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Spatial and temporal variations in soil respiration in relation to stand structure and soil parameters in an unmanaged beech forest

ASTRID R. B. SØE[1–3] and NINA BUCHMANN[1,4]

[1] *Max Planck Institute for Biogeochemistry, Hans-Knoell-Strasse 10, 07745 Jena, Germany*

[2] *Present address: Max Planck Institute for Chemical Ecology, Hans-Knoell-Strasse 8, 07745 Jena, Germany*

[3] *Corresponding author (asoe@ice.mpg.de)*

[4] *Present address: ETH, Institute of Plant Sciences, Universitätsstrasse 2, ETH Zentrum LFW C56, CH-8092 Zürich, Switzerland*

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Summary Soil CO_2 efflux (soil respiration) plays a crucial role in the global carbon cycle and efflux rates may be strongly altered by climate change. We investigated the spatial patterns of soil respiration rates in 144 measurement locations in a 0.5-ha plot and the temporal patterns along a 300-m transect in the 0.5-ha plot. Measurements were made in an unmanaged, highly heterogeneous beech forest during 2000 and 2001. We investigated the effects of soil, roots and forest stand structure on soil respiration, and we also assessed the stability of these spatial patterns over time. Soil temperature alone explained between 68 and 95% of the temporal variation in soil respiration; however, pronounced spatial scatter of respiration rates was not explained by soil temperature. The observed spatial patterns stayed remarkably stable throughout the growing season and over 2 years. The most important structural parameter of the stand was the mean diameter at breast height of trees within a distance of 4 m of the measurement locations (m-dbh4), which explained 10–19% of the variation in soil respiration throughout the growing season. Among the soil chemical parameters, carbon content (bulk as well as dissolved) and magnesium content explained 62% of the spatial variation in soil respiration. The final best model combining soil, root and stand structural parameters (fine root biomass, soil carbon content, m-dbh4 and soil water content) explained 79% of the variation in soil respiration, illustrating the importance of both biotic and abiotic factors.

Keywords: canopy, fine root, soil CO_2 efflux, soil moisture, soil nutrients, soil temperature, tree size.

Introduction

Soils constitute the major carbon reserve in terrestrial ecosystems (Dixon et al. 1994), and it has been estimated that the flux of CO_2 from soil due to respiration is about 60 Pg C or 10 times that from fossil fuel combustion (Schlesinger 1997). Because of the large flux, even small changes in the rate of soil respiration can significantly affect the concentration of CO_2 in the atmosphere (IPCC 2001). However, it is not easy to accurately predict soil CO_2 fluxes because soil respiration is composed of respiration from both roots and microorganisms, which are affected by many biotic and abiotic factors (Raich and Schlesinger 1992, Davidson et al. 1998, Buchmann 2000, Stoyan et al. 2000, Xu and Qi 2001*a*, Reichstein et al. 2003). Consequently, large spatial and temporal variations in soil respiration rates are typically found both within and between most temperate ecosystems (e.g., Raich and Schlesinger 1992, Buchmann 2000, Franzluebbers et al. 2002).

Although factors that control temporal variation of soil respiration are generally well known, those that control spatial variation are not (e.g., Davidson et al. 1998, Buchmann 2000, Xu and Qi 2001*a*). Root distribution and microbial activity due to fine root turnover and root exudates are closely linked to stand structure, i.e., species composition, spatial arrangement of trees and canopy architecture (Stoyan et al. 2000, Savin et al. 2001). In some forest ecosystems, microbial respiration may dominate soil respiration (Tate et al. 1993, Landsberg and Gower 1997). In other forest ecosystems, root respiration has been shown to account for the major fraction of soil-respired CO_2 (Högberg et al. 2001, Laporte et al. 2003). Moreover, Shibistova et al. (2002) showed a close connection between tree density and soil CO_2 flux in an open boreal forest. Furthermore, soil respiration is tightly linked to photosynthetic activity (Högberg et al. 2001, de Neergaard et al. 2002), suggesting a strong link between above- and belowground physiology. The intensity of competition (especially for light and nutrients) and the developmental stage of the trees (e.g., age, height) seem to be important factors affecting root respiration in a forest stand. We therefore hypothesized that stand characteristics have the potential to explain some of the spatial patterns of soil CO_2 efflux in forests.

Several studies in temperate forests have shown that concentrations of macro-nutrients in the soil are important parameters for spatial variation in soil respiration rates. Concentrations of nitrogen, phosphorus and, to some degree, magnesium, have been suggested as the variables that best describe soil respiration (Xu and Qi 2001*a*, Borken et al. 2002, Pangle and Seiler 2002). In some ecosystems, litter moisture

and the thickness of the litter layer have been shown to be the most significant parameters for spatial variation of soil respiration (Brumme 1995, Gärdenäs 2000). Thus, many different factors, ranging from soil chemistry and physics to stand structure and root distribution, may explain the spatial variation of soil respiration.

The objectives of this study were to (1) identify the temporal and spatial variations in soil respiration in the Hainich National Park; (2) assess the importance of stand structure, soil physico-chemical parameters, fine root and microbial parameters for the variation in soil CO_2 efflux rates; and (3) examine the stability of the observed spatial patterns (with hot spots and areas of low soil respiration rates) over time. Our site, a temperate deciduous forest in the Hainich National Park, has been unmanaged for about 60 years and features a mosaic of trees of different species and ages as well as gaps of various sizes. Thus, the Hainich National Park provides a good opportunity to study the spatial variability of soil respiration in relation to stand structure and soil characteristics.

