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Carbon balance in East European tundra

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[1] We studied the carbon dioxide and methane fluxes from early June to mid-September 2001 in the Russian tundra of northeast Europe. Gas fluxes were measured with chamber techniques to determine the seasonal (100 days) carbon gas balance for terrestrial ecosystems representing various vegetation types. Also, the gas balance for aquatic ecosystems in the region was measured. The 2001 fluxes were compared to colder and wetter season fluxes from 1999. The *Sphagnum* sp. dominated peat plateau fen and *Carex* sp. and *Sphagnum* sp. dominated intermediate flarks were carbon sinks of 106 and 110 g C m⁻², respectively. In addition, methane emissions were highest from these sites. Other terrestrial surfaces lost carbon to the atmosphere (28–118 g C m⁻²). The thermokarst lake and the river had seasonal carbon losses of 15 and 34 g C m⁻², respectively. For areal integration, the distributions of the various functional surfaces were classified based on Landsat TM satellite image and on-site validation. This data was used to integrate the carbon fluxes for the entire Lek Vorkuta catchment. The upscaling indicated that the catchment (114 km²) lost 4 (±3.5) Gg C to the atmosphere in summer 2001. The results suggest that predicted warming in the tundra region would induce a substantial loss of carbon. In the warm summer of 2001, the carbon gas released from the whole northeast European tundra (area 205,000 km²) was 8 Tg C when calculated from the Lek Vorkuta data. **INDEX TERMS:** 1615 Global Change: Biogeochemical processes (4805); 1640 Global Change: Remote sensing; 1851 Hydrology: Plant ecology; 0315 Atmospheric Composition and Structure: Biosphere/atmosphere interactions; **KEYWORDS:** carbon balance, tundra

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1. Introduction

[2] Northern wetlands have been a major sink for atmospheric carbon since the last deglaciation. Large areas of arctic and subarctic wetlands are vulnerable to climate change, and owing to their large carbon stocks and presence of permafrost, they can have important feedback mechanisms in global warming [Gorham, 1991; Intergovernmental Panel on Climate Change (IPCC), 2001]. Global peat-forming wetlands, estimated 230–500 Mha, store 270–455 Pg of carbon [Gorham, 1991; Turunen *et al.*, 2001]. The wetland area of Russia is estimated at 150–165 Mha with a carbon pool of 200–215 Pg [Botch *et al.*, 1995]. In the Atlantic-European region of Russia, the palsa and aapa mires occupy 30 and 6.2 Mha of the wetlands, respectively [Botch *et al.*, 1995]. Zamolodchikov and Karelin [2001] estimated the coverage at 23.2 Mha of tundra.

[3] Despite the sequestration of atmospheric carbon, these wetland ecosystems emit large quantities of CH₄ [Billings *et al.*, 1982; Cicerone and Oremland, 1988; Bartlett and Harriss, 1993]. Most of the observed warming over the last 50 years is likely the result of increased greenhouse gas concentrations [Dlugokencky *et al.*, 1998; IPCC, 2001]. The increase in atmospheric CO₂ concentration would increase the net primary productivity of most wetland systems [Oechel *et al.*, 1994, 1993]. The effect of increased temperature becomes important in regulating the hydrology of wetlands through evapotranspiration [Kane, 1997], increasing the nutrient availability [Chapin *et al.*, 1995] and length of the growing season [Oberbauer *et al.*, 1998]. The initial net effect of warming on carbon stores in high-latitude ecosystems is likely to be negative because decomposition may respond more rapidly than primary production [Billings *et al.*, 1982; Oechel *et al.*, 1993].

[4] In addition to the terrestrial ecosystems, CO₂ saturated lakes and rivers are a globally significant source of carbon to the atmosphere [Cole *et al.*, 1994; Hamilton *et al.*, 1994; Semiletov, 1999]. Kling *et al.* [1991] made an estimate that the loss of carbon from tundra lakes and rivers is 20 Tg yr⁻¹. However, the carbon balance estimates seldom include the carbon loss from the aquatic environments, which can be a substantial part of the areal carbon balance [Kling *et al.*, 1991; Hamilton *et al.*, 1994].

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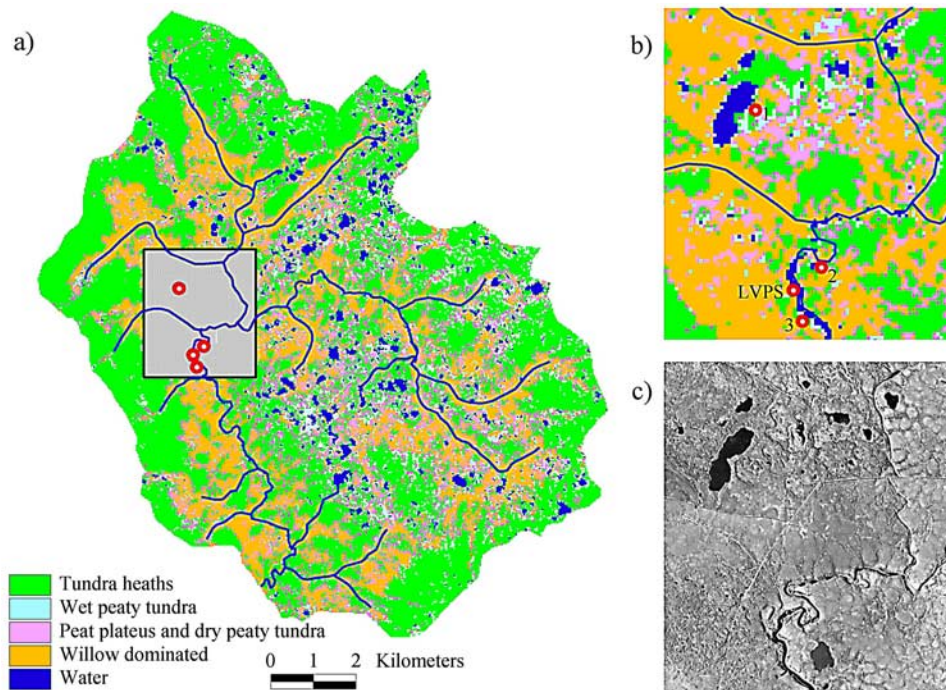


Figure 1. (a) Main vegetation types and river network of the upper part of Lek Vorkuta catchment (114 km²). (b) More detailed view (location indicated by box in Figure 1a) on the study sites: thermokarst lake (1), fen site (2, also studied in 1999), tundra with thin organic soil (3), and meteorological station (LVPS). (c) False color aerial picture from 1970s.

[5] We studied the carbon dioxide and methane fluxes of various terrestrial and aquatic ecosystems in the tundra of Russia, northeast Europe. The objective was to integrate the measured CO₂ and CH₄ gas fluxes over the summer for a seasonal gas balance. The microsites with similar botanical and environmental characteristics were grouped using GIS-based data to calculate the carbon balance for the entire catchment, and further for the whole northeastern European tundra.

2. Material and Methods

2.1. Study Sites

[6] The study was conducted in the discontinuous permafrost zone of the eastern European Russian tundra between June 6 and September 10, 2001 (Julian days 156–252). In addition, the results were compared to the gas fluxes measured in the region during a climatically different year in 1999 [Heikkinen *et al.*, 2002a]. The study sites were located near Lek Vorkuta permafrost monitoring station (LVPS; 67°23′N, 63°22′E) (Figure 1). The mean annual air temperature (MAT) is −5.9°C and the mean annual precipitation (MAP) 548 mm; see Table 1 for monthly means. The long-term average growing season is approximately 80 days.

[7] The study area is south subarctic tundra with large areas of flat terrain. The pools and lakes in the area are predominantly shallow (mean depth approximately 0.5 m) with peaty bottoms and littoral zones near the banks. The pools are mainly formed after peat plateau degradation resulting in steep (up to 3 m) margins between the peat plateau and water.

In valleys and depressions, the accumulated peat with ice layers has formed peat plateaus up to 5 m high. High upland soils have a thin organic (mainly peat and lichens) layer on top of the mineral clay soil. The surface waters have formed numerous small upland streams, which are running to the Lek Vorkuta River (20 m wide; mean water depth 1.2 m at the crossing point near the LVPS).

[8] We established study plots (60 × 60 cm) for three different locations (Figure 1). The study plots (microsites) near the thermokarst lake included the littoral zone of the lake (LM; two collars), various crack succession surfaces on top of the peat plateau (PPC; 8), the wet depression on peat plateau fen (PPF; 2), lichen-dominated peat plateau top (PPL; 2) and a peat plateau with *Sphagnum* sp. vegetation (PPS; 2). On the Lek Vorkuta River bank, plots were characterized by thin humus layers on mineral soil, lichens

Table 1. Monthly Mean Temperatures and Precipitation in Vorkuta Meteorological Station in 2001 and 1999 (69°29′N, 64°01′E, 181 m asl.)^a

Year	May	June	July	August	September
<i>Temperature, °C</i>					
2001	1.0	8.6	10.3	12.4	5.6
1999	−6.2	5.0	11.3	8.6	3.8
1936–1999	−2.7	6.2	12.5	9.4	4.1
<i>Precipitation, mm</i>					
2001	39	38	67	48	26
1999	39	29	91	109	47
1936–1999	36	51	59	62	57

^aLong-term averages for 1936–1999 are also shown.

as dominant vegetation (TTSL; three collars), and microsites with thin tundra peat dominated by shrubs (TTSS; 3). The “true” wetland microsites included intermediate flarks (IF; three collars) and hummocks (HCK; 2) that were also studied in 1999.

[9] In addition, we measured net ecosystem exchange (NEE) with a floating chamber on the main river (mineral bottom) of the catchment, and on a thermokarst lake characterized by a peaty bottom. Respiration (R_{TOT}) on the bare peat plateau was measured with respiration chambers (area 67.9 cm²). The microsites on the bare peat were classified into three groups with respect to peat characteristics. Fine peat (n = 5) was highly degraded with brown color. Coarse peat (n = 3) was slightly degraded with visible stems of vegetation and light brown or yellow in color. The peat with algae (n = 2) occurred on the top of the degrading edge of the peat plateau (just about to fall into the lake). The peat of these microsites was also highly degraded.

