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Heikkinen, J.E.P

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Carbon balance in East European tundra

Juha E. P. Heikkinen, Tarmo Virtanen, Jari T. Huttunen, Vladimir Elsakov, and Pertti J. Martikainen

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1. Introduction

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 for 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., 2000]. 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 Arctic-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.

Despite the sequestration of atmospheric carbon, these wetland ecosystems emit large quantities of CH$_4$ [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 CO$_2$ 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 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].

In addition to the terrestrial ecosystems, CO$_2$ 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].
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 CO$_2$ and CH$_4$ 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

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.

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).

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)\textsuperscript{a}

<table>
<thead>
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<th>August</th>
<th>September</th>
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<tr>
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<td>8.6</td>
<td>3.8</td>
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<tr>
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<td>6.2</td>
<td>12.5</td>
<td>9.4</td>
<td>4.1</td>
</tr>
<tr>
<td>Precipitation, mm</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
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<td>59</td>
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</tbody>
</table>

\textsuperscript{a}Long-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 (RTOT) 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 TTSGL) 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, Hylomium 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\text{AIR}, T_{-5\text{cm}}, and T_{-10\text{cm}}), 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\text{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\text{Air}) 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 R² > 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 (HDSPC: 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 R² > 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\text{TOT}), the gross photosynthesis (P\text{G}) can be calculated from the equation: NEE = P\text{G} - R\text{TOT}. Models using hourly rates of photosynthetically active radiation (PAR), air temperature (T\text{AIR}),
and effective temperature index (ETI) were developed to calculate hourly rates of photosynthesis (equation (1)) and respiration (equation (2)).

\[
P_G = \frac{(Q \times PAR)}{(K + PAR)} + b_1 \times ETI + b_2 \times T_{AIR} + c_1 \quad (1)
\]

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

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 CH\(_4\) 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).

[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 \( CH_4 \) fluxes [see Heikkilä 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 km\(^2\)) 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 km\(^2\)) [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. CO\(_2\) 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 on 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 CO\(_2\)-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 CO\(_2\)-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
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.

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

The seasonal mean respiration was $-12.8$, $-10.7$, and $-26.8$ mg CO$_2$-C m$^{-2}$ h$^{-1}$ for fine peat, coarse peat, and peat with algae, respectively. Highest bare peat respiration ($-34.7$ mg CO$_2$-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 CO$_2$-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 CO$_2$-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 ($R^2 = 0.08–0.14$; $n = 98–229$).

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

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 CH$_4$-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 CH$_4$-C m$^{-2}$ d$^{-1}$) while maximum uptake took place at the lake margin and hummock ($-8.1$ mg CH$_4$-C m$^{-2}$ d$^{-1}$). On drier surfaces (PPL, PPC, TTSL, and TTSS), the fluxes varied between $-6.1$ and 7.9 mg CH$_4$-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 CH$_4$-C in LM and IF, respectively (Figure 5).

### 3.5. Carbon Fluxes From the River and the Lake

The thermokarst lake was a source of CH$_4$ and CO$_2$ to the atmosphere throughout the summer (Figures 6a and 6b).
Table 2. Summary of the Measured Carbon Dioxide Fluxes (mg CO₂·C m⁻²·h⁻¹), Environmental Variables, and Pearson Correlation Statistics in 2001 (JDs 158–248) for Different Vegetation Classes

<table>
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<th>Lichen PP</th>
<th>Bare Peat PP</th>
<th>Crack Succession PPC</th>
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</table>

|                      | Mean          | SD          | Mean      | SD           | Mean                 | SD              | Mean            | SD          | Mean                  | SD          |
|---------------------|---------------|-------------|-----------|--------------|----------------------|-----------------|Mean            | SD          | Mean                  | SD          |
|                      | 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       |
| SD                  | 75.4          | 38.1        | 86.3      | 96.0         | 31.3                 | 27.6           | 11.2            | 64.7        | 61.4                 | 53.9        |
| Min                 | −77.1         | −11.1       | −225      | −20.1        | −88.6                | −25.6          | −0.9            | −224        | −16.8                | −277        |
| Max                 | 249           | −176        | 155       | −418         | 74.5                 | −126           | −73.9           | 182         | −525                 | 73.8        |
| N                   | 62            | 61          | 59        | 63           | 58                   | 66             | 504             | 245         | 260                  | 176         |

