Controlling factors, scaling issues and partitioning of soil respiration

Dissertation

zur Erlangung des akademischen Grades
doctor rerum naturalium
(Dr.rer.nat)

Vorgelegt dem Rat der Biologisch-Pharmazeutischen Fakultät
der Friedrich-Schiller-Universität Jena

Von
Cand.scient (Diplom Biologin) Astrid R. B. Søe
Geboren am 02.03.1971
In Nyborg, Dänemark

Jena 2000 - 2003

Thesis handed in: 30.05.03
Oral exam: 17.07.03
Defence: 26.08.03

Preface

This thesis consists of an introduction chapter that presents the main aspects of soil respiration and the overall objectives of this study. Chapters two to five present the four main aspects that I have dealt with in my scientific work during my PhD. Finally, a discussion chapter sums up the main results and perspectives of my thesis. The work for chapters two and three I have carried out myself in cooperation with technical staff and student helpers, mainly at the Max-Planck-Institute for Biogeochemistry (MPI-BGC) in Jena. The ecosystem respiration (eddy covariance) data in chapter four were kindly provided by Alexander Knohl, MPI-BGC. The $\delta^{13}C$ values of solid samples and the microbial biomass data in chapter five were kindly provided by Dr. Annette Giesemann and Dr. Traute-Heidi Anderson at the Federal German Agricultural Research Center, Braunschweig. Due to the collaborations with other scientists and fruitful discussions with my supervisor and colleagues, I have chosen to use the plural form "we" in the discussions in this thesis. Each of the chapters two to five are submitted or will be submitted as manuscripts in slightly modified versions to the international peer reviewed research journals: *Tree Physiology*, *Basic and Applied Ecology*, *Global Change Biology* and *Plant and Soil*, respectively.

Table of Contents

1 Introduction

After photosynthesis, soil respiration is the second largest flux of carbon in most terrestrial ecosystems (Schlesinger 1997; Raich and Schlesinger 1992; IPCC 2001). Soil respiration (soil CO_2 efflux) originates from autotrophic root respiration and heterotrophic microbial respiration in the bulk soil and in the rhizosphere. Carbon dioxide (CO_2) is taken up from the atmosphere by green plants and assimilated into organic compounds. Due to energy consuming metabolic processes plants respire CO_2 from above and below ground parts (e.g. for active nutrient uptake in the roots) and microorganisms respire CO_2 via decomposition of organic matter (e.g. litter from roots, leaves and branches). During these respiratory processes the carbon is released to the atmosphere again. Since soil respiration has large significance for the carbon cycle (IPCC 2001; Churkina et al. 2003) the work presented in this thesis aimed to understand several aspects of soil respiration, such as the sources for this flux, the influence of biotic and abiotic parameters and the difference between various measurement systems. For this purpose, detailed studies of soil respiration and related parameters were carried out in a highly heterogeneous, unmanaged, deciduous forest in the National Park Hainich (western Thuringia, Germany) and in an elevated CO_2 plot in an agricultural field close to Braunschweig, Germany (see also study site descriptions in chapters 2 and 5).

1.1 Soil respiration and the global carbon cycle

Since the 1970's, it has been known that the atmospheric concentration of carbon dioxide is increasing (Keeling et al. 1976). Various scenarios, mainly regarding CO_2 emission from fossil fuel combustion, have been put forward (IPCC 2001). Based on these scenarios models have estimated that in 2100, the CO_2 concentration in the atmosphere will be between 540 and 970 ppm in comparison to the present day level at about 370 ppm (IPCC 2001). This higher atmospheric CO_2 concentration is thought to lead to climate changes due to enhanced greenhouse effect (i.e. increase in the global mean temperature of about 4°C until 2100, and probably increase of winter precipitation and decrease of summer precipitation (IPCC 2001)). It has been shown that a proportion of the carbon dioxide emitted to the atmosphere by fossil fuel burning and terrestrial

processes (mainly deforestation) is taken up by the oceans and the terrestrial biosphere (Schimel et al. 2001). The current assumption is that the terrestrial ecosystems are a sink of about 1.1 Pg C per year (1 Pg = 10^{15} g; IPCC 2001) (see Fig. 1.1). Results from atmospheric measurements combined with modeled estimates of net primary production have suggested that a major terrestrial carbon sink is located in the Northern hemisphere (Tans et al. 1990).

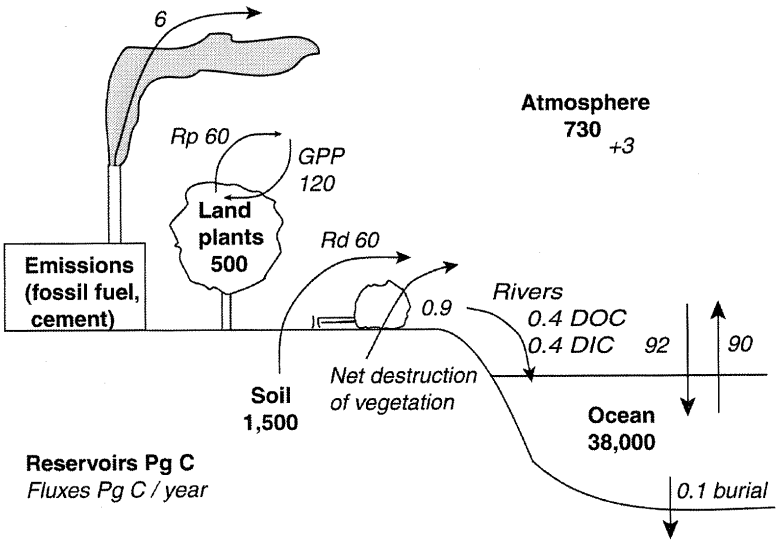


Figure 1.1. The global carbon (C) cycle (after Schlesinger 1997). Living organisms control the largest C fluxes between the atmosphere and the terrestrial reservoirs. During photosynthesis, plants capture solar energy and fix atmospheric CO_2 (gross primary production (GPP)) which is later released by plant respiration (Rp) or by microbial decomposition in soils (Rd). Anthropogenic emissions of CO_2 are small when compared with natural fluxes. Terrestrial ecosystems, in which soils are the largest reservoir, are currently assumed to be a sink for ca. 1.1 Pg C per year (IPCC 2001).

Soils represent the largest terrestrial reservoir of organic carbon, storing between 71 and 81% of the organic carbon (between 1567 and 2011 Pg C) found in terrestrial ecosystems (IPCC 2001). Soil respiration is the main path by which carbon returns from this terrestrial reservoir back to the atmosphere. Soil respiration is one of the largest fluxes in the global carbon cycle. Consequently, small changes in the magnitude of soil respiration could have large effects on the concentration of CO_2 in the atmosphere

(Schlesinger 1997; IPCC 2001; Churkina et al. 2003). Thus, knowledge about soil respiration is highly important in order to understand the global carbon cycle.

The growing concern for the possible global warming potential of increasing CO_2 concentrations in the atmosphere led to the UN Framework Convention on Climate Change in 1992 and its Kyoto Protocol in December 1997. According to this protocol, countries can reduce emissions by limiting fossil fuel consumption and by increasing net carbon sequestration in terrestrial carbon sinks (Murray et al. 2000; Schulze et al. 2002). Forests contain a considerable proportion of the carbon stored in terrestrial ecosystems (IPCC 2000). This carbon, which to a large extend is found in the soil, may be released by changed management (e.g. deforestation) and therefore contribute to the increase in atmospheric CO_2 concentration (WBGU 2003). Within the framework of the Kyoto Protocol, only afforestation and reforestation will be accounted for as sinks, while forests at a later successional stage are expected to be in steady state and therefore not be able to sequester carbon. However, recent studies have shown that unmanaged forests may have (an even fairly large) sink capacity for CO_2 (Schulze et al. 1999; Knohl et al. 2003). Results like these are important, and will possibly change the political decisions.

However, the knowledge about sink capacities of terrestrial ecosystems, particularly of the soil compartment, is often too sparse to serve as basis for firm recommendations. Thus, from a scientific viewpoint the outcome of political negotiations may not always be satisfying (Schulze et al. 2002). Soil respiration is, for example, presumed to increase steadily with increased temperature, but a recent study of soil respiration suggests that the temperature sensitivity of soil respiration will decrease in a future warmer and drier climate (Xu and Qi 2001b). Thus, a better understanding of the important terrestrial CO_2 flux, soil respiration, is needed in order to evaluate to which extend soil can function as long term sink for atmospheric CO_2. Therefore, I carried out detailed studies of soil respiration. Several aspects were investigated such as temperature sensitivity of this flux, the constrains of various parameters on the flux rates, their spatial patterns, and the contribution of recently assimilated versus older carbon sources to this flux.

1.2 Partitioning of sources for soil respiration

The rates of CO_2 respired due to the activity of roots and microbial decomposition of organic material may have different responses to climatic parameters, especially to changes in temperature (Boone et al. 1998). In order to model soil CO_2 fluxes as well as to understand below-ground processes, partitioning of soil respiration into its two components of microbially and root respired CO_2 (or old versus recent carbon) is highly important. However, this partitioning is difficult due to the high variability observed and due to methodological difficulties (Hanson et al. 2000). Experiments have shown that the respiration from roots can range from 10% to 90% of the total soil respiration depending on the season and the ecosystem. Different measurement approaches may also give different results. Four main types of approaches for separating root and microbial respiration have been developed, and a good overview was given by Hanson et al. (2000). One method is the so-called "component integration approach." With this approach, the roots are removed from the soil and both components are measured separately in the lab. However, this method involves a severe physical disturbance of the system, and the results may therefore be imprecise. Another method is to compare respiration from root free soil with total soil respiration *in situ*. The root free plots can be obtained by physical removal of roots, measurements in vegetation gaps (Brumme 1995) or by exclusion of roots by trenching. Several trenching plots have been established in deciduous as well as coniferous temperate forests (Boone at al. 1998; Hart and Sollins 1998: Epron et al. 1999; Buchmann 2000; Rey et al. 2002). With the trenching plot approach root impermeable barriers are dug into the ground to the depth of the maximum root growth to avoid in-growth of roots from the outside. After a year or two, the roots have died and the only respiration is due to decomposition of organic matter. The trenching plot approach is beneficial in the way that no direct physical disturbance of the soil has taken place (Boone et al. 1998; Epron et al. 1999; Buchmann 2000). However, soil moisture conditions are often changed and competition between groups of organisms such as saprophytic and myccorhizal fungi in the soil will be altered. The third approach (only suitable in forests) is tree-girdling. The use of girdling for separation of root and microbial respiration has only recently appeared in the literature. Tree-girdling involves stripping the stem bark to the depth of the current xylem terminating the supply of current