[10] The study area has a wide variety of different vegetation types (Figure 1). Tundra heath (TTSS and TTSL) is the most common vegetation type in the region, typically found in well-drained and slightly elevated sites with thin tundra soils and dominated by dwarf birch (*Betula nana*). Other common shrubs are *Vaccinium vitis-idea*, *V. uliginosum*, and *Empetrum nigrum*. Many lichens and mosses (for example, *Cladonia* sp., *Cetraria* sp., *Polytrichum juniperinum*, *Pleurozium schreberi*, *Hylocomium splendens*, and *Dicranum* sp.) are also found in this vegetation type. In sheltered and lower areas the vegetation is dominated by different willow species (*Salix* sp.), dwarf birches, sedges (*Carex* sp.), grasses, and herbs. Wet peaty tundra surfaces (PPF and IF) are characterized by mosses (*Scorpidium* sp., *Sphagnum* sp.) and sedges. The peat plateaus (PPS and PPL) are dominated by *Rubus chamaemorus*, *Cetraria* sp., *Cladonia* sp. and *Dicranum* sp. On the peat plateau margin (LM), the vegetation is dominated by *Carex aquatilis*, *Comarum palustre*, *Calliergon cordifolium*, and *P. juniperinum*. The wide crack succession microsites (PPC) were covered mainly by *Ledum decumbens*, *R. chamaemorus*, *Arctostaphylos uva-ursi*, and lichens. Smaller cracks were formed on patchy eroded bare peat areas surrounded by the lichens (especially *Cladonia* sp. and *Cetraria* sp.).

2.2. Environmental Variables

[11] The temperatures (T_{AIR} , T_{-5cm} , and T_{-10cm}), photosynthetically active radiation (PAR) (LiCor SA-190, LiCor Inc., Nebraska), wind direction (WD), and wind speed (WS) (Vaisala Inc.) were monitored at 10-min intervals using data loggers (LiCor LI-1000). For backup, we installed laboratory calibrated HOBO Temp temperature loggers (Onset Computer Corp.) on the weather station. Ground temperatures (Fluke 51 k/j thermometer, Fluke Corp., Everett, Washington) and depth of groundwater near the collars were taken for each gas flux sampling date.

2.3. CO₂ Fluxes

[12] Net ecosystem exchange (NEE) was measured with a closed chamber system [Alm et al., 1997; Carroll and Crill, 1997; Heikkinen et al., 2002a; Nykänen et al., 2003]

(volume 0.104 m³) and a portable infrared gas analyzer (LI-6200, LiCor Inc., Nebraska) from pre-installed aluminum collars (60 × 60 cm). The boardwalks were constructed to minimize any disturbance to the collars. The NEE was measured with a transparent chamber (2.3 mm polycarbonate). For total respiration (R_{TOT}) measurements, the chamber was darkened with an opaque shroud. During the measurements, CO₂ concentration, photosynthetically active radiation (PAR), relative humidity (RH), and air temperature inside the chamber (T_{AIRC}) were recorded at 10-s intervals. A total of nine readings were taken. CO₂ flux was calculated from the slope of regression of minimum of five readings after 20 s. Fluxes with correlation coefficient of the slope $R^2 > 0.95$ were accepted to the further analysis.

[13] Soil respiration on the bare peat was monitored with a static chamber technique (PVC chamber, diameter, 9.2 cm, vol. 883 cm³) and LI-6200 CO₂-analyzer. The flow rate of 1.0 L min⁻¹ used in the CO₂ balance studies was reduced to 0.3 L min⁻¹ while the monitoring program remained the same.

2.4. CH₄ Fluxes

[14] Methane fluxes were measured on a weekly basis from JD 157 to JD 250 using a static chamber method [Crill, 1991; Nykänen et al., 1998; Heikkinen et al., 2002a]. Chambers were made from thin aluminum (total volume 0.108 m³). The collars used in the CO₂ balance measurements were also used for the CH₄ measurements. Two air outlets were mounted on the top of the chamber and fan (diameter 7 cm) inside. Gas samples were obtained from the first air outlet while plastic tubing on the second served as a capillary tube to prevent under pressure inside the chamber. The 20-mL glass vials were prefilled with pure nitrogen (99.999% N₂) gas in the laboratory. Four samples were withdrawn at 5-min intervals during the 20-min measuring period. The samples were collected with 60-mL syringes and then moved to 20-mL glass vials (HDSPEC, Sun International Trading Ltd.) with butyl septa (20-B3P, Chromacol Ltd.) and capped with aluminum caps (20-mm Crimp Cap, Chromatography Research Supplies Inc.). The vials were flushed with 40 mL of the sample and over pressurized with the remaining 20 mL.

[15] Samples were returned to the laboratory in Kuopio, Finland, and analyzed for CH₄ and CO₂ within a month of sampling. Analyses were conducted with a Hewlett Packard gas chromatograph with a FID and TCD using a HayeSep Q column. Precision of the analysis (SD) was 0.5% [Nykänen et al., 1998]. We calculated the linear regression (slope) for four sample concentrations collected from the chamber during the 20-min measuring period. Fluxes with correlation coefficient of the slope $R^2 > 0.85$ was accepted for further analysis.

2.5. Modeling Seasonal Fluxes

[16] The carbon balance was constructed between JD 160 to 260 using seasonal photosynthesis and respiration models [Heikkinen et al., 2002a]. By knowing net ecosystem exchange (NEE) and ecosystem respiration (R_{TOT}), the gross photosynthesis (P_G) can be calculated from the equation: $NEE = P_G - R_{TOT}$. Models using hourly rates of photosynthetically active radiation (PAR), air temperature (T_{AIR}),

and effective temperature index (ETI) were developed to calculate hourly rates of photosynthesis (equation (1)) and respiration (equation (2)).

$$P_G = (Q \times \text{PAR}) / (K + \text{PAR}) + b_1 \times \text{ETI} + b_2 \times T_{\text{AIR}} + c_1 \quad (1)$$

$$\ln R_{\text{TOT}} = b_3 \times T_{\text{AIR}} + b_4 \times \text{ETI} + c_2, \quad (2)$$

where Q is an asymptote at the maximum P_G , and K is the light intensity where 50% of the maximum P_G is reached. The constants are marked with c_1 and c_2 . The total respiration, including processes in peat and plant respiration, has an exponential dependence on temperature. Thus the linear regression model was constructed using the log transformed R_{TOT} values.

[17] While the plant growth depends on physiological and environmental factors, we chose the effective temperature sum (ETI) [Alm *et al.*, 1997] to take into account the effect of seasonality in equations (1) and (2). The effective temperature sum index was calculated by dividing daily average temperature when exceeding +5°C by Julian day and standardized to a scale from 0 to 1. ETI was set to zero after the first frost on JD 250. Carbon dioxide uptake is marked positive and carbon emission to the atmosphere is negative.

[18] The measured daily CH₄ fluxes were given for 3 days backward and forward from the sampling date. Daily fluxes were integrated for seasonal balance of 100 days.

2.6. Statistical Analysis

[19] Data analysis was performed with the statistical software SPSS for Windows (Release 9.0.1. SPSS Inc., 1999). One-way ANOVA and Scheffe's Post Hoc test were used to test the differences between the microsites. Correlation statistics were applied to the microsites and grouped microsites to determine the best predictors to the gas flux model. The Pearson's correlation test investigates the correlation between gas fluxes, soil temperatures, air temperature, and height of water table in the early season (158–170), mid-season (171–220), and late season (221–253). Stepwise multiple regressions were used to determine the influence of peat temperature, air temperature, and height of water table on CO₂ and CH₄ fluxes.

[20] Model estimation calculations were performed for each microsite using nonlinear regression analysis with the Levenberg-Marquard method. For each microsite, we randomly selected 70% of the data to construct the model and used the remaining 30% for model validation. For interannual model comparison, the microsites were first grouped and then modeled. The net ecosystem production (NEP) was calculated from summer P_G and R_{TOT} . The seasonal carbon balance and 95% confidence intervals were calculated from P_G , R_{TOT} , and CH₄ fluxes [see Heikkinen *et al.*, 2002a; Nykänen *et al.*, 2003].

2.7. Catchment Scale Estimates

[21] We generalized the flux measurements for the upper part of the Lek Vorkuta catchment (114 km²) using satellite images based on vegetation classification (Figure 1). This area represents the discontinuous and continuous permafrost

tundra of the catchment. Vegetation and land use classifications have been done for the whole Usa basin (93,500 km²) (T. Virtanen *et al.*, Satellite image based vegetation classification of a large area using limited ground truth data: A case study in the Usa Basin, northeast European Russia, submitted manuscript, 2004) (hereinafter referred to as Virtanen *et al.*, submitted manuscript, 2004). For the Lek Vorkuta region, the classification was based on a Landsat TM 5 image (path 166, row 13) acquired on July 31, 1988. Classifications were created based on vegetation ground truthing in the field. Furthermore, oblique photographs taken from the helicopter, and digital topographic maps were used in the work. The pixel size in the classification was 30 × 30 m. In the Lek Vorkuta region, we could classify seven vegetation types (Figure 1; different kinds of tundra heaths are grouped, as also willow stands and meadows). When calculating the fluxes for the catchment, the measured microsites were reclassified to satellite image classification by weighting the microsites using on-site data.

3. Results

3.1. Climatic Conditions

[22] Daily average temperature exceeded 5°C after JD 158, melting the remaining snow and top of the surface frost. A cold period followed the warm week, and vegetation growth started on JD 170 following several rainy days (Figure 2). Highest mean daily temperatures were recorded on JD 191–198 and JD 206–221. During the summer, evening temperatures frequently fell below 5°C, and occasionally below 0°C. The senescence started after JD 250 when evening temperatures dropped below 0°C for several nights. The length of the growing season was then 80 days.