Materials and methods

Site description and experimental layout

The study site is located within the Hainich National Park (51°05′ N, 10°27′ E, 440 m a.s.l.) in central Germany in an area where the climate is suboceanic/subcontinental (Landesanstalt für Wald und Forstwirtschaft 1997). Air temperature averaged 8.4 °C and precipitation was 855 mm year^{-1} for the period 2000 to 2001 (Alexander Knohl, University of California, Berkeley, personal communication).

The Hainich National Park, established in 1997 to protect one of the largest broad-leaved mixed forests in central Europe, covers an area of about 7600 ha. Close to the former East–West German border and used by the military, the forest has been unmanaged for about 60 years. Previously, the forest was managed extensively, with the result that the ages of the trees cover a wide range with a maximum of 250 years (Knohl et al. 2003). The amount of woody debris on the forest floor and standing dead wood is large compared with a managed forest. The forest is dominated (70%) by European beech (*Fagus sylvatica* L.). The remaining 30% is made up of a number of other species, including *Fraxinus excelsior* L., *Acer pseudoplatanus* L., *A. platanoides* L., *A. campestre* L. and *Carpinus betulus* L. The understory vegetation is dominated by geophytes and hemichryptophytes, such as *Allium ursinum* L., *Anemone nemorosa* L. and *Mercurialis perennis* L. The soils are cambisols (clay loam). The A-horizon is 5–15 cm deep, underlaid by clay and, at a depth of 40–60-cm, calcareous bedrock. Litter from trees and plants in the understory decomposes almost completely within 1 year.

The experimental layout consisted of a plot of about 0.5 ha (72 × 72 m) with 36 (in year 2000) and 144 (in year 2001) measurement locations in a regular grid. This large number of locations enabled us to capture the diverse stand structure of our site and to use geostatistical models. To quantify the annual variation in soil respiration rates, 36 permanent locations were measured over the years along a 300-m transect next to the 0.5-ha plot. In 2001, after soil respiration had been measured in the 0.5-ha plot, 122 soil samples were collected for soil and fine root analyses. Soil macro- and micronutrient concentrations were measured only in a subset of 20 samples from locations with the highest or the lowest flux rates, as suggested by Draper and Smith (1998) as a suitable procedure for regression analysis. For the transect, the 36 locations were placed in 10 plots of 1–2 m^2 with 30 m between plot centers. Microbial biomass was measured in 16 separate locations close to the 0.5-ha plot. In these locations, soil respiration was also measured and fine root biomass determined.

Soil respiration and soil climate

Soil respiration was measured in the 0.5-ha plot in July and December 2000, and in May, June and July 2001. During 2000 and 2001, soil respiration rates were measured along the transect every 2 to 6 weeks for a total of 27 measurement campaigns. The measurement campaigns lasted between 1 and 3 days (depending on the number of measurement locations) and were carried out during the daytime.

Soil respiration rates were measured with a closed manual chamber system with an infrared gas analyzer (Li-Cor 6400-09, Li-Cor, Lincoln, NE). A chamber was placed on the soil surface, and CO_2 was scrubbed to below ambient concentration and then allowed to rise above ambient. Five measurement cycles were carried out for each location and a mean of the last four measurements was used to calculate the soil CO_2 efflux.

One week before the first measurement campaign, soil collars were installed at the measurement locations to avoid disturbing the soil at the time of measurement and to allow consecutive measurements at the same positions over time. The collars consisted of PVC tubes about 10 cm in diameter and 7 cm high with stainless steel legs for stabilization. The collars were inserted to a depth of 1 cm (Søe et al. 2004). Each measurement was accompanied by measurements of soil water at 0–6-cm soil depth (ThetaProbe, Delta-T Devices, Cambridge, U.K.) and of soil temperature in the litter layer and at depths of 5, 10 and 15 cm (Li-Cor).

Soil, root and stand structural parameters

After soil respiration was measured, soil samples (three cores of 4.8 cm diameter, 0–8 cm deep) were collected at 122 locations in July 2001. The samples were kept at 4 °C and prepared for analyses, which were performed within 2 weeks. Soil bulk density was determined by drying a defined subsample at 105 °C. Thickness of the litter layer and depth of the A-horizon were measured at the time the soil samples were collected.

Fine roots (diameter < 2 mm) were extracted from fresh soil samples. The samples were washed in a set of sieves (2 mm and 630 µm) to free roots from soil. Living fine roots were dried (70 °C for 48 h) and weighed. In addition, tree and herb roots were separated.

To extract ammonium (NH_4^+), nitrate (NO_3^-) and dissolved organic carbon (DOC) from the soil, 30 g of fresh material was shaken with 100 ml of 1 M KCl for 60 min after roots, stones

and litter had been removed (Mulvaney 1996). Extracts were filtered through filter paper and washed with 1 M KCl prior to filtration. Extracts were kept frozen until analyzed. Concentrations of NH_4^+ and NO_3^- were measured with a continuous flow analyzer (Skalar, Erkelenz, Germany), and DOC with a total organic carbon (TOC) analyzer ("high TOC," Elementar, Hanau, Germany). The pH was measured in 1 M KCl extracts with a pH meter (Wissenschaftlich-Technische Werkstätten GmbH, Weilheim, Germany).