photosynthates to roots without physical disturbance of the delicate root-microbe-soil system. From measurements of soil respiration in girdling and in control plots it is possible to determine the contribution of roots and saprophytic decomposers to soil respiration (Högberg et al. 2001). The fourth method is the isotopical labeling approach. A clear advantage of this method is that disturbance of the root-soil system can almost be avoided. A major disadvantage is that measurements of these kinds are often relatively expensive. Labeled substrates (e.g. from C4 plants) or labeled CO_2 for photosynthesis have been used in several experiments (Rochette and Flanagan 1997; Andrews at al. 1999; Ekblad and Högberg 2000; Pendall et al. 2001). Labeled material can be added either as pulse labeling or as continuous labeling. If CO_2 (depleted or enriched in ^{13}C) is used for the pulse labeling experiments, the timing of labeling and measurements are highly important in order to catch the pulse of respired labeled CO_2 in the measurement scheme. Furthermore, calculations of the fractional contribution of root respiration to total soil respiration can be complex in pulse labeling experiments. The continuous labeling has the advantage that the plants become more homogeneously labeled. Furthermore, a steady state condition is reached, which simplifies calculations. In this study, I took the advantage of a recently developed method of continuous labeling of plants, the "Free Air Carbon dioxide Enrichment experiment" (FACE), where labeled CO_2 is used to rise the CO_2 concentration in plots. The FACE experiments clearly have the advantage that there are no chambers, but the labeled CO_2 is blown directly onto the plants in the open field. Thus, weather and soil conditions are not changed compared to natural conditions. So far, only very few studies have been published, where soil respiration was partitioned by use of a FACE experiment (Andrews et al. 1999; Pendall et al. 2001). The partitioning of soil respiration is further discussed in chapter 5 and the temperature sensitivity of root and microbial respiration is discussed in chapter 4.

1.3 Measurement methods of soil respiration

The main methods for measuring soil respiration are chamber systems and micrometeorological approaches (understory eddy covariance, Janssens et al. 2000; Wilson and Meyers 2001). The chamber systems can be further subdivided into closed manual systems (as used by Davidson et al. 1998; Law et al. 1999a; Buchmann 2000; Xu

and Qi 2001a; Janssens et al. 2001; Rey et al. 2002; Shibistova et al. 2002), open automated systems (as described by Norman et al. 1997; Gärdenäs 2000; Longdoz et al. 2000; Kutsch et al. 2001; Pilegaard et al. 2001; Drewitt et al. 2002; Pumpanen et al. 2003) and closed static systems (Norman et al. 1997; Janssens et al. 1998; Pumpanen et al. 2003). A recent overview of measurement systems is also given by Lankreijer et al. (2003). In the two first mentioned chamber systems, CO_2 concentrations are measured directly with an infrared gas analyzer, while in the closed static system, CO_2 is absorbed chemically in a sodalime trap. The most commonly used systems are the closed manual and the open automated chamber systems. In this study, I used the closed manual soil respiration measurement system Licor 6400-09 (Licor, Inc., Lincoln, Nebraska, USA) (see Fig. 1.2). During the measurement procedure, a chamber is placed on the soil surface and a specific amount of air is pumped from the chamber, into the infrared gas analyzer, and back into the chamber. The CO_2 concentration in the chamber rises to a pre-defined

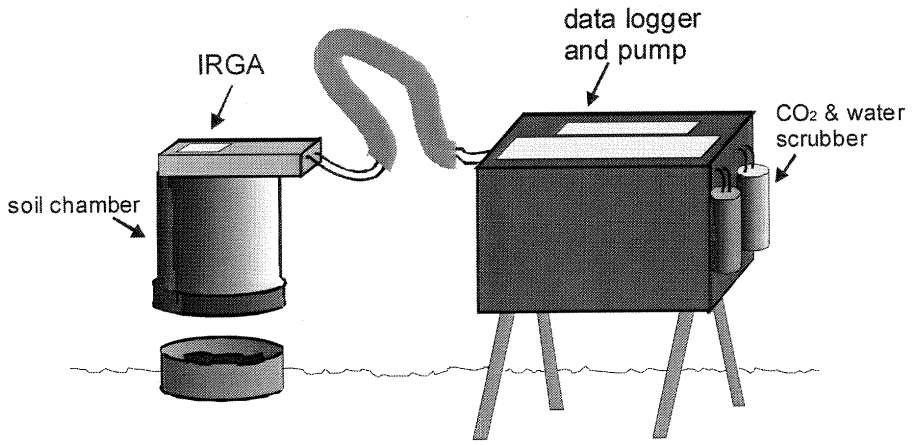


Figure 1.2. Measurement system (Licor 6400-09) for soil respiration. CO_2 concentrations are measured in the soil chamber with an infrared gas analyzer (IRGA), and a specific volume of air is pumped around in a closed circle (for further details see text).

concentration (e.g. 10 ppm above ambient concentration, which was measured beforehand). Then CO_2 is removed from the air with a CO_2 scrubber (sodalime) until a lower pre-defined concentration (e.g. 10 ppm below ambient concentration). Several cycles (normally three to five) of this kind are carried out. From the infrared gas analyzer (IRGA) readings, the soil respiration flux can now be calculated from the increase of CO_2 over time (the first derivative) when the volume of the system and the area covered by the chamber are known. The IRGA readings are corrected for water vapor and air pressure automatically as they also influence the absorption of the infrared light. Soil respiration is calculated in the unit: μmol CO_2 m^{-2} s^{-1}. The clear advantages of the Licor 6400-09 system are that it is a standardized method achieving a high precision (McDermitt et al. 2003; Takle et al. 2003). Furthermore, the system is portable, allowing a large spatial coverage, and it runs on batteries, so locations at a larger distance to a permanent power supply can be measured.

The other main type of measurement system for soil respiration is the automated open chamber method. With this method, an air stream is pumped through a soil camber, and another air stream is pumped parallel to the first one, but not through the chamber. Soil respiration is calculated from the difference in CO_2 concentrations of the two air streams, the flow rate and the area covered by the chamber. With this method, the air in the chamber changes continuously. Therefore, the chamber can be left on the location for longer time intervals than using the closed system. On the other hand biases may occur in the open automated method if CO_2 concentration or pressure in the chamber is different from the natural conditions. Furthermore, the number of measurement locations and the distance between locations are normally limited by the technically possible number of chambers connected to a central gas analyzer, the length of the tubing to the chambers and the presence of permanent power.

Although there are advantages and disadvantages with both of the two chamber systems, the closed manual system was clearly preferable at the Hainich forest site. The reason for this was the high degree of heterogeneity of the site. Thus, although the closed manual system is labor intensive and therefore constrained to a limited number of measurement campaigns, the conditions at the forest site demanded a high spatial

coverage, which was only possible with the closed manual system. More details on measurement systems are given in chapter 4.

1.4 Influencing parameters

Rates of soil respiration are typically dependent upon soil temperature and moisture conditions, at least on an annual basis (e.g. Davidson et al. 1998; Buchmann 2000; Raich and Tufekcioglu, 2000). However, studies dealing with spatial variation in soil respiration rates have suggested several different variables being responsible for this variation. The spatially controlling factors will depend on ecosystem and site characteristics. Several studies in temperate forests have shown that concentrations of macro-nutrients (nitrogen, phosphorus and magnesium) in the soil are the most significant parameters for spatial variation in soil respiration rates (Xu and Qi 2001a; Borken et al. 2002; Pangle and Seiler 2002). Microbial parameters and vegetation structure have also been suggested as controlling factors (Shibistova et al. 2002, Laporte et al. 2003). Furthermore, soil structural parameters could have an influence on soil respiration rates (Janssens et al. 2003). In the literature, contrasting results concerning the most important parameter for soil respiration can often be found. Thus, in this study, a wide variety of parameters were tested. Detailed results are described in chapter 3.

1.5 Objectives of the study

The work for this thesis addressed four main aspects of soil respiration, which are presented in the next four chapters.

Chapter 2 deals with the spatial pattern of soil respiration rates in relation to stand structure. The objectives for this chapter were:

- to evaluate the temporal and spatial variation of soil respiration rates in the Hainich forest,
- to identify the importance of stand structure for the variation in soil respiration rates,
- and to examine the stability of the spatial pattern of hot-spots and areas of low soil respiration rates during the growing season and between years.

Chapter 3 is concerned with factors controlling soil respiration. The objectives of this chapter are:

- to quantify the spatial variation in abiotic and biotic variables affecting soil respiration,
- as well as to identify factors controlling soil respiration.

Chapter 4 deals with soil respiration as a support measurement for ecosystem respiration estimates. For this purpose the chapter addresses the problems in scaling estimates from chambers to the ecosystem. The objectives of this chapter were:

- to determine the effect of spatial variability on annual estimates of soil respiration,
- to evaluate the influence of fine roots on the temperature sensitivity ("Q_{10}") of soil respiration, and
- to recommend the number of sampling locations needed for adequate estimations of annual soil respiration at a forest site with typical heterogeneity.

Finally, results are presented in chapter 5 from measurements in a "Free Air Carbon dioxide Elevated experiment" (FACE). In this chapter the main focus was on separating the amount of CO_2 respired from old and recent carbon. The objectives of this chapter were:

- to quantify soil respiration in a FACE experiment with sugar beet,
- to partition the sources of soil respiration (old vs. recent carbon) in the FACE experiment.

2 Spatial and temporal variation of soil respiration in relation to stand structure

2.1 Introduction

Soils constitute the major carbon reserve in terrestrial ecosystems (Dixon et al. 1994), and the annual flux of CO_2 through soil respiration has been estimated to be about ten times higher than 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 trivial to accurately predict soil CO_2 fluxes because soil respiration is composed of respiration from both roots and microorganisms, affected by many biotic and abiotic factors (Raich and Schlesinger 1992; Davidson et al. 1998; Buchmann 2000; Stoyan et al. 2000; Xu and Qi 2001a, see also chapter 3). Consequently, a large variation in soil respiration rates is typically found both within and between most temperate ecosystems (Raich and Schlesinger 1992; Buchmann, 2000; Franzluebbers et al. 2002).

