

## Vertical and horizontal variation of carbon pools and fluxes in soil profile of wet southern taiga in European Russia

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Vertical and horizontal distributions of soil organic carbon, potential microbial activity and basic soil properties were studied in a boreal mixed forest (Central Forest Reserve, TVER region) to elucidate whether the soil CO<sub>2</sub>-efflux is related to basic soil properties that affect the C pool and activity. Soil cores (0–100 cm depth) were taken from two transects every 50 meters (44 points) immediately after completion of soil CO<sub>2</sub>-efflux measurements. Soil was separated into layers and moisture, bulk density, root density and bacterial counts were determined within one day after soil was taken. Microbial respiration, biomass, CN contents and pH were measured within few months. The variability in the soil CO<sub>2</sub>-efflux and microbial activity was mainly explained by soil bulk density. Results further indicate that laboratory measurements of microbial respiration can represent heterotrophic soil respiration of a distinctive ecosystem in natural conditions, if microbial respiration is measured after the effect of soil handling disappears.

### Introduction

CO<sub>2</sub> released from soil originates mainly from root and microbial respiration. But if measurements are performed without removing the upper soil layer, the measured CO<sub>2</sub>-efflux also includes a measurement of respiration from moss, algae and lichens. It has been estimated that between 28% and 70% of carbon returned to the atmosphere from the soil surface is from autotrophic root respiration with the remainder coming from

soil heterotrophic respiration (Raich and Schlesinger 1992, Ryan *et al.* 1996, Hanson *et al.* 2000).

In recent years, accurate determination of heterotrophic soil respiration rates and factors controlling spatial variability at a range of scales has formed one key area of global change biology (Trumbore 2006, Reichstein and Beer 2008). However this task is arduous due to the enormous spatial variation in microbial quantity and physiological activity together with huge horizontal and vertical heterogeneity of the soil

environment (Wardle 2002, Berg and Bengtsson 2007). Even though our understanding of heterotrophic respiration has been improved in the last decades (Ebklad and Högberg 2001, Ekberg *et al.* 2004, Kuzyakov 2006), it is still unclear which are the principal factors driving spatial variability of heterotrophic soil respiration.

It can be assumed that, in general, the variation of soil heterotrophic activity should be mostly attributed to organic carbon amount and quality, nutrient availability, soil temperature (Hartley and Ineson 2008) and water availability that is strongly affected by geomorphological heterogeneity (Ise and Moorcroft 2006). It is also reasonable to assume that within any ecosystem, horizontal and vertical variation of heterotrophic activity will be affected by different factors. In upper organic soil layers, horizontal variability will be driven mainly by heterogeneities in vegetation cover affecting the amount and quality of litter input (Ettema and Wardle 2002) and variability in microsite water and temperature regimes. On the other hand, vertical variation may be more affected by soil C distribution, supply of fresh carbon and the level of the soil water table (Fontaine *et al.* 2007). Studying spatial variability has mainly focused on horizontal variability but vertical distribution of microbial activity and its variation within one ecosystem remains an additional unresolved question.

In order to address the above questions, the current study was designed to help elucidate the relationships between spatial variation of the *in situ* soil CO<sub>2</sub>-efflux, environmental factors and soil heterotrophic activity (microbial respiration, microbial biomass) at the stand level. We assumed that vegetation cover, soil bulk density, pH, moisture and C and N contents are the main factors explaining the spatial variations. We were also interested in horizontal and vertical variation in soil C pools and how this variation affected soil CO<sub>2</sub>-effluxes. The study was performed in a boreal mixed forest.

