Controlling factors, scaling issues and partitioning of soil respiration

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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.

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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).

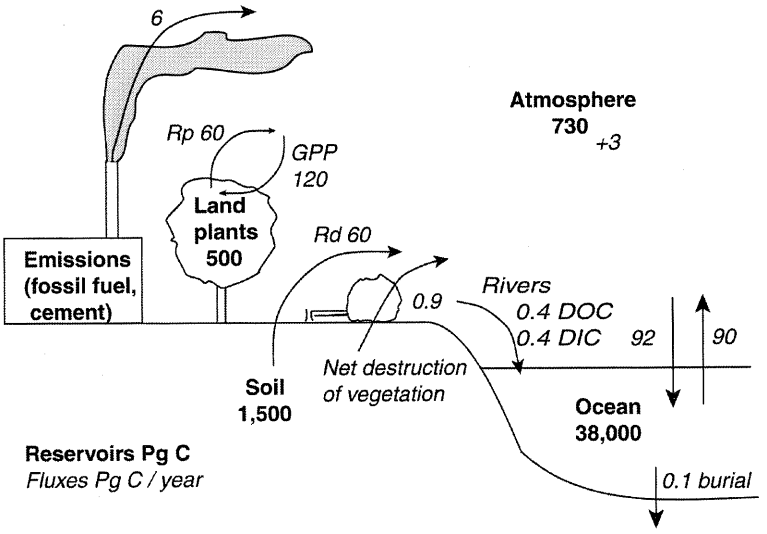

Figure 1.1. The global carbon (C) cycle (after Schlesinger 1997). Living organisms control the largest C fluxes between the atmosphere and the terrestrial reservoirs. During photosynthesis, plants capture solar energy and fix atmospheric CO_2 (gross primary production (GPP)) which is later released by 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

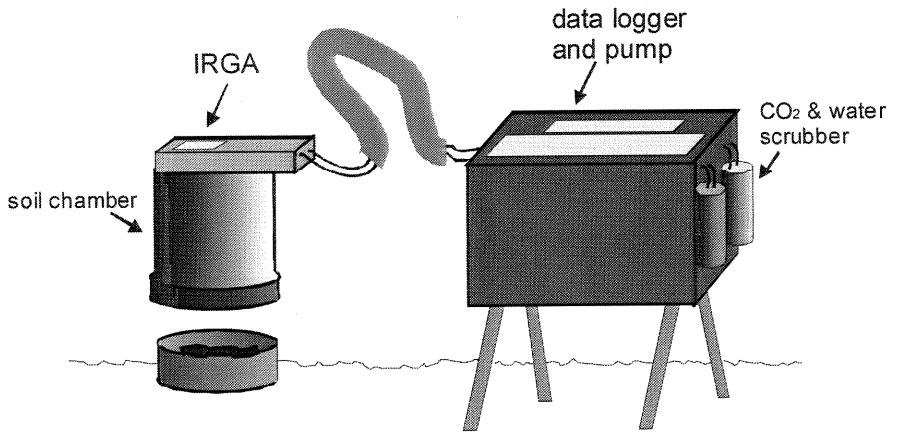

Figure 1.2. Measurement system (Licor 6400-09) for soil respiration. CO_2 concentrations are measured in the soil chamber with an infrared gas analyzer (IRGA), and a specific volume of air is pumped around in a closed circle (for further details see text).

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: $\mu mol\ CO_2\ m^{-2}\ s^{-1}$. 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

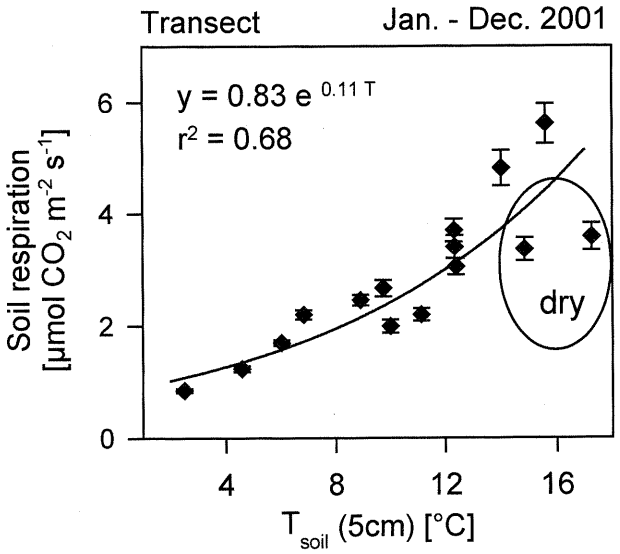

Fig. 2.1. Soil respiration as function of soil temperature during 2001. Mean values and standard error are shown for each of the 16 measurement campaigns along the transect (n = 33). Because of a drought period in late summer (volumetric soil moisture < 23%), soil respiration is better described by a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

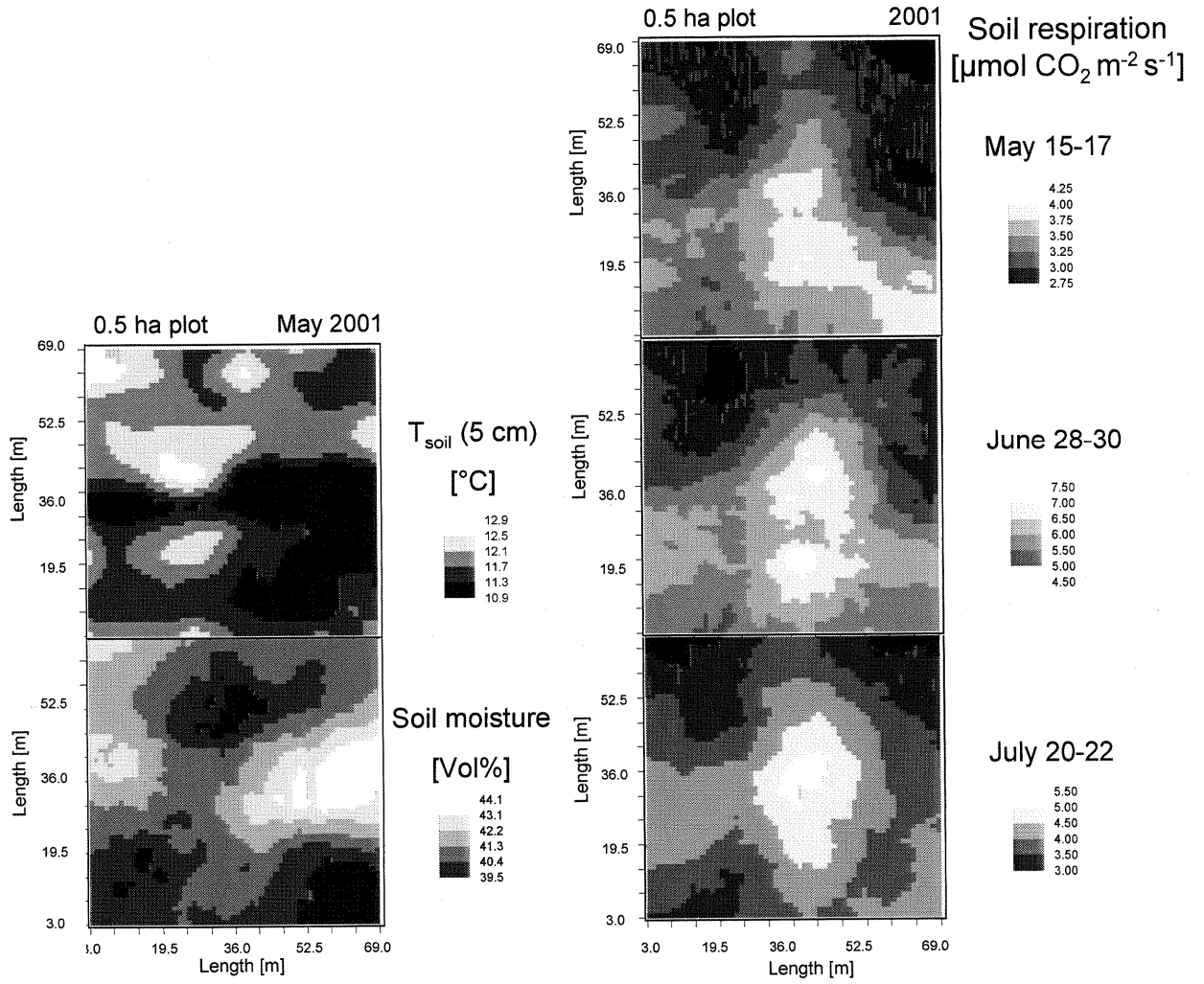

Fig. 2.2. Spatial variability of soil temperature (5 cm depth) and soil moisture (about 6 cm depth) in May 2001 (left panel) as well as soil respiration rates measured during three measurement campaigns in 2001 (right panel). All variables were measured within a 0.5 ha plot at 144 measurement locations 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

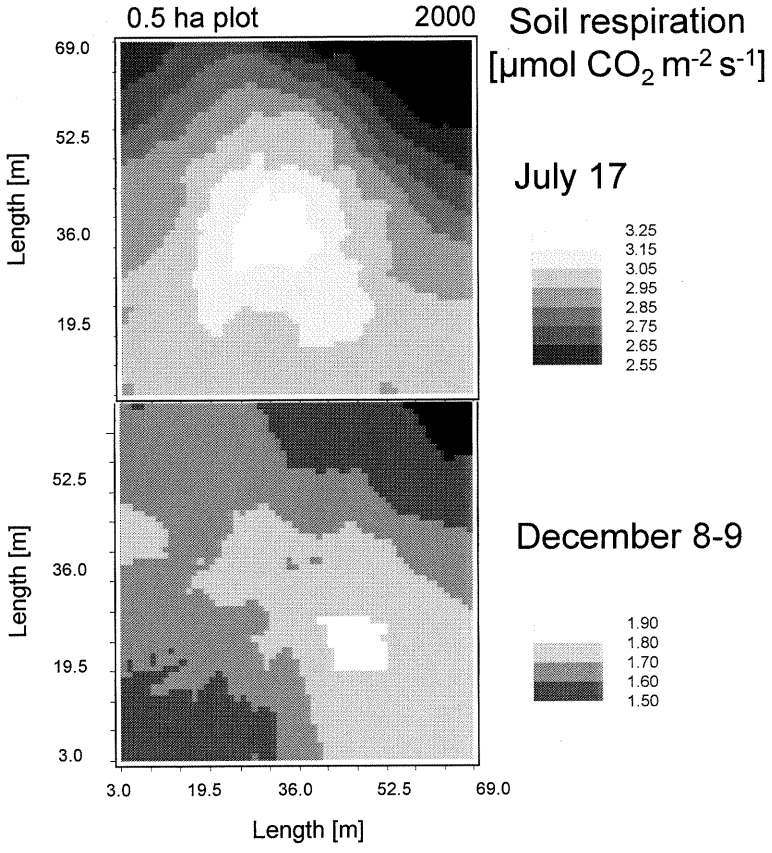

Fig. 2.3. Soil respiration measured within a 0.5 ha plot at 36 measurement locations in summer (July) and winter (December) 2000. Interpolated maps were produced by ordinary block kriging (semivariance analysis and exponential models).

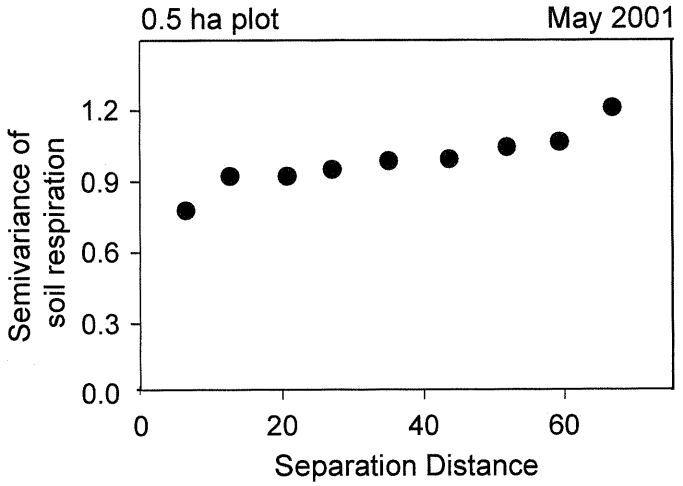

Fig. 2.4. Semivariogram of soil respiration rates measured in a regular grid of 144 measurement locations in May 2001. The smallest distance between measurement locations was 6 m. The fit of an exponential model was r^2 = 0.873.

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).

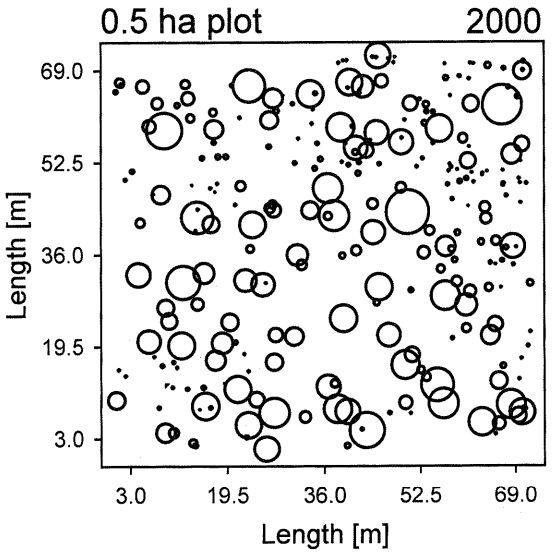

Fig. 2.5. Locations of all living trees within a 0.5 ha plot. Symbol sizes indicate the diameter at breast height of trees, ranging from 1.4 cm to 99 cm (depicted diameters are enlarged for comparison).

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

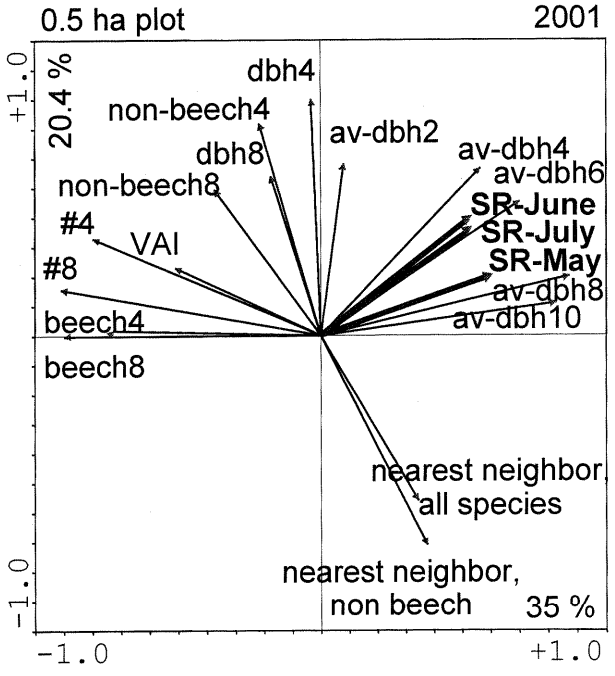

Fig. 2.6. Principal component analysis of soil respiration and stand structural parameters. Abbreviations refer to stand structural parameters in concentric rings with different radii around measurement locations (2, 4, 6, 8, 10 m, respectively). See Table 1 for surther details. Soil respiration was 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

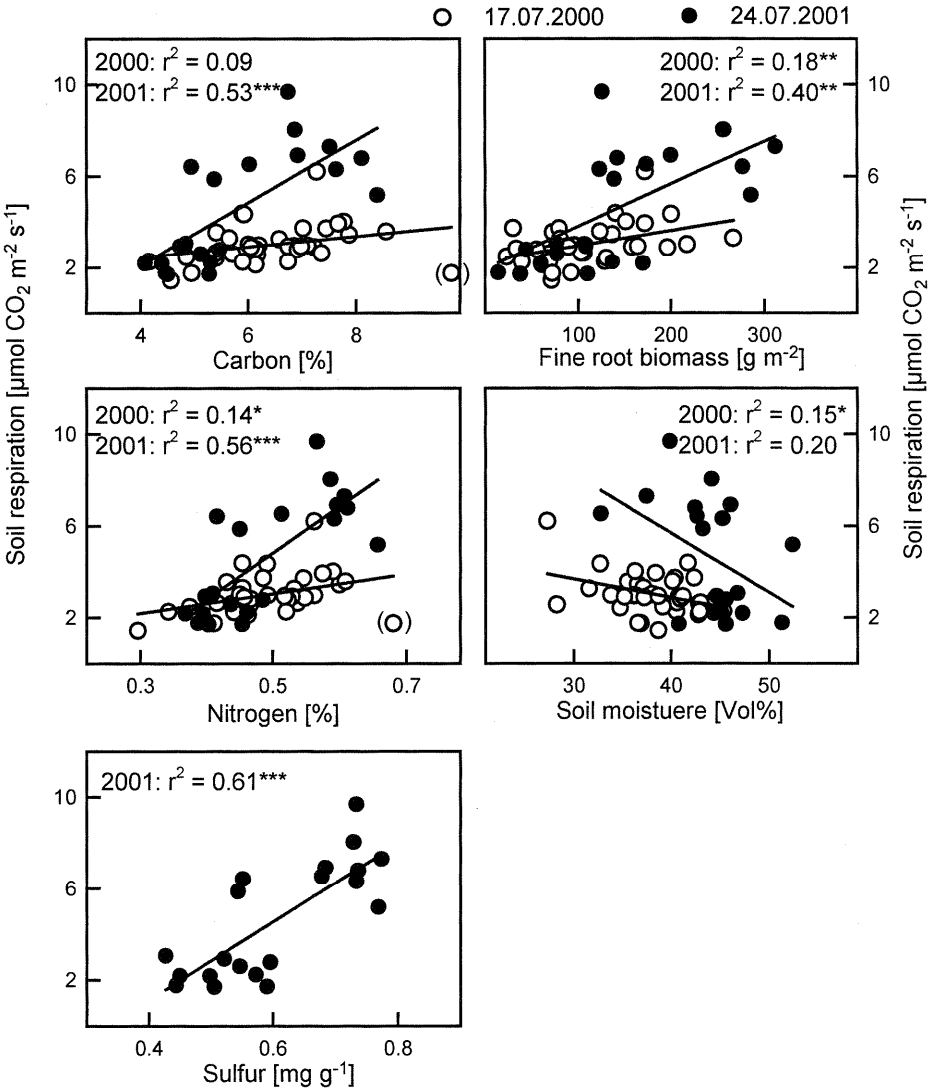

Fig. 3.1. Linear regressions of soil respiration vs. the concentration of various macro-nutrients, soil moisture and fine root biomass in the top-soil. In 2000 the parameters were measured in 36 locations. If one outlier "( )" is removed the fit of soil respiration with C and N were r^2 = 0.25, p = 0.002 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,