One obvious factor, which potentially could influence spatial heterogeneity of soil respiration in a forest, is stand structure. Canopy architecture, root distribution and microbial activity due to fine root turnover and root exudates are closely linked. One could therefore hypothesize that stand and canopy characteristics have the potential to explain spatial patterns of soil CO_2 efflux in forests. Root respiration constitutes the major part of soil respiration in a forest (Högberg et al. 2001; Laporte et al. 2002). For example, Shibistova et al. (2002) found a high correlation between canopy closure and soil respiration in an open boreal forest. Soil respiration has been shown in several studies to be closely linked with photosynthetic activity (Högberg et al. 2001; De Neergaard et al. 2002), the level of competition (especially for light) and the developmental stage of the trees (age, height etc.), important factors for determining root respiration from individual trees. On the other hand turnover, i.e., growth or death of fine roots and thus, the distribution of microbial communities can be the determining factors for soil respiration in forest and agricultural stands (Stoyan et al. 2000; Savin et al. 2001). Furthermore, the temperature sensitivity (Q_{10}) of root respiration may be different from microbial respiration and root respiration, magnifying spatial patterns also at the temporal level (Boone et al. 1998). If a high degree of temporal stability is observed in the spatial patterns of soil respiration rates within a site, information on stand structure might give insight into the controlling factors for soil respiration.

Forest management generally tends to homogenize stand structure. However, where large gaps or two or more canopy structural classes are present considerable variation in soil respiration rates was observed (Shibistova et al. 2002; Laporte et al. 2003). Also death of individual trees, natural regeneration, and forest conservation will typically create a highly heterogeneous stand structure. The temperate deciduous forest in the National Park Hainich has been unmanaged for the last 60 years because of its unique history as a military training area prior to its protection as national park. It is composed by a mosaic of large and small trees of different tree species as well as gaps. Thus, the Hainich national park provides the unique opportunity to test the variability of soil respiration in relation to stand structure (Buchmann et al. 1996; Stoyan et al. 2000; Savin et al. 2002), an aspect often neglected.

The objectives of this study were (1) to identify the temporal and spatial variation of soil respiration in the Hainich forest, (2) to assess the importance of stand structure among abiotic factors for this variation in soil CO_2 efflux rates, and (3) to examine the stability of the observed patterns with hot-spots and areas of low soil respiration rates during the season and between years. Therefore, we used an experimental design with (a) a 0.5 ha plot that enabled us to capture the highly diverse stand structure of the Hainich National Park and (b) a 300 m long transect where more frequent measurements were taken over two years.

2.2 Methods

2.2.1 Site description and experimental layout

The study site was located in Central Germany within the 'National Park Hainich' (51°05' N, 10°27' E, 440 m a.s.l.), close to the city of Eisenach. The National Park Hainich was established in 1997 to protect one of the largest broad-leafed mixed forests in Central Europe, which covers an area of about 7600 ha. The forest has not been managed for about 60 years mainly because of the use as a military training area (close to the former East - West German border). Prior to this, the part of the forest, where the study site was located, was only managed extensively. As a consequence, the trees cover a wide range of age-classes with a maximum of up to 250 years (Knohl et al. 2003). The amount of woody debris on the forest floor and standing dead wood is very large compared to a managed forest. The forest is dominated (70%) by European beech (*Fagus sylvatica* L.). The remaining 30% are made up of other tree species such as *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,

followed by a clay horizon. In about 40-60 cm depth, calcareous bedrock is reached. Only L and partly F horizons are present at the study site because the litter from the forest trees and herbs is nearly totally decomposed within one year. The soil has a pH of about 5, a carbon content of about 6.5% and a nitrogen content of about 0.5% in the upper 8 cm. The study site is located in an area of suboceanic/subcontinental climate (Landesanstalt für Wald und Forstwirtschaft, 1997), with a mean annual air temperature of 8.4 °C and a mean precipitation of 899 mm per year for the period 2000 to 2002 (Alexander Knohl, personal communication).

The experimental layout in this study consisted of a plot, about 0.5 ha (72 x 72 m) with 36 (in year 2000) and 144 (in year 2001) measurement locations. Due to the two dimensional relation of the measurement locations (geographically well defined neighbors in all directions) and the relatively large number of samples, this design enabled the use of geostatistical models. To quantify the annual variation in soil respiration rates, 33 permanent locations were measured along a 300 m transect next to the plot.

2.2.2 Soil respiration, soil climate and forest structure measurements

Soil respiration was measured in the 0.5 ha plot in July and December 2000, and in May, June and July 2001. Along the transect, soil respiration was measured every two to six weeks during 2000, 2001 and 2002. The measurement campaigns lasted between one and three days (depending on the number of measurement locations), and were carried out during daytime. Soil respiration was measured using a closed chamber with an infrared gas analyzer (Li-cor 6400-09, Li-cor, Inc., Lincoln, Nebraska, USA). The measurement protocol suggested by the manual was slightly modified, and five measurement cycles were used instead of three. One week prior to the first measurement campaign, soil collars were installed at the measurement locations to a depth of 1 cm. The soil collars consisted of PVC tubes about 10 cm in diameter and 7 cm high with stainless steel legs for stabilization. The use of such collars avoided disturbance of the soil at the time of measurement and allowed consecutive measurements at the exact same positions over time. Due to technical problems during 2001, measured efflux rates from 2001 were corrected afterwards to enable comparison with data from 2000 and 2002. Each soil respiration measurement was accompanied by measurements of soil moisture at 6 cm soil depth (ThetaProbe, Delta-T Devices Ltd., Cambridge, UK) and of soil temperature in the litter layer, at 5 cm, 10 cm and 15 cm soil depth (Li-cor, Inc., Lincoln, Nebraska, USA).

Tree species were determined and forest structural parameters (geographical locations in the plot and diameter at breast height, dbh) were measured in October 2000. Vegetation

area index (VAI, leaf area index plus stem area index) was measured with a canopy analyzer (LAI 2000, Li-cor, Inc., Lincoln, Nebraska, USA) in July 2001.

2.2.3 Statistical analyses

Mean values, standard deviations and regressions were calculated in JMP (SAS Institute Inc., Connecticut, USA). The sensitivity of soil respiration to changes in temperature (Q_{10} values) were calculated using an exponential relationship between soil respiration and soil temperature (Buchmann, 2000; Xu and Qi, 2001b). A multiple regression model (GLM) for soil respiration was developed with soil temperature and soil moisture as independent variables. In order to maintain the exponential relationship of soil respiration to soil temperature, a logarithmic transformation of the response variable was carried out prior to analysis.

Geostatistical analyses (semivariogram model fitting and kriging) were performed using GS+ (Geostatistics for the Environmental Sciences, vs. 5.1.1, Gamma Design Software,

Table 2.1. Stand structural parameters in a 0.5 ha plot at the Hainich field site. The parameters (except nearest neighbor and VAI estimates) were assessed for concentric rings around each soil respiration measurement location. Rings with a radius (r) of 1 to 10 m were used.

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
av-dbh r	Average 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 to the nearest tree that is not a beech tree
VAI	Vegetation area index (leaf plus stem area) per unit ground

Michigan, USA). We estimated the semivariograms with equation (1).

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

where *n(h)* is the number of lag pairs at distance interval *h*, and *z* is the value of the parameter at location *x* and *x* + *h*. Maps were interpolated using ordinary block kriging. Prior to analyses, outliers were removed as recommended by the GS+ manual. Interpolated maps were also produced by least square functions, resulting in patterns very similar to those in the kriging maps. Since the least square functions produced edge effects in the presentations, only the kriging maps are shown.

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

Table 2.2. Soil respiration (μmol CO_2 m^{-2} s^{-1}) in an unmanaged Central European beech forest. Measurements were taken in a 0.5 ha plot (P) and along a 300 m long transect (T) located next to each other. SD and SE indicates standard deviations and standard errors of the mean, respectively. N presents the number of measurement locations. CV is the coefficient of variation in %.

		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 – Dec.	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
Jan. – Dec.	T	2.8	1.5	0.06	0.4 – 9.7	559	54

2.3 Results

Pronounced variation in soil respiration rates was observed among the measurement locations in the 0.5 ha plot in the Hainich National Park (2000: 36 locations; 2001: 144 locations). In July 2000, the soil respiration varied from 1.4 to 6.2 µmol CO_2 m^{-2} s^{-1} (Table 2.2), while in December 2000, with lower soil temperatures also the soil respiration rates were much smaller. Coefficients of variation in 2000 were between 25 and 30%, in 2001 between 38 and 45%. The measurement campaign in June 2001 was carried out during a warm and sunny period (soil temperatures generally above 14 °C). Therefore, soil respiration ranged from 1.7 to 11.0 µmol CO_2 m^{-2} s^{-1}, spanning the same range as over the whole year along the neighboring transect (from 0.4 to 9.7 µmol CO_2 m^{-2} s^{-1}). The coefficients of variation during both years were higher for the year-round measurements (T: 48 and 54%) than for the short-time measurement campaigns (P: from 25 to 45%).

Soil respiration rates were exponentially correlated with soil temperature at 5 cm depth (for 2001: $r^2 = 0.68$, $Q_{10} = 3.0$, Fig. 2.1). Soil respiration rates in the transect with a minimum of 0.4 µmol CO_2 m^{-2} s^{-1} were observed at low soil temperatures (winter) and rates with a maximum of 9.7 µmol CO_2 m^{-2} s^{-1} were observed at high soil temperatures (summer). In

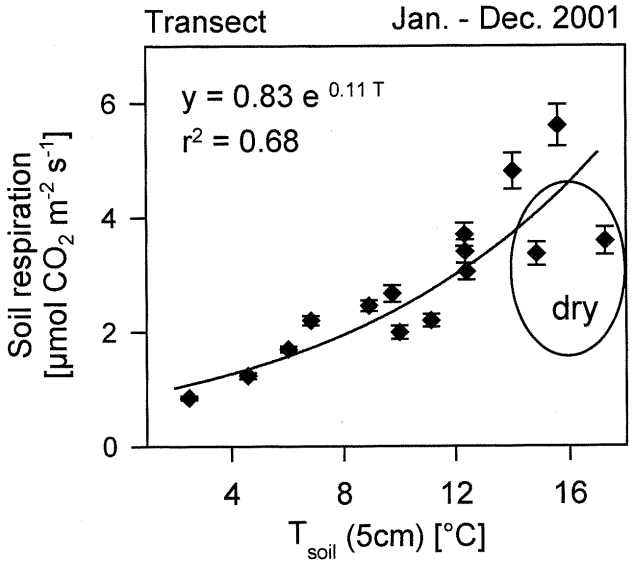


Fig. 2.1. Soil respiration as function of soil temperature during 2001. Mean values and standard error are shown for each of the 16 measurement campaigns along the transect (n = 33). Because of a drought period in late summer (volumetric soil moisture < 23%), soil respiration is better described by a multiple regression model (see text).