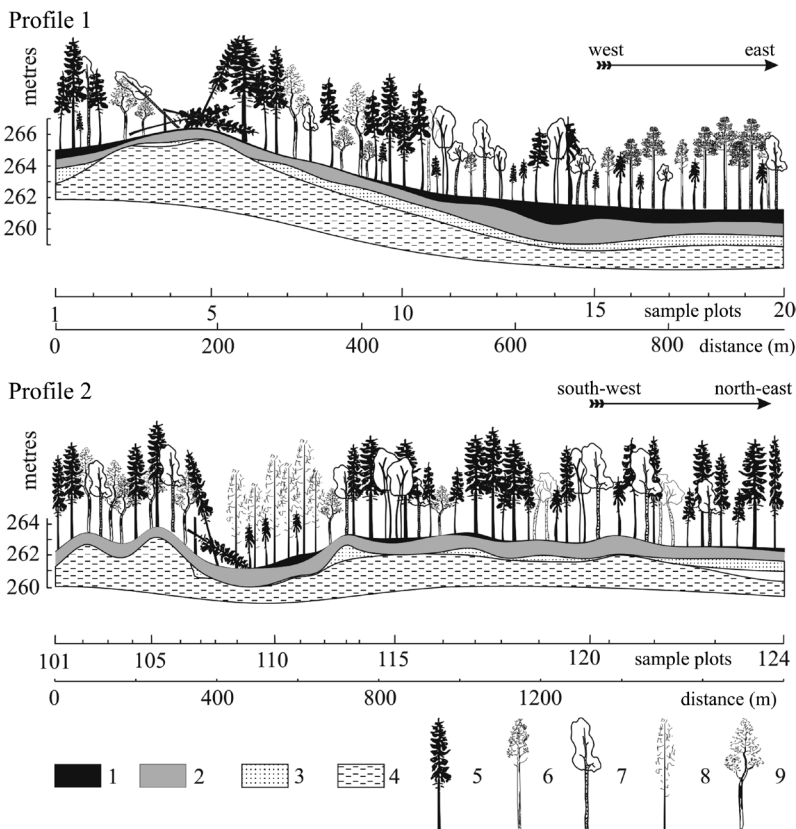
## Material and methods

### Site description

The experimental site was located in the Central

Forest Reserve (CFR) at Fyedorovskoye in the Tver region, about 300 km WNW of Moscow in European Russia (56°2'N, 32°55'E, ca. 220–270 m a.s.l.). The reserve was established in 1931, but in the 1950s and 1960s some commercial logging was permitted. Temperatures in the region range between an average monthly minimum of –9 °C in January and a maximum average of 17 °C in July. Precipitation can vary from 400 mm a<sup>-1</sup> in a dry to 800 mm a<sup>-1</sup> in a wet year (Schulze *et al.* 2002). The vegetation in this area represents the transition between “southern taiga” and a boreal mixed forest of conifers and small leaf species (Schulze *et al.* 2002, Vygodskaya *et al.* 2002). Long term eddy covariance flux measurements took place at the site in two forest types of contrasting soil and moisture regime and in a raised bog (Schulze *et al.* 2002, Milyukova *et al.* 2002, Kurbatova *et al.* 2002, Fig. 1). According to Vygodskaya *et al.* (2002), six main forest sub-types occur within the sampling area (Table 1). The water table level at > 0.40-m depths is characteristic for a spruce forest on sedge bogs and sphagnum peat (vegetation cover classes from 1 to 3 in Table 1), but the typically by the end of growing season the water table is below 0.80 m at the well drained mineral sites.

The mineral soil in all cases was a silty loam, with pH ranging from 3.6 to 6. The water table at well drained sites with mineral soil may rise from 1.0-m to 0.20-m depth in wet years but falls below 1.20-m depth in extremely dry and warm years. In cold and wet summers, soil water content in the main root horizon (0–0.2-m deep) was 75%–86% WHC (water holding capacity) and in the wet and warm summers 55%–65% WHC (Vygodskaya *et al.* 2002). Vegetation cover and *in situ* soil CO<sub>2</sub>-efflux were determined at 44 locations that were selected along two transects every 50 meters in the two areas of the long term eddy covariance measurements. After these soil C flux measurements were completed, soil cores to 1-m depth sampled from the same spot with discrete layers within 0–100 cm soil profile were analyzed for root content, soil properties (pH, C and N content, moisture and bulk density), microbial respiration and bacterial counts. Measurements were carried out in early August 2002. The given growing season was extremely dry.



**Fig. 1.** Vegetation and soil profile on the transects. Legend (at the bottom of the figure): pedogenic substrates: 1 = peat, 2 = dust loam, 3 = Lime lake sand, 4 = moraine loam; trees: 5 = spruce, 6 = pine, 7 = small-leaved trees (birch, aspen), 8 = alder, 9 = broad-leaved trees (maple, elm, lime).

The total precipitation from May to September according to the meteorological station at the reserve was only 146 mm, the long-term average being 388 mm. In particular, the precipitation in July was 13.4 mm, amounting to only 14% of the long-term average.

**In situ soil respiration**

The total CO<sub>2</sub>-efflux from the forest floor was measured using a dynamic closed-chamber gas exchange system (LI-COR 6400, Lincoln, NE, USA). To minimize any influence of mechanical disturbance of soil surface on diffusion rates in the time of measurement, PVC collars were inserted through the forest floor into the depth of 5 cm, projecting not less than 5 cm above the uppermost ground layer. The soil collars were inserted into the soil at least 24 h before the first measurements. The soil CO<sub>2</sub>-efflux measurements, that were repeated 3 to 10 times, started

2 minutes after the LICOR chamber installation. Simultaneously the soil temperature was measured at the depth of 10 cm from surface of the moss layer (Shibistova *et al.* 2002). Chamber CO<sub>2</sub>-efflux measurements were performed in early August 2002, during a one week period always during the day between 11:00 and 18:00 local time. Day-time fluctuations of temperature and the soil CO<sub>2</sub>-efflux, which were measured at 9 points, were low (CV < 0.06) in this time and neither a regular diurnal pattern nor a significant dependence on temperature ( $r^2 = 0.135$ ) was found. Therefore, no normalization for diurnal temperature changes was used.

A total of 44 measurement points were selected every 50 meters along two transects (Fig. 1). For each sampling point, the surrounding vegetation was described, including relative cover of the main groups of mosses and the main species of vascular plants in the herb layer. A more detailed description of the vegetation and soil characteristics of the different forest types

**Table 1.** Characteristics of vegetation cover, CO<sub>2</sub>-efflux from the soil and soil properties of the rooting layer (0 to 30 cm) of the sampling locations. The sampling locations are grouped according to vegetation cover (Vygodskaya et al. 2002).

Vegetation cover (number of locations)	Soil CO <sub>2</sub> -efflux (g m <sup>-2</sup> d <sup>-1</sup> )	Total C pool (g m <sup>-2</sup> )	C/N	pH	Moisture (%)	Temperature °C	Living roots (g m <sup>-2</sup> )
Sphagnum-blueberry spruce forest (4)	8.87 ± 3.21	20.6 ± 12.2	19.7 ± 3.46	3.97 ± 0.16	64.2 ± 16.1	12.2 ± 1.85	392 ± 276
Peat bog with sphagnum-blueberry spruce-pine stand (10)	11.12 ± 5.95	17.3 ± 3.30	31.6 ± 3.08	3.81 ± 0.10	83.5 ± 3.45	16.3 ± 1.38	299 ± 267
Border of sphagnum-blueberry spruce forest (3)	13.79 ± 4.49 7.53 ± 4.37	13.1 ± 3.90 11.1 ± 4.94	17.5 ± 4.25 16.0 ± 5.93	4.52 ± 0.32 4.61 ± 0.43	26.5 ± 7.03 36.6 ± 17.5	12.8 ± 0.49 13.2 ± 1.03	1104 ± 532 869 ± 589
Complex spruce forest (19) Valley with black alder, ash and elm (4)	11.22 ± 6.91 6.39 ± 1.88	16.8 ± 9.51 12.4 ± 10.7	18.2 ± 3.48 15.9 ± 4.59	5.11 ± 0.42 4.76 ± 0.14	47.2 ± 27.3 27.4 ± 4.11	13.3 ± 1.27 13.8 ± 0.29	623 ± 436 984 ± 581
Windfall (4)							

studied along the two transects are presented in Table 1.