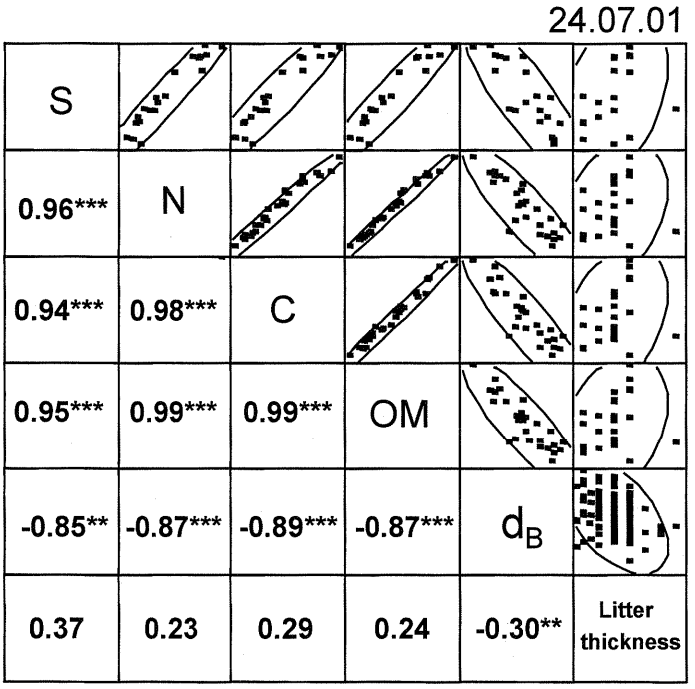

Fig. 3.2. Scatter plot matrix of soil chemical and soil structural parameters that were highly correlated with soil respiration in July 2001 ($p < 0.001$). A 95% bivariate normal density ellipse is imposed on each scatter plot. Correlation coefficients are given in the lower part of the figure. Significance 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

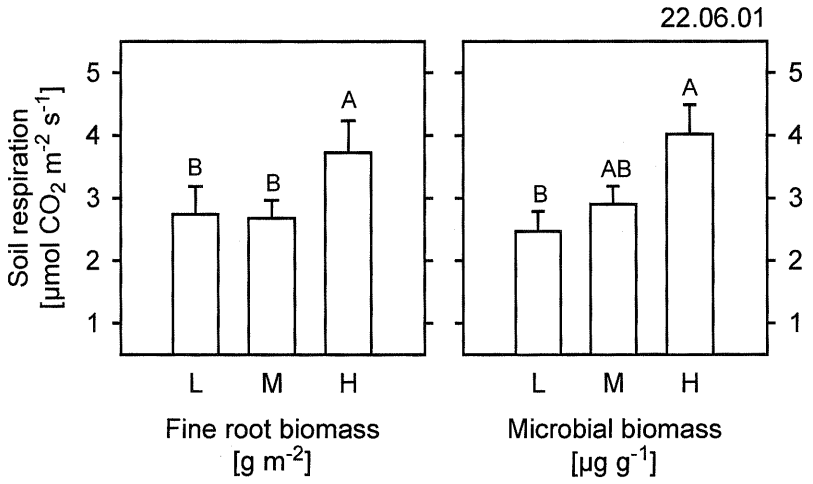

Fig. 3.3. Mean soil respiration rates as function of low (L), medium (M), and high (H) fine root biomass and microbial biomass (in 0 to 8 cm soil depth) from samples collected close to the 0.5 ha study plot. Standard errors of the means are shown. Different letters indicate significantly different means (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

Table 3.3. The best model for soil respiration in the 0.5 ha plot at the Hainich. Measurements were taken in July 2001. For model equation see text.

Parameter	Soil respiration [µmol CO_2 m^{-2} s^{-1}]				
	d.f.	Partial r^2	F	p	AIC
Concentration of sulfur in soil [mg g^{-1}]	1	0.608	5.968	0.027	21.34
Averaged dbh of trees in 4-m radius circular rings [cm]	1	0.084	3.687	0.074	18.48
Fine root biomass [mg m^{-2}]	1	0.043	3.256	0.091	17.55
Soil moisture [Vol%]	1	0.038	2.574	0.130	16.38
Model $r^2 = 0.773$ MS(E) = 1.835	15		12.789	< 0.001	

plot. The presence of old and young trees as well as gaps could explain the high variation (70% CV) of the stand structural parameter av-dbh4 (average diameter at breast height of trees in a circular ring with radius 4 m around the measurement location). Although the difference in coefficient of variation among the parameters was very high, the variation of the individual parameters stayed remarkably stable from year to year. For example, soil temperatures during the measurement campaigns showed only little variation in 2000 and in 2001, while fine root biomass and depth of A-horizon were highly variable among the measurement locations both years. Thus, conditions for soil respiration stayed constant from year to year, and we assumed that the same response of soil respiration to the measured parameters would be seen both years. Furthermore, it was expected that the most important parameters for the variation in soil respiration rates should be sought among those parameters with relatively high coefficients of variation similar to those of soil respiration (30 - 45%), such as av-dbh4, soil chemistry parameters (e.g. C, N, S and DOC) and fine root biomass.

3.4.2 Controlling factors for soil respiration

Sulfur emerged as a key explanatory variable for soil respiration respiration ($p < 0.001$; $r^2 = 0.61$). The present authors have not seen any other studies that address the relationship

between soil respiration and soil sulfur content. However, other macro-nutrients, such as nitrogen, phosphorus and magnesium, have been shown to be correlated with soil respiration (Xu and Qi 2001a; Borken et al. 2002; Pangle and Seiler 2002). More than 90% (in some ecosystems more than 95%) of the sulfur in soil is present in the organic form (Tabatabai 1996; Valeur et al. 2002). In soil organic matter sulfur can be found C-bound and in sulfate esters. The C-S bonds occur in the amino acids cysteine and methionine, which are part of proteins such as biotin, thiamin and coenzyme A. The sulfate esters participate in metabolism and as storage products in plants and microorganisms (Paul and Clark 1996). Thus, sulfur is an essential compound for growth as well as maintenance metabolism in living organisms. The concentrations of sulfur measured at the Hainich site were relatively high (0.4 – 0.8 mg g^{-1}) when compared to the average range of sulfur in soils (0.1 - 0.5 mg g^{-1}) (Tabatabai 1994). Despite the fact that sulfur seemed to be present in the soil at the study site in plenty amount, sulfur, as single parameter, was the one most highly correlated with rates of soil respiration.

Total atmospheric deposition of oxidized sulfur (S_{OX}) in the area of the study site was relatively high, about 2000 mg S m^{-2} yr^{-1} (data from 1997, Umweltsbundesamt 2000). In forests on calcium carbonate poor soils, the oxidized S from atmospheric deposition can (in reaction with water) lower the pH to levels, which may damage the trees. However, at the Hainich site, this was not a problem because of the carbonate bedrock in 40 to 60 cm depth buffering any acidification due to atmospheric deposition. An atmospheric fertilization with S (and N) is therefore expected to increase rather than lower the forest growth at the site. Although S deposition in Central Europe is relatively high, the deposition of S has decreased with about 20% due to industrial changes during the last 20 years (Umweltsbundesamt 2000). Sulfur deficits have even been reported from some Central European agricultural soils during the last few years. The soil at the study site was nutrient rich with a very high soil organic matter pool and a growth rate for beech forest exceptionally high for Central Europe (Martina Mund, personal communication). Since there is almost no leaching from the soil (Gerd Gleixner, personal communication) the ecosystem has a rather closed nutrient cycle. The beech stand is extraordinary in the respect that most soils of equally high quality in Central Europe have been converted into agricultural land. Because of these favorable pedogene characteristics for beech growth combined with a relatively high nitrogen deposition in Central Europe, it is likely that less abundant nutrients, such as sulfur, phosphorous or magnesium could be a limiting factor for biological activity at our site.

However, although the concentration of S was better correlated with soil respiration in our study than the concentration of N, the two parameters were tightly correlated with each

other as well as correlated with the C concentration. Thus, when we made our model for describing soil respiration, sulfur could have been substituted with nitrogen or carbon without changing the fit of the model more than some percentage. This suggests that although sulfur was shown to be a key explaining variable for soil respiration, there may not be a single controlling factor but rather a mixture of inter-correlated parameters controlling rates of soil respiration.

In our best model for describing spatial variability of soil respiration the second and third most important parameters were directly related to the autotrophic respiration. One parameter was a stand structural measure of large trees close to the measurement location (av-dbh4). This parameter was directly linked with tree growth and therefore root respiration. The other parameter was the fine root biomass. We found by simple regression analysis, that fine root biomass explained 18% in July 2000 and 16% in July 2001 of the variation in soil respiration rates and av-dbh4 explained 13% in July 2001. Since root respiration is required for maintenance, growth and ion uptake (Lambers et al 1983; Epron et al. 2001), it is reasonable that tree and root distributions play important roles for soil respiration. Furthermore, in several studies root respiration has been shown in forest ecosystems to be the major source of soil respiration (Epron et al. 1999; Epron et al. 2001; Högberg et al. 2001; Burton et al. 2002; Laporte et al. 2003). Because dominance of large trees (high av-dbh4) in our study was important for soil respiration rates, it was hypothesized that in locations with large trees, there were either 1) more fine roots or 2) the fine roots were more active. The first hypothesis, however, would not be the only answer because the two parameters, fine root biomass and av-dbh4, were not strongly correlated (p = 0.034; $r^2 = 0.04$). The second hypothesis seemed likely, taking into account that recent studies have suggested that most assimilates may be transported to the roots and quickly respired (Law et al. 1999a; Högberg et al. 2001). In order to evaluate the root activity, we measured the nitrogen concentration of the fine roots. Although the fine root N concentration was not directly correlated with soil respiration (p = 0.572), the fine root N per m^2 ground was slightly better correlated with soil respiration than was the simple fine root biomass. However, the fine root N per m^2 ground was not correlated with av-dbh4 (p = 0.462). Although fine root N has been suggested by other authors as a good parameter for root activity (Pregitzer et al. 1998; Burton et al. 2002), this seemed not to be the case in our study. However, the correlation between soil respiration and av-dbh4 suggested that the roots of large trees were more active than those of small trees, i.e. large trees had larger carbon allocation from photosynthesis to root respiration than small trees (Chapter 2).

Among the soil climate parameters, soil moisture was found to be important for variation in soil respiration rates (in the best model). Soil moisture alone explained 13% of the spatial variation in soil respiration rates, by suppressing soil respiration. Soil temperature had very little influence on the spatial variability of soil respiration rates in contrast to the soil moisture. Although temperature was the most important parameters for annual variation in soil respiration at the study site (Chapter 2 and 4), the variation in soil temperature was obviously too small to influence the variation in soil respiration rates during a short measurement campaign. The reason for the suppression of soil respiration by high soil moisture is likely to be anaerobic conditions in the wettest areas, where water logging of the soil can occur due the high amount of clay in the top soil (about 30%, Martina Mund, personal communication). As pointed out by Xu and Qi (2001b), Davidson et al. (1998) and Keith et al. (1997) a high water content in a clay rich forest soil may reduce O_2 diffusion and thereby limit microbial and root activity.

3.4.3 Evaluation of the study site

Several studies have concluded that concentrations of macro-nutrients in forest soils were the most significant factors for spatial variability of soil respiration. Xu and Qi (2001a) and Pangle and Seiler (2002) found in 8 and 2 year old pine plantations in North America that the concentration of nitrogen in the soil was the controlling factor for soil respiration. Soil N explained in their studies 61 and 27% of the spatial variation of soil respiration, respectively. Borken et al. (2002) reported from Central German beech and coniferous forests that soil phosphorus explained most of the variation (74%) in soil respiration rates. Their results showed no significant correlation of soil respiration with soil N. They hypothesized that only a limited amount of soil P was available in the studied forests because of excessive removal of biomass in the past as well as soil acidification. On the other hand, nitrogen was available in excess due to high atmospheric deposition of nitrate and ammonia. Phosphorus was not as highly correlated with soil respiration in our study as in the study by Borken et al. (2002). probably because of different soil characteristics and less removal of biomass in the past. The soil at the Hainich site was a nutrient rich cambisol on calcareous bedrock, while the soils in their study were relatively acidic dystric cambisols on sandstone. Furthermore, the Hainich site was unmanaged while their study sites were managed in a traditional way. However, the concentration of sulfur was not measured in any of the mentioned soil respiration studies. Thus, we cannot say if S may have been such a key explanatory variable for spatial variability in soil respiration in those forests as it was the case at our study site.

Soil bulk density was found to be inversely correlated with soil respiration in our study. In spite of this relationship between density and soil respiration, this parameter was not included in the multiple regression, because soil bulk density was also correlated with the concentration of sulfur. Laporte et al. (2003) found that after forest management soil respiration was 27% lower in the plots with management than in the control plots. They explained that most of the reduction in soil respiration in these plots was due to compaction of the soil, where heavy machines had driven. A compaction could reduce pore space and therefore limit O_2 and CO_2 diffusion (Davidson et al. 1998; Xu and Qi 2001a). On the other hand, without management, mechanical compaction was not likely to be the answer for the inverse correlation of soil respiration and soil bulk density at our study site. The negative correlation could in stead be due to an indirect effect of nutrient concentrations. Several hypothesis for the correlation between soil bulk density and nutrient concentration can be put forward. Firstly, Rodriges-Murillo (2001) found a clear negative correlation between soil bulk density and carbon content in 242 Spanish soils, which partly could be explained by a negative correlation of the density with the clay contents in the soils. Secondly, the areas with a high amount of nutrients could also be the more humus rich areas and therefore they would have a lower soil bulk density. Thirdly, the areas with lower soil bulk density could also be hypothesized to store more organic material, because the soil fauna is more active in the less dense soil and more organic material is therefore incorporated. Thus, we believe that the high correlation of soil respiration with bulk density is an indirect result of the amount of S, N and C in the soil. However, in order to clarify which of the above mentioned hypothesis hold true more studies are needed.

Litter and soil C/N ratios have been shown in some studies to be correlated with soil respiration (Borken et al. 2002; Janssens et al. 2003; Taylor et al. 1989), while in this study no correlation between C/N ratios and soil respiration rates were found. We had expected a larger variance in the C/N ratio because of the species heterogeneity at the study site (ash litter has a lower C/N than beech litter). However the lack of correlation between C/N of the litter and soil respiration may be sought in the fact that the measurement campaigns were in July, so late in the summer that basically all ash and maple litter was decomposed.

When different forest types (deciduous and coniferous) were compared, soil microbial biomass was reported as one of the most important parameters for spatial variability of soil respiration rates (Borken et al. 2002). We found that microbial biomass explained 27% of variation in soil respiration rates in a measurement campaign 22 June 2001 during a warm period. However at this measurement campaign fine root biomass explained even more (34%)

of the variation. Thus at our study site roots seemed to be more important for the spatial variation of soil respiration than microbes, at least during summer under good climatic conditions.

The Hainich site has very good growth conditions for beech. The precipitation is sufficiently high, the climate is relatively warm and the area is not disturbed by humans. It is likely that under such conditions in other forests, the same factors, as the ones we found (mainly macro-nutrients), would be determined as the most significant for variability of soil respiration rates. However, with less favorable conditions (dry, cold, nutrient poor, disturbed etc.), other factors, such as moisture or root density, are likely to be limiting for soil respiration. Because of the high correlation between many of the soil chemical variables (S, N, C and OM), only few parameters were shown to be important using multiple regression techniques on our data. We found that the parameters, most significantly correlated with soil respiration at the Hainich site, were the concentration of sulfur in the soil, large trees close to the measurement location, fine root biomass, and soil moisture. The model containing these four parameters explained 77% of the variability in soil respiration rates at the measurement campaign in July 2001. The most striking result from this study was the high correlation of the concentration of sulfur with the soil respiration (S alone explained 61% of the variation). Although other macro-nutrients may be used to explain spatial variation in soil respiration rates because of the redundancy of those soil chemical parameters, we believe that soil sulfur may be more important for variability of soil respiration than what was previously thought.

4 Respiration estimates based on soil chamber and eddy covariance measurements

4.1 Introduction

Respiration is one of the largest and most important carbon fluxes in terrestrial ecosystems (Valentini et al. 2000). While eddy covariance methods are becoming widely used to measure nighttime total ecosystem respiration, the use of chambers placed over the soil is the most direct way of measuring soil respiration (R_S) originating from the soil and litter layer. Ecosystem respiration (R_E) is composed of respiration from soil, leaves, stems and branches. In a Danish beech forest, soil respiration made up 80% of total ecosystem respiration during summer (Pilegaard et al. 2001). In a coniferous (ponderosa pine) forest in North America, soil respiration made up 76% of the ecosystem respiration (Law et al. 1999b) and in a boreal (*Pinus sylvestris*) forest 80% (Shibistova et al. 2002). Because of the growing concern about the increase in atmospheric CO_2 concentration, and because respiration may be the main determinant of the carbon balance in many ecosystems (Valentini et al. 2000), the study of soil respiration and ecosystem respiration has become highly important.