Total nutrient concentrations of the mineral soil (0–8 cm) were determined in air-dried (35 °C), sieved (2-mm mesh) soil that was ground finely (Ball Mill, Retsch, Haan, Germany) after roots, stones and coarse litter fragments had been removed. Total C and total N concentrations were measured with an elemental analyzer (Vario EL, Elementar). Phosphorus, sulfur, calcium and magnesium concentrations were measured with an ICP-AES (atomic emission spectrometer with inductively coupled plasma, Perkin-Elmer, Norwalk, CT). Soil microbial biomass was determined by substrate-induced respiration (SIR) in 16 fresh soil samples collected close to the 0.5-ha plot on June 22, 2001. Glucose was added to the soil samples (2 mg g^{-1}) and CO_2 fluxes were measured hourly with an automated infrared gas analyzer system (Anderson and Domsch 1978, Heinemeyer et al. 1989).

In October 2000, each tree species was determined as well as each tree's position in the 0.5-ha plot and its diameter at breast height (dbh). Vegetation area index (VAI, leaf area index plus stem area index) was measured with a Li-Cor canopy analyzer (LAI 2000) in July 2001.

Statistical analyses

Mean values, standard deviations and regressions were calculated with a statistical software package (JMP IN, Version 4.0.2, SAS Institute, Cary, NC). Soil respiration was correlated with soil temperature with an exponential equation:

$$SR = ke^{aT_{soil}} \quad (1)$$

where SR is soil respiration (μmol CO_2 m^{-2} s^{-1}), T_{soil} = soil temperature at 5-cm depth (°C), and k and a are constants fitted in the regression analyses.

Because the late summer of 2001 was dry, soil respiration was significantly influenced by soil water content. Therefore we included soil water to arrive at Equation 2:

$$SR = ke^{aT}e^{b\theta} \quad (2)$$

where the parameters are the same as for Equation 1, plus θ = soil water (Vol%) and b is another constant fitted in the regression analyses.

Geostatistical analyses (semivariogram model fitting and kriging) were performed with GS+ (Geostatistics for the Environmental Sciences, v. 5.1.1, Gamma Design Software, Plainwell, MI). We estimated the semivariance ($\hat{\gamma}(h)$) with Equation 3:

$$\hat{\gamma}(h) = \frac{1}{2n(h)}\sum_{x=1}^{n}(z_x - z_{x+h})^2 \quad (3)$$

where $n(h)$ is the number of lag pairs at distance intervals of h, and z_x and z_{x+h} are values of the parameter at location x and $x + h$. The semivariance, expressing the degree of relationship between points on a surface, grows as distance increases between points until the semivariance equals the variance of the whole data set (i.e., the measurement points are independent). The intercept on the y-axis (semivariance versus distance) indicates the rest of the variation that is not captured by the scales used in the experimental design. Further explanations of semivariance analysis are given in, e.g., Stoyan et al. (2000), Savin et al. (2001), Webster and Oliver (2001) and Jansen et al. (2002). Maps were interpolated by ordinary block kriging and exponential semivariance models. Before analysis, outliers were removed as recommended by the GS+ manual. Interpolated maps were also produced by least square functions, resulting in patterns similar to those in the kriging maps. Because the least square functions produced clear edge effects, only the kriging maps are shown.

Stand structural parameters around each measurement location (Table 1) were determined by calculating the number of trees, dbh and species in concentric rings around the measurement locations with a Delphi script (Borland Software, Scotts Valley, CA). Ordinations were calculated in Canoco (Canoco for Windows, v. 4.02, Centre for Biometry, Wageningen, The Netherlands). Because the turnover rate of the variables was only about 1.5 standard deviation units, a linear model (principal component analysis) was used as the basis for the ordination plot. Data were normalized and centered before ordination analysis.

Table 1. Stand structural parameters in a 0.5-ha plot in the Hainich National Park. The parameters (except nearest neighbor and vegetation area index (VAI) estimates) were assessed within concentric rings around each soil respiration measurement location. Rings with a radius (r) of 1 to 10 m were used. Abbreviations: dbh = diameter at breast height (1.3 m).

Parameter	Explanation
#r	Number of trees in a circular ring with radius r
Beech$r$	Number of beech trees in a ring with radius r
Non-beech$r$	Number of non-beech trees in a ring with radius r
dbh$r$	Summed diameter of trees in a ring with radius r
m-dbh$r$	Mean diameter of trees in a ring with radius r
Nearest neighbor all species	Distance between measurement location and the nearest tree
Nearest neighbor non-beech	Distance between measurement location and the nearest tree that is not a beech tree
VAI	Vegetation area index (leaf plus stem area) per unit ground

Results

Temporal variation

Temporal variations in soil respiration rates were well explained by soil temperature at 5-cm depth. For the year 2000, a rather wet year, we found a strong relationship between soil respiration and soil temperature at 5-cm depth ($R^2 = 0.95$; Figure 1, upper panel). For the year 2001, this simple exponential dependency of soil respiration on soil temperature was slightly weaker ($R^2 = 0.68$; Figure 1, lower panel) because of a dry period in August (volumetric soil water < 23%, equivalent to a soil water potential < –1.3 MPa). When we included soil water in the regression model for soil respiration in 2001, the explanatory value of the model increased to $R^2 = 0.84$ ($y = 0.31e^{0.13T}e^{0.02\theta}$).