**Correlations**

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<td>0.58c</td>
<td>0.43c</td>
<td>0.45c</td>
<td>−0.45c</td>
</tr>
<tr>
<td>Min</td>
<td>−0.07</td>
<td>−0.19</td>
<td>−0.08</td>
<td>−0.06</td>
<td>−0.01</td>
<td>−0.48c</td>
<td>−0.31c</td>
<td>−0.38c</td>
<td>0.16</td>
<td>−0.31c</td>
</tr>
<tr>
<td>Max</td>
<td>0.03</td>
<td>0.47c</td>
<td>0.00</td>
<td>0.01</td>
<td>−0.06</td>
<td>−0.48c</td>
<td>−0.31c</td>
<td>−0.38c</td>
<td>0.16</td>
<td>−0.31c</td>
</tr>
<tr>
<td>N</td>
<td>48</td>
<td>100</td>
<td>32</td>
<td>32</td>
<td>100</td>
<td>32</td>
<td>100</td>
<td>32</td>
<td>100</td>
<td>32</td>
</tr>
</tbody>
</table>

*Net 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.

*Measured with respiration chamber (vol. 870 cm³).

*Correlation is significant at the 0.05 level.

*Correlation is significant at the 0.05 level.*
Figure 3. Seasonal patterns of measured daytime (10–18) net ecosystem exchange (NEE) and total respiration (R\textsubscript{TOT}) in various microsites in Lek Vorkuta catchment in summer 2001. Modeled net ecosystem production (NEP), gross photosynthesis (P\textsubscript{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\textsubscript{TOT} with standard deviation and (b) R\textsubscript{TOT} flux in relation with air temperature. The linear regression line R\textsubscript{TOT} = ax + b (a;b;R\textsuperscript{2};m;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).
while the Lek Vorkuta river showed occasional uptake of CO₂ (Figure 6a). The mean CH₄ emissions were 23.9 and 9.9 mg CH₄-C m⁻² d⁻¹ from the lake and the river sites, respectively. The mean CO₂ fluxes were also toward the atmosphere from the lake and the river, 5.4 and 14.5 mg CO₂-C m⁻² 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 P₆₅. When including the high CH₄ emissions, the LM acted as a carbon source to the atmosphere.

3.7. Model Validation

[33] The seasonal CO₂ 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 R² 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 P₆₅ model results were similar (Table 3). The modeled respiration was higher in 2001, as were the mean respiration values, −107 and −142 mg CO₂-C m⁻² h⁻¹ in 1999 and 2001, respectively. As a result of high respiration, the NEP was negative in hummocks. Carbon balances for different microsites were estimated based on the specific seasonal regression models or integrating the seasonal mean over 100 days (Table 4).
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

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Gross CO₂ Exchange Parameters</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( Q )</td>
<td>348 (115)</td>
<td>230 (127)</td>
<td>348 (123)</td>
</tr>
<tr>
<td>( K )</td>
<td>1070 (787)</td>
<td>104 (125)</td>
<td>999 (947)</td>
</tr>
<tr>
<td>( b_1 )</td>
<td>16 (26)</td>
<td>158 (16)</td>
<td>80 (29)</td>
</tr>
<tr>
<td>( b_2 )</td>
<td>2.8 (1.7)</td>
<td>7 (1)</td>
<td>1.9 (1.7)</td>
</tr>
<tr>
<td>Constant ( c_1 )</td>
<td>2.9 (25)</td>
<td>118</td>
<td>172</td>
</tr>
<tr>
<td>Modeled ( P_G )</td>
<td>214</td>
<td>5, 101</td>
<td>5, 104</td>
</tr>
<tr>
<td>( N ), collars</td>
<td>3</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>( R^2 ) (%)</td>
<td>48</td>
<td>63</td>
<td>65</td>
</tr>
<tr>
<td>df( \text{reg} ), df( \text{res} )</td>
<td>5, 107</td>
<td>3, 77</td>
<td>3, 68</td>
</tr>
</tbody>
</table>

| Respiration Parameters |
| TAIR, \( b_3 \) | 0.030 (0.009) | 0.065 (0.011) | 0.028 (0.008) | 0.078 (0.008) |
| ETL, \( b_4 \) | 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 \( R_{\text{TOT}} \) | –93 | –75 | –290 | –182 |
| \( N \), collars | 3 | 5 | 2 | 7 |
| \( R^2 \) (%) | 10 | 70 | 26 | 65 |
| df\( \text{reg} \), df\( \text{res} \) | 3, 107 | 3, 77 | 3, 68 | 3, 103 |