Ecosystem and soil respiration are partly caused by different processes as ecosystem respiration includes the aboveground respiration. Furthermore, the measurement procedures are highly different (normally eddy covariance nighttime data and chamber measurements). Therefore, the two sets of measurements can compliment each other very well in describing the respiration fluxes in an ecosystem. The eddy covariance system has the advantages that there are no chamber effects, the system integrates over a large area and the measurements are almost continuous (normally measurements every night). Advantages with the chamber methods are that measurements are less elaborate – a tower does not need to be build before the measurements can be carried out. Furthermore, if the scope of a study is to investigate the spatial variability and controlling factors for fluxes, the chambers with their spatially well defined measurements, are highly suited. On the other hand, the chamber system, used in this work (a closed path manual system), also had disadvantages. The soil respiration data were limited to measurement campaigns, and therefore special events such as drought or physiological events may not have been measured. Additionally, a certain amount of spatial (i.e. time consuming) replicates have to be measured to cover spatial heterogeneity. However, there is a clear synergetic advantage of using both systems simultaneously. When both systems are used the spatial variation and controls of fluxes can be examined by results from

the soil respiration chambers while the temporal resolution can be studied by the eddy covariance system.

Several systems have been developed for measuring soil respiration. The portable manual system used in this study (Licor 6400-09) is a frequently used system (e.g. Davidson et al. 1998; Law et al. 1999a; Buchmann 2000; Xu and Qi 2001a; Shibistova et al. 2002). In this method a chamber is placed on the soil surface and a specific amount of air is pumped from the chamber, into an infrared gas analyzer, and back into the chamber. The CO_2 concentration in the chamber cycles around the ambient CO_2 concentration (increase of CO_2 concentration from soil respiration intermixed with chemical removal of CO_2). There are no pressure or concentration problems by the measurements since the pressure is constant in the chamber (a volume of air is pumped around in a circuit), and the concentration is kept close to the ambient concentration from the measurement procedure. Soil respiration rates are calculated form the increase in concentration in the chamber, the volume of the system and the area covered by the chamber. Several experiments have been set up to exclude that systematic errors could occur during the measurement procedure (McDermitt et al. 2003; Takle et al. 2003). Another system, which also measures soil respiration by pumping air around in a closed cycle from a chamber into an infrared gas analyzer and back into the chamber, leaving the concentration to rise in the chamber, is the so called "PP-system" (Le Dantec et al. 1999; Janssens et al. 2000 and 2001; Rey et al. 2002). However, the PP-system has been reported to produce higher values than most other systems, probably by disruption of concentration gradient above the soil caused by a fan in the chamber (Le Dantec et al. 1999; Janssens et al. 2001). As an alternative to the manual closed path system, several automated open path systems have been developed (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). With the open path method fresh air is continuously sucked into the soil chamber and out of the chamber again. Soil respiration is calculated by the difference between infrared gas analyzer measurements of air from the chamber (measurement cell) and an air stream that runs parallel to the first one but not through the chamber (reference cell). A clear advantage of the automated systems is that measurements are continuous. Thus, diurnal differences and special events such as drought, wetting, budbreak or leaf fall are very well captured. However, these systems may have disadvantages, such as pressure and concentration problems in the chamber, which do not occur with the Licor 6400-09 system. The main disadvantage in these systems is that they normally do not capture spatial variation in soil respiration rates very well. The automated, open systems generally have a few chambers

connected by tubing to a central infrared gas analyzer. Thus, only few locations not far away from each other can be measured at a site. Furthermore, the position of the infrared gas analyzer is normally constrained by the necessity of power supply to the system. A few other options for measuring soil respiration are described in the literature. One method is a static system, where CO_2 is collected chemically in a soda lime trap placed in a chamber (underestimates often fluxes, Norman et al. 1997; Pumpanen et al. 2003; Janssens et al. 1998). Another method is a closed chamber, where air samples are collected with a syringe and measured on a gas chromatograph (Borken et al. 2002). The last method described here is the below canopy eddy covariance system (Janssens et al. 2000; Wilson and Meyers 2001; Shibistova et al. 2002). This last system has the same advantages of the above canopy eddy covariance system for measuring ecosystem respiration. The measurements are continuous and the system integrates over a larger area. However, this system often suffers from problems due to insufficient turbulence below the canopy, especially in dense forest types.

When soil respiration is measured in campaigns, a good model is necessary in order to make a reliable estimate of the annual soil CO_2 efflux. Also when respiration is measured continuously (automated chamber or tower system), models are needed for gap filling and to extrapolate from night to day data. In temperate forest ecosystems with a relatively high precipitation, soil temperature is normally the most important factor for temporal variation in respiration rates (e.g. Davidson et al. 1998; Buchmann 2000). The most frequently used models for soil and ecosystem respiration are those with a simple exponential relationship between soil temperature and respiration (e.g. Buchmann 2000) and an extended Arrhenius function (Lloyd and Taylor 1994). However, also linear, power and sigmoid functions have been suggested in the literature (Janssens et al. 2003). Furthermore, in dry ecosystems soil moisture can be just as important as soil temperature for rates of soil respiration, and it may be necessary to include soil moisture in the model (Rey et al. 2002).

High spatial variability in soil respiration rates from one plot to another within forests was shown by, for example, Buchmann (2000), Davidson et al. (1998) and Xu and Qi (2001a). Also the temperature sensitivity (Q_{10}) of the soil respiration can be highly variable among plots within a forest. Davidson et al. (1998) reported a range of Q_{10} values from 3.5 to 5.6 among deciduous forest sites with different drainage at the Harvard forest in Massachusetts. The wettest sites having the largest Q_{10} values. From a Danish beech forest Q_{10} values of 6.3 and 2.8 were published from a wet and a dry year, respectively (Pilegaard et al. 2001; Janssens et al. 2003). Xu and Qi (2001b) presented a positive correlation between soil temperature and Q_{10} values calculated over short time intervals within one year. In their

study, soil temperature explained 45% of the Q_{10} variation and the temperature sensitivity was stronger at cold temperatures (in winter) than at warm temperatures. Furthermore, the temperature sensitivity was dependent on the depth in which soil temperature was measured. At more shallow depths the soil temperature was highly variable, and the Q_{10} values therefore smaller, while deeper down in the soil, the range in temperature was smaller, and the Q_{10} values therefore larger. Boone et al. (1998) showed in a root exclusion experiment in a mixed temperate forest that root and microbial respiration have different temperature sensitivity. The Q_{10} was considerably higher for the root (4.6) than for the microbial respiration (2.5). Although some knowledge has been gathered about soil and ecosystem respiration, there are still unsolved aspects of factors controlling these fluxes, the spatial variability and the effect of experimental designs (e.g. number of samples) on the estimates of the fluxes. Thus, we carried out a detailed study of soil and ecosystem respiration in an unmanaged mixed beech forest in the National Park Hainich.

The objectives of the study were (1) to determine the effect of spatial variability on annual estimates of soil respiration in the source area of an eddy covariance tower, (2) to evaluate the influence of fine roots on the temperature sensitivity ("Q_{10}") of soil respiration, and (3) to recommend the number of sampling locations needed for adequate estimations of annual soil respiration at a forest site with typical heterogeneity.

4.2 Methods

4.2.1 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.) (for more detail see chapter 2).

Ecosystem respiration was measured with the eddy covariance technique from a 43.5 m tall tower (about 10 m above the canopy). Dominant wind direction was from the south eastern direction. Calculations with an analytical footprint model (Schuepp et al. 1990) showed that under neutral atmospheric conditions, the source weight function peaked at approximately 80 m distance from the tower and 50% of the integrated source weight function was reached at 200 m. Soil respiration was measured within this main footprint (=source area) with a portable measurement system at 36 permanent locations in 10 plots along a 300 m transect in the south eastern direction from the eddy covariance tower. In each plot three to five measurement locations were placed with about one meter distance from each other, and the distance between plots was 30 m. Soil respiration was measured every two to six weeks

from May 2000 through December 2002 while ecosystem respiration was measured continuously during this period.

4.2.2 Measurements of respiration

Ecosystem respiration was calculated from nighttime measurements of carbon dioxide mixing ratios and vertical wind speed at the top of the tower using the eddy covariance technique. The flux system consisted of a triaxial sonic anemomenter at the top of the tower (Gill Solent R3, Gill Instruments, Lymington, UK) and a fast response CO_2/H_2O infrared gas analyzer in absolute mode placed at ground level (LiCor 6262-3, LiCor Inc. Lincoln, NE, USA). Air was drawn through tubing from the inlet on the top of the tower to the gas analyzer at the bottom. Full details of the eddy covariance measurements are given in Knohl et al. (2003). In close vicinity to the tower, soil temperature was measured at several depths (2, 5, 15, 30 and 50 cm) using PT-100-temperature sensors and soil moisture at several depths (5, 15, 30 cm) using Theta-probes (ML-2x, DeltaT, Cambridge, UK). These data were collected every ten seconds and stored as 10 min. average values with a data logger (CR23x and CR10X, Campbell Scientific, Logan, UT, USA).

Soil respiration was measured with a portable infrared gas analyzer and a closed chamber system (Li-cor 6400-09, Li-cor, Inc., Lincoln, Nebraska, USA). Each soil respiration measurement was accompanied by measurements of soil temperature in the litter layer, at 5 cm, 10 cm and 15 cm soil depth, and of soil moisture at 6 cm depth (ThetaProbe, Delta-T Devices Ltd., Cambridge, UK) (see also chapter 2).

We participated in a calibration experiment in Finland in 2002 (Pumpanen et al. 2003), where our soil respiration system was tested against fixed efflux rates. The system measured highly reliable values (0 - 2% higher rates than the true fluxes at rates between 0 and 6μmol CO_2 m^{-2} s^{-1}, P. Anthoni and W. Ziegler, unpublished data).

4.2.3 Root analyses

Two soil samples (0 - 8 cm) were collected in each of the 10 plots along the transect in June 2001 close to the permanent soil respiration measurement locations. Fine roots were extracted from the 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 (diameter smaller than 2 mm) were dried (70°C, 48 hours) and weighed. Data from 9 of the plots were used for further analyses, while data from the plot closest to the tower were not included due to problems with the soil sample.

4.2.4 Statistical analyses and calculations

Mean values, standard deviations, regressions and ANOVA's were calculated in JMP (SAS Institute Inc., Connecticut, USA).

Soil respiration was modeled with exponential models of data from a whole year assuming no changes in temperature response of soil respiration. A multiple regression model (GLM) for soil respiration was developed with soil temperature and soil moisture as independent variables. In order to maintain an exponential relationship of soil respiration to soil temperature, a logarithmic transformation of the response variable was carried out prior to analysis. The resulting equation was:

$$R_S = k\, e^{a\,T}\, e^{b\,\theta}, \qquad (1)$$

where R_S is soil respiration [µmol CO_2 m^{-2} s^{-1}], T = soil temp (5cm) [°C], θ = soil moisture [Vol%] and k, a and b are constants fitted in the regression analyses. The temperatures and moisture data collected at the time and place of soil respiration measurements were used for the models. However, for annual estimates, temperature and moisture data from the logger close to the tower was used for the models and calculations of the amounts of annual CO_2 efflux in order to be consistent with the calculation of ecosystem respiration from the eddy covariance measurements. In 2000 and 2002 the soil respiration rates calculated by the software in the Licor 6400 were used for further data processing. However, the data from 2001, due to a calibration problem, data were normalized to the level in 2000 and 2002. Thus, data from 2001 were only used for illustrative purposes and not for comparisons.

Ecosystem respiration (R_E) was calculated from the night time flux measurements. Data under low turbulence conditions (u_* of 0.4 m s^{-1} in summer and 0.5 m s^{-1} in winter), during rain (precipitation larger then 0.1 mm per 30 minutes) and with unrealistic large variance in CO_2 mixing ratio measurement (variance > 3.5, equals top 2.5%) were excluded from regression analysis and night averages were only calculated if more than 2.5 hours of valid data were available. Extrapolations from nighttime measurements to daytime estimates and gap filling was done using three different models:

The above mentioned model 1 with data from a whole year was also used for ecosystem respiration estimates.

Another model was used, where only soil temperature was included as independent variable:

$$R_E = k\, e^{a\,T}, \qquad (2)$$

where R_E is ecosystem respiration [µmol CO_2 m^{-2} s^{-1}], T = soil temp (5cm) [°C] and k and a are constants fitted in the regression analyses.

Finally an extended Arrhenius function (Lloyd and Taylor, 1994), which expresses the dependency of R on soil temperature (T_s) as follows:

$$R_E = R_{10} e^{A\left(\frac{1}{B-C}-\frac{1}{T-C}\right)} \quad (3)$$

where R_{10} denotes ecosystem respiration at 10 °C, A, B and C are constants (A = 308.56 K, B = 283.15 K, C = 227.13 K, Lloyd and Taylor, 1994). For equation 3 data from monthly intervals were used for the calculations.

The sensitivity of soil respiration to changes in temperature (Q_{10} values) were calculated using the exponential relationship between soil respiration and soil temperature in equation 2 (Buchmann 2000; Xu and Q, 2001b).

$$Q_{10} = e^{10a}, \quad (4)$$

where a is the constants that was fitted in equation 2.

The number of respiration measurements needed for various degrees of precision were calculated using a power function:

$$n = \left[\frac{ts}{range/2}\right]^2 \quad (5)$$

where t is the t-statistics, s is the standard deviation and range is the range around the mean value by the wanted precision (Davidson et al. 2002).

4.3 Results

Soil respiration measured during three years showed that minimum rates of 0.4 µmol CO_2 m^{-2} s^{-1} were observed at low soil temperatures (winter) and rates with a maximum of about 10 µmol CO_2 m^{-2} s^{-1} were observed at high soil temperatures (summer) (Fig. 4.1). The soil temperature showed the same pattern over the years. Ecosystem respiration followed the same pattern as soil respiration and temperature, but with a higher temporal resolution due to the continuous measurements.

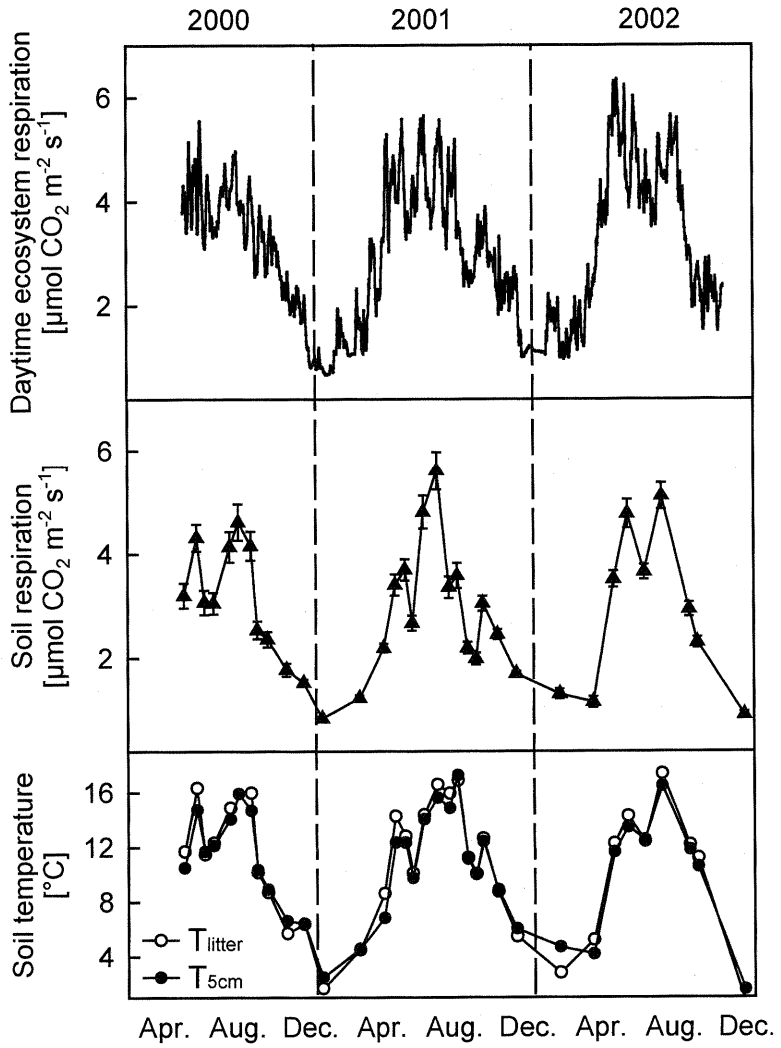

Fig. 4.1. Daytime ecosystem respiration, soil respiration and soil temperature during three years. Daytime ecosystem respiration was extrapolated from nighttime eddy covariance measurements. Soil temperatures followed the same pattern as the respiration. Soil respiration and soil temperature: n = 33, 35 measurement campaigns, error bars indicate standard error of the mean. Ecosystem respiration: one measurement tower, continuous measurements.

Soil respiration and ecosystem respiration vs. soil temperature showed that respiration rates were exponentially correlated with temperature (Fig. 4.2). There was more scatter in the data calculated from the eddy covariance measurements (ecosystem respiration) than in the chamber data (soil respiration). Thus, the models for soil respiration had better fits to the measured data (r^2 = 0.68 – 0.95) than the ecosystem respiration models (r^2 = 0.56 – 0.62). In the wet year 2000 a very strong correlation between soil respiration and soil temperature at 5 cm was found (r^2 = 0.95). On the other hand, in 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 model for soil respiration in 2001, the explanatory value of the model increased remarkably (r^2 = 0.68 with a simple exponential equation, r^2 =

0.90 with the equation: $y = 0.24\ e^{0.14\ T}\ e^{0.02\ \theta}$, T = soil temp (5cm) [°C] and θ = soil moisture [Vol%]). This drought limitation is further illustrated in the residual plot (Fig. 4.2, lower panel), where the respiration rates at the two dry measurements campaigns clearly were below the values expected from the temperature regression in 2001. Although the regression lines from the soil respiration and the ecosystem respiration seem to be very similar in this figure, the Q_{10} values form the soil respiration (3.3, 3.0 and 3.7 for 2000, 2001 and 2002, respectively) were higher than those from the ecosystem respiration (2.9, 2.9 and 2.7 for 2000, 2001 and 2002, respectively).