## Soil profile measurements

Soil samples were collected from 42 of the 44 selected points, immediately after completion of the soil CO<sub>2</sub>-efflux measurement. This was achieved by taking soil cores of 0.1 m diameter (the same diameter as the PVC collars) and 1 m depth from the exact location where each soil CO<sub>2</sub>-efflux rate determination had been made using a motorized window auger. These cores were separated into 5 cm layers from the surface to the 20 cm depth and then in 10 cm increments to 100 cm. The litter layer was not removed but rather included into the uppermost layers. Once the individual soil layers had been separated, 1–2 g of soil from each layer was fixed in 2 ml of 3% formaldehyde in the field and subsequently stored at 4 °C until analyzed for bacterial counts. Moisture, bulk density and root density were determined within one day after soil was taken. Root density was calculated from dry weight of roots that were picked out from each core and layer in the day of the sampling.

For microbial respiration and CN measurements, the soil was dried in a thin layer at the room temperature immediately after sampling and removing roots, and then stored at 4 °C until analyzed in the laboratory. Analyses were performed in homogenized but not sieved soil as all sampling sites were on alluvial sandy area with no stones and gravel. Moisture, bulk density and root density were determined in each sampled layer, while microbial parameters as well as C and N contents were measured only in the layers 0–5, 5–10, 10–15, 15–20, 20–30, 50–60 and 90–100 cm.

Microbial respiration was determined at 45 °C using HP 5890 gas chromatograph (Agilent, USA), equipped with two parallel steel columns — a 0.53 mm × 15 m HP Plot Q column (Agilent, USA) and 0.53 mm × 15 m HP-Plot Molecular Sieve 5A column (Agilent, USA) — and with a thermal conductivity detector, using helium as the carrier gas. All measurements were performed in 3–4 replicates. Prior to the analyses, the air-dried soil had been moistened to

60% WHC and incubated for 6 days. Microbial respiration was measured for 24 hours between the 5th and 6th days of incubation, after the flush of respiration upon soil wetting had ceased and respiration stabilized. Direct counts of bacteria were carried out using the fluorescence microscopy and DAPI (4',6-diamidino-2-phenylindole) staining method (Bloem *et al.* 1992). Conversion factor of 80.8 fg C bacterial cell<sup>-1</sup> was used to calculate bacterial biomass ( $C_{\text{bact}}$ ) (Taylor *et al.* 2002). In addition microbial biomass was measured in nine out of 42 cores using SIR method (West and Sparling 1986). Nine cores were chosen to be representative for the soil profiles in the area. Total C ( $C_{\text{tot}}$ ) and N were measured from finely grounded soil using elemental NC 2100 Soil analyzer (ThermoQuest, Italia). Soil pH in water suspension (soil: water, 1:2.5, w/v),  $C_{\text{bact}}/C_{\text{tot}}$  (%) and  $\text{CO}_2/C_{\text{tot}}$  ( $\text{mg g}^{-1} \text{h}^{-1}$ ) ratios were used as a measure of C availability.

To interpret the data on the ecosystem level and compare them with the soil  $\text{CO}_2$ -efflux, microbial respiration and C pools were expressed on per square meter basis:

$$C_{\text{resp}}(C_{\text{pool}}) = C_c DL \quad (1)$$

where  $C_c$  is C content and/or respiration per 1 kg dry soil,  $D$  is bulk density ( $\text{kg m}^{-3}$ ),  $L$  is depth of the layer in question (m).

To estimate microbial  $\text{CO}_2$  flux and C pools in the entire 0–100-cm soil column, the missing values of C content at respiration at depths of 40, 50, 70 and 80 cm were derived from the values measured in neighborhood layers by means of a linear interpolation and then expressed on per-square-meter basis using measured  $D$ .

The Lloyd-Taylor temperature dependency model (Lloyd and Taylor 1994) was used for the standardization of the soil  $\text{CO}_2$ -efflux and microbial respiration to 10 °C to compare the rate of the soil  $\text{CO}_2$ -efflux and microbial respiration.

Coefficient of variation (CV) was used to express spatial variabilities in soil and vegetation parameters (Kleb and Wilson 1997). This allows for comparisons that are independent of scale. One-way ANOVA was used to test differences among groups after checking the normality of distribution. Multivariate and non-linear regressions were used for testing dependence between

measured variables. Calculations were carried out in STATISTICA 7.

## Results

### *In situ* soil $\text{CO}_2$ -efflux

The average *in situ* soil  $\text{CO}_2$ -efflux from the forest floor along the transects as calculated from 44 measurement points was  $9.4 \text{ g C m}^{-2} \text{ d}^{-1}$  with a relatively low spatial variability ( $\text{CV} = 0.55$ ). The mean soil temperature during the time of measurements was 13.9 °C ( $\text{CV} < 0.13$ ) and no significant dependence between the soil  $\text{CO}_2$ -efflux and soil temperature was found ( $r = 0.0248$ ).

When grouped according to vegetation type and/or moss cover (Table 1), no significant difference in soil  $\text{CO}_2$ -efflux rates between the six groups was found. Subsequently, we examined the observed variation in soil  $\text{CO}_2$ -efflux rates in relation to the soil parameters measured (total and microbial C pools, microbial respiration, pH, moisture and bulk density) at the point of measurement. To do this, we considered the mean soil properties expressed per unit area for the upper soil layer (0 to 30 cm), this being the main rooting zone (roots were distributed in the upper 0–30 cm layer in all the sampled profiles and less than 2% of living roots penetrated below 30 cm) and the most biologically active part of the soil profile. Multiple regression analysis ( $r^2 = 0.418$ ,  $p < 0.020$ ) revealed a highly significant relationship only between the soil  $\text{CO}_2$ -efflux and bulk density ( $r^2 = 0.587$ ,  $p < 0.007$ ) and significant relationship between the soil  $\text{CO}_2$ -efflux and pH ( $r^2 = 0.530$ ,  $p < 0.035$ ). The relationships between the soil  $\text{CO}_2$ -efflux and the total C pool ( $r^2 = 0.265$ ,  $p < 0.342$ ), the microbial C pool ( $r^2 = 0.425$ ,  $p < 0.372$ ), the microbial respiration ( $r^2 = 0.308$ ,  $p < 0.650$ ) and moisture ( $r^2 = 0.530$ ,  $p < 0.316$ ) were all insignificant.