2001, there was a distinct drought period in August (volumetric soil moisture < 23%, which equals soil water potential < -1.3 MPa). When soil moisture was included in the regression model for soil respiration in 2001, the explanatory value of the model increased remarkably ($y = 0.24\ e^{0.14\ T}\ e^{0.02\ \theta}$, $r^2 = 0.90$, T = soil temperature at 5 cm [°C] and θ = soil moisture [Vol%]). The year 2000 was in general a wet year, and a strong correlation between soil

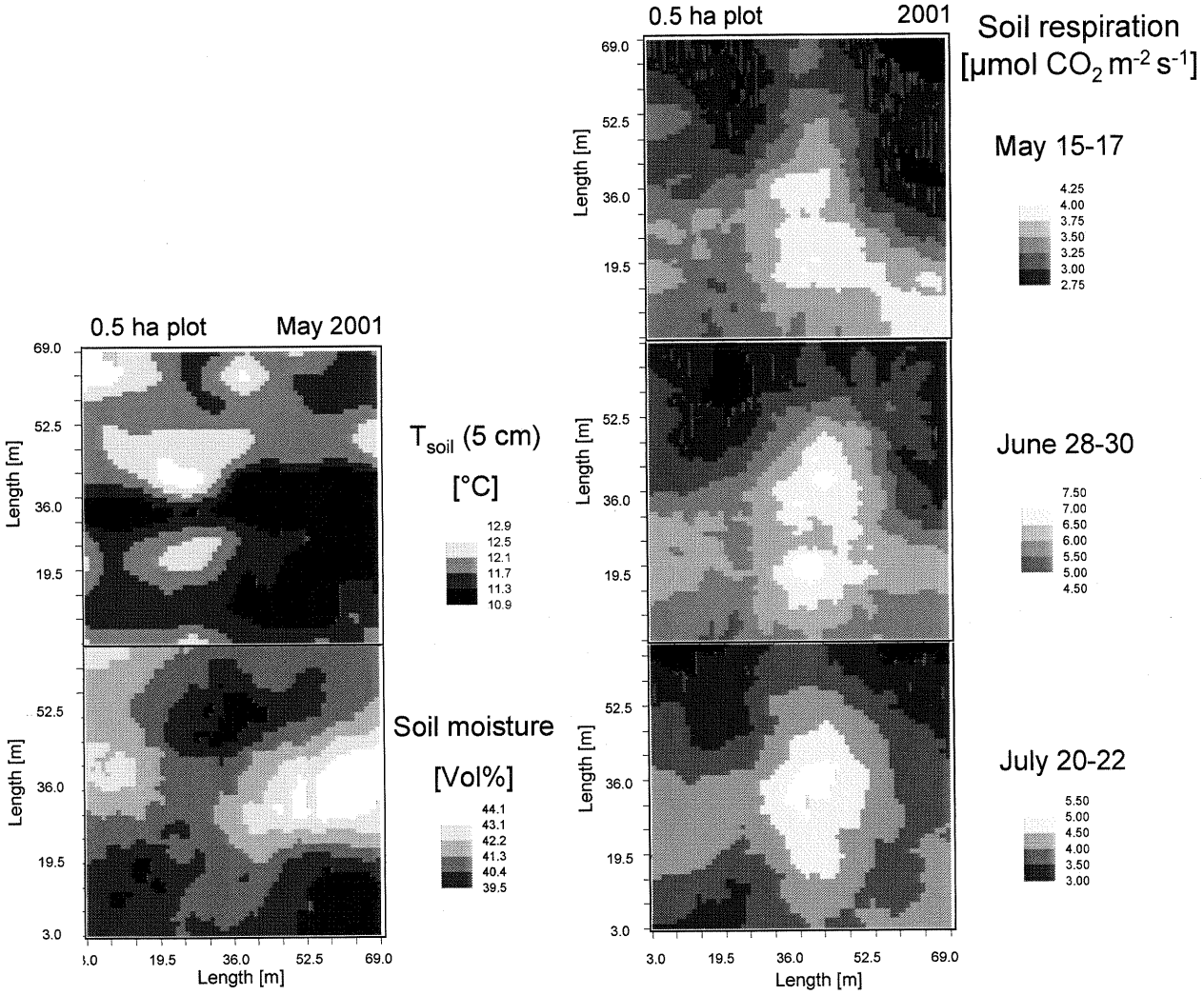


Fig. 2.2. Spatial variability of soil temperature (5 cm depth) and soil moisture (about 6 cm depth) in May 2001 (left panel) as well as soil respiration rates measured during three measurement campaigns in 2001 (right panel). All variables were measured within a 0.5 ha plot at 144 measurement locations in a regular grid with the mesh size of 6 m. Interpolations were done by ordinary block kriging, using exponential models on the semivariance data. White areas indicate high values (top of the mountain), dark areas indicate low values (valleys).

respiration and soil temperature at 5 cm was found (2000: r^2(without θ) = 0.97, Q_{10} = 3.3, data not shown).

In contrast to the annual variations, the spatial variability was not determined by soil temperature. Little variation in soil temperature was seen (only few degrees Celsius). During the measurement campaigns in the 0.5 ha plot (Fig. 2.2, left panel). Therefore, the spatial temperature pattern was not correlated (or weakly correlated) with the patterns found for soil respiration (May: $r^2 = 0.00$, $p = 0.80$; June: $r^2 = 0.05$, $p = 0.01$; July: $r^2 = 0.03$, $p = 0.04$). On the other hand, soil moisture was found to be negatively correlated with soil respiration, although rather weak (May: $r^2 = 0.07$, $p < 0.001$; June: $r^2 = 0.06$, $p = 0.003$; July: $r^2 = 0.13$,

$p < 0.001$) (Fig. 2.2, left and right panels). Spatial variations in soil respiration remained quite constant over the growing season (Fig. 2.2, right panel). Areas of high soil respiration in May (e.g. in the center of the plot in the lower right hand corner) stayed high during June and July, while areas of low soil respiration (e.g. in the upper right and left corners) stayed low during the summer. The same pattern of variation in soil respiration was detected during the measurement campaigns in July and in December 2000 (Fig. 2.3), despite the fact that soil respiration rates were much lower during the winter campaign. For all kriging maps, exponential models were used for the semivariograms. The fit (r^2) of the models to the soil respiration data were in July and December 2000 (36 measurement locations) 0.45 and 0.38, respectively. In May, June and July 2001 (144 locations), the r^2 values were 0.87, 0.55 and 0.65, respectively. The nugget (i.e., the noise) was relatively large in comparison to the sill (i.e., the distance where measurement locations are independent) (Fig. 2.4, in May: nugget = 0.7 and Sill = 0.9 at 15 m). Furthermore, there seemed to be an increase in semivariance after a separation distance of 50 - 60 m.

The stand structure within the 0.5 ha plot was highly heterogeneous (Fig. 2.5). Although areas of mainly large or mainly small trees can be recognized, measurements of the vegetation area index (VAI) showed a relatively dense canopy over the entire plot. Among

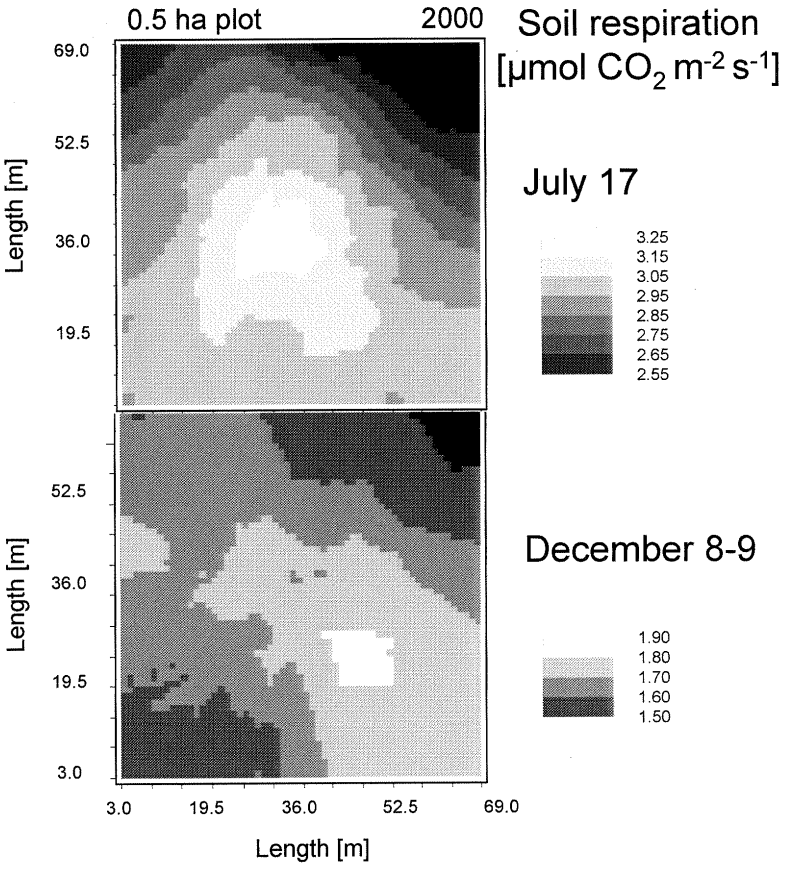


Fig. 2.3. Soil respiration measured within a 0.5 ha plot at 36 measurement locations in summer (July) and winter (December) 2000. Interpolated maps were produced by ordinary block kriging (semivariance analysis and exponential models).