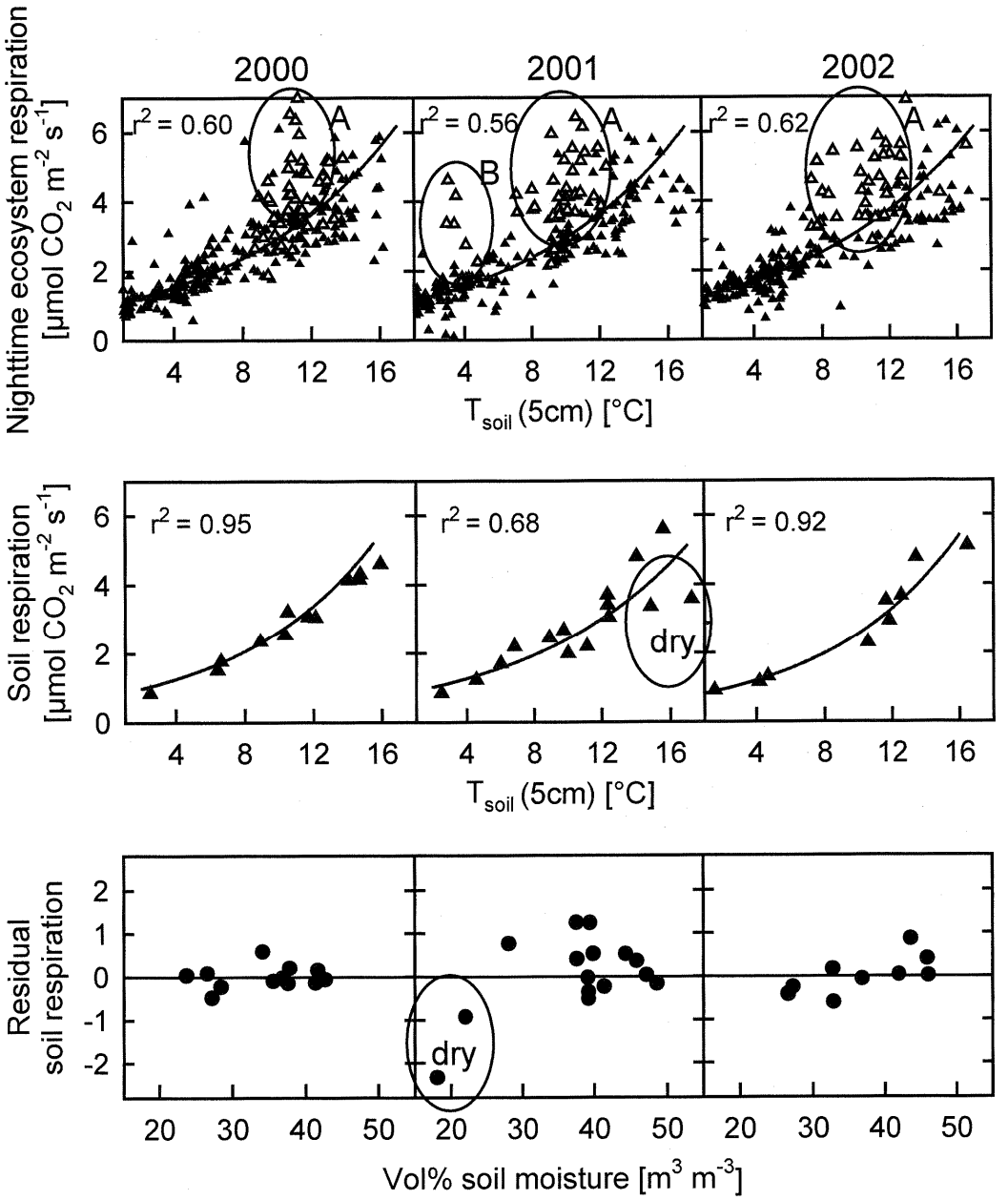

Fig. 4.2. Ecosystem respiration (R_E) and soil respiration (R_S) were exponentially correlated with soil temperature (upper two panels, for R_E in 2000: $y = 1.01\ e^{0.11\ T}$; 2001: $y = 1.03\ e^{0.11\ T}$; 2002: $y = 1.13\ e^{0.10\ T}$, for R_S in 2000: $y = 0.72\ e^{0.12\ T}$; 2001: $y = 0.83\ e^{0.11\ T}$; 2002: $y = 0.72\ e^{0.13\ T}$). Relatively high ecosystem respiration rates were observed during budbreak (A) and after leaf fall (B). The residuals from the regressions of soil respiration vs. temperature are plotted in the lower panel. Soil respiration rates are mean values of 33 measurements.

Large variation in the annual efflux of soil CO_2 was found among plots at different distance to the tower (Fig. 4.3). However, the variation from year to year in efflux at a given plot was relatively small (small error bars). Thus, plots with high soil CO_2 efflux rates (e.g. the first and the last plot) always had high efflux rates, while those locations in the middle of the transect with lower efflux rates always had lower rates.

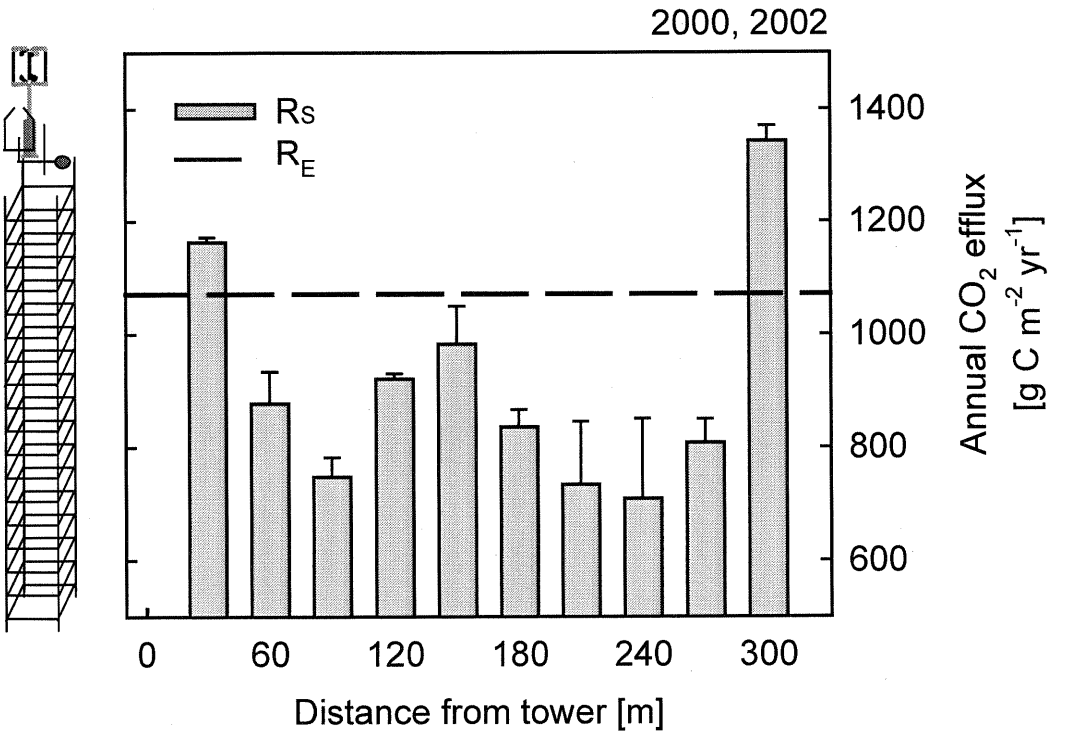

Fig. 4.3. Annual soil respiration (R_S) from plots at different distance from the eddy covariance tower as well as the ecosystem respiration (R_E) from the footprint. Soil respiration was almost twice as large at the plot with highest soil respiration compared to the plot with lowest. Number of measurements at each plot: 3 - 5, error bars indicate standard error of the mean efflux from 2000 and 2002. R_E is the average from year 2000 and 2002 calculated by three different models (see text).

Among 36 locations, most of the annual soil CO_2 efflux estimated were around 900 g C m^{-2} yr^{-1}, but when only those five locations with the lowest efflux rates were included, the estimate was around 500 g C m^{-2} yr^{-1}, while the estimate based on the five locations with highest efflux was almost three times greater (Fig. 4.4).

Those plots with the highest soil CO_2 efflux were characterized by a different stand structure (older trees) than the other plots. At the first plot (closest to the tower) a few large ash and maple trees dominated and at the last plot the measurement locations were next to a very large beech tree and close to a canopy opening (i.e. intense sun radiation). The temperature response of soil respiration was highly correlated with the fine root biomass at

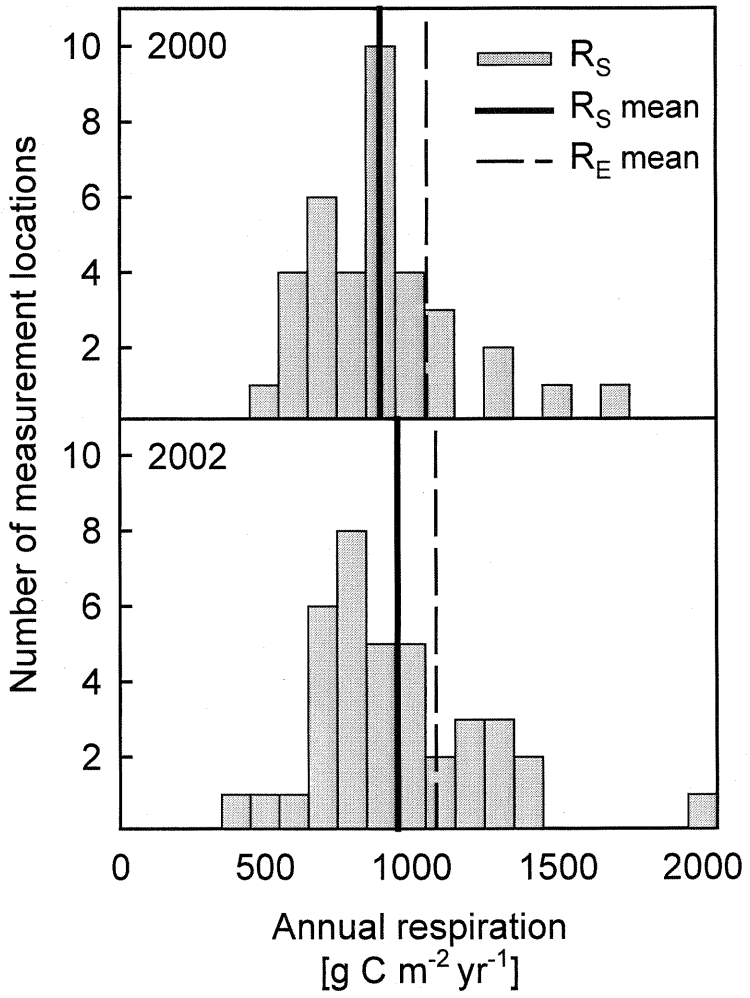

Fig. 4.4. Annual soil respiration (R_S) in 2000 and 2002 from 36 separate locations along the transect. If the five locations with lowest efflux are chosen, the estimate is about 500 g C m^{-2} yr^{-1}. If the annual efflux is based on the five location with highest soil respiration the estimate is almost three times greater. Mean ecosystem respiration (R_E mean) is the mean of estimates from three different models (see text).

the plots (Fig. 4.5). The Q_{10} values varied from 3.1 to 4.7 among 9 plots, while the Q_{10} value from a root free plot was 1.9 ± 0.3.

Ecosystem respiration (including stem and leaf respiration) was about 15% higher than the soil respiration, when data from the whole year 2002 were used for the models (table 4.1). When regressions for ecosystem respiration were made separately for each month the annual estimates were about 7% higher than when one model was used for the whole year. This was mainly due to higher estimates by the monthly models in the month March, May, October and November (table 4.1 and Fig. 4.2).

The precision of efflux estimates depended on the number of samples used for the estimate (table 4.2). At a 95% confidence level, 7 random locations in the transect should be measured for an estimate within 30% of the full population mean. At 20% precision 13 locations were needed, and to reach 10% precision 47 locations should have been measured. Also the contribution of soil respiration to total ecosystem respiration depended highly on the number and locations of measurements (table 4.3).

4.4 Discussion

4.4.1 Temporal and spatial variation in respiration rates

The large temporal variation of soil and ecosystem respiration rates in our study (0.4 – 10 μmol CO_2 m^{-2} s^{-1}) were well described with exponential functions. A simple exponential function explained 95% of the annual variation in soil respiration rates in the wet year 2000. However, due to drought in August 2001, a model with only soil temperature explained no more than 68% of the variation in soil respiration rates during 2001. On the other hand, when soil moisture was included in the model, the model could explain 90% of soil respiration variation. Davidson et al. (1998) proposed a similar model for a North American hardwood forests. In their study the precision of the estimate also increased considerably by including soil moisture. We found that the threshold where low soil water conditions were limiting for soil respiration was about 23% volumetric water contents, which is similar to the 20% threshold that was found by Rey et al. (2002) in a Mediterranean oak forest. Thus, in an ecosystem where drought occasionally can limit soil respiration, it can be recommended to use a soil respiration model that includes soil moisture, in stead of using a simple temperature exponential model or an Arrhenius type equation (Janssens et al. 2003).

In our experiment, the difference in soil respiration measured among plots in a 300 m transect was considerable. Soil respiration from the plots at 30 m and 300 m distance from the

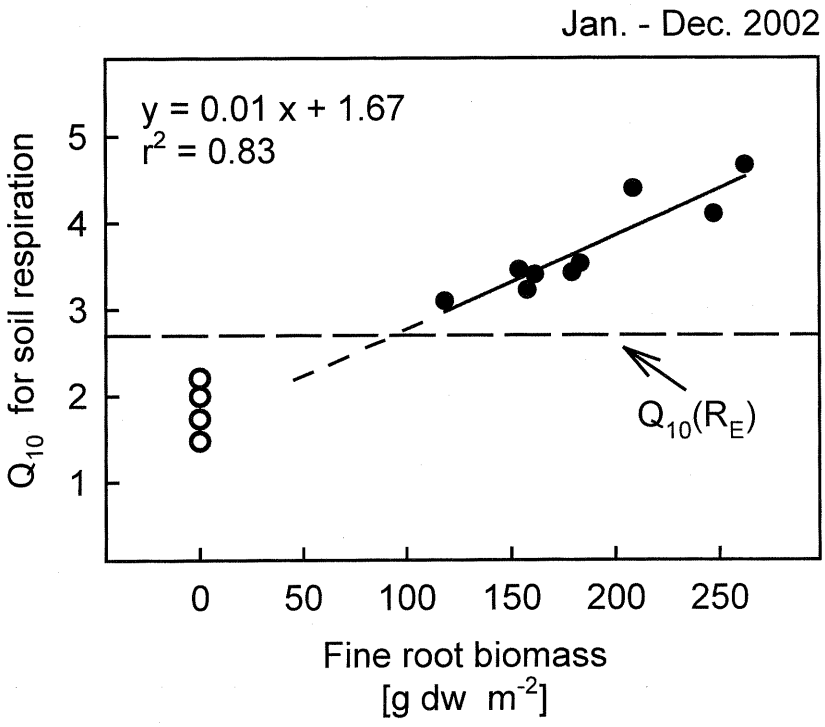

Fig. 4.5. Temperature sensitivity (Q_{10}) of soil respiration is correlated with the fine root biomass. Root biomass and soil respiration were measured in nine plots along the transect. For comparison soil respiration Q_{10} values from four locations within two nearby root exclusure plots (trenching plots) are depicted in the graph. Q_{10} of ecosystem respiration in year 2002 is shown as a dashed line.

Table 4.1. Estimates of total soil and ecosystem respiration per month during 2002. The model for soil respiration was based on data from the whole year, and the monthly estimates were calculated using soil temperature and moisture data. For estimates of ecosystem respiration three different models were used (see text).

[g CO_2 m^{-2} $month^{-1}$]	R_S (50-200m)	R_E(annual exponential)	R_E(monthly exponential)	R_E(monthly Lloyd-Taylor)
Jan.	24	43	42	41
Feb.	33	46	42	42
Mar.	35	50	51	48
Apr.	50	67	84	87
May	94	122	164	162
Jun.	123	147	149	150
Jul.	131	140	133	134
Aug.	161	161	155	158
Sep.	97	96	97	100
Oct.	59	68	75	74
Nov.	46	59	67	67
Dec.	29	40	50	50
Σ	882	1037	1109	1113

tower was almost twice as large as soil respiration at 90 m, 210 m and 240 m distance. Similar high spatial variability from plot to plot within forests was shown by Buchmann (2000), Davidson et al. (1998) and Xu and Qi (2001a). In our study, not only the soil respiration rates, but also the sensitivity of soil respiration to temperature (Q_{10}) varied considerably from one plot to another, and the Q_{10} value for ecosystem respiration (2.9) was lower than the Q_{10} values for soil respiration (3.1 - 4.7) in 2002. Several explanations for the relatively low Q_{10} value for ecosystem respiration are likely. If the temperature sensitivity of soil respiration is

much higher than that of the other components of ecosystem respiration (stem, branch and leaf respiration), this would explain the low Q_{10} by ecosystem respiration. The Q_{10} values are especially sensitive to changes in the data at low temperatures. Thus, if the temperature sensitivity of the different processes is particularly pronounced at low temperatures, this would explain differences in Q_{10} values which may not be reflected in the annual CO_2 fluxes (because the flux rates are small anyway at low temperatures). Although the differences in Q_{10} values may be explained by differences in physiological processes, the possibility of biases by the measurement methods cannot be excluded. If the temperature sensitivity really was the same, but the soil respiration system generally measured slightly too low values in winter or

Table 4.2. Required number of soil respiration measurement locations to achieve various degrees of precision (within ±10 to 30% of the full population mean) and at various confidence levels (80 - 99%). Calculations are based on a population of 36 measurements in the National Park Hainich 6 June 2002 (mean = 4.77 µmol CO_2 m^{-2} s^{-1}, SD = 1.57).