[23] The mean temperature of the summer months was 2°C higher in 2001 than in 1999. However, in both years, July was colder than the long-term average of 12.5°C (Table 1). The precipitation in May was close to the long-term average, while in June, August, and September 2001 the precipitation was 66% of the long-term average. Precipitation in June, July, and August in 1999 was 50% higher than in 2001 (Table 1).

3.2. CO₂ Fluxes on Various Terrestrial Microsites

[24] Summary statistics of the measured NEE and R_{TOT} fluxes from different surfaces are shown in Table 2. The seasonal mean NEE was positive at the peat plateau wet fen, peat plateau margin, thin tundra soil growing shrubs, and intermediate flark microsites. The highest respiration was found at the peat plateau margin and shrub (mainly *B. nana*) dominated microsites.

[25] The peat plateau crack succession (PPC) microsites were different in NEE and R_{TOT} with respect to the size of cracks and vegetation coverage. At the wide old cracks with dominant *L. decumbens* microsites, the seasonal mean NEE and R_{TOT} were −46.4 and −164 mg CO₂-C m^{−2} h^{−1}, respectively (n = 34). Small cracks on the top of the plateau were occupied with lichens, and the seasonal mean NEE and R_{TOT} were −38.2 and −83.0 mg CO₂-C m^{−2} h^{−1}, respectively (n = 31).

[26] Seasonal NEE and R_{TOT} flux dynamics were different between microsites (Figure 3). A high water table delayed

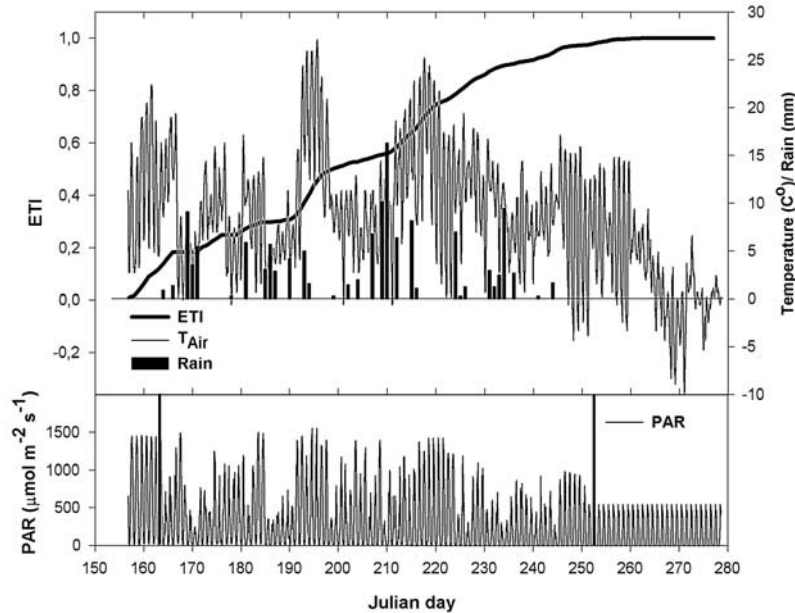


Figure 2. Measured environmental parameters at Lek Vorkuta permafrost monitoring station (LVPS) in summer 2001. Effective temperature index (ETI) was calculated as cumulative daily average temperatures exceeding 5°C and normalized on scale 0 to 1. The data were continuous between JD 163 and JD 252, also marked as vertical lines on photosynthetically active radiation (PAR) curve.

sedges emergence, while shrub-dominated drier hummocks emerged when the top 10 cm of the soil melted in spring. In most cases, the NEE grew to the maximum around JD 210 following the ETI and vegetation growth characteristics. The *Sphagnum* sp. and lichen-covered surfaces showed steady growth in NEE until the frost. The senescence started from *Carex* sp. in wetter microsites and was followed several days later in the drier microsites covered by shrubs.

[27] Of the vegetated surfaces, the R_{TOT} rate was lowest at the lichen-dominated microsites and highest in the shrub microsites (Figure 3). Seasonal development in the R_{TOT} was connected to the NEE, vegetation growth, and ETI in most microsites. The maximum R_{TOT} took place early in the season (TTSS and TTSL), late mid-season (PPF, PPS, IF, HCK), and autumn (PPC). At the lake margin, the R_{TOT} peaked early midseason after several days of warm weather when the ground surface temperature was 15°C.

3.3. Soil Respiration on the Eroded Peat Plateau Without Vegetation

[28] The seasonal mean respiration was -12.8 , -10.7 , and -26.8 mg CO₂-C m⁻² h⁻¹ for fine peat, coarse peat, and peat with algae, respectively. Highest bare peat respiration (-34.7 mg CO₂-C m⁻² h⁻¹) was measured from the fine peat microsite on JD 225. On the same day, on algae-covered surfaces, the highest respiration was -73.9 mg CO₂-C m⁻² h⁻¹. The variation in fluxes increased at all microsites until midsummer (JD 223). The R_{TOT} decreased on the peat with algae microsites until JD 210, then jumped up to 60 mg CO₂-C m⁻² h⁻¹ (JD 218), and finally decreased toward the end of summer. Similar smaller

peaks were also seen at fine and coarse peat microsites around JD 220 (Figure 4a). There was no correlation between respiration and ETI on grouped microsites over the growing season ($R^2 = 0.08-0.14$; $n = 98-229$).

[29] Respiration on the whole bare peat plateau correlated best (-0.32) with temperature at a depth of 10 cm in soil, while there was no correlation between air temperature and respiration (Table 2). When the data were separated into fine peat, coarse peat, and peat with algae, the correlation between air temperature and R_{TOT} was obvious (Figure 4b). The R_{TOT} response to the air temperature was different in peat with algae compared to the fine and coarse peat microsites (Scheffe's Post Hoc test of significance = 0.000).

3.4. Methane Fluxes From Terrestrial Microsites

[30] The seasonal mean (and SD) methane fluxes were 136 (70.4), 107 (82.0), 26.2 (14.0), 3.8 (3.8), and 5.8 (12.4) mg CH₄-C m⁻² d⁻¹ at the intermediate flark, lake margin, PP wet fen, PP Sphagnum fen, and hummock, respectively ($n = 23-87$). Maximum emission was found at the intermediate flark (323 mg CH₄-C m⁻² d⁻¹) while maximum uptake took place at the lake margin and hummock (-8.1 mg CH₄-C m⁻² d⁻¹). On drier surfaces (PPL, PPC, TTSL, and TTSS), the fluxes varied between -6.1 and 7.9 mg CH₄-C m⁻² d⁻¹, the mean being close to zero. The seasonal methane flux integrated over 100 days was 12.9 and 13.6 g CH₄-C in LM and IF, respectively (Figure 5).

3.5. Carbon Fluxes From the River and the Lake

[31] The thermokarst lake was a source of CH₄ and CO₂ to the atmosphere throughout the summer (Figures 6a and 6b),

Table 2. Summary of the Measured Carbon Dioxide Fluxes ($\text{mg CO}_2\text{-C m}^{-2} \text{h}^{-1}$), Environmental Variables, and Pearson Correlation Statistics in 2001 (JDs 158–248) for Different Vegetation Classes^a

	PP Wet Fen		PP Sphagnum		PP Lichen		PP Bare Peat		PP Crack		TTS Lichen		TTS Shrubs		Lake		Intermediate		Hummock	
	NEE	R_{TOT}	NEE	R_{TOT}	NEE	R_{TOT}	NEE	R_{TOT}	NEE	R_{TOT}	NEE	R_{TOT}	NEE	R_{TOT}	NEE	R_{TOT}	NEE	R_{TOT}	NEE	R_{TOT}
Mean	82.7	-52.5	-5.9	-133	-9.5	-66.6	-	-14.8	-35.5	-122	-13.5	-73.8	5.8	-140	59.9	-162	84.0	-42.7	-32.3	-142
SD	75.4	38.1	86.3	96.0	31.3	27.6	-	11.2	64.7	61.4	53.9	49.8	97.5	110	115	74.7	72.3	27.1	98.1	55.0
Min	-77.1	-11.1	-225	-20.1	-88.6	-25.6	-	-0.9	-224	-16.8	-277	-18.6	-374	-2.3	-198	-62.3	-47.8	-6.0	-286	-15.5
Max	249	-176	155	-418	74.5	-126	-	-73.9	182	-525	73.8	-281	238	-610	315	-422	309	-133	166	-264
N	62	61	59	63	58	66	-	504	245	260	176	182	226	96	93	96	189	187	117	126
	PP Wet Fen		PP Sphagnum		PP Lichen		PP Bare Peat ^b		PP Crack		TTS Lichen		TTS Shrubs		Lake		Intermediate		Hummock	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
WT, cm	0.8	3.5	3.5	3.3	-	-	-	-	-	-	-	-	-	-	9.9	2.2	3.8	2.0	>20	-
PF, cm	86	66	66	11.5	52	11.6	60	10.4	55	10.0	136	140	140	12.3	>140	60	60	48	48	-
$T_{5\text{cm}}$, °C	12.3	3.0	11.5	3.0	11.6	3.7	10.4	4.8	10.0	3.5	9.6	9.6	9.6	3.5	12.3	3.6	11.3	4.3	11.7	4.6
$T_{20\text{cm}}$, °C	7.6	3.0	6.2	2.9	5.3	3.2	5.2	4.7	4.2	3.2	5.8	5.7	5.7	3.2	8.8	3.9	7.1	2.9	5.3	3.6
Correlations	-0.35 ^c	-	-0.32 ^d	-	0.15	-	0.49 ^c	-	0.49 ^c	-	0.73 ^c	0.22 ^c	0.22 ^c	-	-0.55 ^c	-	-0.53 ^c	-	0.49 ^c	-
PAR	0.59 ^e	-	0.52 ^c	-	0.20	-	0.33 ^c	-	0.33 ^c	-	0.16 ^d	0.19 ^c	0.19 ^c	-	0.58 ^c	-	0.43 ^c	-	0.45 ^c	-
WT	0.24	-0.55 ^c	-0.07	-0.19	-	-	-	-	-	-	-	-	-	-	0.16	-0.31 ^c	-0.27 ^c	-0.43 ^c	-	-
T_{air}	0.36 ^e	-0.41 ^c	0.13	-0.47 ^c	-0.08	-0.60 ^c	-0.06	-0.06	0.01	-0.48 ^c	-0.31 ^c	0.11	0.11	-0.52 ^c	0.36 ^c	-0.60 ^c	0.32 ^c	-0.29 ^c	0.18	-0.45 ^c
$T_{5\text{cm}}$	0.19	-0.57 ^c	-0.09	-0.58 ^c	-0.26 ^d	-0.47 ^c	-0.30 ^c	-0.30 ^c	-0.14 ^d	-0.39 ^c	-0.20 ^c	0.15 ^d	0.15 ^d	-0.43 ^c	0.35 ^c	-0.63 ^c	0.30 ^c	-0.47 ^c	0.05	-0.28 ^c
$T_{10\text{cm}}$	0.17	-0.57 ^c	-0.03	-0.48 ^c	-0.16	-0.39 ^c	-0.32 ^c	-0.32 ^c	-0.14 ^d	-0.33 ^c	-0.02	0.23 ^c	0.23 ^c	-0.34 ^c	0.40 ^c	-0.56 ^c	0.29 ^c	-0.53 ^c	0.00	-0.31 ^c
$T_{15\text{cm}}$	0.21	-0.57 ^c	0.10	-0.39 ^c	-0.01	-0.28 ^d	-0.26 ^c	-0.26 ^c	-0.11	-0.28 ^c	0.09	0.10	0.26 ^c	-0.26 ^c	0.34 ^c	-0.40 ^c	0.32 ^c	-0.59 ^c	-0.07	-0.41 ^c
$T_{20\text{cm}}$	0.27 ^d	-0.55 ^c	0.17	-0.35 ^c	0.09	-0.19	-0.17	-0.17	-0.10	-0.27 ^c	0.19 ^d	0.25 ^c	0.25 ^c	-0.18 ^c	0.30 ^c	-0.26 ^c	0.34 ^c	-0.63 ^c	-0.11	-0.43 ^c