Based on these findings, the soil cores and the corresponding soil  $\text{CO}_2$ -effluxes were grouped according to bulk density into three groups: (1) deep peaty soils with organic horizon deeper than 30 cm ( $n = 13$ ; average bulk density =  $0.52 \text{ g cm}^{-3}$ ), (2) peaty soils with a shallow organic horizon (< 30 cm,  $n = 8$ ; average bulk density =  $1.16 \text{ g cm}^{-3}$ ) and (3) mineral well drained soils



**Table 2.** Soil characteristics, C pools ( $C_{\text{tot}}$ , bacterial and microbial), microbial respiration in upper 0–30 cm layer of soil (weighed mean  $\pm$  SD). The sampled cores were grouped according to bulk density — see text for more detail. Except for absolute values, a relative contribution (%) of the values from the upper 0–30 cm layer to the values from the whole 0–100 cm profile is shown. Different letters denote significant difference between groups of soils at significance level  $p < 0.01$  (one-way ANOVA and Fisher post-hoc test  $n = 42-44$ ).

Group of soils ( $n$ cores)	Bulk density ( $\text{g cm}^{-3}$ )	Moisture ( $\text{g}_{\text{H}_2\text{O}} \text{cm}^{-2}$ )	pH	C/N	$C_{\text{tot}}$ pool		Bacterial C pool	Microbial C pool*		Microbial respiration ( $\text{g C m}^{-2} \text{d}^{-1}$ )	Microbial respiration (%)
					( $\text{kg m}^{-2}$ )	(%)		( $\text{g m}^{-2}$ )	(%)		
Deep peat ( $n = 13$ )	$0.128 \pm 0.007^a$	$18.7 \pm 0.91^c$	$3.92 \pm 0.11^a$	$30.3 \pm 1.55^c$	$19.7 \pm 1.74^b$	28	$77.5 \pm 9.6^a$	$266.5 \pm 6.7^a$	$50$	$6.22 \pm 1.32^a$	50
Shallow peat ( $n = 8$ )	$0.297 \pm 0.026^b$	$11.2 \pm 1.51^b$	$4.50 \pm 0.21^b$	$21.0 \pm 2.27^b$	$20.1 \pm 3.18^b$	54	$105.9 \pm 23.4^a$	$556.0 \pm 1.1^b$	54	$7.42 \pm 0.79^a$	53
Mineral ( $n = 23$ )	$0.937 \pm 0.041^c$	$8.24 \pm 0.50^c$	$4.65 \pm 0.08^b$	$15.0 \pm 0.99^a$	$11.0 \pm 1.06^a$	82	$111.5 \pm 10.5^a$	$281.4 \pm 17.7^a$	71	$7.83 \pm 1.05^a$	76

\* only three cores from each group were analysed for microbial C pool.

( $n = 23$ ; average bulk density =  $1.38 \text{ g cm}^{-3}$ ). Bulk densities of these groups were significantly different (Table 2). Soil acidity, however, was similar in the groups of peaty soils and significantly different in the group of mineral soils (Table 2). The variation in soil  $\text{CO}_2$ -effluxes within each group was low (Table 3;  $\text{CV} < 0.14$ ). Well drained mineral soils differed from the deep peat soils having lower temperatures and moss covers, higher root densities and lower total C pools (Table 3). Differences between the mineral soils and the shallow peat soils were not as high as those between the mineral soils and the deep peat soil, being significant only for moss covers and total soil C pool. The two peaty soils differed significantly in temperature, moss cover, living roots and microbial C pool (Table 3).

### Variability of soil parameters

Bulk density increased with soil depth and the remaining parameters decreased being closely negatively correlated to the bulk density (Table 4). All the measured soil parameters were interdependent (Table 4). Relationships between the bulk density and moisture,  $C_{\text{tot}}$  and  $C_{\text{bact}}$  contents and microbial respiration, respectively, were not linear but exponential (Fig. 2). Microbial biomass C being measured only in nine cores using SIR was closely related to the  $C_{\text{bact}}$  and microbial respiration of the respective cores (Fig. 3).

Division of soil cores into three groups decreased variation of the measured soil parameters. The three groups were significantly different in distribution of soil moisture, C/N and  $C_{\text{tot}}$  content in the soil profile, whilst the distributions of pH,  $C_{\text{bact}}$  content and microbial respiration were apparently similar (Figs. 4 and 5). Recalculating  $C_{\text{bact}}$  content and microbial respiration per unit of  $C_{\text{tot}}$ , which denote C availability, however, revealed the significant difference in C availability, especially in deeper parts of the soil profile (Fig. 6). In general, C availability slightly decreased in deep peat soils and increased in the mineral soils (Fig. 6).

The upper soil layers constituted the most biologically active part of the soil profile and the upper 0–30 cm contributed 82% to the  $C_{\text{tot}}$  pool at 0–100 cm depth for the mineral soils, which

is about 50% or less than in the peaty soils, this depending on the thickness of the organic layer (Table 2). Similarly, about 70% and 50% of the estimated  $C_{\text{bact}}$  pool and microbial respiration in the 0–100 cm soil profile was in the upper layer in mineral soils and peat soils, respectively.