Precision [%]	99% confidence	95% confidence	90% confidence	80% confidence
±10	81	47	33	20
±20	23	13	10	6
±30	12	7	5	4

the ecosystem respiration rates were estimated too high in winter, this could explain the differences. Furthermore, the low number of measurements at low temperatures in the soil respiration data could lead to impreciseness in the Q_{10} values calculated from the soil respiration data. Concerning the difference in Q_{10} values for soil respiration among plots, we found a positive correlation between Q_{10} of soil respiration and the fine root biomass. In our experiment the differences in the fine root biomass explained 83% of the variation in Q_{10} values. The linear regression line could even be extended to data from root free plots (similar to the experimental setup by Boone et al. 1998). This further supports the relationship between soil respiration Q_{10} and the fine root biomass, which became apparent from our transect plot data. That temperature sensitivity of soil respiration can be linked to root activity is further supported by results from an experiment by Boone et al. (1998), who demonstrated

that root respiration has a higher temperature sensitivity than microbial respiration. They showed a higher Q_{10} for root respiration (4.6) than for microbial respiration (2.5) using root free plots in a mixed temperate North American forest. Janssens et al. (2003) also reported a higher Q_{10} value for roots (3.86) than for microbes (2.34) in a French beech forest. Thus, the spatial heterogeneity of the soil respiration temperature-sensitivity, can partly be explained by differences in root density. Since soil processes are often modeled as a "black box", this result stresses the need for detailed soil compartments in carbon models, especially for estimating the carbon balance under changed climatic conditions.

4.4.2 Manual chambers and micrometeorological methods

Soil respiration measured in the main source area of the eddy covariance tower (50 - 200m from the tower) constituted 79 - 85% of the total ecosystem respiration, well within the range of what is reported in the literature (Law et al. 1999a; Pilegaard et al. 2001; Shibistova et al. 2002). However, when soil respiration was measured only at the 5 locations closest to the tower, soil respiration was estimated to contribute between 105 and 113% of the ecosystem respiration. Ecosystem respiration is composed of soil respiration, foliage, branch and stem respiration. Thus, a soil respiration fraction above 100% is of course unrealistic and it reflects the untypical stand structure next to the tower. Therefore, in a heterogeneous ecosystem the location of measurements is highly important for the measured flux rates, and a severe over (or under) estimations may be detected when comparisons are made to the spatially integrating ecosystem respiration measured by the micrometeorological eddy covariance method.

Table 4.3. Contribution of soil respiration to total ecosystem respiration. Ecosystem respiration was estimated using three different models (see text), soil respiration was estimated using three different plot sizes. The main footprint ranged from 50 – 200m.

	N	R_S [g CO_2 m^{-2} yr^{-1}]	R_E(annual exponential)	R_E(monthly exponential)	R_E(monthly Lloyd-Taylor)
R_S(0-50m)	5	1172	113%	106%	105%
R_S(0-300m)	36	913	88%	82%	82%
R_S(50-200m)	19	882	85%	80%	79%

Soil respiration was measured with a closed manual system (Licor 6400-09), where the CO_2 efflux from the soil was calculated from measurements of concentration over time in a chamber placed on the soil surface. Ecosystem respiration was calculated from nighttime eddy covariance measurements of CO_2 mixing ratios and wind speed on top of a tower. The two sets of data supplement each other well. The chamber measurements are good in representing the spatial resolution of soil respiration and its control, while the ecosystem data have a very fine temporal resolution. The regressions of soil respiration to temperature and moisture data could only be applied on an annual basis due to the low number of samples. The eddy covariance regressions were applied on annual as well as on monthly basis. For the ecosystem respiration, the monthly regressions resulted in an annual ecosystem estimate that was about 7% higher than when the annual regression was applied. This was mainly due to high physiological activity at budbreak (during April and May) and increased respiration after litter fall (mainly October). These phenological effects were also reported from a study of soil respiration in a Danish beech forest (Pilegaard et al. 2001). Thus, the eddy covariance measurements were good in capturing seasonal events. A potential problem by both systems is the timing of the measurements. For manual chamber systems, measurements are normally only carried out during day hours, while for the eddy system, only the nighttime measurements reflect ecosystem respiration while daytime data integrate respiration and photosynthesis. If there are large differences in day and night fluxes (high flux rate during daytime which cannot be explained by soil temperature differences) calculations based on soil respiration data will overestimate, while ecosystem respiration will lead to underestimated fluxes. However, diurnal cycles of soil respiration were measured at the Hainich site in August 2000 and 2002. During these campaigns, no significant difference (not caused by temperature) was detected between day and night measurements (data not shown). Results from a study by Buchmann (2001) in a Central German Coniferous forest support our findings. She found no diurnal pattern in soil respiration rates, which could not be explained by soil temperature. However, diurnal patterns have been reported from studies in a wheat field and a North American hardwood forest (Davidson et al. 1998; Kuzyakov and Cheng 2001). Especially in the wheat field, the diurnal pattern was rather strong, most likely due to recent photosynthesates being respired within few hours after assimilation. Thus, in our study, diurnal differences could be ignored, but in other ecosystems this feature may be of large importance, especially by smaller crops, where the transport way from leaves to roots is shorter and quicker. In our study the ecosystem respiration data had a relatively large scatter around the temperature regressions. Parts of the scatter represents the influence of

atmospheric stability on the vertical exchange of air. Thus, on calm nights less carbon dioxide is exchanged vertically than on windy nights, although the biological flux could be the same. A systematic error can occur when the tower is located on a slope and at night cold air inside the canopy drains down the slope. Then CO_2 respired from soil or stems may never reach the top of the tower, but can be lost into the valleys via horizontal air movement (Aubinet et al. 2002). However, in our study we identified periods of cold air drainage and excluded those data from further analysis (Knohl et al. 2003). Another part of the scatter seen in the temperature regression was caused by the phenological events in spring and fall, such as increased metabolism during bud break and increase respiration rates after leave fall, respectively. (Knohl et al. 2003). All in all, both systems have their advantages, and the information about ecosystem respiration and soil respiration is essential for a proper carbon budget of an ecosystem. Care has to be taken to avoid biases in the measurements, but then chamber and eddy covariance measurements can with benefit supplement each other (e.g. Law et al. 1999; Shibistova et al. 2002).

Soil respiration is generally measured with a chamber in a portable, manual, closed path systems or a automated, more stationary, open path systems. Our own comparison of the closed path (Licor 6400-09) and the open systems by Pilegaard et al. (2001) and by Kutsch et al. (2000) have shown that the automated open system gave lower results than our system, especially at high flux rates (unpublished data). This is further supported in a study by Longdoz et al. (2000), but in contrast to the studies by Norman et al. (1997) and by Pumpanen et al. (2003). However, the automated open systems are all very different, so different performance can be expected. The forest in the national park Hainich has a very heterogeneous stand structure and large variability in soil respiration. If the soil respiration rates were measured at only a few locations, which is the normal scheme by automated chambers (e.g. Pilegaard et al. 2001; Drewitt et al. 2002), the estimates of soil respiration could easily have been significantly over or under estimated in our study – no matter at how high time resolution the data were collected. Ideally, our measurement scheme could have been supported by a few automated chambers in order to cover the temporal variation better, as long as this would not have implemented savings on the spatial coverage. However, combining the data from the closed chamber with the ecosystem respiration from the eddy covariance measurements allowed us to study spatial patterns as well as temporal dynamic of respiration.

4.4.3 Annual estimates of soil respiration – problems and considerations

The high spatial variability at our study site clearly created a challenge for precise upscaling of soil respiration chamber measurements. If soil respiration was measured in the main source area for the eddy covariance tower, the annual soil CO_2 efflux was estimated to 882 g C m^{-2} s^{-1}. However, if we had measured only in the five 5 locations closest to the tower, the annual efflux would have been estimated to 1172 g C m^{-2} s^{-1}, which is an overestimation of 33% compared to the main source area. In the extreme case, if the five locations with the lowest soil respiration rates by chance were chosen as "representative" for the forest, the annual estimate would have been about 500 g C m^{-2} s^{-1}. In contrast, if the locations with the highest rates were chosen, the estimated annual soil respiration would have been almost three times larger. In a boreal forest site, Shibistova et al. (2002) found a very heterogeneous stand structure with obvious patches of closed canopy and patches of open vegetation. In the open areas, soil respiration rates were only 50% of the rates under dense canopy. In order to take the heterogeneity of their site into account, they made a stratified measurement scheme, where they chose the number of measurement locations under dense canopy and the number in the open areas, representative for the coverage by each of the two types of vegetation. In a study by Davidson et al. (1998), wet and dry areas in a forest were identified and the experimental layout of measurement locations was stratified in relation to their soil moisture classification. However, the areas of high respiration (hotspots) or those with low efflux rates are not always easily identified. At our study site, the canopy was dense all along the transect, and the soil moisture was relatively constant form location to location. The main driving factor of soil respiration was the concentration of macro-nutrients in the soil (see chapter 3), a parameter that cannot be identified at a glance in the forest.

Large numbers of measurements are ideal for evaluation of soil respiration, but logistical constrains of labor and time often limit the number of measurements that are feasible. Davidson et al. (2002) presented some helpful calculations to identify the number of randomly located measurements needed in a tropical grassland to obtain certain levels of precession in their soil respiration estimates for the site. They showed that at a 95% probability level, 41 measurements were needed to give an estimate within ±10% of the full population mean, 10 measurements were needed to give an estimate within ±20% and 5 measurements were needed to give an estimate within ±30%. Similar results were found by Yim et al. (2003) in a Japanese larch plantation, who showed that 27 – 33 measurement locations were needed in order to stay within 10% of the population mean and 7 - 8 measurements to stay within 19% of the populations mean. Davidson et al. (2002) concluded

from their measurements that 6 – 8 flux measurements were necessary to describe the site in a proper way. However, this entails a deviation of ±20% or ±30% of the population mean, which in our study would have resulted in an annual estimate of 882 ± 88 or 882 ± 176 g C yr^{-1}. We find this deviation is too large to accept in a study like ours. We would rather recommend to stay within 10 – 20 % of the full population mean. Thus, for estimates of soil respiration to use as basis for a reliable carbon budget in a heterogeneous forest (with a similar structure than at the studied site), we recommend about 20 measurement locations spaced randomly in the area of interest, for example, the source area of the eddy covariance tower. However, the number of measurement locations needed for a given precision is site specific and changes from campaign to campaign. For a site with large spatial variation in soil respiration rates, a large number of sampling locations is needed for a precision of 10 – 20% of the population mean, while for a highly homogeneous site a lower number of locations is needed. We calculated the number of locations needed for each of the measurement campaigns during 2002 at our study site. The number needed for a precision of 10% of the population mean at a 95% probability varied between 25 and 70 and a precision of 20% varied between 6 and 18 locations. There was no specific pattern over the year to detect in the number of locations needed for a given precision. Thus, a strategy for a new study site would be to measure about 40 locations at a few measurement campaigns to get an estimate of the spatial variability and then calculate the number needed for a good cover of spatial variability. The number of location in the following measurements should be adjusted to that first estimate. This procedure would result in the soil respiration being described in a satisfactory way within time constrains.

4.4.4 Conclusions

Scaling from soil to ecosystem level is one of the main challenges that carbon cycle projects face. Especially, in long-term studies with many sites, e.g. CarboEurope (Valentini 2000) or Ameriflux (Wofsi and Hollinger 1998), a consistent and robust method to deal with spatial variability is essential for successfully scaling soil respiration to ecosystem respiration. From the results of our study we see potential in a two-fold approach. In a first step, spatial variability is captured in several intensive measurement campaigns in the first year. Based on this knowledge, a representative subset of plots is selected for chamber measurements in the following years. This approach will combine time limitations within the framework of a study with the requirement for precision of respiration estimates due to the objectives of the study.

5 Influence of elevated CO_2 on soil respiration and its partitioning into recently assimilated and older carbon sources

5.1 Introduction

Since the 1970s, it has been known that atmospheric concentrations of carbon dioxide are steadily increasing (Keeling et al. 1976). Models have predicted that from the present-day level of about 370 μmol mol^{-1} (ppm), atmospheric CO_2 concentrations will reach 550 μmol mol^{-1} in only 30 years (IPCC 2001). Recent literature suggest that plant growth and biomass production is generally stimulated at higher CO_2 levels (Amthor 2001). Beginning in the late 1980s (Hendrey et al. 1993), the Free Air Carbon-dioxide Enrichment (FACE) technique has offered the opportunity to study the influence of high CO_2 on plant and soil gas exchange while altering the ecosystem as little as possible (e.g. ambient soils, ambient climate, no chamber effect). Many FACE studies have shown that an increase in the level of atmospheric CO_2 will result in higher crop production (for example: wheat: Kartschall et al. 1995; grassland: Daepp et al. 2001). It is also well established that elevated CO_2 results in a higher fine-root production (wheat: Wechsung et al. 1999; cotton: Prior et al. 1994). Furthermore, Nitschelm et al. (1997) suggested that carbon storage increases in a grassland soil under elevated CO_2. However, only little information is available on soil CO_2 efflux and thus carbon sequestration in agricultural stands exposed to elevated CO_2 under otherwise natural conditions. Pendall et al. (2001) found a 40 - 70% increase of soil CO_2 efflux in a FACE experiment with wheat; Craine et al. (2001) measured a 13% increase in soil CO_2 efflux after CO_2 and N treatments in grassland.

Soil respiration is due to root activity and microbial decomposition of organic material. In this study, we define "recent" soil respiration as CO_2 derived from recently assimilated C, i.e. root respiration, respiration of root exudates and decomposition of new fine roots. On the other hand, we define "old" soil respiration as CO_2 derived from decomposition of organic material produced in previous years. Although the ability to partition these two carbon sources for CO_2 fluxes is critical to understand below-ground

processes, partitioning of soil respiration is still difficult (Hanson et al. 2000). Data obtained from greenhouse, open top chambers or laboratory studies may not reflect natural conditions since climatic and soil variables are excluded (or altered). Also destructive methods such as root exclusion alter soil conditions, particularly the soil water regime. However, using differences in natural ^{13}C abundances among plants and isotopic tracing techniques are useful for estimating the contribution of the two components of soil respiration with almost no soil or root disturbance (Rochette and Flanagan 1997; Ekbladt and Högberg 2000). Particularly FACE experiments, using CO_2 from a fossil source under otherwise natural conditions provide an approach with an isotopic tracer for the CO_2 assimilated by plants, which allows separation of the contributions of recent and old CO_2 to the total soil CO_2 efflux. However, although FACE experiments have been established in many different vegetation types, very few of these experiments usually have used the distinct isotopic signature of tank CO_2 to partition soil respiration into its two components. For a wheat field, Pendall et al. (2001) reported variation in the rhizosphere respiration from 0 - 65% of the total respiration over the growing season. For a loblolly pine forest, Andrews et al. (1999) calculated this contribution to be about 55% late in the season. Since only one FACE experiment with agricultural crops (Pendall et al. 2001) has provided insights into these below-ground processes, the aim of our study was to investigate soil CO_2 fluxes and their partitioning in a FACE experiment with sugar beet in Germany. We used the carbon isotopic tracer provided by the CO_2 gas in the fumigated FACE rings to quantify the contributions of recently assimilated C (from roots and rhizosphere) and of old C (from microbial respiration decomposition of older organic material) to total soil respiration. Furthermore, we tested the effect of two levels of nitrogen fertilization on these contributions.

5.2 Material and methods

5.2.1 Study site and plants

The FACE treatment has been applied since May 2000 in four rings (20m diameter) in an agricultural field at the experimental farm of the Federal Agricultural Research Center (FAL) in Braunschweig, Lower Saxonia, Germany (10°26′ E 52°18′ N, 79 m a.s.l). The design was according to Hendrey et al. (1993). Each ring was surrounded by vertical vent

pipes that extended to the top of the crop canopy. In the two replicated CO_2 treatment rings ("elevated rings"), CO_2 concentrations were maintained during the daytime in the growing season at approximately 550 μmol mol^{-1}, regulated according to wind speed, wind direction, and current CO_2 concentration. Two control rings ("ambient rings") were fumigated with ambient air only (about 370 μmol mol^{-1} CO_2). The four rings were located 100 m from each other to avoid increased CO_2 in the non-fumigated rings (Weigel and Dämmgen 2000). The research site has been used for agriculture for at least 30 years, and the vegetation has always consisted of C3 plants. The soil at the site is a cambisol/loamy sand (Parabrown Earth), with a pH of 6.3 - 6.5. The concentrations of soil organic carbon and nitrogen were 0.99% ± 0.07 and 0.09% ± 0.01% (0 - 20 cm), respectively. All soil, irrigation, fertilizer and pesticide management routines were carried out according to local farming practices. However, nitrogen fertilizer was applied in a split-plot design: half of each ring received the normal amount of N fertilizer (+N), while the remainder received half of this amount (-N) (in 2001: the +N treatment received 136 kg N ha^{-1}, and the -N treatment, 63 kg N ha^{-1}).

The crop in the year of experiment (2001) was sugar beet (*Beta vulgaris* subsp. *rapacea* (KOCH) DÖLL cv. Wiebke), while the previous year's crop was barley. Crop management practices were those typical for the region. The soil within the rings was plowed in the beginning of April 2001. One week later, the sugar beet seeds were sown. Two weeks later (14 May 2001), when seeds had germinated, fumigation started (daytime only). By the end of July, plants had reached their full height. Beets were allowed to grow until the end of September, when they were harvested and fumigation was terminated (25 September 2001). By mid-summer (June 2001), all plants looked healthy (above and below ground) and thus all data from our first measurement campaign in June were used. However, later in the season, *Rhizomania*, one of the most serious diseases of sugar beet, heavily infected the plants in two rings (one elevated and one ambient). *Rhizomania* is a virus (Beet Necrotic Yellow Vein Virus), which is transmitted by a soil-borne fungus (*Polmyxa betae kestin*) and infects beet roots. As a result, infected plants produce smaller beets with lower sugar content and a large proportion of fine roots, which die quickly. Due to the occurrence of this disease, data collected during our second campaign (August) were separated according to infected and non-infected rings.

5.2.2 Measurement of soil respiration

Soil respiration was measured in 40 locations, five in each N treatment per ring, both close to beet plants as well as between rows. The measurements were carried out with a Li-cor 6400-09 (a closed chamber system with an infrared gas analyzer for measuring CO_2 fluxes in the field). The protocol suggested by the manual was slightly modified, and five measurement cycles were used instead of three at all locations (Li-cor, Inc., Lincoln, Nebraska, USA). Each soil respiration measurement was accompanied by measurements of soil moisture at 6 cm (ThetaProbe, Delta-T Devices Ltd., Cambridge, UK) and soil temperature at 5 cm (Li-cor, Inc., Lincoln, Nebraska, USA). Measurements were carried out twice during the season: on a warm sunny day at the height of the growing season (27 June 2001), and on a cold, overcast day later in the season (6 August 2001). Each measurement campaign was spread over the day so that the order of measurements did not confound results. 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 collars prevented the soil from being disturbed at the time of measurement and allowed consecutive measurements to be made at the exact same positions over time.