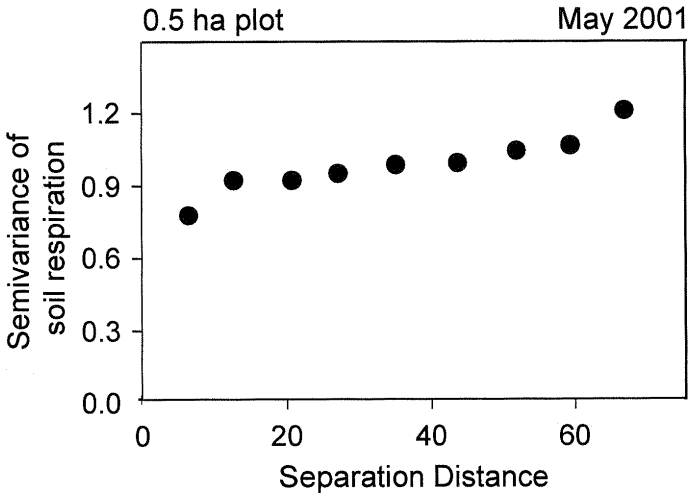


Fig. 2.4. Semivariogram of soil respiration rates measured in a regular grid of 144 measurement locations in May 2001. The smallest distance between measurement locations was 6 m. The fit of an exponential model was r^2 = 0.873.

the stand structural parameters, the average diameter at breast height (av-dbh) of trees (4 - 6 m away from the measurement location were highly correlated with soil respiration (Fig. 2.6). Especially the average dbh in circular rings with 4 m radius (av-dbh4; $r^2 = 0.13$, $p < 0.001$ for July 01) remained very close to the soil respiration also in the third and fourth dimension of the principal component analysis. The number of beech trees (beech4 and 8) as well as the total number of trees (#4 and 8) in a 4 or 8 m radius around the measurement location were negatively correlated with soil respiration. Distance to nearest neighboring tree, sum of dbh, and number of non-beech trees seemed to have no effect on soil respiration. Models with 9 to 12 stand structural parameters from the total of 53 measured parameters (Table 1.1) (forward stepwise regression using Akaike's Information Criterion) explained about 40% of the variation in soil respiration rates. The model for May included the 9 variables: av-dbh7, non-beech8, dbh10, av-dbh4, dbh8, #7, #beech7, dbh9, dbh2 and VAI ($r^2 = 0.39$). In June 9 variables were chosen in the stepwise procedure: av-dbh4, non-beech9, dbh7, av-dbh10, dbh2, VAI, dbh10, dbh8 and #beech7 ($r^2 = 0.39$). In July 12 variables were chosen: av-dbh9, dbh2, #2, #1, VAI, av-dbh1, dbh10, #non-beech9, #7, #8, dbh1 and av-dbh4 ($r^2 = 0.42$). Only three parameters were included in the regressions for all campaigns: av-dbh4, dbh10 and VAI, with av-dbh4 explaining the most variation (for May, June and July: av-dbh-4: $r^2 = 0.09$, 0.13 and 0.19, $p < 0.001$, respectively; dbh10: $r^2 = 0.02$, 0.00 and 0.01, $p > 0.05$, respectively; VAI: $r^2 = 0.05$, 0.05 and 0.09, $p < 0.05$, respectively).

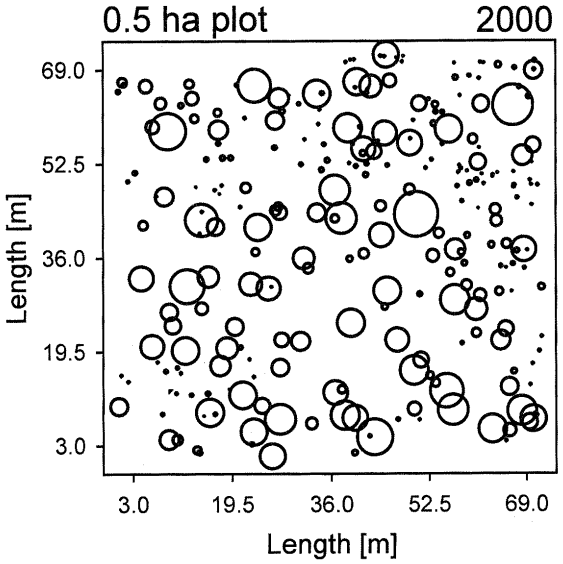


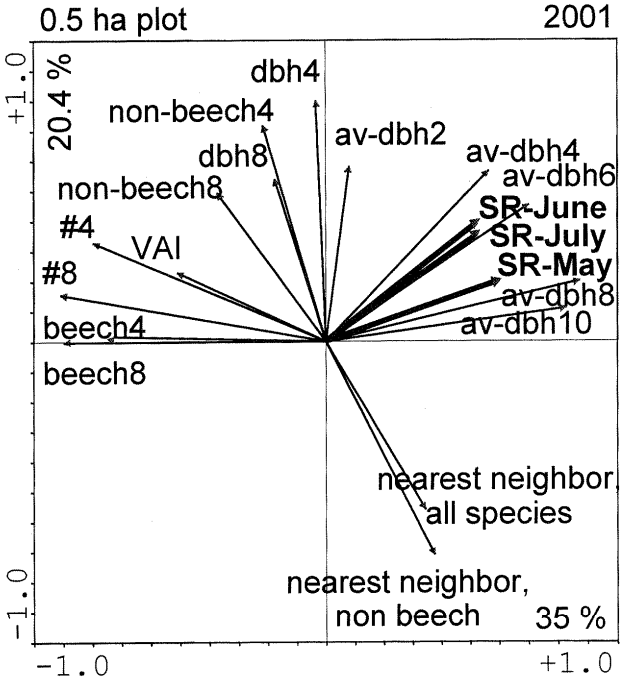
Fig. 2.5. Locations of all living trees within a 0.5 ha plot. Symbol sizes indicate the diameter at breast height of trees, ranging from 1.4 cm to 99 cm (depicted diameters are enlarged for comparison).

2.4 Discussion

2.4.1 Variation in soil respiration rates over time

Soil temperature was shown to be the most important factor for temporal variations in soil respiration rates on an annual basis. In the present study, soil temperature explained 95% of the variation in soil respiration in the moist year of 2000, and 68% in the drier year of 2001. The sensitivity of soil respiration to temperature (Q_{10}) in year 2000 and 2001 were 3.3 and 3.0, respectively, well within the range of Q_{10} values reported in the literature (Raich and

Fig. 2.6. Principal component analysis of soil respiration and stand structural parameters. Abbreviations refer to stand structural parameters in concentric rings with different radii around measurement locations (2, 4, 6, 8, 10 m, respectively). See Table 1 for surther details. Soil respiration was measured in May, June and July 2001. 1st and 2nd ordination axes are shown. Variables were centered and normalized prior to analyses. N = 144.



Schlesinger 1992; Davidson et al. 1998; Buchmann 2000). However, we found, similar to Xu and Qi (2001a), that this parameter could not explain spatial variation in soil respiration.

The second most important parameter for annual variation of soil respiration rates is typically soil moisture, especially in very dry or very wet habitats (Raich and Schlesinger 1992; Buchmann et al. 1997; Conant et al. 1998; Davidson et al. 1998; Xu and Qi 2001a). In our study, low soil water content was generally not a limiting factor due to high precipitation and a good soil water holding capacity of the clay rich soil. However, during the period of drought in August 2001, the soil water content clearly sank to very low values, probably limiting biological activities (volumetric soil moisture < 23%, which equals soil water potential < -1.3 Mpa).

2.4.2 Stability of spatial soil respiration patterns

Remarkable stability in the spatial patterns of high and low soil respiration rates were seen among the measurement campaigns and from year to year. The hot-spot for soil respiration (in the center of the plot) was even detectable in winter. This observed stability of the spatial patterns in soil respiration rates must be due to characteristics of the underlying processes. It is well known from the literature, that soil respired CO_2 is a result of the activity of plant roots (directly from the roots, from mycorrhizae or from microbes accessing root exudates) and from microbial decomposition of organic material (Andrews et al. 1999; Buchmann 2000). A larger variation in soil respiration rates in summer than in winter was seen in this study. However, the soil respiration hot-spot was also a hot-spot during the winter measurement campaign. Since microbial decomposition of soil organic matter should be similar across the entire 0.5 ha plot, the presence of hot-spots indicates the dominant influence of plants on soil respiration, either directly via root respiration or indirectly via root exudates or root and leaf litter turnover. This hypothesis is supported by several recent studies that have shown that root (and rhizosphere) respiration constitutes at least half of the soil respiration in temperate forests (Epron et al. 2001; Laporte et al. 2003) and in boreal forest (Högberg et al. 2001). Another source of variation in soil respiration could be the below-ground activity of understory vegetation, which was actively photosynthesizing in May but not at the later measurement campaigns. However, our spatial soil respiration patterns were about the same in all campaigns. Thus, our results suggest that the main forest canopy is highly important for our observed stability of spatial patterns of soil respiration.

2.4.3 Spatial patterns of soil respiration

The geostatistical method used in this study for presenting spatial variation of soil respiration was appropriate and convincing due to the good agreement among different algorithems (kriging and least square functions) and the observed stability over time (see above). However, the semivariograms had a relatively large nugget. This suggests that soil respiration was spatially correlated at a smaller scale than the chosen 6 m distance between measurement locations, enabling us to treat our measurement locations as independent samples for inferential statistics.

Stand structure is rarely assessed when soil respiration measurements are carried out despite its clear effects on below-ground activities. In a boreal pine forest, where large gaps occurred naturally, Shibistova et al. (2002) found that soil respiration was about 50% lower in gaps than under dense canopy. Laporte et al. (2003) described that in a Canadian hardwood forest, soil climate changed in gaps created in the canopy by forest management. Soil temperatures increased, and as a result, soil moisture decreased because of evaporation. However, at our study site without forest management, no effects of gaps were seen. These gaps (mainly created from single fallen trees) were only small and the canopy remained relatively dense, leading to no significant effect on soil climate (as proposed by Ellenberg 1996). Pangle and Seiler (2002) showed that rates of soil respiration were consistently higher near the base of loblolly pine seedlings than between seedlings. However, in our study, we found no correlation between distance to nearest neighboring tree and soil respiration. Respiration rates were consistently higher in areas with high average dbh than in areas with many trees. Thus, large trees (high av-dbh) resulted in higher soil respiration rates than many small tress (e.g. in gaps with regeneration). It could be speculated on the one hand that large trees have a large fine root system and therefore respire more intensively than many small trees. On the other hand, large trees may remove soil water by transpiration leading to drier and more favorable conditions for the microbial community. However, none of the two hypotheses held true. Av-dbh in rings with a radius of 4 m was not very strongly correlated with fine root biomass ($p = 0.034$; $r^2 = 0.037$) nor with soil moisture ($p = 0.015$; $r^2 = 0.049$) (see also chapter 3). Thus, our results suggest that the roots of large trees are more active than those of many small trees, i.e., large trees may have larger carbon allocation from photosynthesis to root respiration than small trees.