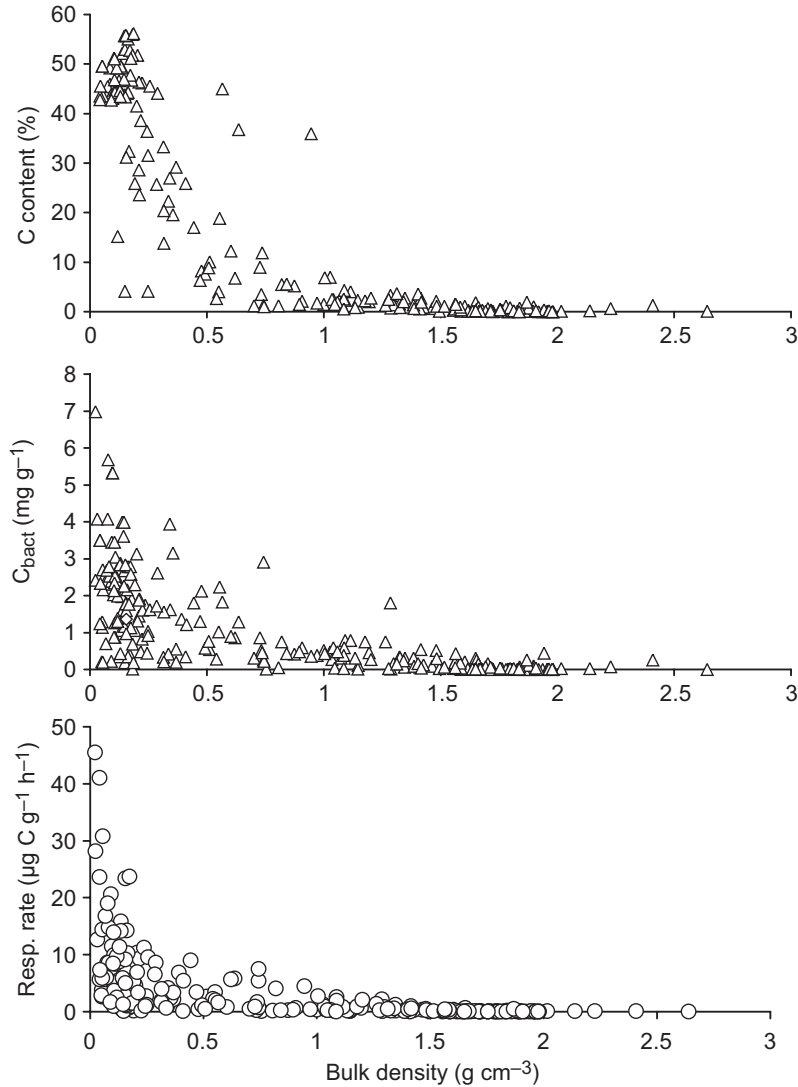
To compare microbial respiration with the *in situ* soil  $\text{CO}_2$ -efflux, all measured values were standardized to 10 °C. This calculation showed that although the soil  $\text{CO}_2$ -efflux was significantly higher in the shallow peat soils than in the deep peat and mineral soils, the microbial respiration did not differ significantly (Table 5). Thus, the potential contribution of microbial respiration to the total soil  $\text{CO}_2$ -efflux in the upper soil layer (0–30 cm) was higher in the mineral soils (62%) than in the deep and shallow peat soil (39% for both). Microbial C respiration in 0–100 cm profile followed the similar pattern as microbial respiration in the upper layer and did not exceed 65% of the total soil  $\text{CO}_2$ -efflux in any case.

## Discussion

The study has shown that spatial variability of the soil  $\text{CO}_2$ -efflux,  $C_{\text{tot}}$  pool, C/N ratio and pH in the upper part of the soil profile within the boreal ecosystem studied was mainly related to the soil bulk density. Although we expected that the vegetation cover should affect the soil  $\text{CO}_2$ -efflux, microbial biomass and respiration, and C/N ratio in the upper soil layer, this influence was not proved. Further, the bulk density in the soil profile correlated with the remaining soil parameters. It is not necessarily the case that the bulk density affects the microbial activity and the soil  $\text{CO}_2$ -efflux per se, but it is an integrating factor, reflecting differences in moisture regime, water level, C content and quality and vegetation cover. This is supported by the interdependency of soil abiotic and biotic drivers and by the significant differences in moisture, moss cover, pH, C pool and its C/N ratio among the three soil groups determined according to differences in the bulk density distribution in the soil profile. Variations in the soil bulk density were mainly accountable in terms of variations in the extent of organic matter accumulation in the soil, itself driven

**Table 3.** Soil  $\text{CO}_2$  effluxes measured in situ, temperature at the time of sampling, ground cover, root biomass and  $C_{\text{tot}}$  pool in the 0 to 100cm profile in the area close to the core samplings. The soils were grouped according to bulk density (BD; weighed mean  $\pm$  SD), see text for more detail. Different letters denote significant difference between groups of soils at significance level  $p < 0.01$  (one-way ANOVA and Fisher post-hoc test,  $n = 42-44$ ).