5.2.3 Soil analyses

After the final measurement campaign, soil collars were removed and soil beneath the measurement locations was collected. Active soil microbial biomass was determined using the substrate-induced respiration technique (SIR), described by Anderson and Domsch (1978). Addition of 2 mg glucose g^{-1} soil was sufficient to reach maximum CO_2 efflux. CO_2 fluxes were measured hourly using an automated infrared gas analyzer system (Heinemeyer et al. 1989). In addition, active microbial biomass had been measured in randomly collected soil cores before and after the first measurement campaign (on 7 June and 12 July 2001). Stable carbon isotope ratios ($\delta^{13}C$) of soil and fine roots were measured on dried, ground material from the soil respiration collars using a mass spectrometer at the German Federal Agricultural Research Center, Braunschweig (Finnigan MAT Delta S coupled to a Carlo Erba NA 1500, Finnigan, Bremen, Germany).

Carbon contents of the soil were measured with an elemental analyzer (Elementar Analysensysteme GmBH, Hanau, Germany).

5.2.4 Stable carbon isotope analyses

Stable carbon isotope ratios ($\delta^{13}C$) are expressed in parts per thousand (‰) using the accepted PDB carbonate standard (Craig, 1957):

$$\delta^{13}C = [(({}^{13}C/{}^{12}C)_{sample}/({}^{13}C/{}^{12}C)_{standard})-1] \times 1000, \quad (1)$$

The CO_2 used for fumigation was derived from natural gas and was therefore strongly depleted in ^{13}C ($\delta^{13}C$ = -45‰ vs. PDB). Using this tank CO_2, the atmospheric CO_2 concentration was increased from 370 µmol mol^{-1} to 550 µmol mol^{-1}, which changed the atmospheric $\delta^{13}C$ in the elevated rings from -7.82 ± 0.10‰ to -20.51 ± 2.99‰.

To determine the $\delta^{13}C$ of soil CO_2 efflux, soil-respired air was sampled from four locations in each ring prior to soil collection in August 2001. Sample collection was spread over the day to avoid bias in the data due to diurnal trends. A cylinder made of PVC plastic with a metal lid was placed on the pre-installed soil collars to create a headspace above the soil surface with a total height of 10 cm and a diameter of 10 cm. The lid of the upper cylinder and the juncture of the two cylinders were sealed gas-tight with a rubber ring and a plastic-coated metal ring, respectively. In the metal lid, a three-way valve (Swagelock, Ohio, USA) connected the headspace of the chamber through a drying column (with magnesium perclorate) to a vacuum pump to the one side and a capillary with a syringe needle to the other side. Air samples were collected via the syringe needle to 12 ml glass vials with rubber septa (Europa Scientific Ltd., Crewe, UK). For air collection, the vial and the sampling line were first evacuated and then flushed twice with soil-respired air before an air sample was collected for stable isotope analysis. The chamber was left on the measurement location for 15 min, during which five air samples were collected. Since only very small volumes of air were used to flush and sample in the vials, the pressure in the chamber only experienced a minute change, which was corrected for in the calculations. The CO_2 concentration in the samples was determined by measuring the initial soil respiration rates (with a Li-cor 6400) and

extrapolating to subsequent samples according to this production rate. Results of earlier tests showed no significant fractionation during vial storage for one week. Thus, all samples were analyzed within one week after sampling. The stable carbon isotope ratios in air were measured with an isotope ratio mass-spectrometer (IRMS) (Delta XL, Finnigan MAT, Bremen, Germany) in combination with a Gasbench II and an autosampler at the Max-Planck-Institute for Biogeochemistry, Jena. Furthermore, in each ring, three air samples were collected just above the crop canopy in order to determine the atmospheric $\delta^{13}C$ value.

The air in each sample was a mixture of soil-respired air and atmospheric air. The $\delta^{13}C$ of pure soil-respired air at each measurement location was calculated using so-called "Keeling-plots" (Keeling, 1958, 1961). This means that $\delta^{13}C$ was plotted against the reciprocal of the CO_2 concentration in the sample vials, and the $\delta^{13}C$ value of soil-respired CO_2 was determined as the y-axis intercept of a geometric mean regression line through the five measurement points (Sokal and Rohlf, 1997).

5.2.5 Mixing model

The contribution of recent respiration to soil-respired CO_2 was calculated using a two-component mixing model:

$$\delta^{13}C_{\text{soil-respired air}} = a\,(\delta^{13}C_{\text{recent}}) + b\,(\delta^{13}C_{\text{old}}), \qquad (2)$$

$$a + b = 1 \qquad (3)$$

where a is the proportion of CO_2 generated from recent respiration, and b represents the proportion of respired CO_2 originating from the older active carbon pool (soil organic matter). The $\delta^{13}C_{\text{recent}}$ values were set equal to that of roots at the measurement location (assuming no fractionation by plant respiration, as suggested by Lin and Ehleringer (1997)). $\delta^{13}C_{\text{old}}$ values were those of root-free soil.

5.2.6 Statistical procedures

Analyses of variance, comparison of means, simple regressions and multiple regressions were carried out in JMP (SAS Institute Inc., Connecticut, USA). Soil microbial biomass

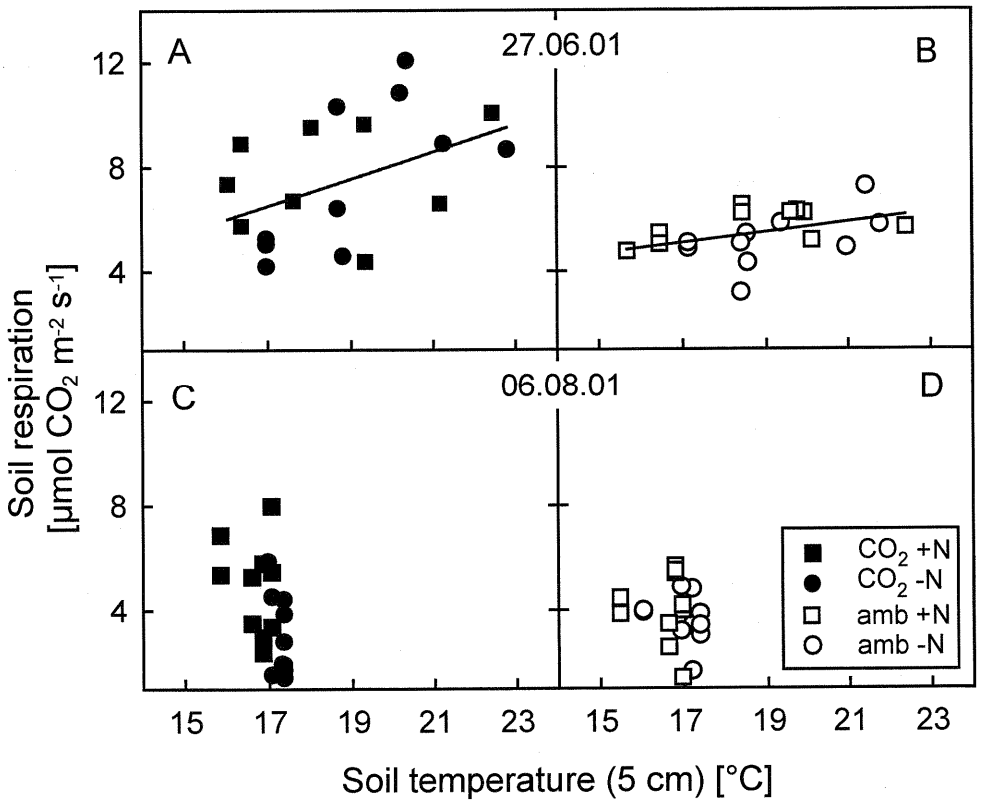

Fig. 5.1. Soil respiration as a function of soil temperature in the Braunschweig FACE experiment (A and B, 27 June 2001; C and D, 6 August 2001). Elevated rings (fumigated with tank CO_2) are indicated with filled symbols; ambient rings (with atmospheric air) are represented with open symbols. High and low nitrogen levels are indicated with squares and circles, respectively. In total, soil respiration was measured in 40 measurement locations per campaign. Linear regression lines are fitted to the June data (for further explanation, see text).

was measured in 8 replicate soil samples per treatment in June/July and in 10 replicate samples per treatment in August. Soil respiration was measured at 40 locations in both June and August, giving 10 replicates per treatment. A general statistical problem in FACE experiments is the low number of replicate rings due to the very high expenses of running a FACE site (Filion et al. 2000). The trade-off between statistical power and experimental cost has been discussed in the literature in the light of avoiding the problem of pseudo-replication (Hurlbert 1984; Filion et al. 2000). Suggestions have been made to build more FACE rings at the sites, change the α-value for statistical analysis from 0.05 to 0.1, pool data from different FACE sites or only present data as percentage

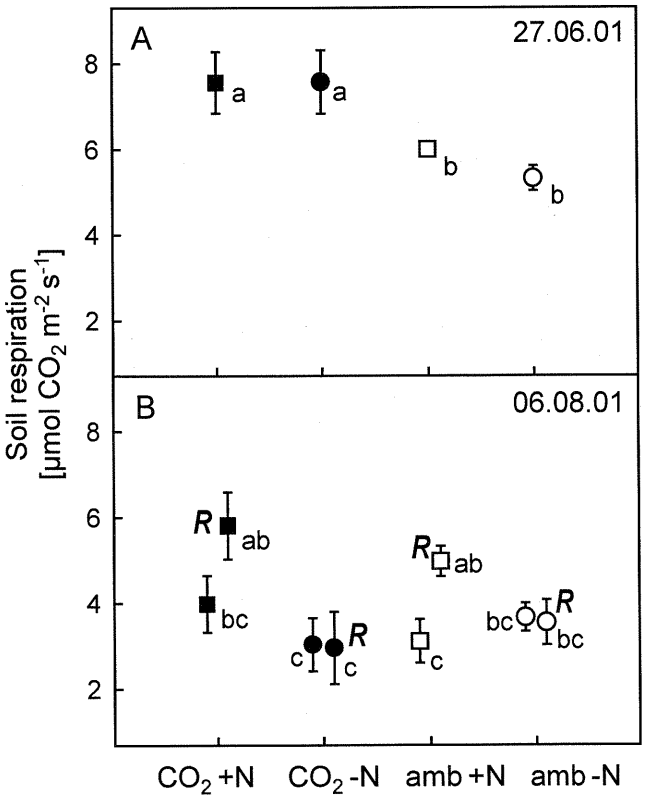

Fig. 5.2. Soil respiration for the different treatments in the Braunschweig FACE experiment in June 2001 (A, data have been normalized to the mean soil temperature at 5 cm soil depth, 19.06 °C), and in August 2001 (B, no temperature correction was applied). Elevated rings are indicated with filled symbols; ambient rings with open symbols. High and low nitrogen levels are indicated with squares and circles, respectively. Measurement locations, where plants were heavily infected by the disease *Rhizomania,* are marked with '***R***'. Means and S.E. (n = 5) are presented. Letters indicate significant differences among means (LSD, α = 0.05).

comparisons of mean values (Andrews et al., 1998; Filion et al. 2000). All of these solutions were either not wanted or possible in the Braunschweig FACE experiment. Because of the problems created in two of the rings by the infection of the beet plants in the late summer, nested ANOVA's were not possible in this study. Thus, we chose to run ordinary statistical analysis on the data, and the results from the inferential statistical analysis should therefore be interpreted under consideration of the points discussed above.

5.3 Results

Soil respiration rates measured in June on a warm sunny day tended to increase with increasing soil temperatures (Fig. 5.1. A: $y = 0.52\,x - 2.29$, $r^2 = 0.18$, $p = 0.064$ for elevated rings, and Fig. 5.1. B: $y = 0.20\,x + 1.74$, $R^2 = 0.16$, $p = 0.077$ for ambient). For further comparisons among treatments, we normalized the June soil respiration rates to the mean soil temperature at 5 cm depth (19.06 °C). Soil water content was not correlated

with soil respiration rates (p = 0.865; data not shown). During the August measurement campaign (cold, cloudy day), only small variations in soil temperature and soil respiration rates were observed. The functional relationship between soil respiration and soil temperature was therefore not significant (p > 0.1; Fig. 1. C and D), and no temperature correction was necessary for further analysis. Soil moisture content also in August was not correlated with soil respiration rates (p = 0.136).

In June, soil CO_2 efflux in the elevated rings was significantly higher (by 34%, p = 0.001) than that in the ambient (control) rings, whereas the N-level had no influence on soil respiration (all data: p = 0.586; elevated: p = 0.992; ambient: p = 0.060) (Fig. 5.2. A). In contrast, during the August measurement campaign the CO_2 treatment had no significant influence on soil respiration (p = 0.778; Fig. 2. B). In addition, due to the *Rhizomania* infection, all three main factors, the disease itself, the N level and the interaction *Rhizomania* X N were significant (p = 0.049, p = 0.010 and p = 0.030, respectively). Thus, August results from infected locations were separated for all further analyses.

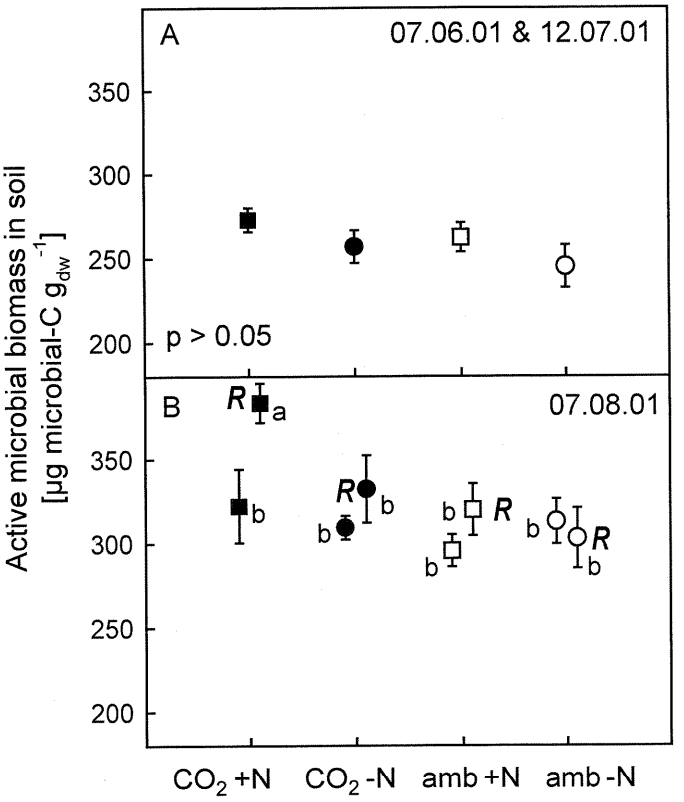

Fig. 5.3. Active microbial biomass measured in June-July (A) and in August 2001 (B). Filled and open circles indicate elevated and ambient rings, respectively. Squares and circles represent high and low N treatments, respectively. Symbols marked with '***R***' indicate measurement locations with infected plants. Means and S.E. are presented (A: n = 4; B: n = 5). Letters indicate significant differences among means (LSD, α = 0.05).

Table 5.1. $\delta^{13}C$ values (‰) for canopy air, foliage, roots, and top-soil from the Braunschweig FACE experiment. The $\delta^{13}C$ value of the tank-CO_2 used for fumigation was -45‰. Means and S.E. are given (air: $n = 3$; foliage: $n = 4$; roots: $n = 6$; soil: $n = 20$). Significant levels for t-tests: *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

	elevated	ambient	difference
$\delta^{13}C_{air}$	-20.52 ± 2.99	-7.82 ± 0.10	12.7 *
$\delta^{13}C_{foliage}$	-43.39 ± 0.20	-28.99 ± 0.38	14.4 ***
$\delta^{13}C_{roots}$	-40.49 ± 0.14	-27.39 ± 0.25	13.1 ***
$\delta^{13}C_{soil}$	-27.15 ± 0.12	-26.74 ± 0.06	0.4 **

Active soil microbial biomass did not differ significantly among any treatments in June and July 2001 ($p = 0.284$ for CO_2; $p = 0.104$ for N; Fig. 5.3. A), nor in August (Fig. 5.3. B). One exception was the soil microbial biomass in one infected ring of the CO_2 + N treatment, which differed significantly from all other rings ($p = 0.013$).

Pronounced effects of the CO_2 enrichment were seen for all carbon isotope analyses (Table 5.1). While the source air CO_2 in the ambient plots reflected atmospheric CO_2 with a $\delta^{13}C$ of about -7.8‰, the $\delta^{13}C$ values of CO_2 in the elevated rings averaged -20.52 ± 2.99‰, due to mixing with the strongly depleted tank CO_2 (see methods). This carbon isotopic difference of source air CO_2 for assimilation was 12.7‰ depleted in the elevated rings in comparison to the ambient rings. This difference was carried over into sugar beet leaves (14.4‰ depletion), and subsequently to roots (13.1‰ depletion). However, the difference of the $\delta^{13}C$ of the soil in the CO_2-enriched and the ambient rings was only 0.4‰, reflecting the low proportion of soil organic matter accumulated during the short time the FACE experiment had been operated.

