4 is consumed in the oxic layer by CH_4 metabolizing bacteria and liberated as CO_2 (King 1990). Saarnio et al. (1997) detected the highest variation in reconstructed CH_4 emission in dry hummocks and lowest emissions in wet *Carex* lawns. Our results revealed a high variation in moist lawns where the CH_4 production and emission was predicted by temperature and water table. In lawns, the height of CH_4 oxidation zone depended on the water table and the small difference in daily CH_4 emission between microsites was presumably a result of vegetation composition, i.e. number of *Carex* stems (Table 2). In water-saturated flarks, the temperature was found to be the factor predicting the CH_4 flux (Table 6). In summary, in wet and partly anoxic microsites, the vegetation composition is the primary predictor of the methane flux while temperature represents a secondary predictor.

Differences between plant communities in the timing of emergence, growth, reproduction and senescence account for some of the differences in methane fluxes (see also Joabsson et al. 1999). Bubier & Moore (1994) concluded that ebullition and active vascular plant transport are important CH_4 emission mechanisms where the water table is at or above the peat surface but diffusion predominates when the water table is below the peat surface. The aerenchyma tissues in vascular species can act as a gas conduit, transporting methane from the anoxic production zone to the atmosphere and oxygen to the roots; thus the oxic zone mainly represents the rooted zone of the vascular species (Bubier & Moore 1994; Joabsson et al. 1999). Therefore, the species composition and coverage is significant for the overall CH_4 flux (Bubier 1995). This was seen in flarks and lawns where the CH_4 flux increased with the emergence of *Carex* spp. The absence of *Carex* spp. in some flark subsurfaces reduced the maximum emission to the range of 0 to 50 mg CH_4-C m^{-2} d^{-1} (with *Carex* spp. 50 to 200 mg CH_4-C m^{-2} d^{-1}). The emergence of vegetation favoured the CH_4 flux in flarks and lawns in early summer, but later senescence reduced the CH_4 flux by destroying the vegetation pathways for gas fluxes.

This study was conducted in highly patterned peatland where topography plays an important role in vegetation and moisture regime. The means (and ranges) in methane fluxes reported here 55.3 (-4.3 to 402) mg m^{-2} d^{-1} are in agreement with those reported by Whalen & Reeburgh (1990) for the Alaskan Haul Road study, 52 (-0.3 to 265) mg m^{-2} d^{-1}. The emissions of CH_4 are commonly coupled with the hydrological and thermal regime of the surface soil. Statistical relationships between flux controlling variables are often hard to detect when feedback times range from a few hours to days. Despite the known lag, many studies have found water table to be the primary controller of CH_4 efflux (Roulet et al. 1992; Bubier 1995; Nykänen et al. 1998). Roulet et al. (1992) found that CH_4 emissions from northern peatlands are more sensitive to changes in the moisture regime than to fluctuations in temperature within the range of changes predicted for $2 \times CO_2$ scenarios. The soil temperature and water table are strongly interrelated because the water content controls the heat diffusion in peat.

Areal fluxes of carbon dioxide and methane

The variation in gas fluxes occurs on a much smaller scale than can be detected in spatially integrated NEE estimates from eddy covariance technique. The spatial variability in NEE is caused by variations in hydrology and vegetation as described above. When the chamber results are integrated over the relative coverage of different surfaces, the areal NEE is within the range of eddy covariance results despite that they gave smaller results when used simultaneously. According to these results, in future it will be possible to use areally integrated respiration results with eddy covariance results to estimate the seasonal and annual carbon balance for the fen.

The inaccuracy in determining the relative areal coverage cannot explain the two-fold difference between the areal CH_4 fluxes by chambers and micrometeorology. The emergence of moist lawns under the water table decreased the area of flarks. One explanation for the higher chamber fluxes could be that the measurements disturbed the delicate system in flarks and lawns, leading to an overestimation of the fluxes. However, there were no samples with clear ebullition characteristics; all samples were qualified to further analysis. A second explanation would be diurnal variation, which was not taken into account in the chamber studies. Our summer season CH_4 flux is an underestimate of the annual CH_4 flux. Nonetheless, it was two times greater than the emission reported by Waddington & Roulet (2000) for a boreal patterned peatland in northern Sweden, i.e. 3.9 to 4.1 g CH_4-C m^{-2} y^{-1}. A third explanation would be that the chambers were not usually within the "footprint" of the micrometeorological measurements and that, due to the spatial heterogeneity of the site, it would not be reasonable to expect a good agreement between the methods.

Implications

In this study, single factor relationships were found to be unable to explain in full the variation in carbon flux. Despite the variation and intercorrelation of parameters, the predictors of carbon dioxide and methane from northern Finnish aapa mire were identified.

In the prevailing climatic and geomorphological conditions, it is believed that climate change in northern peatlands will disrupt the thermal and moisture patterns (IPCC 1996). Should there be less summertime precipitation, higher evaporation, warmer average temperature and an increase in the growing season length is still a question. In this kind of highly patterned peatland, the differences in hydrology and temperature regimes between flarks and lawns indicate that global changes can induce shifts in the areal balance from wet flarks to lawns, promoting carbon exchange between vegetation and atmosphere. Consequently, lowering water table reduces the overall methane emissions and may cause a decrease in radiative forcing (a cooling effect).

Severe spring floods and a short growing season hamper the carbon accumulation in flarks and lawns. The string formation, along with the vegetation, is the key for carbon fluxes in highly patterned fens. At some stage during string formation, the rate of carbon sequestration increases, though the accumulation does not necessarily increase. The accumulated peat shows that fen has been a sink for atmospheric carbon. However, unpublished micrometeorological results (M. Aurela) indicate that the fen has been a source for atmospheric carbon during recent years.

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