In July 2000, soil respiration rates varied from 1.4 to 6.2 μmol CO_2 m^{-2} s^{-1} (Table 2), whereas in December 2000, when soil temperatures were lower, soil respiration rates were much lower (from 0.9 to 2.7 μmol CO_2 m^{-2} s^{-1}; see Table 2). During the measurement campaign in June 2001, which was carried out during a warm and sunny period (soil temperatures were generally above 14 °C), soil respiration within the 0.5-ha plot ranged from 1.7 to 11.0 μmol CO_2 m^{-2} s^{-1} (Table 2), higher than for May or July 2001 and spanning the same range as that for the whole year, along the neighboring transect (from 0.4 to 9.7 μmol CO_2 m^{-2} s^{-1}; see Table 2). The coefficients of variation during both years were higher for the year-round measurements along the transect (48 and 54% in 2000 and 2001, respectively) than for the short-term measurement campaigns in the plot (from 25 to 45%). Furthermore, coefficients of variation were smaller in winter than in summer.

Spatial variation

The spatial arrangement of trees and their dbh were highly heterogeneous (Figure 2, left panel, top graph). Although areas of mainly large or mainly small trees were recognizable, measurements of VAI showed a relatively dense canopy over the entire plot (VAI = 5.9 ± 0.5). In contrast to the variation over the year, the spatial variability in soil respiration was not determined by soil temperature (Figure 2), probably because spatial variation in soil temperature during each measurement campaign was small. Therefore, the correlation between soil respiration and soil temperature was weak (May 2001: $R^2 < 0.001$, $P = 0.80$; June 2001: $R^2 = 0.05$, $P = 0.01$; July 2001: $R^2 = 0.03$, $P = 0.04$). Soil water explained only a small proportion of the spatial variation in soil respiration during these campaigns (May 2001: $R^2 = 0.07$, $P < 0.001$; June 2001: $R^2 = 0.06$, $P = 0.003$; July 2001: $R^2 = 0.13$, $P < 0.001$; Figure 2). In the geostatistical analyses, relatively large *y*-axis semivariance intercepts (data not shown) suggested that soil respiration was spatially correlated on a scale smaller than the chosen 6 m in-

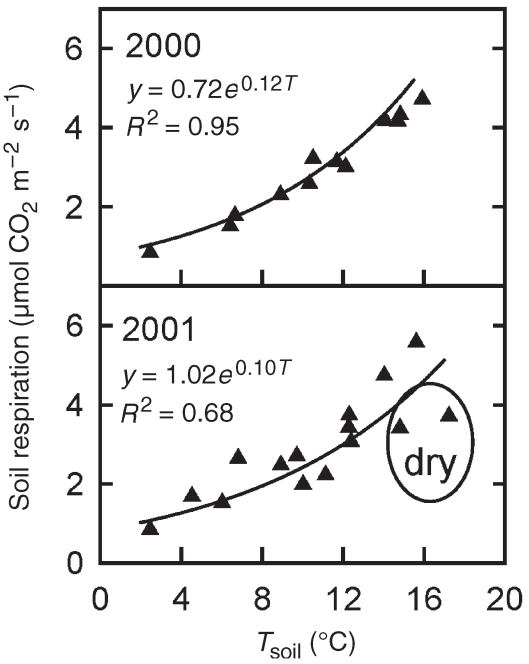

Figure 1. Soil respiration as a function of soil temperature (T_{soil}) at 5-cm depth during 2000 and 2001. Mean values are shown for each of the 27 measurement campaigns along the transect (number of measurement locations = 36). Because of a dry period in late summer 2001 (volumetric soil moisture < 23%), soil respiration is better described by a multiple regression model (see text).

Table 2. Soil respiration (μmol CO_2 m^{-2} s^{-1}) in an unmanaged central European beech forest in Hainich National Park. Measurements were taken in a 0.5-ha plot (P) and along an adjacent 300-m-long transect (T). Abbreviations: SD = standard deviation; SE = standard error of the mean; *n* = number of measurement locations; and CV = the coefficient of variation in %.

	Location	Mean	SD	SE	Range	*n*	CV
2000							
July 17	P	3.0	0.9	0.15	1.4–6.2	36	30
December 8–9	P	1.6	0.4	0.07	0.9–2.7	36	25
May–December	T	3.1	1.5	0.08	0.9–10.6	394	48
2001							
May 15–17	P	2.9	1.1	0.09	0.9–6.2	143	38
June 28–30	P	4.8	2.0	0.17	1.7–11.0	144	42
July 20–22	P	3.3	1.5	0.13	1.2–7.5	144	45
January–December	T	2.8	1.5	0.06	0.4–9.7	559	54