We calculated the $\delta^{13}C$ values of soil-respired CO_2 (using the Keeling plot approach) (Fig. 5.4). The relationships between the inverse of CO_2 concentration and the corresponding $\delta^{13}C$ value was significant for all non-infected plots ($r^2 > 0.995$, $p < 0.024$), while some of the relationships for the *Rhizomania* infected plots were not significant ($r^2 > 0.959$, $p < 0.124$). The $\delta^{13}C$ of soil-respired CO_2 from the elevated rings

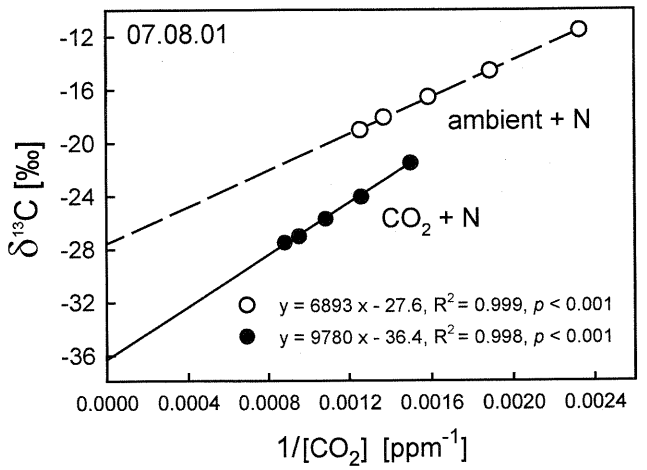

Fig. 5.4. Representative Keeling plots from elevated and ambient treatment rings of the FACE experiment in Braunschweig (n = 5 per regression). The intercepts of the linear regression lines represent $\delta^{13}C$ values of soil-respired CO_2.

was significantly lower than that from the ambient rings (on average 9.6‰ depletion, $p < 0.001$, Fig. 5.5. A, non-infected rings), whereas no difference was observed among the N treatments. Due to the large variability of $\delta^{13}C$ values of soil-respired CO_2 of infected rings (S.E. 0.89 to 4.55‰) compared to non-infected rings (S.E. 0.09 to 0.95‰) (Fig. 5.5. A and B), infected rings were not considered in partitioning calculations.

The contribution to soil respiration originating from recently assimilated versus older carbon was calculated using the $\delta^{13}C$ values of soil-respired CO_2 from the Keeling plots (Fig. 5.5) and the $\delta^{13}C$ values of roots and soil organic matter from the corresponding locations (Table 5.1). In the non-infected elevated ring, the contribution of recent carbon (i.e. roots and their rhizosphere) to total soil respiration was about 70%, the contribution from old carbon (microbial decomposition of older soil organic matter) accounted for the remaining 30% (Table 5.2). These relative proportions of recently fixed, root respired versus older soil organic matter, microbially respired CO_2 were not affected by the levels of nitrogen fertilization ($p = 0.982$). Whether the measurement locations were close to or far away from a plant did also not affect the proportion of root-respired carbon either.

5.4 Discussion

Using stable carbon isotopes to partition the total soil CO_2 efflux into respiration of recently assimilated carbon versus respiration of older soil organic matter, about 70% of

the soil-respired carbon originated from recent assimilation. This was true independent of the N level. Although soil respiration rates have more frequently been measured at FACE sites during the last few years (e.g. Craine et al. 2001; King et al. 2001; Pendall et al. 2001), the partitioning of soil respiration into recent and older components has been done in very few FACE experiments. Andrews et al. (1999) found that root respiration contributed 55% to total soil respiration late in the growing season in a loblolly pine forest. Pendall et al. (2001) showed for a wheat FACE experiment, that in winter no respiration of new carbon occurred, and that the proportion of root respiration increased until a maximum of 65% of total soil respiration was reached early in the growing season. The importance of roots for the overall response of plants to increased atmospheric CO_2 concentrations has been demonstrated by an increase of fine root biomass in most FACE

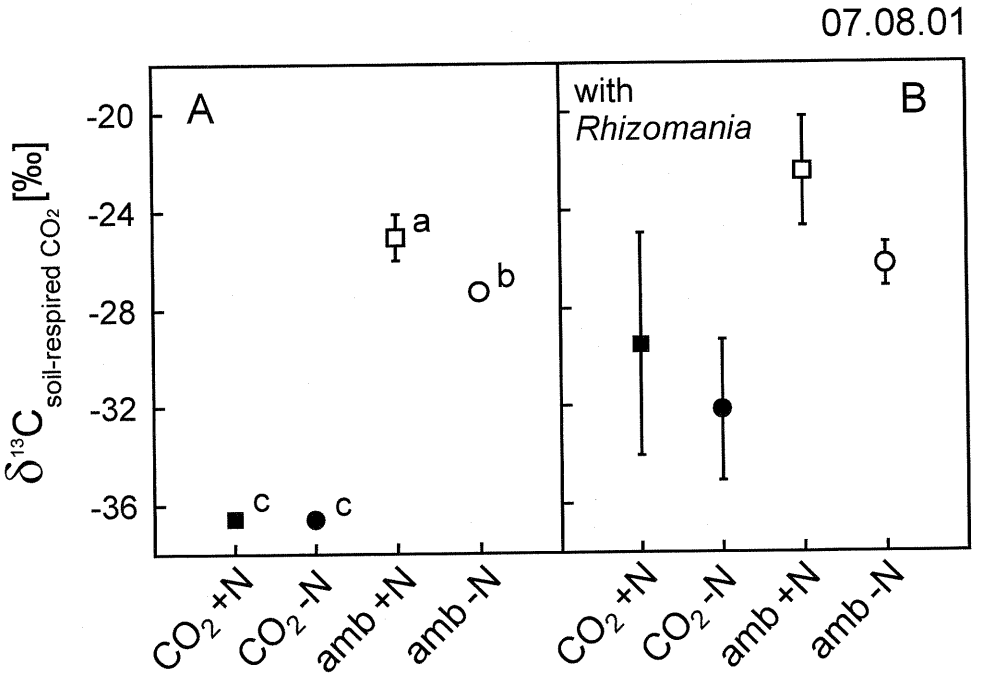

Fig. 5.5. $\delta^{13}C$ values of soil-respired CO_2 from the different treatments in the Braunschweig FACE experiment. Data from rings with healthy plants (A) were separated from those rings with infected plants (B). Filled and open circles indicate elevated and ambient rings, respectively. Squares and circles represent high and low N treatments, respectively. Means and S.E. (n = 2) are presented. Letters indicate significant differences among means (LSD, α = 0.05).

Table 5.2. Proportions of active C pool originating from recently assimilated carbon (roots and rhizosphere) and older carbon (soil organic matter). Estimates were calculated for the four locations in the uninfected FACE ring with elevated CO_2 in August 2001.

location	CO_2 +N		CO_2 –N	
	recent C	old C	recent C	old C
near beet plant	70%	30%	68%	32%
between beet plants	69%	31%	73%	27%

experiments (e.g. Prior et al. 1994; Wechung et al. 1999; King et al. 2001). At the Braunschweig FACE site fine root biomass during summer 2001 was about 35% higher in the high CO_2 compared to the ambient rings (Bernd Kleikamp, personal communication), while leaf biomass of the sugar beet plants had not increased due to the CO_2 enrichment (Remy Manderscheid, personal communication). The proportionally larger influence of elevated CO_2 on root than on leaf biomass is well established in the literature (e.g. Rogers et al. 1996). However, so far the effect of short-term environmental changes in radiation or temperature (sunny vs. overcast day) on root or total soil respiration, as seen in our study, has not been reported before. Soil respiration rates on a sunny day were 34% higher under high CO_2 compared to ambient conditions. This increase of soil respiration is in accordance with results from other FACE experiments, e.g. in wheat crop (Pendall et al. 2001) and in deciduous forest (King et al. 2001). However, on an overcast day soil respiration rates did not differ between elevated and ambient treatments. Thus, we hypothesize that due to the large contribution of recently assimilated carbon, we found large differences in soil respiration among CO_2 treatments during conditions favorable for plant activity (sunny day), but not under cold, overcast conditions. Since soil temperatures were similar in all rings within a measurement campaign, these temporal differences in soil respiration under high CO_2 indicate a strong

impact of plant photosynthesis on soil CO_2 efflux, just as demonstrated in a large-scale girdling experiment in Northern Sweden (Högberg et al. 2001). This is further supported by the fact that on the sunny day, the temperature response in the elevated rings seemed stronger than in the ambient rings (Fig. 5.1. A and B), although the interaction term Temp X CO_2 was not significant ($p = 0.3$).

N fertilization showed no effect on soil respiration rates, microbial biomass, or $\delta^{13}C$ values of soil-respired air in our study at the Braunschweig FACE experiment (neglecting results from infected plots, see below). Although plants produced more leaf biomass in plots that received high N (136 kg N) compared to those in plots with low N (63 kg N) (Remy Manderscheid, personal communication), this pattern was not reflected in fine root biomass (Bernd Kleikamp, personal communication) or in soil respiration rates. While Brooks et al. (2001) and Daepp et al. (2001) also reported higher biomass production by CO_2 and N treatments in wheat and grassland, respectively, no information was available in those studies on soil respiration. Craine et al. (2001) found an increase in soil respiration by high N and CO_2 levels in a grassland community, which was relatively poor in N. Thus, in our study (at a nutrient rich agricultural site) N seemed not to be a controlling factor for soil respiration.

The low contribution (only 30%) of microbial decomposition of old soil organic carbon to total soil CO_2 efflux under high CO_2 is supported by measurements of microbial biomass that did not differ among treatments during our study. Similar results were found in a grassland FACE (Schortemeyer et al. 1996) and a pine FACE (Allen et al. 2000), where microbial biomass did not increase as response to high CO_2. We measured higher soil respiration rates and microbial biomass in only one CO_2+N plot where plants were infected with *Rhizomania*, a plant root-virus. However, this increase was probably due to the presence of large amounts of dead roots, substrate for increased microbial decomposition. The high percentage of root respiration by elevated atmospheric CO_2 concentration demonstrates the vulnerability of the plant/soil system to quickly loose much of the surplus carbon assimilated under high CO_2 through root (and rhizosphere) respiration, a phenomenon often ignored by terrestrial carbon models.

Whether increased atmospheric CO_2 concentrations will lead to increased soil organic matter decomposition ('priming effect') and therefore to a net loss of soil organic

carbon, or to increased soil carbon accumulation is still a matter of debate (Torbert et al. 1997; Pendall et al. 2001). Pendall et al. (2002) found an enhanced decomposition of slow C, but even faster rates of new C input, resulting in a net C accumulation under elevated CO_2. We found no significant changes in the soil carbon content in the upper 10 cm in the elevated rings compared to the ambient rings (data not shown; $p = 0.180$, t-test, $n = 20$). Nor did we find changes in soil density among treatments ($p > 0.05$). Furthermore, the $\delta^{13}C$ of soil organic matter was depleted by only 0.4‰ in the elevated CO_2 treatment compared to the ambient, although large $\delta^{13}C$ depletion (13 – 14‰) were detected in roots and soil-respired air. Though significant, this 0.4‰ depletion in the soil $\delta^{13}C$ could have been due to minute amounts of root material that might not have been removed despite careful sieving and hand picking roots out of the soil samples. Thus, no (or only very little) recently assimilated carbon was stored in the soil of the Braunschweig FACE experiment during the first two years of CO_2 fumigation. Traditional harvest practices and soil treatments, i.e. ploughing twice a year, might counteract the detection of carbon accumulation in the top soil. Results from other experiments with elevated CO_2 in wheat and grassland only showed an increase of the labile soil carbon pool (Hungate et al. 1997; Cheng and Johnson, 1998; Gill et al. 2002), which was lost from the system almost immediately, resulting in no detectable changes in the bulk soil carbon pool. On the other hand, Nitschelm et al. (1997) reported an increase in new soil C input of 1 t ha^{-1} after one year of elevated CO_2 concentration compared to ambient conditions. However, three years later, this large C sequestration in soils under elevated CO_2 was not detected any more, and species composition rather than CO_2 treatment seemed to be the driving factor for soil C pools (van Kessel et al. 2000). Thus, in general, the proposed capability of soils (Tans et al. 1990) to act as long-term storage pools for the increased carbon inputs into the ecosystem under high CO_2 conditions seems to be either highly variable or – most probably - very small if any (Gill et al. 2002).

6 Concluding discussion

Soil carbon (C) pools and soil respiration are large in comparison to C pools in the atmosphere and net ecosystem fluxes (IPCC 2001). Consequently, small changes in the magnitude of soil respiration can significantly alter the atmospheric CO_2 concentration (Jenkinson et al. 1991; Schlesinger 1997; Churkina et al. 2003). I order to predict future changes in soil respiration and to develop sustainable mitigation strategies we aimed to: (1) identify temporal and spatial controls of soil respiration, (2) partition soil respiration into recent and older carbon sources (processes may have different sensitivity to temperature), (3) investigate soil respiration in changing climate, and (4) scale from soil (chambers) to ecosystem level.

6.1 Temporal and spatial controls of soil respiration

Soil temperature was shown to be the most significant factor for temporal variation in soil respiration rates at a single location (or for mean values from a specific set of locations) at the forest site in the National Park Hainich (see chapter 2 and 4). During drought we found that low soil water contents were limiting for soil respiration. We demonstrated a higher threshold for drought limitation (23 Vol%) than what was reported by Davidson et al. (1998) for a North American hardwood forest (about 10 Vol%). The different response to soil moisture could be referred to the high clay content (reducing the plant available water content) in the soil at the Hainich site. Thus, although soil moisture is often not included in models for soil respiration (Lloyd and Taylor 1994; Buchmann 2000), we showed that even for a relatively moist forest, including soil moisture strengthened the explaining model for soil respiration considerably (r^2 increased from 0.68 to 0.90 in a year with a dry period).

Spatially, soil respiration was shown to be almost as variable as it was the case temporally. However, for this variation, soil temperature only played a minor role. Concentration of sulfur in the soil was the parameter that was most highly correlated with soil respiration spatially (explained 61% of variation, see chapter 3). Sulfur is present in organic material (e.g. in many proteins) and, thus, an essential component in the metabolism of all living organisms. However, to our knowledge, we are the first to

investigate soil respiration in relation to sulfur in a forest ecosystem. The soil at the Hainich site is nutrient rich, and therefore excellent for beech growth. Furthermore, there is a high nitrogen deposition in this area of Central Europe (Umweltsbundesamt 2000), and the site is shown to have a relatively closed nutrient cycle since almost no leaching could be detected (Gerd Gleixner, personal communication). The above mentioned facts make it plausible that the biological activity of the system may not necessarily be limited by nitrogen or carbon, but might also be limited by other nutrients, such as sulfur, phosphorus or magnesium. It could be hypothesized that sulfur measured in the soil was either present in the organic matter, possibly in readily available amino acids, or that it was present in microbial cells, and as such high sulfur concentrations would indicate increased microbial activity/biomass. Since other studies have shown that under normal conditions more than 90% of sulfur in soil is present in organic matter (Tabatabai 1996) and only up to 5% is found in microbial biomass (Paul and Clark 1996), we believe that sulfur in our soil samples mainly was present in organic matter.

Although sulfur being the parameter, best correlated with soil respiration, we also found a high correlation of soil respiration with concentrations of nitrogen and carbon in the soil. Furthermore, the concentrations of the three components were highly inter correlated, indicating a relatively constant ratio between C, N and S at the study site. The importance of macro-nutrients in the soil (mainly N and P) for spatial variability of soil respiration was also found in other temperate forest ecosystems (Xu and Qi 2001a; Pangle and Seiler 2002; Borken et al. 2002). Soil bulk density was highly correlated with rates of soil respiration, possibly via the influenece of the concentrations of macro-nutrients (due to clay contents, humus or soil fauna, for further details see chapter 3). Thus, the parameters related with the concentration of macro-nutrients were shown to be the key explaining variables in the Hainich forest.

At the study site we detected a pattern of high and low soil respiration rates that stayed surprisingly constant over the growing season as well as between years. This result is remarkable in the respect that only very few studies have investigated spatial patterns of soil respiration (Stoyan et al. 2000; Savin et al. 2001). The reason for the stability of this must be sought in a stability of some factors controlling soil respiration. Thus we correlated soil respiration with fine root biomass and with several stand structural

parameters. Although sulfur was the most highly correlated parameter with soil respiration, fine root biomass and one stand structural parameter (average diameter of trees in a 4-m circular ring, av-dbh4) were also highly correlated with soil respiration. The fine root biomass was correlated with sulfur, which may be explained by either more roots where plenty of sulfur was present or more sulfur (from root exudates or root litter) where the fine roots density was high. However, a clear conclusion cannot be drawn without more studies. Several hypothesis why the presence of large trees (high av-dbh4) was significant for soil respiration can be put forward: (1) large trees might have relatively large root biomass compared to the above ground biomass for supporting purposes, or (2) large trees possibly have high maintenance metabolism due to the large stem biomass, or (3) in the competition the large trees could have an advantage over the smaller trees in the way that the upper canopy trees gets more light than the lower canopy trees. Since the fine root biomass was not highly correlated with av-dbh4, the first hypothesis can be rejected and hypothesis two or three (or both of them) seem to be correct. 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.

The role of stand structure for soil respiration may be of great consequence for ecosystem models as well as management recommendations. In ecosystem models, such as BIOME-BGC, the stand structure is not explicitly added as a parameter (Churkina et al. 2003). Either a steady state or a certain age of the forest is used as starting point for the model iterations. However, our results suggest that the actual stand structure of the forest is relevant for ecosystem processes, since large trees were found to respire at higher rates than small trees. This may shift the balance between autotrophic and heterotrophic respiration as well as nutrient availability or utilization. We therefore suggest to calibrate ecosystem models with stand structural parameters before running a model on an ecosystem.

In the light of the Kyoto protocol, more focus has in recent years been put on the role of forests as sinks for atmospheric CO_2 (Murray et al. 2000; Schulze et al. 2000). Our result have shown that roots from old trees respire more than roots from young trees, this may, however, not implicate that an older forest has a higher net carbon loss than a

young forest. In contrast recent literature has pointed to a high carbon sequestration in old stands (Schulze et al. 1999; Knohl et al. 2003). Thus, a sustainable management strategy would not be to minimize soil respiration, but rather to retain old forest, because an undisturbed soil-plant system may sequester more carbon than a disturbed system (Schulze at al. 2000).