^aNet ecosystem exchange (NEE) was measured with the transparent chamber and total respiration (R_{TOT}) with the opaque chamber. The depth of permafrost (PF) is reported for JD 240. The carbon uptake is marked positive and emission from the ecosystem to the atmosphere is negative. See text for other abbreviations.

^bMeasured with respiration chamber (vol. 870 cm^3).

^cCorrelation is significant at the 0.01 level, a is measured with respiration chamber (vol. $x \text{ cm}^3$).

^dCorrelation is significant at the 0.05 level.

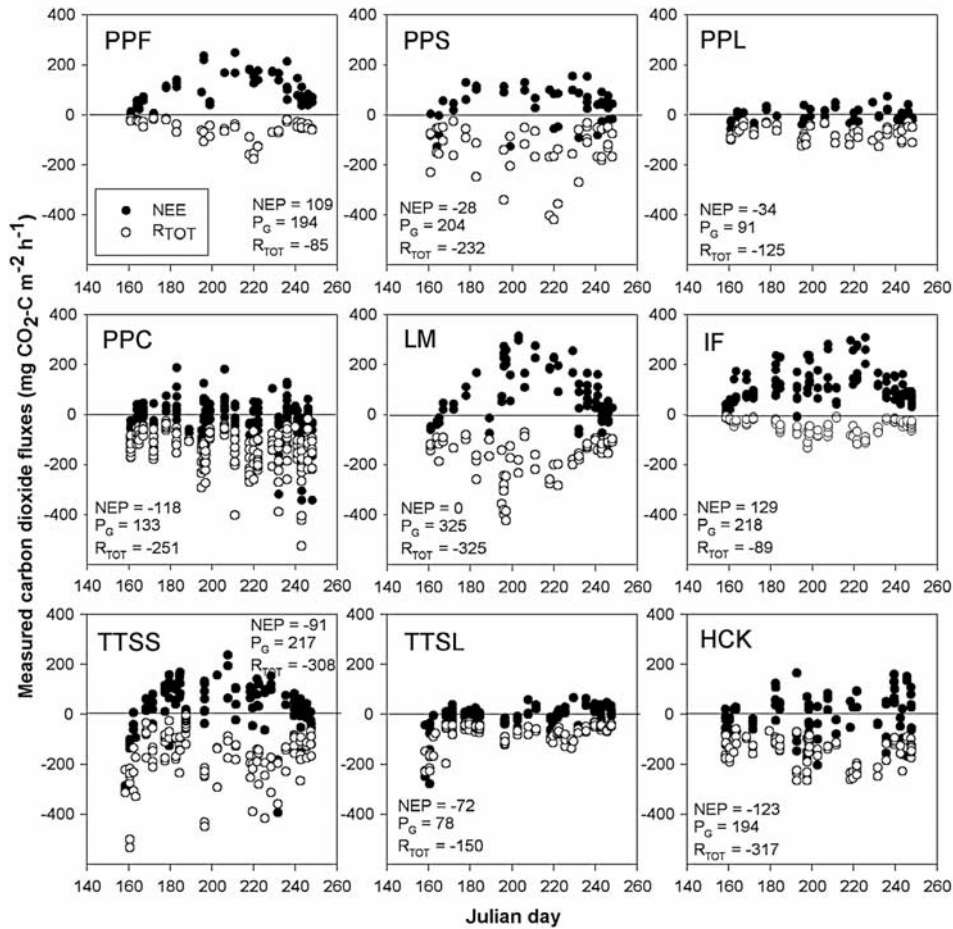


Figure 3. Seasonal patterns of measured daytime (10–18) net ecosystem exchange (NEE) and total respiration (R_{TOT}) in various microsites in Lek Vorkuta catchment in summer 2001. Modeled net ecosystem production (NEP), gross photosynthesis (P_G), and respiration are given in each plot.

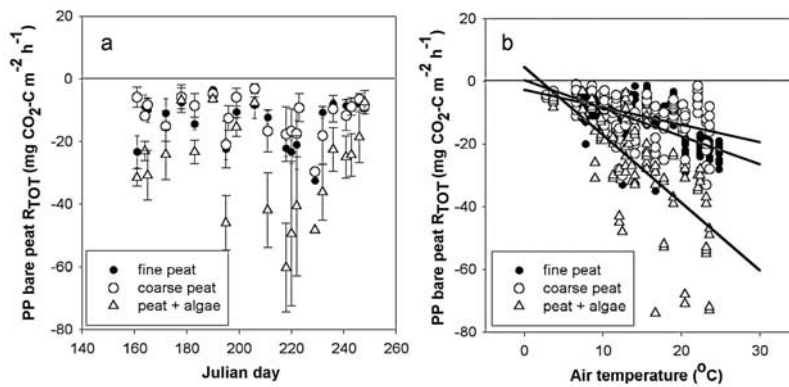


Figure 4. Comparison of respiration dynamics in three different microsites at peat plateau bare peat. (a) Seasonal pattern of measured R_{TOT} with standard deviation and (b) R_{TOT} flux in relation with air temperature. The linear regression line $R_{TOT} = ax + b$ ($a; b; R^2; n; F$) is shown for fine peat ($-0.896; 0.434; 50; 227; 233$), coarse peat ($-0.555; -2.77; 19; 175; 40.6$), and peat with algae ($-2.16; 4.47; 51; 96; 101$).

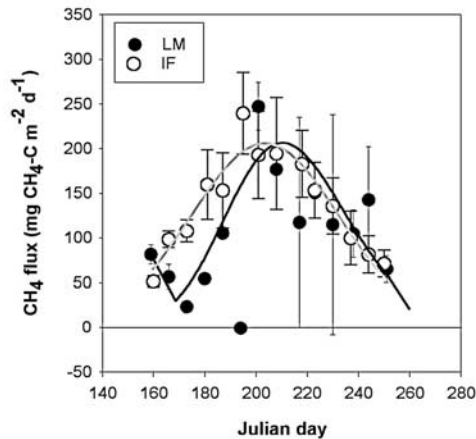


Figure 5. Methane fluxes from lake margin (LM) and intermediate flarks (IF). Methane emission between JD 160 and 260 was calculated integrating daily values from regression line (LM black line and IF shaded line).

while the Lek Vorkuta river showed occasional uptake of CO_2 (Figure 6a). The mean CH_4 emissions were 23.9 and 9.9 $\text{mg CH}_4\text{-C m}^{-2} \text{d}^{-1}$ from the lake and the river sites, respectively. The mean CO_2 fluxes were also toward the atmosphere from the lake and the river, 5.4 and 14.5 $\text{mg CO}_2\text{-C m}^{-2} \text{h}^{-1}$, respectively. There was no correlation between the carbon gas fluxes and water temperature.

3.6. Seasonal Fluxes

[32] Seasonal fluxes were modeled integrating hourly fluxes over 100 days according to the model parameters calculated for each microsite. The mean photosynthesis, respiration, and net ecosystem production values for grouped microsites are shown in Figure 3. The wet peaty tundra soil microsites gained carbon during the summer, while other microsites lost carbon to the atmosphere. The NEP on LM was zero despite having the highest mean P_G .

When including the high CH_4 emissions, the LM acted as a carbon source to the atmosphere.

3.7. Model Validation

[33] The seasonal CO_2 balance with chambers is based on the regression models constructed for the season when the measurements were done. Issues to be determined were whether the models, calibrated for a particular summer, could also apply in other summers, or are the models valid only for specific weather conditions during a summer. Therefore the regression models (based on 70% of the data) were cross-tested in intermediate flarks and hummocks with respect to the parameters and years 1999 and 2001 (Table 3). Notably, the microsites in hummocks were the same in 1999 and 2001, while wet flarks measured in 1999 and 2001 were classified as intermediate flarks in 2001 (and are here compared with 1999 intermediate flarks) due to the water table drop in 2001, the mean drop being 4 cm (see Table 2). In 2001, the R^2 values in IF and HCK respiration models were 0.10 and 0.26, respectively. Only a minor improvement in regression was achieved when the model was drawn from the mid-season measurements only.