Group of soils (number of cores)	Soil $\text{CO}_2$ efflux ( $\text{g C m}^{-2} \text{d}^{-1}$ )	Temperature (°C)	Moss (%)	Sphagnum (%)	Living roots ( $\text{g m}^{-2}$ )	$C_{\text{tot}}$ pool ( $\text{kg C m}^{-2}$ )
Deep peat ( $n = 13$ ) BD = 0.52 $\text{g cm}^{-3}$	11.79 $\pm$ 1.6 <sup>b</sup>	15.8 $\pm$ 0.44 <sup>b</sup>	71.5 $\pm$ 6.2 <sup>c</sup>	49.4 $\pm$ 7.4 <sup>b</sup>	280 $\pm$ 77.4 <sup>a</sup>	78.0 $\pm$ 5.74 <sup>c</sup>
Shallow peat ( $n = 8$ ) BD = 1.16 $\text{g cm}^{-3}$	10.29 $\pm$ 1.94 <sup>ab</sup>	12.6 $\pm$ 0.55 <sup>a</sup>	49.4 $\pm$ 13.4 <sup>b</sup>	43.4 $\pm$ 14.4 <sup>b</sup>	721 $\pm$ 245 <sup>b</sup>	37.8 $\pm$ 6.64 <sup>b</sup>
Mineral ( $n = 23$ ) BD = 1.38 $\text{g cm}^{-3}$	7.22 $\pm$ 0.73 <sup>a</sup>	13.2 $\pm$ 0.19 <sup>a</sup>	9.39 $\pm$ 2.26 <sup>a</sup>	3.11 $\pm$ 1.39 <sup>a</sup>	931 $\pm$ 97.5 <sup>b</sup>	13.7 $\pm$ 1.26 <sup>a</sup>



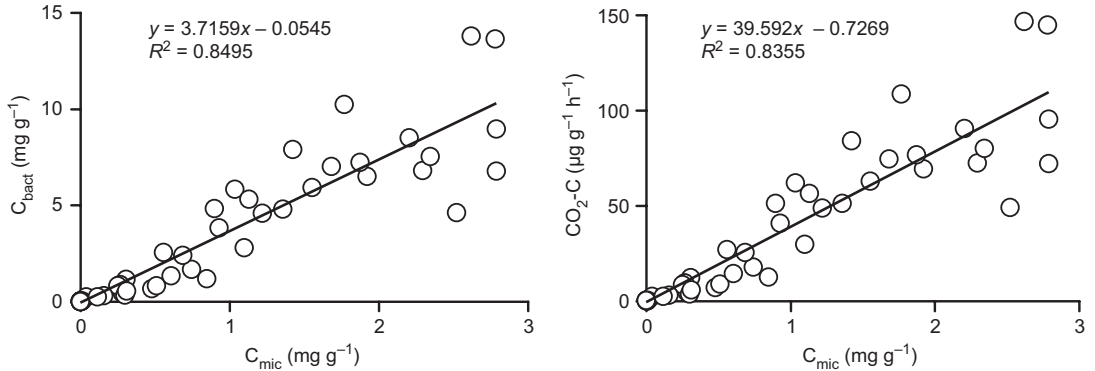
**Fig. 2.** Dependency of  $C_{tot}$ ,  $C_{bact}$  and microbial respiration on soil bulk density.

**Table 4.** The correlations among soil bulk density, moisture, pH, total ( $C_{tot}$ ) and bacterial carbon ( $C_{bact}$ ) contents, C/N and microbial respiration measured at 42–44 sampling points in the 0–100 cm profile. All correlations are significant at  $p < 0.01$  ( $n = 252$ ).

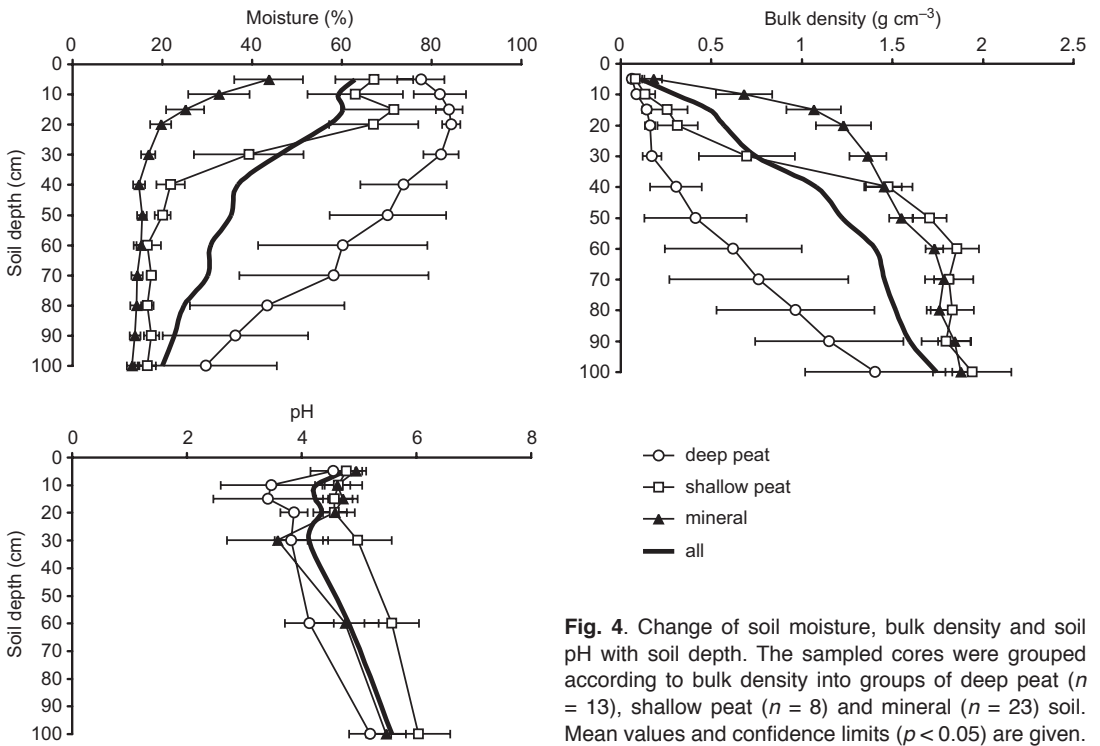
Parameter	Bulk density	Moisture*	pH	$C_{tot}$ *	C/N	$C_{bact}$ *	Microbial respiration*
Bulk density	1.000	-0.892	0.587	-0.934	-0.518	-0.824	-0.863
Moisture*		1.000	-0.571	0.886	0.602	0.759	0.760
pH			1.000	-0.613	-0.315	-0.556	-0.531
$C_{tot}$ *				1.000	0.582	0.884	0.892
C/N					1.000	0.409	0.411
$C_{bact}$ *						1.000	0.874
Microbial respiration*							1.000

\* Logarithmic values were used to calculate the correlation matrix.