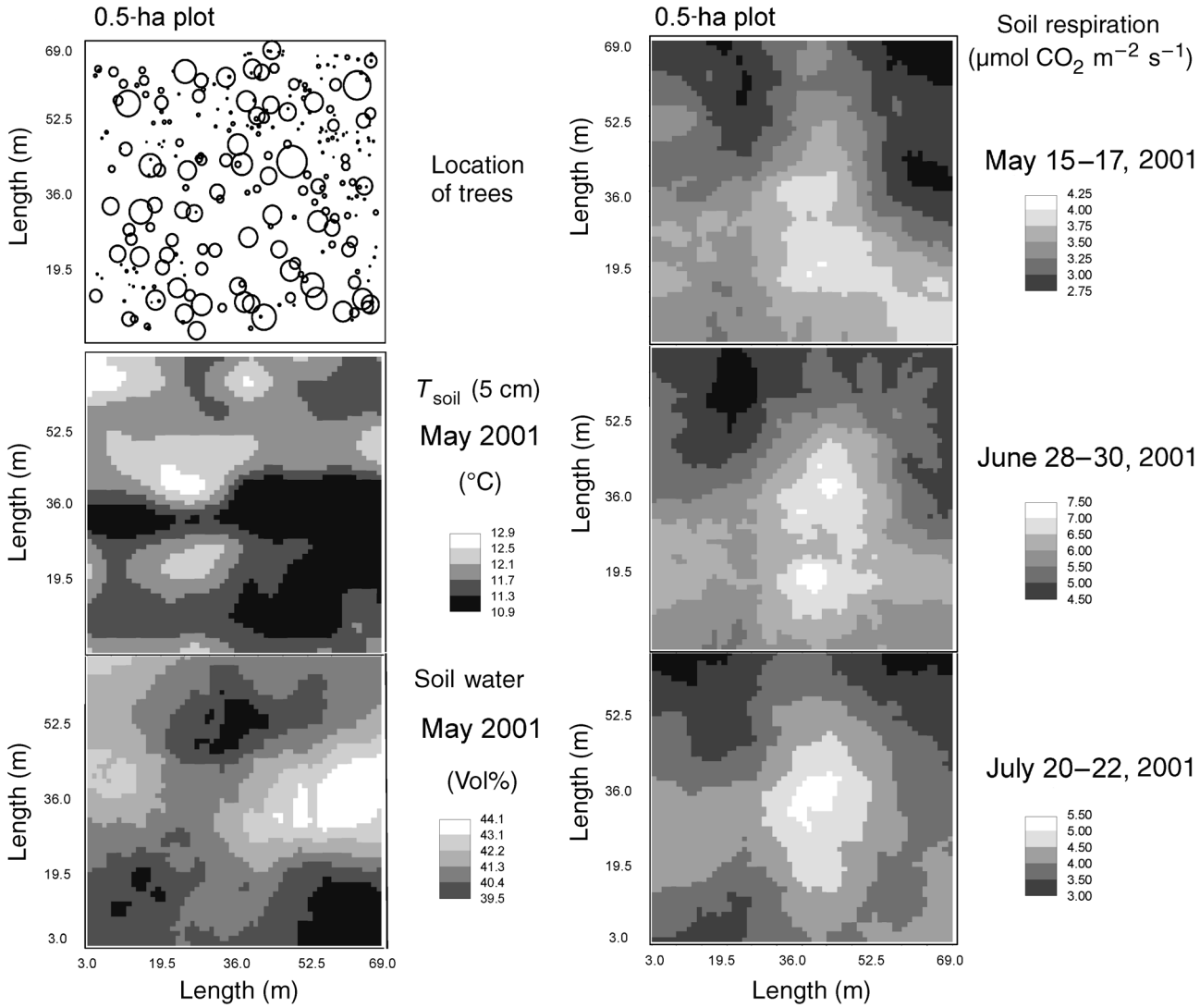

Figure 2. Spatial patterns within the study site. Locations of all living trees within a 0.5-ha plot are shown in the left top panel. Symbol sizes indicate the diameter at breast height of trees, ranging from 1.4 to 99 cm (depicted diameters are enlarged for comparison). Spatial variability of soil temperature (T_{soil} at a depth of 5 cm) and soil water (0–6 cm deep) in May 2001 are shown in the left panel. Soil respiration rates measured during three measurement campaigns in 2001 are shown in the right panel. All variables were measured within a 0.5-ha plot at 144 measurement locations in a regular grid with a mesh size of 6 m. Interpolations were done by ordinary block kriging, using exponential models on the semivariance data. White areas indicate high values and dark areas indicate low values.

terval between measurement locations (144 locations in 0.5 ha in 2001). This finding enabled us to treat our measurement locations as independent samples for inferential statistics. Spatial patterns of soil respiration remained remarkably constant over the growing season (Figure 2, right panel). Areas of rapid soil respiration in May (e.g., the center of the plot and the lower right-hand corner) remained high during June and July, whereas areas of less rapid soil respiration (e.g., the upper right- and left-hand corners) also remained low during summer. Soil respiration rates were highly correlated between the measurements made in May and June ($R^2 = 0.42$, $P < 0.001$) and between the measurements made in June and July ($R^2 = 0.67$, $P < 0.001$). The same pattern of spatial variation in soil respiration rates was detected in July and even in December 2000 (Figure 3), although soil respiration rates were much lower during the winter.

Soil respiration rate was strongly related to a subset of the stand structural parameters: mean diameter at breast height (m-dbh) of trees 4, 6, 8 and 10 m away from the measurement locations (Figure 4). The mean dbh of trees in concentric rings with a 4- and 6-m radius (m-dbh4, m-dbh6) remained close to the soil respiration in a principal component analysis (Figure 4). Mean-dbh4 also stayed close to soil respiration in the third and fourth dimension of the principal component plot, whereas other parameters (e.g., m-dbh6) were diverted from soil respiration in the third and fourth dimension (data not shown). Therefore, m-dbh4 was the preferred structural pa-