[34] Photosynthesis potential in the intermediate flark was higher in 2001 due to the lower water table and higher above ground plant biomass. In the intermediate flark, the respiration parameters were different between 1999 and 2001. The 2001 model parameters overestimated the NEP in 1999 environmental data, and the 1999 model parameters underestimated the NEP in 2001. There was no change in vegetation growth dynamics in hummocks between 1999 and 2001. Despite the difference in seasonal weather in 1999 and 2001, both of the P_G model results were similar (Table 3). The modeled respiration was higher in 2001, as were the mean respiration values, -107 and $-142 \text{ mg CO}_2\text{-C m}^{-2} \text{h}^{-1}$ in 1999 and 2001, respectively. As a result of high respiration, the NEP was negative in hummocks.

[35] Carbon balances for different microsites were estimated based on the specific seasonal regression models or integrating the seasonal mean over 100 days (Table 4).

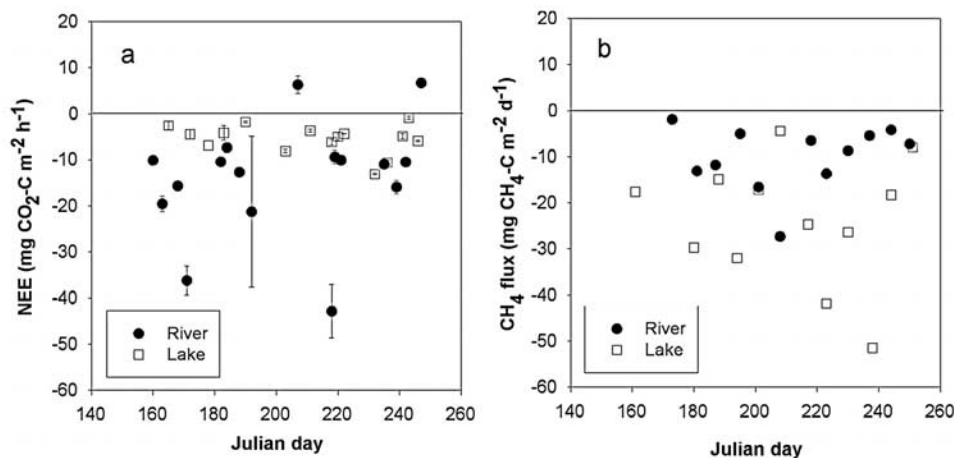


Figure 6. Carbon fluxes in the Thermokarst Lake and Lek Vorkuta River. (a) Net ecosystem exchange was measured with transparent chamber, and (b) methane fluxes were measured with opaque aluminum chamber. Positive values represent uptake and negative values represent emission.

Table 3. Comparison Between 1999 and 2001 Parameter Estimates Used to Reconstruct the Hourly Gross CO₂ Exchange and Total Respiration for Different Microsites Between JDs 160 and 260^a

	Flark 2001	Intermediate Flark 1999	Hummock 2001	Hummock 1999
	<i>Gross CO₂ Exchange Parameters</i>			
Q	348 (115)	230 (127)	348 (123)	339 (48)
K	1070 (787)	104 (125)	999 (947)	529 (370)
ETI, b_1	16 (26)	158 (16)	80 (29)	110 (18)
T _{AIR} , b_2	2.8 (1.7)	7 (1)	1.9 (1.7)	5 (1)
Constant c_1	2.9 (25)	-246 (143)	-47 (31)	-124 (48)
Modeled P_G	214	118	172	179
N _i collars	3	5	2	7
R ² (%)	48	63	65	55
df _{reg} , df _{res}	5, 101	5, 104	5, 44	5, 131
	<i>Respiration Parameters</i>			
TAIR, b_3	0.030 (0.009)	0.065 (0.011)	0.028 (0.008)	0.078 (0.008)
ETI, b_4	0.27 (0.19)	2.14 (0.22)	0.53 (0.16)	0.90 (0.15)
Constant c_2	3.18 (0.18)	1.56 (0.17)	4.22 (0.14)	3.10 (0.11)
Modeled R_{TOT}	-93	-75	-290	-182
N _i collars	3	5	2	7
R ² (%)	10	70	26	65
df _{reg} , df _{res}	3, 107	3, 77	3, 68	3, 103

^aModeled values represent the carbon flux (g CO₂-C m⁻²). Standard error of the estimate (SE in parentheses), coefficient of determination (R²; min – max), degrees of freedom for regression (Df_{reg}), and residuals (Df_{res}, min – max) are also shown for the microsites.

Standard error (SE) of the NEP (including the P_G and R_{TOT}) was used to evaluate the uncertainty of microsites. The wide range of confidence interval is a result of high variation in measured fluxes at the microsites. This variation was especially high in shrub-dominated tundra heaths.

3.8. Areal Flux Estimates

[36] For the catchment scale carbon balance estimates, we reclassified the microsites by weighting the microsites with their areal abundance (Table 4). Areally, wet peaty tundra gained 109 g m⁻² while other surfaces lost from -5 to -91 g m⁻² carbon. According to upscaling, Lek Vorkuta catchment (114 km²) lost about 4 Gg C (34.6. g m⁻² as a mean) in summer 2001 (Table 5). Variation was especially

large within the most common vegetation type, shrub-dominated tundra heaths, which again causes relatively high uncertainty levels for our estimate of the total balance estimates.

4. Discussion

4.1. Growing Season CO₂ Fluxes

[37] The growing season in 2001 was 10 days longer, and was drier and warmer than summer 1999. In most wet microsites (wet flarks) where the water table was above or at the vegetation surface in 1999, the mean water table was 4 cm below the surface in 2001, which increased the plant biomass for carbon sequestration. The vegetation growth dynamics, especially emergence, growth, and senescence of

Table 4. Comparison of Seasonal Carbon Fluxes From Various Microsites at Lek Vorkuta Catchment (67°24'N, 63°22'E)^a

Site/Microsites	CO ₂ Fluxes Summer					CH ₄ Flux Summer, ^b g m ⁻²	Seasonal C Balance (±SE), g m ⁻²	Areal Reclassification	Percent of the Class Area
	MWT	N	P _G , g m ⁻²	R _{TOT} , g m ⁻²	NEP, g m ⁻²				
Peat plateaus									
<i>Sphagnum</i> dominated	5–10	2	204	-232	-28	-0.4	-28 (±65)	peat plateau	20
Lichen dominated	-	2	91	-125	-34	0.2	-34 (±16)	peat plateau	70
Crack succession	-	8	133	-251	-118	0.0	-118 (±14)	peat plateau	5
Bare peat surfaces	-	10	-	-28 ^b	-	-	-28 (±1)	peat plateau	5
Wet peaty tundra soils									
<i>Carex</i> + <i>Sphagnum</i>	0–5	2	194	-85	109	-2.6	106 (±18)	wet peaty tundra	35
Intermediate flarks	0–5	3	217	-93	124	-13.6	110 (±23)	wet peaty tundra	65
Dry peaty tundra soils									
Hummocks	>20	2	194	-317	-123	-0.5	-123 (±72)	dry peaty tundra	100
Thin tundra soils									
Lichen dominated	-	3	78	-149	-72	0.0	-72 (±10)	tundra heath	20
Shrubs dominated	-	3	217	-308	-91	0.0	-91 (±59)	tundra heath	80
Thermokarst lakes, profundal	-	1	-	-13 ^b	-	-2.4	-15	lake, profundal	100
Lake and pond margins	10	2	325	-325	0	-5.4	-5 (±9)	lake and pond margins	100
River	-	1	-	-33 ^b	-	-1.0	-34	river	100

^aThe positive values represent a gain to the ecosystem; negative values represent a carbon loss. Column “Percent of the Class Area” indicates the weight used for the microsite within vegetation class when calculating areal estimates in Table 5. MWT, mean water table; N, number of microsites.

^bMean integrated over 100 days.

Table 5. Areal Estimates of Carbon Stocks and Fluxes in Lek Vorkuta Catchment (Area 114 km²)^a

Classes Within the Terrestrial and Aquatic Ecosystems Used in the Areal Integration	Area, %	C Stock in Vegetation, ^b g m ⁻²	C Stock in Soil, ^c (g m ⁻²) × 10 ³	C Flux, g m ⁻²	Areal Flux A = 114 km ² (±SE) (g) × 10 ⁶
Wet peaty tundra	12.9	260	41.3	109	1597 (±313)
Dry peaty tundra	3.2	275	46.2	-123	-449 (±263)
Peat plateau	9.0	210	125.4	-37	-377 (±256)
Tundra heath	46.8	290	13.9	-87	-4652 (±2625)
Willow dominated stands ^d	24.3	1070	23.5	0	0
Thermokarst lakes, profundal ^e	3.3	0	20.4	-15	-58
Lake and pond margins	0.1	120	46.3	-5	-1 (±1)
Rivers ^f	0.3	0	8	-34	-10
Mean (weighted by area)		457	31.1	-34.6	-
SUM	100	-	-	-	-3950(±3457)

^aC flux measurements from individual microsites were weighted (see Table 4).

^bCalculations were based on field measurements (trees and large shrubs) and samples (dwarf shrubs, other field layer) by T. Virtanen et al., and will be published in more detail elsewhere.

^cKuhry et al. [2002]; P. Kuhry, Arctic Centre, Rovaniemi, personal communication. Carbon stocks in upland soil are reported to 1 m depth. In peat and lake deposits to the contact with mineral subsoil.

^dWillow stands were not measured in this study. These surfaces, mainly situated in depressions, have a high carbon stock in phytomass and an average carbon stock in soil. No literature data available on annual carbon balance. Values probably in between wet peaty tundra and tundra heath classes. Therefore we assume that present carbon balance is close to zero.