3 Factors controlling spatial variability of soil respiration

3.1 Introduction

Carbon dioxide is an end product of microbial respiration during the process of organic matter decomposition, and of respiration by live roots. Because of the complexity of soil biological processes many factors are of importance for the increase or decrease of soil CO_2 fluxes. Annual variations in soil respiration in temperate forest ecosystems have been explained mainly by variation in temperature (Lloyd and Taylor 1994; Davidson et al. 1998; Buchmann 2000; Pilegaard et al. 2001). However, considerable spatial variation in soil respiration rates (not due to temperature) was also found in several studies (e.g. Buchmann 2000; Stoyan et al. 2000: Xi and Qu 2001a).

In order to evaluate the controlling factors for soil respiration, the spatial variability as well as the temporal stability in these factors are important to study. Several studies in temperate forests have shown that concentrations of macro-nutrients in the soil are the most important parameters for spatial variation in soil respiration rates. Thus, concentrations of nitrogen, phosphorus and to some degree magnesium have been suggested as the best describing variables for soil respiration (Xu and Qi 2001a; Borken et al. 2002; Pangle and Seiler 2002). However, in a disturbed ecosystem or under less favorable climatic conditions for forest growth, other factors may be controlling for soil respiration. Gärdenäs (2000) found in a boreal forest with large variation in moisture and a thick litter layer, that the moisture of this layer was the parameter that correlated the best with soil respiration. In forest areas with large gaps (due to harsh climate conditions or forest management), the location of gaps and dense forest might be the most important parameter for variation in soil respiration rates (Brumme 1995; Shibistova et al. 2002, Laporte et al. 2003). Thus, there is a potential impact of many different kinds of variables such as concentration of various macro-nutrients, stand structural and root parameters as well as soil physical and climate parameters on the variation of soil respiration.

We carried out measurements in an undisturbed (unmanaged) deciduous forest in Central Europe. The ages of the trees at our study site (in the National Park Hainich) ranged from 0 to about 250 years. The stand consisted of about 70% beech while the remaining was mainly made up of ash and maple. The growth conditions at the site were ideal for beech growth because of the temperate climate with relatively high precipitation and a nutrient rich soil (calcareous bedrock, a clay layer, and partly a loess layer on top). Under these favorable

conditions it could be speculated that nitrogen was not necessarily limiting for biological processes, but other nutrients, such as phosphorus or sulfur could be controlling factors. Due to the diverse chemical characteristics of the leaves of the main tree species at the study site, it was further hypothesized that differences in soil respiration rates could be due to chemical differences (C/N ratios) of the litter at the soil respiration measurement locations.

We conducted an intensive study in the in the National Park Hainich with the aim to quantify the spatial variation in abiotic and biotic variables affecting soil respiration and to identify those factors controlling soil respiration.

3.2 Methods

3.2.1 Site description and experimental layout

The study site was located in the 'National Park Hainich' (for further details see chapter 2).

The experimental layout consisted of a plot of about 0.5 ha (72 X 72 m) with 36 (in 2000) or 144 (in 2001) measurement locations, as well as 16 separate locations close to the plot. In 2000 the 36 measurement locations were placed in the plot after a stratified random design. Although this design is beneficial if there is a structure which repeats itself with a specific distance in the landscape, the design is more time consuming than a regular grit. Since we did not detect such a repeated structure in the first year, we decided to use a regular grit in the second year. In order to optimize our coverage of the spatial variation, we chose to measure soil respiration and other parameters in more locations in the second year than it was done in the first year. The soil respiration measurement campaign in July 2000 lasted one day, while the campaign in July 2001 lasted three days. However, in July 2001 each location was measured twice during the three days using two Li-cor 6400-09 chamber systems at the same time. All regressions of soil respiration versus other parameters were done with the mean value of these two measurements. In 2001, due to time constraints, the macro- and micro-nutrient concentrations of dried soil were only measured in samples from locations, which had the highest or lowest rates of soil respiration, like suggested by Draper and Smith (1998) as a suited procedure for regression analysis.

3.2.2 Soil respiration, soil temperature and moisture measurements

Soil respiration was measured with a portable infrared gas analyzer in a closed chamber system (Li-cor 6400-09, Li-cor, Inc., Lincoln, Nebraska, USA). Soil temperature was measured in the litter layer, at 5 cm, 10 cm and 15 cm soil depth, with a thermometer (Li-cor,

Inc., Lincoln, Nebraska, USA) and of soil moisture at 6 cm depth (ThetaProbe, Delta-T Devices Ltd., Cambridge, UK) (see also chapter 2).

3.2.3 Soil, root and stand structural analyses

After soil respiration was measured, soil samples with a known volume were collected at the locations (36 samples in July 2000 and 122 samples in July 2001). In 2000, the samples were subdivided into two depths, 0-5 cm and 5-10 cm. In 2001, soil samples were collected 0-8 cm and not subdivided, since the separate samples did not bring significantly more information than the pooled data. In 2000 (not in 2001), litter was collected at the measurement locations and dried at 70 °C. Thickness of litter layer and depth of A-horizon were measured both years at the time the samples were collected. Soil and litter samples were kept at 4° C and prepared for analyses within two weeks after collection.

Ammonium (NH_4^+), nitrate (NO_3^-), and dissolved organic carbon (DOC) were extracted from the soil or litter shaking 30 g of fresh material with 100 ml 1M KCl for 60 min, after removal of roots, stones and litter from the soil samples (Mulvaney 1996). Extracts were filtered with filter paper, which had been washed with 1M KCl prior to filtration (for DOC analysis: folded filters 604 ½, Ø = 185 mm; for NH_4^+ and NO_3^- analysis: 589[3], blue ribbon, Ø = 90 mm; Schleicher & Schuell, Düren, Germany). Extracts were kept frozen until analysis. NH_4^+ and NO_3^- were measured with a Continuos Flow Analyzer (Skalar, Erkelenz, Germany), and DOC with a TOC Analyzer ("high TOC", Elementar, Hanau, Germany). pH was measured in 1M KCl extracts with a pH-meter (Wissenschaftlich-Technische Werkstätten GmbH, Weilheim, Germany).

Total nutrient concentrations of the mineral soil were determined using air dried (35°C), sieved soil (2 mm mesh size), which was finely ground (Ball Mill, Retsch, Haan, Germany) after removal of roots, stones and coarse litter fragments. In 2000, all 36 samples were ground and analyzed. From the results in the first year (2000) it became apparent that no single parameter, among those measured, could explain the large variability in soil respiration rates. Due to the lack of one single explaining parameter and because of the highly nutrient rich soil at the site, we chose to extend our measurement program in 2001 and include measurements in the soil of concentration of the following macro- and micro-nutrients: phosphorus, sulfur, calcium and magnesium. In 2001, soil from locations with high and low soil respiration were analyzed (26 soil samples, see experimental layout). Total C and total N concentrations were measured with an Elemental Analyzer (Vario EL, Elementar, Hanau, Germany). Phosphorus, sulfur, calcium and magnesium concentrations were measured with an ICP-AES (Atomic Emission Spectrometry with Inductively Coupled Plasma, Perkin-

Elmer, Norwalk, USA). Organic material (OM) was measured using a thermogravimetrical method. For this method, dried, ground soil and litter material was heated from 35 to 1000 °C (5 °C per min) in the presence of oxygen (Thermo-scale: TGA/SDTA851, Mettler-Toledo, Gießen, Germany). Peaks of weight loss were determined from the first derivative of the sample weight against the temperature of the oven. The total weight loss in the temperature range from 120°C to 560°C was used to determine the amount of organic material in the sample. Separate weight loss peaks during the temperature increase was used to determine the amount of organic compounds in the sample from easily to less decomposable (e.g from glucose to lipids) (Jakab et al. 1997; Siewert and Nitschke 1998). Soil microbial biomass was determined using the substrate-induced respiration technique (SIR) in 16 fresh soil samples, collected close to the 0.5 ha plot on 22.06.01. Glucose was added to the soil samples (2 mg g^{-1}) and CO_2 fluxes were measured hourly using an automated infrared gas analyzer system (Anderson and Domsch 1978; Heinemeyer et al. 1989).

Fine roots (diameter smaller than 2 mm) were extracted from fresh soil samples with known weight and volume. The samples were washed in a set of sieves (630 µm and 2 mm) to free roots from soil. Living fine roots were dried (70°C, 48 hours) and weighed. Whether roots were living or dead was determined visually and by texture. In 2001, a further separation between tree and herb roots was carried out. Tree species were determined and forest structural parameters (location and diameter at breast height) were measured in October 2000.

3.2.4 Statistical analyses

All descriptive statistics, regressions (simple, multiple least square, and stepwise), correlations, Akeike's Information Criterion, ANOVA's, and comparisons of mean values (Tukey HSD test) were calculated in JMP (SAS Institute Inc., Connecticut, USA). Coefficient of variation (CV%) was calculated as 100 SD/mean. The average diameter of trees in circular rings with radius 4 m around the measurement locations (av-dbh4) represents the most important structural parameter (see chapter 2) and was calculated using a Delphi script (Borland Software Cooperation, Scotts Valley, California, USA).

3.3 Results

The ranges in soil temperatures were relatively small among the 36 locations measured during the campaign in July 2000, about 4 °C in the litter layer and about 0.5 °C deeper down in the

Table 3.1. Descriptive statistics and linear regressions of soil, litter and root parameters measured in 2000 versus rates of soil respiration. Significance levels: *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$. Samples were taken on 17.07.00. N = 36. All soil chemical and root parameters were measured in soil samples from 0-5 cm depth except when otherwise noted. CV indicates coefficient of variation (in %). Soil and litter chemical parameters have been corrected for water content in the samples.