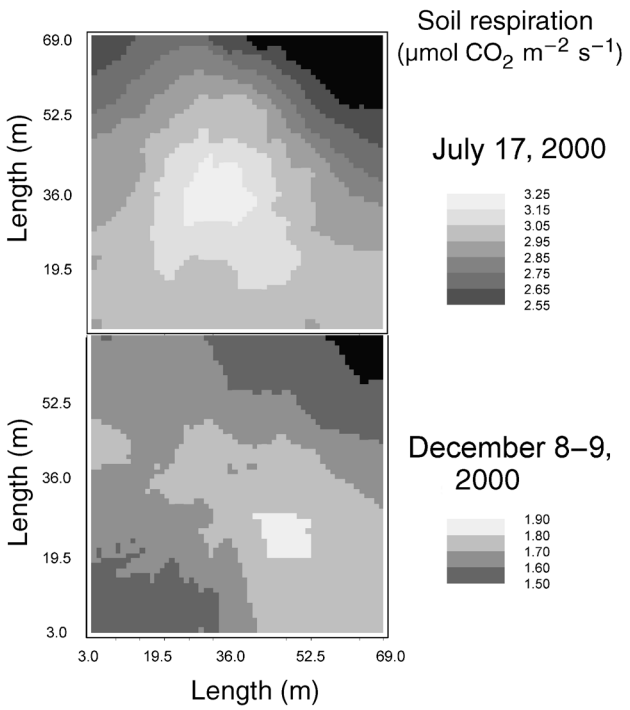

Figure 3. Soil respiration measured within a 0.5-ha plot at 36 measurement locations in summer (July) and winter (December) 2000. Interpolated maps were produced by ordinary block kriging (semivariance analysis and exponential models).

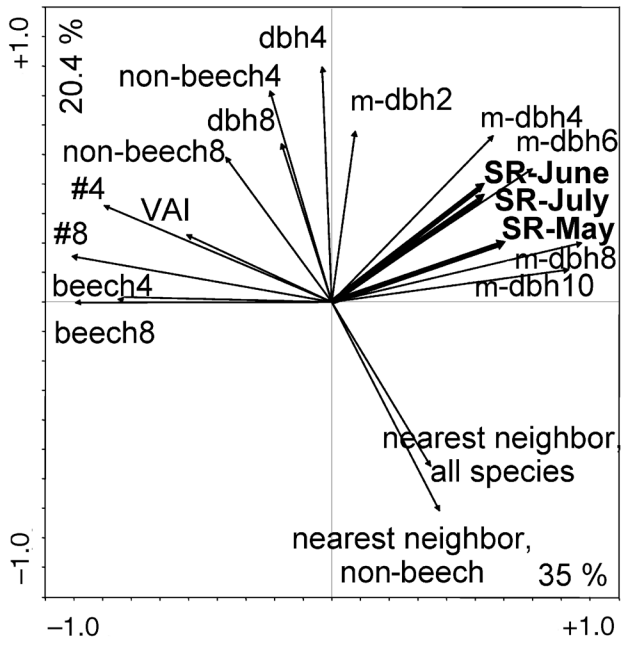

Figure 4. Principal component analysis of soil respiration (SR), vegetation area index (VAI) and stand structural parameters of a 0.5-ha plot in 2001. Abbreviations refer to stand structural parameters in concentric rings with different radii around measurement locations (2, 4, 6, 8 and 10 m, respectively); see Table 1 for further details. Soil respiration was measured in May, June and July 2001. First and second ordination axes are shown. Variables were centered and normalized prior to analyses. $n = 144$.

rameter for further analyses. The number of beech trees (beech4 and beech8) as well as the total number of trees (#4 and #8) in a 4- or 8-m radius around the measurement locations were negatively correlated with soil respiration. In contrast, the distance to nearest neighboring tree, sum of dbh and the number of non-beech trees seemed to have no effect on soil respiration. When multiple regression models (forward stepwise) were calculated based on all stand structural parameters from Table 1, the models contained 9 to 12 parameters and explained 39 to 40% of the variation in soil respiration rates in the three campaigns in summer 2001.

To further assess potential driving factors, we tested a range of root and soil parameters measured in 2001 (Table 3). Although some factors were positively related to soil respiration, such as litter depth, fine root biomass and various soil chemical parameters, others were negatively related, such as soil water, soil bulk density and magnesium content of the soil. Subsequently, all soil chemical parameters that showed a significant relationship with soil respiration (Table 3) were used in a multiple (forward stepwise) regression analysis (Table 4). The model included bulk carbon (C), DOC and magnesium (Mg) contents and explained 62% of the spatial variation in soil respiration rates in July 2001. In a final step, to reduce the number of potential driving factors, the stand structural (m-dbh4) and soil chemical factors (C, DOC and Mg contents) were used in a multiple regression analysis in which root, soil climate and soil structure parameters correlated significantly with soil respiration (except soil bulk density, because this variable was used to convert all soil chemical and root parameters from concentration (g g^{-1}) to content (g m^{-2}); Table 5). From this final regression, the "best model" for spatial variation in soil respiration was found to contain the parameters fine root biomass, soil C content, m-dbh4 and soil water. This combination of parameters explained 79% of the spatial variation in soil respiration rates in July 2001.

With an additional set of measurements, we tested the effect of soil microbial biomass on soil respiration in June 2001 (Figure 5). However, this microbial parameter showed no significant relationship with soil respiration, whereas fine root biomass again explained about one third of the spatial variation in soil CO_2 efflux (compared with a partial R^2 of 0.40 in Table 5).

Discussion

Notable stability in the spatial patterns of high and low soil respiration rates was seen within the growing season and from year to year. Although variation in soil respiration rates was larger in summer than in winter, soil respiration hot spots were also detectable during the winter measurement campaign. The observed stability of the spatial patterns in soil respiration rates must be associated with relatively stable characteristics of the underlying processes.