^eAll lakes in the region were classified as thermokarst lakes.

^fRiver area was calculated using the river layer in GIS and assuming mean river width of 8 m in the catchment.

mosses, followed the ETI curve, while in sedge- and shrub-dominated surfaces the maximum growth occurred between JDs 200 and 220 [see also Heikkinen et al., 2002a].

[38] The mean NEE fluxes on intermediate flarks and hummocks were about 10–30% higher in 2001 than in 1999. In intermediate flarks, the mean NEE were only 10% higher, while in hummocks, the NEE and R_{TOT} were 21 and 33% higher, respectively. The NEE/ R_{TOT} ratio was 1.91 (1.96) for flarks and 0.23 (0.37) for hummocks in 2001 and (1999) [Heikkinen et al., 2002a]. This suggests that warmer and drier conditions increased the carbon loss from the hummocks. Since the vegetation of hummocks remained unchanged between these two years, the carbon loss originated presumably from the unfrozen peat, that is, from the active peat layer. In addition, the mean peat temperature at 5 cm was 1° and 2°C higher in 2001 than in 1999 in flarks and hummocks, respectively. There was some difference in the mean permafrost depth in hummocks between 1999 and 2001, for example, 50 cm in 1999 and 54 cm in 2001. We concluded that in hummocks, the increase in respiration, which is a sum of autotrophic and heterotrophic respiration, is a result of temperature-induced decomposition. The permafrost melting dynamics follow the pattern of ETI and were autocorrelated to the respiration dynamics.

[39] Griffis et al. [2000] suggested that climatic conditions during the pre-growth period are critical to the sink/source strength of the wetland over the growing season. In this study the early season respiration fluxes were 3–4 times the reported seasonal mean hourly fluxes at the thin tundra soil microsites. The early season thawing peak is important on a seasonal scale [see also Oechel et al., 1997; Oberbauer et al., 1998]. Most likely, a great part of the interannual labile carbon is released from the soil soon after the frost melting. In our study sites, the mean NEE during summer was positive only at the TTS with shrubs. There is a high carbon circulation in shrub-dominated surfaces [Heikkinen et al., 2002b], but the mean net ecosystem production,

calculated from the difference between seasonal photosynthesis and respiration, was close to zero [Heikkinen et al., 2002b]. On lichen-dominated thin soils, the photosynthesis and respiration had little variation throughout the growing season. At the time, some of the fresh organic carbon was transported to the roots in the form of carbohydrates for later use. There is reason to believe that the thawing peak is a result of decomposition of fine root and root exudates (carbon hydrates) and mechanical release of gas molecules trapped into the soil [Oechel et al., 1997].

[40] The peat plateau crack succession is thought to release a substantial amount of carbon [Bubier et al., 1995a; Liblik et al., 1997]. We compared eight microsites with various crack types including small surface cracks with thin vegetation coverage and wider and older cracks with evergreen vegetation, especially *R. chamaeomorus* and *B. nana*. In all cases, the carbon was released to the atmosphere. On microsites with cracks, the photosynthesis and respiration potential depended on the present vegetation. In addition, the temperature of the soil further controlled respiration. On smaller cracks, the CO₂ emissions were at the same level with the bare peat emissions.

[41] The bare peat respiration from coarse and fine peat surfaces showed a similar response to the air temperature. When algae were introduced to the system, the temperature response changed rapidly. Algae growth increases the R_{TOT} potential on the system. The respiration potential doubled when temperature exceeded 20°C, and it is very likely that the carbon circulation is high. However, this can explain only part of the increase in respiration. An increase in soil moisture, availability of nutrients, and microbial activity can explain the rest of the higher respiration at algae dominated peat surfaces [Hamilton et al., 1994].

4.2. Growing Season CH₄ Fluxes

[42] The pattern of CH₄ fluxes followed the vegetation growth pattern on the wetter intermediate flark and peat

plateau margin. The drier surfaces showed no distinct pattern. Therefore the seasonal flux was calculated from the annual means. In intermediate flarks, the seasonal CH₄ emission in 2001 was 13.6 g m⁻², whereas in 1999, it was 5 g m⁻² [Heikkinen *et al.*, 2002a]. The 2.5-fold increase in CH₄ fluxes is clearly a result of a 2°C increase in the monthly mean temperature and a 4-cm drop in the seasonal mean water table level in 2001, thus supporting better plant growth. These results stressed the fact that in spite of the small drop in the water table in wet tundra, the CH₄ emission increased with increasing temperature. In a recent European research project, temperature was found to be the key driving force for the CH₄ emissions from northern wetlands [Christensen *et al.*, 2003]. However, if a drop in water table is high enough, it can overcome the importance of temperature in the CH₄ release because the good aeration causes basic changes in microbiology and vegetation of wetlands [Nykänen *et al.*, 1998; Moore and Roulet, 1993].

[43] The lake margin had a seasonal CH₄ flux of 5.4 g C m⁻² season⁻¹, which is in the range reported from boreal littoral ecosystems in Finland [Juutinen *et al.*, 2001, 2003]. The methane emission from LM peaked after the snowmelt and decreased until vegetation growth started. Later, the CH₄ emission followed the vegetation growth dynamics. Possibly, in the beginning of the season the methane flux originates from the winter CH₄ production accumulated and trapped on ice [Michmerhuizen *et al.*, 1996]. In addition, high water table and cold soil and water conditions after the melting process effectively inhibited the methane production and emission to the atmosphere [Heikkinen *et al.*, 2002a]. The rapid increase in methane emissions could be boosted by the increase in the number of gas conducting stems of sedges, and increased soil temperature [Bubier, 1995; Morrissey *et al.*, 1993].

[44] On drier microsites, there was occasional CH₄ uptake, but the seasonal balance was close to zero. Most likely the peat in the old peat plateau is not anaerobic enough to support methanogenesis. Furthermore, the availability of plant-derived substrates is low in these microsites.

4.3. Gas Fluxes From the River and Thermocarst Lake

[45] There are a limited number of seasonal carbon gas flux studies from aquatic ecosystems in the Russian Arctic. Our results from the thermocarst lake and the Lek Vorkuta River in the west Siberian tundra indicated that aquatic ecosystems in this region are important sources of both CH₄ and CO₂ to the atmosphere, as are lakes and rivers in other arctic areas [Kling *et al.*, 1991, 1992; Ramlal *et al.*, 1994; Zimov *et al.*, 1997]. Zimov *et al.* [1997] estimated an average CH₄ emission of 1.8 g CH₄ m⁻² yr⁻¹ (May–July) for north Siberian lakes, which is somewhat lower than the summer CH₄ emission from the thermocarst lake in this study (3.2 g CH₄ m⁻² season⁻¹). The mean daily CH₄ fluxes from the thermocarst lake and the Lek Vorkuta River (32 and 13 mg CH₄ m⁻² d⁻¹, respectively) were at least twice the CH₄ emissions reported for nine lakes (1.3–16.4 mg CH₄ m⁻² d⁻¹) and the Kuparuk River (5.8 mg CH₄ m⁻² d⁻¹) on the north slope of arctic Alaska [Kling *et al.*, 1992]. In comparison, Whalen and Reeburg [1990]

reported the average CH₄ efflux of 21 mg CH₄ m⁻² d⁻¹ (range 4.6–131) for some ponds and lakes in arctic Alaska. The daily mean CO₂ emissions from the thermocarst lake and the Lek Vorkuta River in this study (5.4 and 14.5 mg CO₂-C m⁻² h⁻¹, respectively) correspond to the average CO₂ emission of 10.5 (range from –2.78 to 29.9) mg CO₂-C m⁻² h⁻¹ reported for 25 lakes and four rivers on the north slope of arctic Alaska [Kling *et al.*, 1992] or 3.4 mg CO₂-C m⁻² h⁻¹ for an Arctic tundra lake on the Tuktoyaktuk Peninsula, Canada [Ramlal *et al.*, 1994].

[46] It is unlikely that the decomposition of autochthonous organic matter could alone maintain the observed total carbon (CH₄ + CO₂) effluxes of 15.4 and 35.8 g C m⁻² yr⁻¹ from our mesotrophic (the summertime epilimnic total nitrogen, total phosphorus, and total organic carbon concentrations were 418–833 µg L⁻¹, 13–29 µg L⁻¹, and 7–13 mg L⁻¹, respectively (Lauri Arvola, Lammi Biological Station, unpublished data, 2000)) lake and river sites, respectively. Thus we suggest that the aquatic CH₄ and CO₂ emissions were derived mainly from the respiration of allochthonous organic matter, and dissolved CH₄ and CO₂ leached from the catchment. Terrestrial ecosystems are important sources of C into tundra lakes, where low nutrient availability could limit autochthonous production; thus arctic lakes conduct terrestrial carbon to the atmosphere [Kling *et al.*, 1991, 1992; Ramlal *et al.*, 1994; Zimov *et al.*, 1997]. Kling *et al.* [1991, 1992] estimated that lakes and rivers on the north slope of Alaska release an average of 24 g of carbon C m⁻² yr⁻¹ to the atmosphere, which could equal to up to 20–50% of the net C accumulation rates in arctic tundra.

[47] The CH₄ and CO₂ emissions presented here for the open water period actually underestimate the annual carbon gas release at the aquatic study sites, since we did not measure the gas exchange during the cold season. Both CH₄ and CO₂ are produced in arctic lakes under ice during winter. The gas stores accumulated in the water columns are largely released to the atmosphere from holes appearing in the ice during winter or during water column circulation after the spring ice melt [Ramlal *et al.*, 1994; Zimov *et al.*, 1997]. According to Zimov *et al.* [1997], north Siberian lakes could release as much as 75% of their annual CH₄ emission during winter, and the CO₂ release in 2 weeks after spring ice melt by degassing of CO₂ from the water column was estimated to account for almost half of the annual CO₂ emission from an Arctic tundra lake on the Tuktoyaktuk Peninsula, Canada [Ramlal *et al.*, 1994]. In addition, our results did not take into account the riverine losses of dissolved and particular C from the study area, of which much of the young dissolved fraction becomes decomposed in the rivers and coastal waters and is subsequently released to the atmosphere before entering the oceans [Raymond and Bauer, 2001].