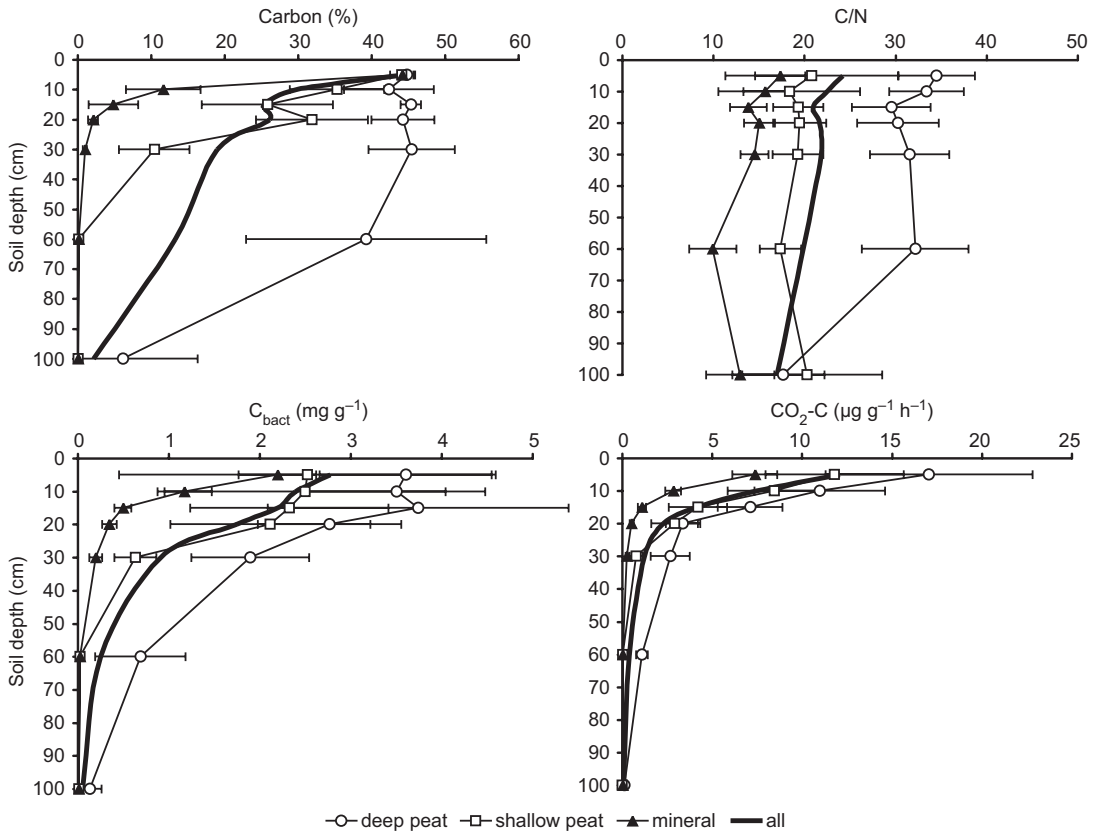
**Fig. 3.** Correlation between microbial ( $C_{mic}$ ) and bacterial ( $C_{bact}$ ) biomass and between microbial biomass and microbial respiration in the soil profile. Data from nine cores representative for the studied area are given.



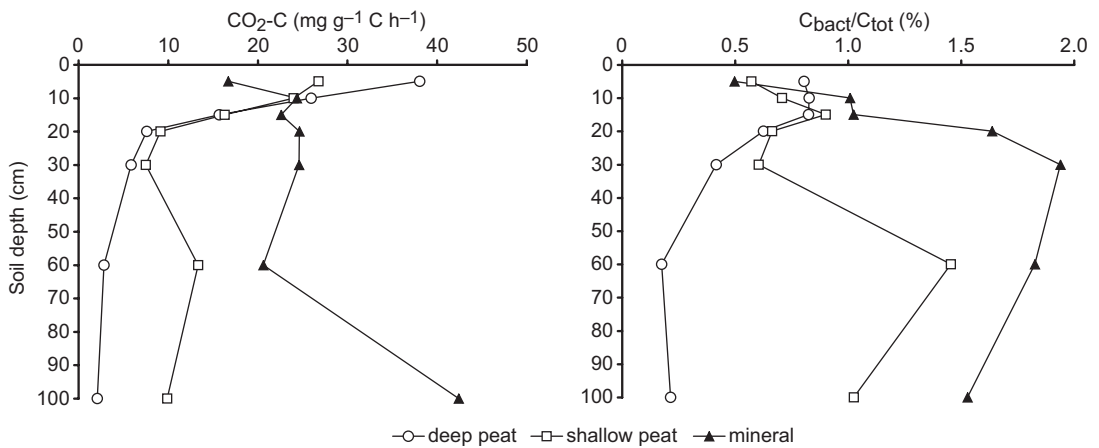
**Fig. 4.** Change of soil moisture, bulk density and soil pH with soil depth. The sampled cores were grouped according to bulk density into groups of deep peat ( $n = 13$ ), shallow peat ( $n = 8$ ) and mineral ( $n = 23$ ) soil. Mean values and confidence limits ( $p < 0.05$ ) are given.

**Table 5.** In situ soil  $CO_2$ -efflux and microbial respiration in the soil profiles 0–30 cm and 0–100 cm standardized to 10 °C. See text for more details. Different letters denote significant difference between groups of soils at  $p < 0.01$  (one-way ANOVA and Fisher post-hoc test,  $n = 42–44$ ).