A relatively stable characteristic of any forest ecosystem is stand structure. The presence of stable respiration hot spots

Table 3. Descriptive statistics and linear regressions of biotic and abiotic parameters versus rates of soil respiration. Significance: * = $P < 0.05$; ** = $P < 0.01$; and *** = $P < 0.001$. Soil and root samples were collected on July 24, 2001. Depth of samples was 0–8 cm. Abbreviations: T_{soil} = soil temperature; DOC = dissolved organic carbon; m-dbh4 = mean diameter at breast height in a 4-m-radius plot; SD = standard deviation; and n = number of measurement locations.

Parameter	Unit	Mean	SD	Range	n	R^2
Stand structure						
m-dbh4	cm	25.1	17.5	0–71.6	144	0.126 ***
Soil climate						
T_{soil}, 0 cm	°C	5.4	1.2	13.0–18.8	144	0.031 *
T_{soil}, 5 cm	°C	14.2	1.2	12.7–18.0	144	0.031 *
T_{soil}, 10 cm	°C	13.9	1.3	12.6–17.9	144	0.022
T_{soil}, 15 cm	°C	13.6	1.4	12.5–17.8	144	0.016
Soil water[1]	Vol%	45.2	4.0	32.2–55.8	144	0.131 ***
Soil structure						
Litter depth	cm	1.3	0.7	0.2–3.5	122	0.157 ***
A-horizon depth	cm	7.2	3.0	1.5–16.0	122	0.061 **
Soil bulk density[1]	g cm^{-3}	0.8	0.1	0.6–1.1	122	0.164 ***
Fine roots						
Total biomass	g m^{-2}	128.5	75.9	7.2–374.8	122	0.157 ***
Tree roots only	g m^{-2}	38.9	45.3	0–286.6	122	0.042 *
Herb roots only	g m^{-2}	89.5	66.6	0–268.5	122	0.098 ***
Root N	g N m^{-2}	2.5	1.4	0.4–5.3	25	0.234 *
Soil chemistry						
pH		5.4	0.7	3.3–6.5	20	0.062 **
$[C_{total}]$	g m^{-2}	3681	431	2949–4445	20	0.362 **
$[N_{total}]$	g m^{-2}	310.6	28.6	248–362	20	0.227 *
C/N		11.8	0.6	11.1–13.2	20	0.300 **
$[P_{total}]$[1]	g m^{-2}	62.6	7.3	50.7–78.8	20	0.122
$[S_{total}]$	g m^{-2}	38.3	4.3	31.9–46.9	20	0.227 *
$[Ca_{total}]$	kg m^{-2}	0.45	0.1	0.2–0.6	20	0.000
$[Mg_{total}]$[1]	kg m^{-2}	0.56	0.1	0.4–0.7	20	0.273 *
$[NH_4^+–N]$	g m^{-2}	0.39	0.2	0.2–0.8	20	0.042
$[NO_3^-–N]$[1]	g m^{-2}	0.40	0.3	0.1–1.1	20	0.021
[DOC–C]	g m^{-2}	4.4	1.4	3.0–9.0	20	0.224 *

[1] Negatively correlated with soil respiration; all other parameters were positively correlated.

Table 4. Multivariate regression of soil chemical parameters that significantly explained spatial variation of soil respiration rates in the Hainich 0.5-ha plot in July 2001. Abbreviations: DOC = dissolved organic carbon; C = carbon; and Mg = magnesium.

Parameter	Soil respiration (μmol CO_2 m^{-2} s^{-1})			
	df	Partial R^2	F	P
Carbon content of the soil (g m^{-2})	1	0.36	9.13	0.008
DOC content of the soil (g m^{-2})	1	0.16	4.47	0.051
Magnesium content of the soil (kg m^{-2})	1	0.10	4.30	0.055
Model $R^2 = 0.62$[a]	16	8.77	0.001	

[a] Model equation: $y = 0.003C + 0.59DOC – 10.5Mg – 2.46$.

may indicate the influence of plants on soil respiration, either directly via root respiration, or indirectly via root exudates or root and leaf litter turnover. If the spatial variation in soil respiration rate is caused mainly by plant activity (above- and belowground), this could imply a dominance of root respiration in total respiration at the study site. This hypothesis is supported by several recent forest studies where tree root (and rhizosphere) respiration constituted at least half of the soil respiration in temperate forests (Epron et al. 2001, Laporte et al. 2003, Subke et al. 2004) and in a boreal forest (Högberg et al. 2001). Furthermore, fine root biomass was the most important variable in our final best model, explaining 30–40% of spatial variation in soil respiration rates (see Table 5 and Figure 5). We further assume that the impact of understory vegetation on soil respiration rate is lower than that of forest trees, because the understory vegetation actively photosynthesized in May, but not during later measurement campaigns; our spatial soil

Table 5. The best model for explaining soil respiration in the 0.5-ha plot. Measurements were taken in July 2001. Soil bulk density was used in the calculation of many of the parameters for the model and is therefore excluded from this analysis. Abbreviation: DOC = dissolved organic carbon; dbh = diameter at breast height; C = carbon; and H_2O = water.

Parameter	Soil respiration (μmol CO_2 m^{-2} s^{-1})			
	df	Partial R^2	F	P
Fine root biomass (g m^{-2})	1	0.40	13.88	0.002
Carbon content of the soil (g m^{-2})	1	0.23	7.18	0.017
Mean dbh of trees in plots with 4 m radius (cm)	1	0.11	5.11	0.039
Soil water (Vol%)	1	0.04	2.58	0.129
Model $R^2 = 0.79$[a]	15		13.74	< 0.001

[a] $y = 0.014\text{roots} + 0.002\text{C} + 0.042\text{m-dbh4} - 0.13\text{soil } H_20 - 0.04$

respiration patterns, however, were similar during all measurements.