4.4. Seasonal Carbon Balance

[48] Regression models for hourly P_G and R_{TOT} fluxes have been widely used to fill in missing data between measurements with reasonable accuracy [Alm *et al.*, 1999; Bubier *et al.*, 1998, 1999; Griffis *et al.*, 2000; Heikkinen *et al.*, 2002a; Kettunen *et al.*, 2000]. The models and model parameters drawn from seasonal flux measurements are not

capable of interseasonal predictions. Despite the different model parameters, the models may give similar results mainly because most of the environmental parameters are not independent.

[49] The seasonal models estimating flux from each microsite were good because there was limited variation in WT (hydrology), and vegetation followed the growth pattern and ETI. Unfortunately, the real ecosystem carbon balance is vulnerable to short-term changes in hydrology (precipitation), length of growing season, and, presumably, the permafrost level [Billings *et al.*, 1982]. The explanatory power of the models would be better if, for example vegetation, soil characteristics, and cumulative precipitation are included, especially when integrating over longer time-scales and varying vegetation. However, by considering the confidence intervals of the models, we can conclude that wet surfaces gained carbon and dry surfaces lost carbon from June to September 2001.

[50] The lake margin at the littoral zone of the thermokarst lake showed close to zero carbon balance. T. Larmola (personal communication, 2003) has also found that seasonal respiration can counterbalance the seasonal gross photosynthesis in the littoral zones of two boreal lakes. In thermokarst lakes, the margin (littoral zone) is generally narrow, about 2 m in this study. The margin, with its dense vegetation, may efficiently trap the nutrients and carbon derived from the eroding peat around the lake. Nutrients and carbon then fuel decomposition and the CO₂ and CH₄ production at the margin. Therefore the littoral zone has a great importance in the lake gas dynamics in northern lakes [Michmerhuizen *et al.*, 1996].

4.5. Areal Carbon Estimates and Their Uncertainty

[51] The Lek Vorkuta catchment lost 4 Gg of carbon within the summer 2001. Winter fluxes would increase the annual carbon loss from 2 to 24% [Heikkinen *et al.*, 2002a]. Extrapolation of the results from the Lek Vorkuta catchment for the whole European side tundra (205,000 km²) assuming the corresponding vegetation structure and their responses in the whole region, gives seasonal carbon emission of -7.2 Tg (35 g C m⁻²). Methane emissions account 3.5% (1.36 g CH₄ m⁻²) of the areal emissions during the summer. For comparison, Reeburgh *et al.* [1998] estimated regional flux of 20.9 Gg CH₄ yr⁻¹ (0.795 g CH₄ m⁻² yr⁻¹) for the Kuparuk River basin, which is dominated by wetlands and open water. In addition, Roulet *et al.*'s [1992] estimation for the Hudson Bay Lowland was 538 Gg CH₄ yr⁻¹ (1.681 g CH₄ m⁻² yr⁻¹). All of these studies address the importance of the areal coverage of the dry and wet surfaces on the methane emissions.

[52] The assumption that the vegetation composition is the same for the whole European tundra is subject to some bias. For example, the landscape becomes more patterned toward the north where the presence of ponds and peat plateaus increases and heaths and willows disappear. However, when the fluxes were integrated over tundra regions in the Usa basin (49,500 km²) using satellite image based vegetation classification (Virtanen *et al.*, submitted manuscript, 2004), and then farther to the European continental side of tundra (assuming for the whole region same vege-

tation composition as in the Usa basin), the flux estimate changes only slightly, to -8.1 Tg. Zamolodchikov and Karelin [2001] estimated 0.8 ± 11.3 Tg mean annual carbon loss for the east European tundra. The study was based on a few CO₂ flux measurements in terrestrial ecosystems during field seasons from 1993 to 1998. The warm summer in the present study is the probable reason for the high carbon loss, suggesting that the tundra carbon balance is highly sensitive to climatic warming, especially in drier habitats.

[53] There is a high temporal and spatial variation in measured fluxes. Variation was found to be especially large within the most common vegetation type, shrub-dominated tundra heaths. This is mainly due to the coverage differences of dominant species in our replicate microsites. This again causes relatively high uncertainty levels for our areal estimate of the total fluxes. Our findings indicate that in the future it would be important to focus carbon balance studies intensively also on tundra heaths, not only on peatlands.

[54] The carbon balance in the dry tundra surfaces was shown to be the most sensitive to warming. The dry tundra biomes, which have the highest potential to loose carbon to the atmosphere, presently contain 60% of the carbon stock in the eastern European tundra soils (Table 5). It was important that a single dry summer could induce remarkable carbon loss. In summer 2001, the dry peaty tundra and tundra heath lost 0.3 and 0.7% of their carbon stocks, respectively. When the C loss is calculated to the active layer of about 50 cm in depth, the loss percentage would be more than 1% because the carbon stocks are determined for the soil depth of 1 m (Table 5).

[55] Plant assemblages are useful carbon flux predictors, as water table position and ground temperatures cannot be well estimated by remote sensing [Bubier, 1995]. Satellite image based classifications including the terrestrial surfaces and aquatic ecosystems are the most feasible way to make regional flux estimates for remote areas. In tundra, the main ecosystems can be identified and matched with reasonable accuracy [Rees *et al.*, 2002; Virtanen *et al.*, submitted manuscript, 2004]. Rivers, ponds, heaths, and willows can easily be identified in remote sensing data. Furthermore, bryophytes have unique spectral signatures [Bubier *et al.*, 1997] that allow the identification of differences in moisture and thus separate the drier shrub-dominated hummock sites from sedge-dominated wet sites (flarks).

[56] There might be some error in our areal carbon balance calculations due to inaccuracies in the satellite image classification. In our 2001 case, the main uncertainties due to vegetation classification inaccuracies would arise if the coverage estimate of the wet sites (as they were only carbon-fixing surfaces) would be largely erroneous. The accuracy testing of the satellite images is not a simple issue [Foody, 2002]. In an accuracy test studying how correctly individual pixels of the main vegetation types (forests, willow-dominated stands and meadows, peatlands, tundra heaths, mainly unvegetated areas, and water bodies) for the whole Usa basin were classified, we found out that 84% of the independent test points were classified correctly (Virtanen *et al.*, submitted manuscript, 2004). This is already good accuracy, when compared to results achieved in other studies [Foody, 2002]. Second, and when thinking

of the upscaling calculations, the more relevant question is “are the relative proportions of different vegetation types in the classification correct, or are there such biases that some types are over- or under-presented?” For this we cannot present numerical tests, but based on some general Russian thematic maps, experience gained during the fieldwork, general knowledge of the landscape structure, and the several hundred photographs taken in the field, we believe that the proportions of different vegetation types in our classification are not far from reality. Another potential error source would be if the measured sites would not be representative for vegetation classes. We believe that this was not the major problem.

5. Conclusions

[57] The results showed that in the eastern European Russian tundra, only the wetlands are able to gain carbon in warm summers when all the other terrestrial and aquatic environments lost carbon. The respiration already exceeds the photosynthesis during summer, and if winter and leaching of carbon were included, the loss could be greater than reported here. There is no indication that summer temperature has increased in the region continuously during the last decades. However, the models predict an increase both in summer and winter temperatures in the region, which would be a big threat to the global carbon balance. Only 2°C increase in the mean temperature during summer doubled the CH₄ emissions from the wet surfaces, supporting the recent hypothesis of the key importance of temperature in methane dynamics in northern wetlands.

[58] This study is the first attempt to assess the seasonal carbon balance in tundra based on gas flux studies in both terrestrial and aquatic ecosystems. Despite the uncertainties, the results strongly suggest that the carbon balance in the region is highly sensitive to the global warming.