Parameter	Unit	Mean	SD	Range	CV	r^2
Soil climate						
T_{soil}, 0 cm	°C	12.5	0.6	11.8 - 15.5	5	0.10
T_{soil}, 5 cm	°C	11.8	0.2	11.4 - 12.1	2	0.00
T_{soil}, 10 cm	°C	11.6	0.1	11.4 - 11.9	1	0.01
T_{soil}, 15 cm	°C	11.5	0.1	11.2 - 11.7	1	0.11*
Litter moisture	Weight%	58.2	5.7	48.1 - 69.3	10	0.15*
Soil moisture§	Vol%	38.2	4.2	27.3 - 45.3	11	0.15*
Soil structure						
Litter thickness	cm	0.9	0.5	0.2 - 2.0	56	0.10
F-horizon thickness	cm	0.02	0.1	0 - 0.2	500	0.02
A-horizon depth	cm	9.3	2.8	4.0 - 15.0	30	0.12*
Soil bulk density§	g cm^{-3}	0.8	0.1	0.5 - 1.2	13	0.01
Soil chemistry						
$[NH_4^+ - N]$	µg g^{-1}	4.3	2.6	1.0 - 11.1	60	0.00
$[NO_3^- - N]$	µg g^{-1}	16.6	11.9	5.0 - 62.7	72	0.03
[DOC – C]	µg g^{-1}	81.1	23.5	50.1 - 157.1	29	0.03
pH		4.2	0.2	3.7 - 4.6	5	0.03
Total C	%	6.5	1.1	4.2 - 9.7	17	0.09
Total N	%	0.5	0.1	0.3 - 0.7	20	0.14*
C/N		13.1	0.7	12.03 - 15.40	5	0.02
Litter chemistry						
$[NH_4^+ - N]$	µg g^{-1}	18.4	28.7	2.9 - 151.1	156	0.02
$[NO_3^- - N]$	µg g^{-1}	31.8	30.8	2.0 - 135.4	97	0.02
[DOC – C]	µg g^{-1}	473.1	172.4	55.3 - 1074.5	36	0.03
pH		6.4	0.4	5.4 - 6.9	6	0.02
Total C	%	46.0	1.1	42.3 - 47.4	2	0.02
Total N	%	1.4	0.1	1.3 - 1.7	7	0.00
C/N		32.0	2.0	27.5 - 35.5	6	0.00
Fine roots						
Biomass (0 - 10 cm)	g m^{-2}	110.0	56.6	23.0 - 266.8	51	0.18*
Biomass (0 - 5 cm)	g m^{-2}	64.0	37.9	2.2 - 127.3	59	0.14*
Biomass (5 - 10 cm)	g m^{-2}	46.0	32.9	7.1 - 139.5	72	0.11
Total C	%	36.5	2.4	30.6 - 41.5	7	0.00
Total N	%	1.7	0.2	1.3 - 2.4	12	0.01

§ Negatively correlated with soil respiration, all other parameters were positively correlated.

Table 3.2. Descriptive statistics and linear regressions of biotic and abiotic parameters measured in 2001 versus rates of soil respiration. Significance levels: *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$. Soil and root samples were collected 24.07.01. Sampling depth was 0 – 8 cm. Av-dbh4 is averaged diameter at breast height (dbh) in a 4-m radius circular ring. CV indicates coefficient of variation (in %). Soil chemical parameters have been corrected for water content in the samples.

Parameter	Unit	Mean	SD	Range	CV	N	r^2
Stand structure							
Av-dbh4	cm	25.1	17.5	0 - 71.6	70	144	0.13***
Soil climate							
T_{soil}, 0 cm	°C	15.4	1.2	13.0 - 18.8	8	144	0.03*
T_{soil}, 5 cm	°C	14.2	1.2	12.7 - 18.0	8	144	0.03*
T_{soil}, 10 cm	°C	13.9	1.3	12.6 - 17.9	9	144	0.02
T_{soil}, 15 cm	°C	13.6	1.4	12.5 - 17.8	10	144	0.02
Soil moisture§	Vol%	45.2	4.0	32.2 - 55.8	9	144	0.13***
Soil structure							
Litter thickness	cm	1.3	0.7	0.2 - 3.5	54	122	0.16***
A-horizon depth	cm	7.2	3.0	1.5 - 16.0	42	122	0.06**
Soil bulk density§	g cm^{-3}	0.8	0.1	0.6 - 1.1	13	122	0.16***
Soil chemistry							
$[NH_4^+ - N]$	µg g^{-1}	6.3	3.4	2.2 - 18.0	54	122	0.00
$[NO_3^- - N]$	µg g^{-1}	6.7	4.0	1.0 - 19.0	60	122	0.00
[DOC – C]	µg g^{-1}	67.7	23.5	25.9 - 200.0	35	122	0.04*
pH		5.4	0.7	3.3 - 6.5	13	122	0.06**
Organic material (thermogravimetry)	%	13.8	2.3	10.3 - 18.9	17	27	0.41***
Total C	%	5.9	1.2	4.1 – 8.4	20	27	0.42***
Total N	%	0.5	0.1	0.4 - 0.7	20	27	0.44***
C/N		11.8	0.5	11.1 – 13-2	4	27	0.20*
[P]total	mg g^{-1}	1.0	0.1	0.8 - 1.2	10	20	0.22*
[S]total	mg g^{-1}	0.6	0.1	0.4 - 0.8	17	20	0.61***
[Ca]total	mg g^{-1}	7.1	1.7	2.9 - 9.5	24	20	0.18
[Mg]total	mg g^{-1}	8.6	0.8	7.0 - 9.8	9	20	0.06
Fine roots							
Biomass	g m^{-2}	128.5	75.9	7.2 - 374.8	59	122	0.16***
Tree roots only	g m^{-2}	38.9	45.3	0 - 286.6	116	122	0.04*
Herb roots only	g m^{-2}	89.5	66.6	0 - 268.5	74	122	0.10***
Total C	%	45.6	2.0	41.9 - 49.4	4	25	0.01
Total N	%	1.8	0.3	1.0 - 2.1	17	25	0.01
Root N	g N m^{-2}	2.5	1.4	0.4 – 5.3	56	25	0.23*

§ Negatively correlated with soil respiration, all other parameters were positively correlated.

soil profile (Table 3.1). The coefficients of variation of the soil climate parameters were small (1-11%) compared to the other types of measured parameters and compared to the coefficients of variation of soil respiration (30% in July 2000 and 45% in July 2001). Litter moisture was positively correlated with soil respiration (p = 0.022; $r^2 = 0.15$), while soil moisture was negatively correlated (p = 0.020; $r^2 = 0.15$). Among soil structural parameters, A horizon depth was positively correlated with soil respiration (p = 0.043; $r^2 = 0.12$). At this measurement campaign no correlation between soil respiration and litter thickness or soil bulk density could be detected ($p = 0.063$ and $p = 0.531$). The F-horizon was in most locations not present and the coefficient of variation was unrealistically high (500%). Among the soil chemical parameters only total N was correlated with soil respiration (p = 0.024; $r^2 = 0.14$), but if one outlier was removed the fit improved considerably for N ($p < 0.001$; $r^2 = 0.29$, Fig. 3.1) as well as for C (p = 0.002; $r^2 = 0.25$). The concentrations of NH_4^+ and NO_3^- were high (4.33 µg g^{-1} and 16.56 µg g^{-1}) and the variations relatively large (Hart et al. 1994), but not correlated with soil respiration rates. The pH value in 1M KCl was quite low (4.15) taking

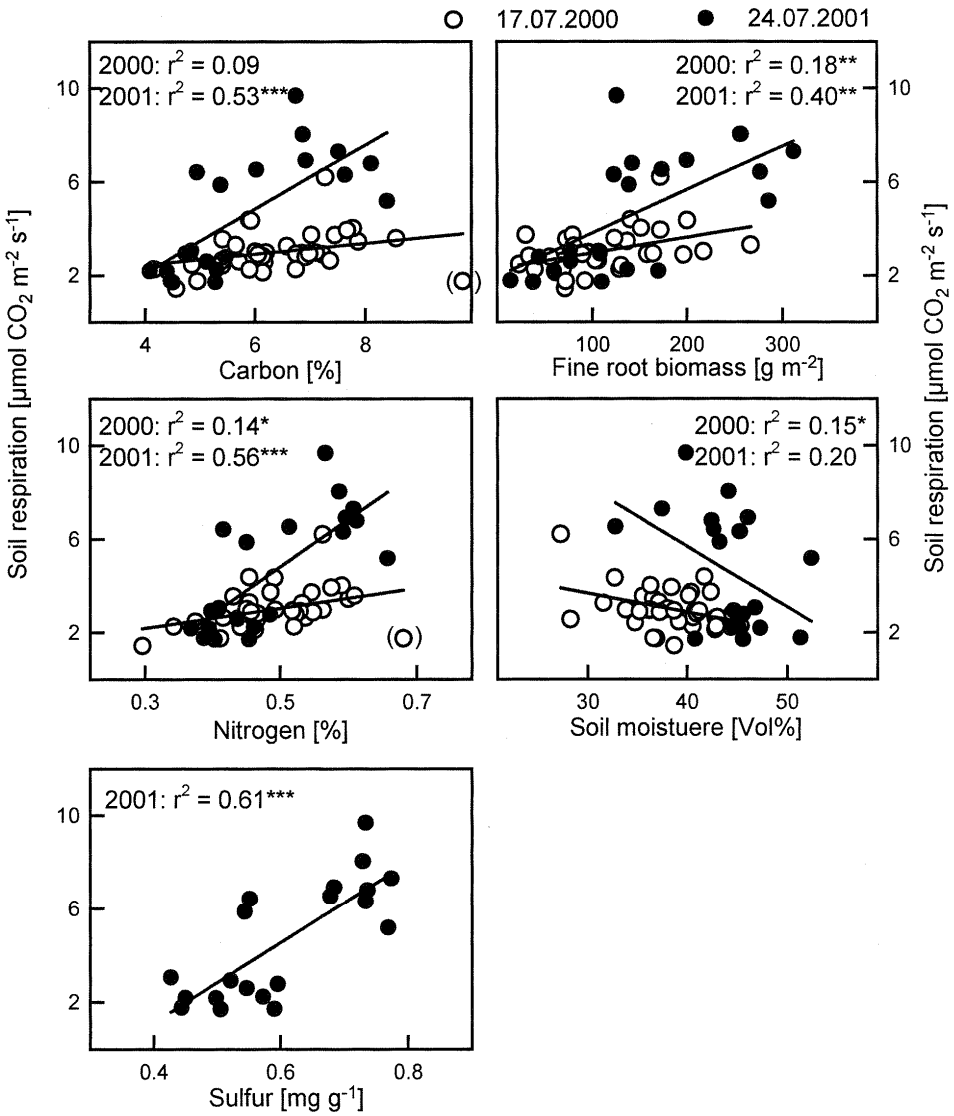


Fig. 3.1. Linear regressions of soil respiration vs. the concentration of various macro-nutrients, soil moisture and fine root biomass in the top-soil. In 2000 the parameters were measured in 36 locations. If one outlier "( )" is removed the fit of soil respiration with C and N were r^2 = 0.25, p = 0.002 and r^2 = 0.29, $p < 0.001$, respectively. In 2001 results are shown from the 20 soil samples where either the highest or the lowest soil respiration rates had been measured. Significance levels: *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