The importance of autotrophic respiration was also seen in the influence of large trees in explaining spatial patterns of soil respiration. In our study, respiration rates were consistently higher in areas with high mean dbh (i.e., large trees, e.g. m-dbh4) than in areas with many small trees. Pangle and Seiler (2002) showed that rates of soil respiration were consistently higher near the bases of loblolly pine seedlings than between seedlings. However, in our study, we found no correlation between distance to the nearest neighboring tree and soil respiration. We therefore hypothesized that, in locations with large trees, either (1) there were more fine roots or (2) the fine roots were more active. The first possibility, however, was not supported by our data because fine root biomass and m-dbh4 were not strongly correlated ($r^2 = 0.04$, $P = 0.034$). The second possibility is more likely, because recent studies have shown that a considerable amount of assimilate is transported to the roots and respired there quickly (Law et al. 1999, Högberg et al. 2001). Furthermore, we found a negative correlation (Figure 4) between soil respiration and the number of beech trees that surround each measurement location. The reason for this observation may be twofold. First, in our study, many small trees seem to respire less per unit ground area than large trees. Second, when there were many beech trees, there were fewer trees of other species. Thus, soil respiration rates were higher when ash and maple trees were present, probably due to more easily decomposable litter or because of increased root respiration. To evaluate root activity, we measured the nitrogen (N) concentration of fine roots. Although fine root N concentration was not directly correlated with soil respiration (P = 0.572), fine root N per m^2 ground was slightly better correlated with soil respiration than was fine root biomass. However, the fine root N per m^2 ground was not correlated with m-dbh4 ($P = 0.462$), although it has been viewed by other authors as a good estimator of root activity (Pregitzer et al. 1998, Burton et al. 2002). Thus, in our study, the large trees may have had a greater (but root-N-independent) belowground C allocation than small trees.

Soil C content, calculated on an area basis, was the single factor with the largest effect on soil respiration, explaining 36% of the variation (Table 4). It is unclear why C was more important than N and phosphorus availability, which have been shown to determine soil respiration patterns in other forest ecosystems (Xu and Qi 2001*a*, Borken et al. 2002, Pangle and Seiler 2002). However, we observed a strong correlation between C content and N ($R^2 = 0.83$, $P < 0.001$). Furthermore, C content was not correlated with the structural parameter m-dbh4 ($R^2 = 0.12$, $P = 0.13$). Thus, the effect of C content on soil respiration seemed unrelated to the respiration of trees, but was related to soil (or microbial) properties. One of the four most important parameters for explaining spatial variation of soil respiration was soil water, which had a negative relationship to soil CO_2 efflux. Suppression of soil respiration by high soil water is likely to be associated with anaerobic conditions in the wettest areas, where waterlogging of the soil can occur

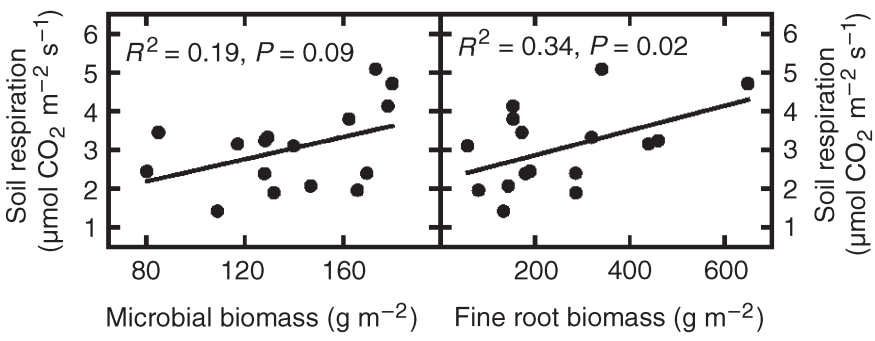

Figure 5. Soil respiration rates as a function of microbial biomass and fine root biomass (at 0–8 cm soil depth) from samples collected close to the 0.5-ha study plot on June 26, 2001. The two parameters were not correlated with each other ($P = 0.34$).

because of the high clay content of the topsoil at our site (about 30%, Martina Mund, Max Planck Institute for Biogeochemistry, Germany, personal communication). As pointed out by Xu and Qi (2001*b*), Davidson et al. (1998) and Keith et al. (1997), a high water content in a clay-rich forest soil may also reduce O_2 diffusion and thereby limit microbial and root activity. Soil respiration rates are determined by highly localized processes, where water saturation of a clump of clay may limit respiration rates. On the other hand, dry clay-rich soil had a negative effect on soil respiration (as seen in the dry period in August 2001). The strong impact of soil water on soil respiration was also shown at a much larger spatial scale (and this time with a positive correlation) for Mediterranean forests and scrublands by Reichstein et al. (2003).

In conclusion, the highly significant influences of tree roots and forest structure on soil CO_2 fluxes indicate that the spatial heterogeneity of soil respiration in the Hainich plot can be partly explained by the spatial variation of gross primary production. This result is supported on much larger spatial scales by the results of Janssens et al. (2001) and Reichstein et al. (2003). However, on smaller scales, our study shows that combining measurements of root, soil and stand structure parameters is promising and will help us to understand mechanisms underlying soil respiration rates and the role of soil respiration in the ecosystem C budget.

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