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

Standard error (SE) of the NEP (including the \( P_G \) and \( R_{\text{TOT}} \)) was used to evaluate the uncertainty of microsites. The wide range of confidence intervals 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). Areal, wet peaty tundra gained 109 g m⁻² while other surfaces lost from –5 to –91 g m⁻² carbon. According to upscaling, Lek Vorhuta catchment (114 km²) lost about 4 Gg C (34.6. g m⁻²) 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 5. Areal Estimates of Carbon Stocks and Fluxes in Lek Vorkuta Catchment (Area 114 km²)¹

<table>
<thead>
<tr>
<th>Classes Within the Terrestrial and Aquatic Ecosystems Used in the Areal Integration</th>
<th>Area, %</th>
<th>C Stock in Vegetation, g m⁻²</th>
<th>C Stock in Soil, (g m⁻²) × 10³</th>
<th>C Flux, g m⁻²</th>
<th>Areal Flux A = 114 km² (±SE) (g × 10⁶)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wet peaty tundra</td>
<td>12.9</td>
<td>260</td>
<td>41.3</td>
<td>109</td>
<td>1597 (±313)</td>
</tr>
<tr>
<td>Dry peaty tundra</td>
<td>3.2</td>
<td>275</td>
<td>46.2</td>
<td>−123</td>
<td>−449 (±263)</td>
</tr>
<tr>
<td>Peat plateau</td>
<td>9.0</td>
<td>210</td>
<td>125.4</td>
<td>−37</td>
<td>−377 (±256)</td>
</tr>
<tr>
<td>Tundra heath</td>
<td>46.8</td>
<td>290</td>
<td>13.9</td>
<td>−87</td>
<td>−4652 (±2625)</td>
</tr>
<tr>
<td>Willow dominated stands³</td>
<td>24.3</td>
<td>1070</td>
<td>23.5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Thermokarst lakes, profundal²</td>
<td>3.3</td>
<td>0</td>
<td>20.4</td>
<td>−15</td>
<td>−58</td>
</tr>
<tr>
<td>Lake and pond margins</td>
<td>0.1</td>
<td>120</td>
<td>46.3</td>
<td>−5</td>
<td>−1 (±1)</td>
</tr>
<tr>
<td>Rivers²</td>
<td>0.3</td>
<td>0</td>
<td>8</td>
<td>−34</td>
<td>−10</td>
</tr>
<tr>
<td>Mean (weighted by area)</td>
<td>100</td>
<td>457</td>
<td>31.1</td>
<td>−34.6</td>
<td>−3950(±3457)</td>
</tr>
</tbody>
</table>

¹C flux measurements from individual microsites were weighted (see Table 4).
²Calculations 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.
³Kuhry 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.
⁴Willow 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.
⁵All lakes in the region were classified as thermokarst lakes.
⁶River 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].

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 were 33% higher, respectively. The NEE/Rₜₒᵗₑᵢₛ were 21 and 33% higher, respectively. The NEE/Rₜₒᵗₑᵢₛ 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°C 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.

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 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].

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.

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 Rₜₒᵗₑᵢₛ 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

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 growth. These results stressed the fact that in spite of the monthly mean temperature and a 4-cm drop in the seasonal ecosystems in this region are important sources of both CH4 and CO2 to the atmosphere, as are lakes and rivers in other

Our results from the thermokarst 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].

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.

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 Thermokarst Lake

There are a limited number of seasonal carbon gas flux studies from aquatic ecosystems in the Russian Arctic. Our results from the thermokarst 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 thermokarst lake in this study (3.2 g CH4 m⁻² season⁻¹). The mean daily CH4 fluxes from the thermokarst 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 thermokarst 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].

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].

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.

4.4. Seasonal Carbon Balance

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 timescales 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 vegetation 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].
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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V. Elsakov, Institute of Biology, Komi Science Centre, Kommunisticheskaya Str. 28, 167610, Syktyvkar, Russia.

J. E. Heikkinen, J. T. Huttunen, and P. J. Martikainen, Department of Environmental Sciences, University of Kuopio, Bioteknia 2, P.O. Box 1627, 70211, Kuopio, Finland. (juha.heikkinen@uku.fi; pertti.martikainen@uku.fi)

T. Virtanen, Department of Ecology and Systematics, University of Helsinki, Biocenter 3, Viikinkkaari 1, 00014, Finland.