into consideration that the site was on calcareous bedrock. None of the chemical parameters measured in the litter were significantly correlated with soil respiration. The overall best-correlated parameter in 2000 was the fine root biomass in the total soil sample (p = 0.009; r^2 = 0.18).

Biotic and abiotic parameters measured in the 0.5 ha plot in 2001 (Table 3.2) showed mainly the same relationship with soil respiration as it was the case the year before, and also the coefficients of variation of the parameters were quite stable from 2000 to 2001. However, the rates of soil respiration were in general higher in 2001 (3.3 ± 1.5) than in 2000 (3.0 ± 0.4). The stand structural parameter av-dbh4 (average diameter of breast height of the trees in circular rings with 4 m radius around the measurement locations) was positively correlated with soil respiration rates and had a high coefficient of variation (70%). Soil moisture was also this year negatively correlated with soil respiration ($p < 0.001$; r^2 = 0.13). Litter thickness and A horizon depth were positively and soil bulk density negatively correlated. The fine root biomass was, in the same way as the year before, highly correlated with soil respiration ($p <$ 0.001; r^2 = 0.16). To our surprise the herb root biomass seemed to be stronger correlated with soil respiration ($p < 0.001$; r^2 = 0.10) than tree root biomass (p = 0.024; r^2 = 0.04), which may, however, be due to problems by separation. The fine root N content was not directly correlated with soil respiration (p = 0.572), but fine root N per m^2 ground was slightly better correlated with soil respiration than the pure fine root biomass was (p = 0.014; r^2 = 0.23 for fine root N per m^2 ground, while p = 0.023; r^2 = 0.20 for simple fine root biomass per m^2 ground in the same samples). Several macro-nutrients were measured in dried soil samples from 2001. The soil samples from the locations with the highest and the lowest rates of soil respiration were used for the analysis (see experimental layout). Total C and total N explained 42 and 44%, respectively. If fewer samples were used (the samples where sulfur had been measured), the regressions of N and C versus soil respiration resulted in r^2 values of 0.56 and 0.53, respectively (Fig. 3.1). Organic material measured by thermogravimetrical analysis (120°C-560°C) explained 41% of the variance in the soil respiration rates (the weight loss over the whole temperature range explained variation soil respiration better than any separate peaks). The concentration of phosphorus showed a weak positive correlation with soil respiration (p = 0.038; r^2 = 0.22). Furthermore, C:N and C:S ratios were not correlated with soil respiration (r^2 = 0.04 for both regressions). The concentration of sulfur was the parameter, which in 2001 had the strongest positive correlation with soil respiration ($p < 0.001$; r^2 = 0.61,

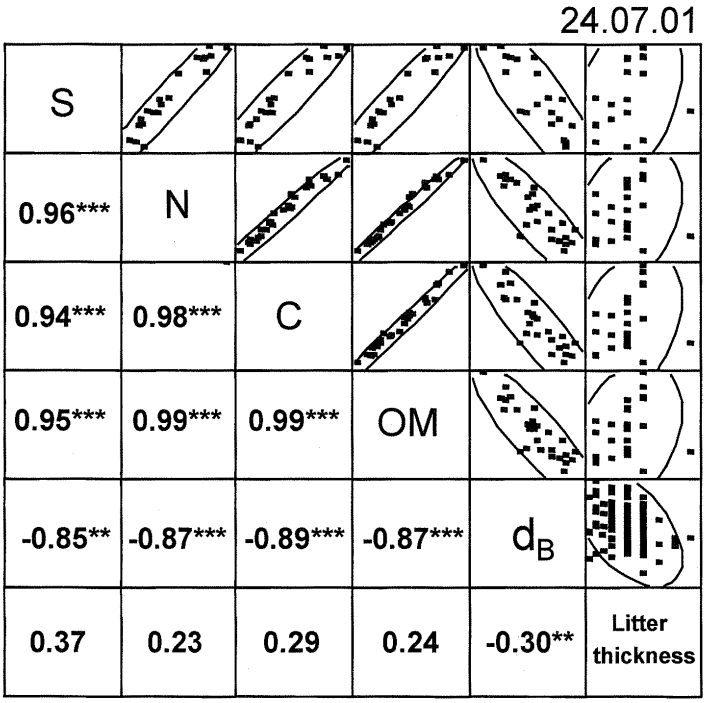


Fig. 3.2. Scatter plot matrix of soil chemical and soil structural parameters that were highly correlated with soil respiration in July 2001 ($p < 0.001$). A 95% bivariate normal density ellipse is imposed on each scatter plot. Correlation coefficients are given in the lower part of the figure. Significance levels: *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$. Units: S: mg g^{-1}; N: weight%; C: weight%; OM (organic matter): % weight loss; d_B (soil bulk density): g cm^{-3}; Litter thickness: cm.

Fig. 3.1). All these soil chemical parameters were positively correlated with each other ($p < 0.001$) and negatively correlated with soil bulk density ($p < 0.001$), while litter thickness was not correlated with the soil chemical parameters (p between 0.113 and 0.260, Fig. 3.2).

The range of microbial biomass, which had been measured close to the main plot at an extra campaign in June 2001, was split into three equal intervals (low, medium and high biomass, respectively). Locations with high microbial biomass had higher soil respiration than those with low microbial biomass ($p = 0.033$; $r^2 = 0.29$, linear regression). Fine root biomass measured at the same locations was also split into three equal intervals. Locations with high fine root biomass had higher soil respiration than those with low or medium fine root biomass (explained 34% of the variation in soil respiration rates in a linear regression) (Fig. 3.3).

The best model for spatial variation in soil respiration rates was calculated with stepwise forward regression using Akaike's Information Criterion (Table 3.3). Those parameters, which were highly correlated with soil respiration at the measurement campaign in July 2001 were used for the analysis. In the regression the parameters most highly correlated with soil respiration at the study site were the concentration of sulfur, large trees close to the measurement locations (av-dbh4), fine root biomass, and soil moisture. This model explained 77% of the spatial variation in soil respiration rates at the measurement campaign in July 2001. The model equation was:

$SR = 2.9 + 9.2\ S + 0.04$ av-dbh4 $+ 8$ root $- 0.1\ \theta$,

where SR is soil respiration (in μmol CO_2 m^{-2} s^{-1}), S is total concentration of sulfur in the

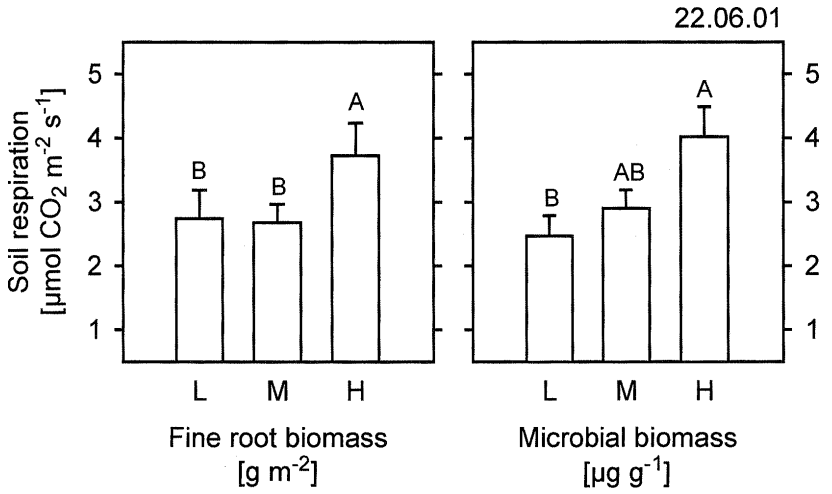


Fig. 3.3. Mean soil respiration rates as function of low (L), medium (M), and high (H) fine root biomass and microbial biomass (in 0 to 8 cm soil depth) from samples collected close to the 0.5 ha study plot. Standard errors of the means are shown. Different letters indicate significantly different means (Tukey HSD test, $\alpha = 0.05$, N = 5 - 6). The two parameters were not correlated with each other ($p = 0.096$).

upper 8 cm soil (in mg g^{-1}), av-dbh4 is averaged diameter at breast height of trees in circular rings with 4 m radius (in cm), root is fine root biomass in the upper 8 cm soil (mg m^{-2}) and θ is volumetric soil moisture (in Vol%).

3.4 Discussion

3.4.1 Variability of biotic and abiotic parameters

The parameters measured in the 0.5 ha plot had different degrees of variation. The variance ranged from 1% CV for soil temperatures (10 and 15 cm depth) in 2000 to 500% CV for the thickness of the F-horizon. The variability of the soil climate parameters was relatively small (1-11% CV) because of stable climatic conditions during the short-time measurement campaigns. The reason for the extremely high variation in the F-horizon thickness was that this horizon generally was not present. Thus, the distribution was highly skew (most values being zero) and the high coefficient of variation was only an artifact from the distribution. The low variation in the C/N ratio of the litter and the soil points towards a rather constant quality of the organic matter available for decomposition at the Hainich site within the 0.5 ha