Group of soils (number of cores)	Soil $CO_2$ -efflux <sub>10</sub> (g C m <sup>-2</sup> d <sup>-1</sup> )	Microbial respiration <sub>10</sub> (g C m <sup>-2</sup> d <sup>-1</sup> )	
		0–30 cm	0–100 cm
Deep peat ( $n = 13$ )	7.11 ± 1.01 <sup>ab</sup>	2.69 ± 0.46 <sup>a</sup>	5.38 ± 0.75 <sup>b</sup>
Shallow peat ( $n = 8$ )	8.17 ± 1.62 <sup>b</sup>	3.22 ± 0.25 <sup>a</sup>	6.08 ± 0.15 <sup>b</sup>
Mineral ( $n = 23$ )	5.40 ± 0.57 <sup>a</sup>	3.38 ± 0.37 <sup>a</sup>	4.45 ± 0.31 <sup>a</sup>



**Fig. 5.** Change of  $C_{tot}$ ,  $C_{bact}$ , soil C/N ratio and microbial respiration with soil depth. The sampled cores were grouped according to bulk density into groups of deep peat ( $n = 13$ ), shallow peat ( $n = 8$ ) and mineral ( $n = 23$ ) soil. Mean values and confidence limits ( $p < 0.05$ ) are given.



**Fig. 6.** Change of  $C_{bact}/C_{tot}$  and  $CO_2/C_{tot}$  ratios with soil depth. The sampled cores were grouped according to bulk density into groups of deep peat, shallow peat and mineral soil. Mean values are given.

by variations in temperature, moisture regime, especially where bulk densities were lower than  $1 \text{ g cm}^{-3}$ , i.e. in the upper 0–30 cm layer (see

Fig. 4 and Table 2). In deeper layers, other factors may be of greater importance with moisture regime, ground water level and transport of fine

particles and available C to the depression being the principal factors. The effects of the soil moisture regime and level of the water table may be quite complex, affecting moss cover, root and tree abundance, decomposition rate of organic material and, consequently, the size of the soil organic C pool and its quality as reflected by the C/N ratio (Berg and McLaugherty 2008). Soil porosity, which may further affect the soil CO<sub>2</sub>-efflux, soil aeration status and the character of microbial processes will also be affected. Thus according to our interpretation of the results, the local soil moisture regime, drainage and water level were the driving forces of the soil C-efflux and C pools heterogeneity and that the soil bulk density within a soil profile can be used as a reliable indicator of it.

The present study has two main limitations: (1) The application of soil collars could lead to a certain underestimation of the total CO<sub>2</sub>-efflux due to the damage of roots when inserting collars in the soil (Wang *et al.* 2005). In our study, the collars were inserted to the depth of 5 cm, at which mean proportion of roots was 14%, varying from 7% in the peat bog to 18% in the mineral soils. Assuming that maximum contribution of root respiration to the total soil respiration is 60% (Högberg *et al.* 2001, Subke *et al.* 2004, Högberg and Read 2006), the maximum underestimation of the soil CO<sub>2</sub>-efflux could be only from 5% to 8%. (2) The total soil CO<sub>2</sub>-efflux was measured and soil was sampled in a single week during August and numerous parameters that control soil respiration (e.g. input of labile C, composition of soil microbial community, water availability) may change seasonally. We suppose, however, that our data are representative for the growing season in the studied ecosystem, as water limitation is very rare there. In general, established dependency (correlations and/or regressions) among biotic and abiotic drivers of soil C pools and fluxes would hardly change over the year. Only particular relationships or significances of the dependency can be seasonally shifted.

Microbial respiration assessed for the upper 0–30 cm layer in the laboratory was estimated to contribute between 38% and 62% of the total soil CO<sub>2</sub>-efflux. This is in the range of values estimated in the field conditions using a girdling method (e.g. Högberg *et al.* 2001, Subke *et al.*

2004, Högberg and Read 2006) suggesting that laboratory measurements, if performed after soil conditions were equilibrated and flush of respiration due to soil handling ceased, may be representative for potential heterotrophic soil respiration that is characteristic for given soil. This is also supported by the data on microbial biomass and direct count of bacteria as microbial biomass correlated with both, microbial respiration and the direct counts of bacteria (Fig. 3). Microbial biomass was measured at the same time as microbial respiration, after the respiration rate was equilibrated, while direct counts of bacteria were carried out in the soil, which was fixed in formalin immediately after taking the core in the field. Direct counts, therefore, represent the amount of bacteria present in an undisturbed soil profile and microbial biomass represents the amount of active microorganisms at the time of measurement. These correlations of bacterial biomass with microbial biomass and microbial respiration indicate that the measured microbial biomass and microbial respiration also reflected the *in situ* conditions.

Microbial respiration that we measured was about half of that measured by Borken *et al.* (2002a) in forest soils of comparable C<sub>tot</sub> pool and quality, but soil C-efflux that we measured *in situ* was higher (*see* fig. 1 in Borken *et al.* 2002b). The difference between the two studies can be explained by the difference in the methods used for the measurement. While Borken *et al.* (2002a) measured microbial respiration in first hours after soil handling and increase of temperature, we performed the measurement after soil conditions satbilized and flush of respiration due to handling ceased. Our estimate of C<sub>tot</sub> pool in the 0–100-cm profile is a bit higher than the data summarized for the world life zones (Post *et al.* 1982, Schlesinger 1984) which could be explained by the fact that the litter layer was included in our estimates but excluded from the world profiles. The litter was included in our study as this layer is a very important place of biological activity in forest ecosystems (Šantrůčková *et al.* 2005).

The present study suggests that (i) variability of soil CO<sub>2</sub>-fluxes within one ecosystem can be indicated by the soil bulk density, which is related to moisture regime and ground water

level and, consequently, to different composition of vegetation cover and soil organic C pool and microbial transformation processes, and that (ii) laboratory measurements of microbial respiration represent potential heterotrophic soil respiration of distinctive studied ecosystem in natural conditions, if microbial respiration is measured after effect of soil handling disappears.

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