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References

- Alm, J., A. Talanov, S. Saarnio, J. Silvola, E. Ikkonen, H. Aaltonen, H. Nykänen, and P. J. Martikainen (1997), Reconstruction of the carbon balance for microsites in a boreal oligotrophic pine fen, Finland, *Oecologia*, *110*, 423–431.
- Alm, J., L. Schulman, J. Walden, H. Nykänen, P. J. Martikainen, and J. Silvola (1999), Carbon balance of a boreal bog during a year with an exceptionally dry summer, *Ecology*, *80*, 26–39.
- Bartlett, K. B., and R. C. Harriss (1993), Review and assessment of methane emissions from wetlands, *Chemosphere*, *26*(1–4), 261–320.
- Billings, W. D., J. O. Luken, D. A. Mortensen, and K. M. Peterson (1982), Arctic tundra: A source or sink for atmospheric carbon dioxide in a changing environment, *Oecologia*, *53*, 7–11.
- Botch, M. S., K. I. Kobak, T. S. Vinson, and T. P. Kolchugina (1995), Carbon pools and accumulation in peatlands of the former Soviet Union, *Global Biogeochem. Cycles*, *9*(1), 37–46.
- Bubier, J. L. (1995), The relationship of vegetation to methane emission and hydrochemical gradients in northern peatlands, *J. Ecol.*, *83*, 403–420.
- Bubier, J. L., T. R. Moore, L. M. Bellisario, and N. T. Comer (1995), Ecological controls on methane emissions from a northern peatland complex in the zone of discontinuous permafrost, Manitoba, Canada, *Global Biogeochem. Cycles*, *9*(4), 455–470.
- Bubier, J. L., B. N. Rock, and P. M. Crill (1997), Spectral reflectance measurements of boreal wetland and forest mosses, *J. Geophys. Res.*, *102*(D24), 29,483–29,494.
- Bubier, J. L., P. M. Crill, T. R. Moore, K. Savage, and R. K. Varner (1998), Seasonal patterns and controls on net ecosystem CO₂ exchange in a boreal peatland complex, *Global Biogeochem. Cycles*, *12*(4), 703–714.
- Bubier, J. L., S. E. Frohling, P. M. Crill, and E. Linden (1999), Net ecosystem productivity and its uncertainty in a diverse boreal peatland, *J. Geophys. Res.*, *104*(D22), 27,683–27,692.
- Carroll, P., and P. M. Crill (1997), Carbon balance of a temperate poor fen, *Global Biogeochem. Cycles*, *11*(3), 349–356.
- Chapin, F. S. III, G. R. Shaver, A. E. Giblin, K. J. Nadelhoffer, and J. A. Laundre (1995), Responses of arctic tundra to experimental and observed changes in climate, *Ecology*, *76*(3), 694–711.
- Christensen, T. R., A. Joabsson, L. Ström, N. Panikov, M. Mastepanov, M. Öquist, B. H. Svensson, H. Nykänen, P. J. Martikainen, and H. Oskarsson (2003), Factors controlling large-scale variations in methane emissions from wetlands, *Geophys. Res. Lett.*, *30*(7), 1414, doi:10.1029/2002GL016848.
- Cicerone, R., and R. Oremland (1988), Biogeochemical aspects of atmospheric methane, *Global Biogeochem. Cycles*, *2*(4), 299–327.
- Cole, J. J., N. F. Caraco, G. W. Kling, and T. K. Kratz (1994), Carbon dioxide supersaturation in the surface waters of lakes, *Science*, *265*, 1568–1570.
- Crill, P. M. (1991), Seasonal patterns of methane uptake and carbon dioxide release by a temperate woodland soil, *Global Biogeochem. Cycles*, *5*(4), 319–334.
- Drugokencky, E. J., K. A. Masarie, P. M. Lang, and P. P. Tans (1998), Continuing decline in the growth rate of the atmospheric methane burden, *Nature*, *393*, 447–450.
- Foody, G. M. (2002), Status of land cover classification accuracy assessment, *Remote Sens. Environ.*, *80*, 185–201.
- Gorham, E. (1991), Northern peatlands: Role in the carbon cycle and probable responses to climatic warming, *Ecol. Appl.*, *1*, 182–195.
- Griffis, T. J., W. R. Rouse, and J. M. Waddington (2000), Interannual variability of net ecosystem CO₂ exchange at a subarctic fen, *Global Biogeochem. Cycles*, *14*(4), 1109–1121.
- Hamilton, J. D., C. A. Kelly, J. W. M. Rudd, R. H. Hesslein, and N. T. Roulet (1994), Flux to the atmosphere of CH₄ and CO₂ from wetland ponds on the Hudson Bay lowlands (HBL's), *J. Geophys. Res.*, *99*(D1), 1495–1510.
- Heikkinen, J. E. P., V. Elsakov, and P. J. Martikainen (2002a), Carbon dioxide and methane dynamics and annual carbon balance in tundra wetland in north east Europe, *Russia*, *Global Biogeochem. Cycles*, *16*(4), 1115, doi:10.1029/2002GB001930.
- Heikkinen, J. E. P., M. Maljanen, M. Aurela, K. J. Hargreaves, and P. J. Martikainen (2002b), Carbon dioxide and methane dynamics in a sub-arctic peatland in northern Finland, *Polar Res.*, *21*(1), 49–62.
- Intergovernmental Panel on Climate Change (2001), The carbon cycle and atmospheric carbon dioxide, in *Climate Change 2001: The Scientific Basis*, edited by J. T. Houghton, et al., pp. 183–237, Cambridge Univ. Press, New York.
- Juutinen, S., J. Alm, P. J. Martikainen, and J. Silvola (2001), Effects of spring flood and water level draw-down on methane dynamics in the littoral zone of boreal lakes, *Freshwater Biol.*, *46*, 855–869.
- Juutinen, S., J. Alm, T. Larmola, J. T. Huttunen, M. Morero, S. Saarnio, P. J. Martikainen, and J. Silvola (2003), Methane (CH₄) release from littoral wetlands of boreal lakes during an extended flooding period, *Global Change Biol.*, *9*(3), 413–424.
- Kane, D. L., (1997), The impact of hydrologic perturbations on arctic ecosystems induced by climate change, in *Global Change and Arctic Terrestrial Ecosystems*, edited by W. C. Oechel, et al., pp. 63–81, Springer-Verlag, New York.
- Kettunen, A., V. Kaitala, J. Alm, J. Silvola, H. Nykänen, and P. J. Martikainen (2000), Predicting variations in methane emissions from boreal peatlands through regression models, *Boreal Environ. Res.*, *5*, 115–131.
- Kling, G. W., G. W. Kipphut, and M. C. Miller (1991), Arctic lakes and streams as gas conduits to the atmosphere: Implications for tundra carbon budgets, *Science*, *251*, 298–301.
- Kling, G. W., G. W. Kipphut, and M. C. Miller (1992), The flux of CO₂ and CH₄ from lakes and rivers in arctic Alaska, *Hydrobiologia*, *240*, 23–36.
- Kuhry, P., G. G. Mazhitova, P.-A. Forest, S. V. Deneva, T. Virtanen, and S. Kultti (2002), Upscaling soil carbon estimates for the Usa Basin

- (northeast European Russia) using GIS-based vegetation and soil classification schemes, *Danish J. Geogr.*, *102*, 11–25.
- Liblik, L. K., T. R. Moore, J. L. Bubier, and S. D. Robinson (1997), Methane emissions from wetlands in the zone of discontinuous permafrost: Fort Simpson, Northwest Territories, Canada, *Global Biogeochem. Cycles*, *11*(4), 485–494.
- Michmerhuizen, C. M., R. G. Striegl, and M. E. McDonald (1996), Potential methane emission from north temperate lakes following ice melt, *Limnol. Oceanogr.*, *41*(5), 985–991.
- Moore, T. R., and N. T. Roulet (1993), Methane flux:water table relations in northern wetlands, *Geophys. Res. Lett.*, *20*, 587–590.
- Morrissey, L. A., D. B. Zobel, and G. P. Livingston (1993), Significance of stomatal control on methane release from Carex-dominated wetlands, *Chemosphere*, *26*, 339–355.
- Nykänen, H., J. Alm, J. Silvola, K. Tolonen, and P. J. Martikainen (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 Biogeochem. Cycles*, *12*(1), 53–69.
- Nykänen, H., J. E. P. Heikkinen, L. Pirinen, K. Tiilikainen, and P. J. Martikainen (2003), Annual CO₂ exchange and CH₄ fluxes on a subarctic palsamire during climatically different years, *Global Biogeochem. Cycles*, *17*(1), 1018, doi:10.1029/2002GB001861.
- Oberbauer, S. F., G. Starr, and E. W. Pop (1998), Effects of extended growing season and soil warming on carbon dioxide and methane exchange of tussock tundra in Alaska, *J. Geophys. Res.*, *103*(D22), 29,075–29,082.
- Oechel, W. C., S. J. Hastings, G. L. Vourlitis, M. A. Jenkins, G. H. Riechers, and N. E. Grulke (1993), Recent change of Arctic tundra ecosystems from a net carbon dioxide sink to a source, *Nature*, *361*, 520–523.
- Oechel, W. C., S. Cowles, N. Grulke, S. J. Hastings, B. Lawrence, T. Prudhomme, G. Riechers, B. Strain, D. Tissue, and G. L. Vourlitis (1994), Transient nature of CO₂ fertilization in Arctic tundra, *Nature*, *371*, 500–503.
- Oechel, W. C., G. L. Vourlitis, and S. J. Hastings (1997), Cold season CO₂ emission from arctic soils, *Global Biogeochem. Cycles*, *11*(2), 163–172.
- Ramlal, P. S., R. H. Hesslein, R. E. Hecky, E. J. Fee, J. W. M. Rudd, and S. J. Guildford (1994), The organic carbon budget of a shallow Arctic tundra lake on the Tuktoyaktuk Peninsula, N.W.T., Canada, *Biogeochemistry*, *24*, 145–172.
- Raymond, P. A., and J. E. Bauer (2001), Riverine export of aged terrestrial organic matter to the North Atlantic Ocean, *Nature*, *409*, 497–500.
- Reeburgh, W. S., J. Y. King, S. K. Regli, G. W. Kling, N. A. Auerbach, and D. A. Walker (1998), A CH₄ emission estimate for the Kuparuk River basin, Alaska, *J. Geophys. Res.*, *103*(D22), 29,005–29,013.
- Rees, G., I. Brown, K. Mikkola, T. Virtanen, and B. Werkman (2002), How can the dynamics of the tundra-taiga boundary be remotely monitored?, *Ambio Spec. Rep.*, *12*, 56–62.
- Roulet, N. T., T. Moore, J. Bubier, and P. Lafleur (1992), Northern fens: Methane flux and climatic change, *Tellus, Ser. B*, *44*, 100–105.
- Semiletov, I. P. (1999), Aquatic sources and sinks of CO₂ and CH₄ in the polar regions, *J. Atmos. Sci.*, *56*, 286–306.
- Turunen, J., A. Pitkänen, T. Tahvanainen, and K. Tolonen (2001), Carbon accumulation in West Siberian mires, Russia, *Global Biogeochem. Cycles*, *15*(2), 285–296.
- Whalen, S. C., and W. S. Reeburgh (1990), A methane flux transect along the trans-Alaska pipeline haul road, *Tellus, Ser. B*, *42*, 237–249.
- Zamolodchikov, D. G., and D. V. Karelin (2001), An empirical model of carbon fluxes in Russian tundra, *Global Change Biol.*, *7*, 147–161.
- Zimov, S. A., Y. V. Voropaev, I. P. Semiletov, S. P. Davidov, S. F. Prosiannikov, F. S. Chapin III, M. C. Chapin, S. Trumbore, and S. Tyler (1997), North Siberian lakes: A methane source fueled by Pleistocene carbon, *Science*, *277*, 800–802.
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