6.2 Partitioning of soil respiration into recent and older carbon sources

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 and recent carbon) is essential. To obtain a mechanistic understanding of these processes in a future changed climate, we chose to carry out a part of our study in the "Free Air Carbon dioxide Elevated experiment" (FACE) in an agricultural field close to Braunschweig (see chapter 5). This site, in contrast to the Hainich forest site, was a simple ecosystem, relatively homogenous, with only a single species. We had full control to manipulate the ecosystem in order to elevate the CO_2 and manipulate the nitrogen fertilization. Due to the fumigation-gas depleted in ^{13}C, the experiment provided us with a site where parts of the system became isotopically labeled. With the aim to partition soil respiration, we developed a chamber and a measurement procedure, where the isotopical signal of the respired CO_2 could be calculated. Thus, our method used in the FACE experiment was optimal for (1) understanding processes in an experimental setup where the delicate soil-root-microbe community could be left almost undisturbed, (2) explore the potential of stable isotopes to partition soil respiration into respiration of recently assimilated carbon versus older soil organic matter, and (3) investigate soil respiration in changing climate. Using the stable carbon isotopes to partition the total soil CO_2 efflux into recent and older carbon, we calculated that about 70% of the soil-respired carbon originated from recent assimilates. Although, FACE experiments provide an ideal experimental setup for partitioning soil respiration and study soil respiration processes under changed climate, only in very few FACE experiments soil respiration has been partitioned. Pendall et al. (2001) and Andrews et al. (1999) found that recent carbon constituted 65 and 55% of the total soil respiration during summer in FACE experiments in a wheat field and a pine forest, respectively. The high percentage of root respiration by

elevated atmospheric CO_2 concentration demonstrates the vulnerability of the plant/soil system to quickly loose much of the surplus carbon assimilated under high CO_2 through root (and rhizosphere) respiration, a phenomenon often ignored by terrestrial carbon models.

6.3 Investigation of soil respiration in changing climate

Effects of climate changes were studied indirectly in the forest ecosystem at the Hainich site and directly in the FACE experiment. A higher atmospheric CO_2 concentration in the future is considered to lead to climate changes due to enhanced greenhouse effect (increase in the global mean temperature and most likely increase of winter precipitation and more pronounced summer droughts (IPCC 2001)). At the forest site the temperature sensitivity (Q_{10}) in a root free plot was 1.9, while in plots with high fine root biomass the measured Q_{10} values were as high as 4.7 (see chapter 4). The differences in the fine root biomass explained 83% of the variation in Q_{10} of the soil respiration flux. Thus, our results (from relatively short term measurements) suggest that soil respiration will increase proportionally more in areas with large root activity than in other areas in response to an increase in temperature. If higher soil respiration rates are connected with a similar size increase in photosynthesis, surplus soil respiration will only be caused by direct root respiration and respiration of the labile carbon pool (root exudates and root turnover). Under this scenario the more permanent soil carbon pool will therefore not be affected and no (negative or positive) feedback on the atmospheric CO_2 concentration will occur. However, increased carbon storage with higher temperature could occur if the biomass production would increase and part of this would be incorporated into the more permanent soil carbon pool. On the other hand, loss of carbon from the soil pool has also been suggested in the literature as response to an increased soil respiration, due to the so-called "rhizosphere priming effect" (Kuzyakov Y. 2002). Living plants change the local environment in the rhizosphere and consequently affect the rate of soil organic matter decomposition. The increase in microbial activity in the rhizosphere through utilization of additional easily available carbon sources may lead to a subsequent intensive microbial mobilization of nutrients from the more permanent soil organic matter. The understanding of interactions between root and microbial respiration and their distinct

responses to changing temperature and substrate availability is therefore essential in order to predict to which extend forests may react as sinks or sources for carbon in a future climate.

In the Braunschweig FACE experiment we found that soil respiration rates on a sunny day were 34% higher under high CO_2 compared to ambient conditions, similar to the increase in fine root biomass by CO_2 treatment (see chapter 5). However, on an overcast day soil respiration rates did not differ between elevated and ambient treatments. Thus, we hypothesize that due to the large contribution of recently assimilated carbon and the larger fine root biomass in the elevated plots, we found large differences in soil respiration among CO_2 treatments during conditions favorable for plant activity (sunny day), but not under cold, overcast conditions. Increased atmospheric CO_2 concentration could lead to either a net gain (via increased biomass production) or loss (via rhizosphere priming effect) from the soil carbon pool (Torbert et al. 1997; Pendall et al. 2001). Pendall et al. (2002) found a net C accumulation under elevated CO_2, while Hungate et al. (1997), Cheng and Johnson (1998) and Gill et al. (2002) showed an increase only in the labile soil carbon pool, which was lost from the system almost immediately, resulting in no detectable changes in the bulk soil carbon pool. In our experiment, the bulk soil carbon pool had not changed remarkably after two years of FACE experiment in an agricultural field. Although soils have been proposed to be able to act as long-term storage pools for the increased carbon inputs into the ecosystem under high CO_2 conditions (Tans et al. 1990), our results suggest that this hypothesis may not hold true.

Nitrogen fertilizer was added in the FACE experiment in the normal (136 kg N ha^{-1}) and a lower amount (63 kg N ha^{-1}) (see chapter 5). Although the leaf biomass increased by high fertilization (Remy Manderscheid, personal communication), no significant effect of N was detected in the rates of soil respiration, nor in the balance between autotrophic and heterotrophic respiration. We hypothesize that the agricultural soil at the study site was so rich in nitrogen (due to fitilization in former years) that a reduction in nitrogen addition did not influence soil respiration. If the treatments are carried out over longer time, it is possible that effects will be observed. With high CO_2 levels, the C/N ratio of biomass may increase leading to slower litter decomposition. Slower respiration of organic matter could increase the soil carbon pool, but may also

decrease plant growth, which might have large implications for the world food production. A general conception is that photosynthesis and biomass production will be enhanced with higher levels of CO_2 (Amtor 2001), but if a counter reaction with nitrogen occurs negative socio-economical effect or environmental consequences (due to excessive fertilization) may be the result.

6.4 Scaling from soil (chambers) to ecosystem level

Soil respiration, measured in chambers, is often used in combination with measurements of ecosystem respiration. When ecosystem respiration is measured with the eddy covariance system, the measurements integrate over a larger area, whereas, the soil respiration chambers each cover a small area. Therefore, the high spatial variability at our study site required a detailed experimental design to successfully scale from soil respiration measurements from chambers to the ecosystem. A task that is necessary in order to calculate a robust carbon budget and evaluate ecosystem models (Churkina et al. 2003; Kimball et al. 1997). With our study we managed to evaluate the spatial and temporal variability of soil respiration rates at the forest study site, and developed a design that produces robustly upscaled estimates of the flux rates (see chapter 4). If the five locations with the lowest soil respiration rates by chance were chosen as "representative" at the forest site, the annual estimate would have been about 500 g C m^{-2} yr^{-1}. In contrast, if the locations with the highest rates were chosen, the estimated annual soil respiration would have been approximately three times larger. The same estimate based on a more representative set of measurement locations (between 19 and 36 locations) was 882 to 913 g C m^{-2} yr^{-1}. If clear differences can be detected at a study site, such as gaps versus dense vegetation or wet versus dry areas, a stratified design of measurement locations may be applied (Shibistova et al. 2002; Davidson et al. 1998). However, at our study site no obvious distinct classes of subplots could be identified. Large numbers of measurements are ideal for evaluation of soil respiration, but logistical constrains of labor and time often limit the number of measurements that are feasible. In order to cover the spatial variability in soil respiration rates in the source area of an eddy covariance tower, we measured 40 locations. Afterwards, using a power analysis we estimated the number of soil respiration measurement locations needed for given levels of

precision. About 20 measurement locations would have been necessary for a precision of 10 - 20% of the full population mean using a 95% confidence interval. For carbon cycle projects, e.g. CarboEurope (Valentini 2000) or Ameriflux (Wofsi and Hollinger 1998), a consistent and robust method to scale from soil respiration measurements to a larger area (e.g, the main source area of an eddy covariance tower) is essential. Our results suggest a two-fold strategy. Firstly, to capture the spatial variability in a few intensive measurement campaigns. Secondly, to select a representative subset of plots for chamber measurements in the following long-term campaigns. This approach would optimize the precision of respiration estimates under labor and financial constrains.

6.5 Future perspectives

With this study we have achieved to present a comprehensive picture of soil respiration at various temporal and spatial scales. Despite complexity and large natural variability in soil processes, we could firstly partition the sources of soil respiration, secondly scale soil respiration to ecosystem level in a robust manner, and finally acquire a good understanding of spatial patterns in soil respiration rates. Our research contributes to a better understanding of soil processes. Furthermore, this project provide background for several potential follow-up projects.

Since we showed empirically that sulfur was a key explaining variable for soil respiration, an interesting experiment would be to fertilize with sulfur (and maybe also with nitrogen). This manipulation would prove if sulfur was the limiting factor for soil respiration, if in reality nitrogen was just as important, and if soil bulk density was correlated directly with soil respiration or indirectly via the concentration of sulfur (or another macro-nutrient). The next step would be to measure if sulfur also is a key explaining variable in beech forests on less nutrient rich soil. This is imporatant in order to test if sulfur is generally a key explaining variable or if the Hainich site is an extraordinary site in that respect. Further studies on the nutrient balance of trees (e.g. nutrient contents in leaves) would also be appropriate.

Despite the obvious relevance of stand structure to soil respiration, only very few studies have made this link (Buchmann et al. 1996; Stoyan et al. 2000; Savin et al. 2002). An interesting project would be to test if the best structural parameter (av-dbh4), which

indicates the presence of mainly large trees, is also the most important structural parameter in less favorable (more typical) beech stands. It is hypothesized that in more open stands other structural parameters, such as the simple distance to nearest tree, may play a larger role than it was the case at the Hainich site. The work might include programming and geostatistical methods. We see a potential in a tighter link between forest population ecology work and more process/flux-oriented research.

Our procedure of scaling chamber measurements to the ecosystem level may be a valuable method, since spatial variability can cause impreciseness of scaled carbon estimates. In the large carbon projects (e.g. CarboEurope and Ameriflux), standardized robust procedures are necessary because results are compared over different levels and scales (bottom up and top down), and data are collected at a wide range of sites by different researchers. A method similar was tested by Davidson et al. (2002) in a tropical grassland and Yim et al. (2002) in a Japanese larch plantagen. They obtained results comparable to ours. The next logical step would be to test if the method is generally applicable for all kinds of ecosystems. The tests could include measurements of the stability of soil respiration patterns over longer time scales. Only in ecosystems where the spatial patterns stay constant or change randomly the method would be fully valid. Whereas, if the patterns of soil respiration in an ecosystem changes from, for example, homogeneous to heterogeneous, the initial number of required measurement locations would in a later stage be insufficient. The project would include data compiling from existing literature and field measurements in selected ecosystems that are characterized by different degrees of heterogeneity.

Finally, the chamber and the procedure developed for determining $\delta^{13}C$ values of soil respired CO_2 was proven to be highly suitable for the purpose. The chamber has already been used in an experiment, where the transport time for assimilates from photosynthesis to respiration was calculated at the Hainich forest site. We took advantage of the natural labeling of the photosynthesis product under dry conditions (by stomata closure), and compared the course of water vapor deficit with that of the isotopic signal of respired CO_2. Furthermore, we carried out a pilot study, where a labeled substrate for saprophytic respiration was added (in our case a C4 sugar). The results from this study seemed promising, and showed that there is a potential for partitioning root and microbial

respiration in this manner. Thus, there is a whole array of process-studies, which are possible with this method.

7 Summary

Soil respiration plays a crucial role in the global carbon cycle and efflux rates may be strongly altered by climate change. Since the spatial patterns and the processes controlling soil respiration are only poorly known, the work in this dissertation was carried out in order to bring new insight into temporal and spatial aspects of soil respiration. Soil respiration and related parameters were measured in an unmanaged, highly heterogeneous beech forest and in an agricultural field in a "Free Air Carbon dioxide Enrichment experiment" (FACE).

On an annual basis, soil temperature alone explained between 68 and 95% of the variation in soil respiration rates at the forest site with soil moisture as the second most important parameter (values ranged from 0.4 to 10.6 μmol CO_2 m^{-2} s^{-1}). However, concerning the spatial aspect, a substantial scatter in respiration rates (about 9 μmol CO_2 m^{-2} s^{-1}), which could not be explained by soil temperature, was also found. On a spatial scale, rates of soil respiration were correlated with several different types of parameters. Especially, the concentration of sulfur in soil was a good predictor of soil respiration rates (explained 61% of the variation in this flux). Although sulfur appeared to be a key explanatory variable for soil respiration, the macro-nutrients (carbon, nitrogen and sulfur) were also highly correlated with each other, suggesting that when models are made for predicting soil respiration rates, concentrations of the macro-nutrients may be substituted with each other as redundant variable. Since root respiration is required for maintenance, growth and ion uptake, it is reasonable that the tree and root distributions play essential roles for soil respiration. The fine root biomass and the stand structural parameter, av-dbh4 (average diameter in breast height of trees within a radius of four meters from the measurement location), were both highly correlated with soil respiration, but not correlated with each other. Since av-dbh4 is an indicator for large trees close to the measurement location, the results suggest that although the fine roots in general were important for soil respiration, the roots from larger trees were more active (had larger carbon allocation) than those from smaller trees.

In order to calculate an ecosystem carbon budget, soil respiration, measured in chambers was combined with measurements of ecosystem respiration with an eddy

covariance system. Due to the spatially variable soil respiration rates, estimates of annual efflux could vary from 500 to 1500 g C m^{-2} yr^{-1}. Since a precise upscaling of soil respiration may be highly important for carbon budgets, we suggested a two-fold strategy to solve this problem. Firstly: to capture the spatial variability in a few intensive measurement campaigns and secondly: to select a representative subset of plots for chamber measurements in the following campaigns in order to obtain the time course. Using this method, we calculated that at our study about 20 randomly placed measurement locations would be adequate to achieve a sufficient precision. This approach combines time limitations within the framework of a study with the requirement for precision of respiration estimates due to the objectives of the study.

Finally, we determined the temperature sensitivity of different processes (autotrophic and heterotrophic) involved in soil respiration. We found that root free plots had much lower temperature sensitivity (Q_{10} about 1.9) than plots with high fine root biomass (Q_{10} about 4.7). Furthermore, using stable carbon isotopes we estimated that about 70% of the soil-respired carbon originated from recent assimilation in the FACE experiment with 550 ppm. This observed dominance of recently assimilated carbon (originating from root activity) and a minute alteration in the carbon isotope ratio of the top soil under high (depleted) CO_2 adds major uncertainties to the anticipated increase of soil carbon storage in the future. This is an important finding since the world faces an increase in atmospheric CO_2 and the role of ecosystems in the global carbon budget is not fully understood.

8 Zusammenfassung

Bodenatmung spielt eine entscheidende Rolle im globalen Kohlenstoffkreislauf, und die Atmungsraten können durch den Klimawandel stark verändert werden. Da die räumlichen Muster und die Prozesse, die die Bodenatmung steuern, nur in geringem Maße bekannt sind, sollte diese Dissertation neue Einsichten in die räumlichen und zeitlichen Aspekte der Bodenatmung erbringen. Die Bodenatmung und mit ihr verwandte Parameter wurden in einem unbewirtschafteten, stark heterogenen Buchenwald sowie auf einer landwirtschaftlichen Fläche, die Teil eines „Free Air Carbon dioxide Enrichment (FACE) – Experiments ist, gemessen.

Die Bodentemperatur erklärte im Jahresverlauf 68 bis 95% der Variation der Bodentemperatur des Waldstandortes, während Bodenfeuchte die zweitwichtigste Variabel darstellte (Einzelwerte lagen zwischen 0.4 und 10.6 µmol CO_2 $m^{-2}s^{-1}$). Räumlich streuten die Werte stark (etwa 9 µmol CO_2 $m^{-2}s^{-1}$), was nicht durch die Bodentemperatur erklärt werden konnte. Auf räumlicher Ebene waren die Bodenatmungsraten mit verschiedenen Parametern korreliert. Die Konzentration von Schwefel im Boden war ein besonders guter Indikator für Bodenatmungsraten (erklärte 61% der Variabilität). Obwohl Schwefel eine Schlüsselrolle bei der Vorhersage der Bodenatmungsraten spielte, waren die Makro-Nährstoffe Kohlenstoff, Stickstoff und Schwefel auch stark miteinander korreliert. Dies führt zu der Annahme, dass bei der Erstellung von Modellen zur Vorhersage von Bodenatmungsraten die Konzentrationen der Makro-Nährstoffe als redundante Variablen gegeneinander austauschbar sind. Da Wurzelatmung zum Erhaltungsstoffwechsel, zum Wachstum und zur Ionenaufnahme notwendig ist, scheint es nahe liegend, dass Baum- und Wurzelverteilungen von großer Bedeutung für die Bodenatmung sind. Die Feinwurzelbiomasse und strukturelle Parameter wie der av-dbh4 (mittlerer Brusthöhendurchmesser der Bäume im Umkreis von vier Metern Entfernung zur Messstelle) waren jeweils stark mit der Bodenatmung korreliert, jedoch nicht miteinander. Die Ergebnisse lassen darauf schließen, dass Feinwurzeln zwar generell wichtig für die Bodenatmung waren, dass jedoch die Wurzeln größerer Bäume aktiver waren als die kleinerer (d. h. eine stärkere Kohlenstoffallokation hatten).

Um die Kohlenstoffbilanz eines Ökosystems zu berechnen, wurden Messungen der Bodenatmung in Bodenkammern mit Messungen der Ökosystematmung mittels Eddy-Kovarianz-System kombiniert. Wegen der hohen räumlichen Variabilität der Bodenatmungsraten variieren Schätzungen des jährlichen Kohlenstoffflusses der Bodenatmung von 500 bis 1500 g C m^{-2} a^{-1}. Da eine präzise Hochrechnung der Bodenatmung für die Ermittlung einer Kohlenstoffbilanz sehr wichtig ist, gingen wir folgendermaßen zur Lösung des Problems vor: zum ersten wurde die räumliche Variabilität in wenigen Intensivkampagnen erfasst, zum zweiten wurde ein repräsentativer Anteil an Messpunkten ausgewählt, um im Folgenden den Jahresgang der Bodenatmung zu bestimmen. Mit dieser Methode ermittelten wir, dass 20 zufällig platzierte Messpunkte zur Erlangung einer ausreichenden Genauigkeit erforderlich wären. Diese Herangehensweise ermöglicht eine den Zielen der Untersuchung angemessene Genauigkeit innerhalb des zur Verfügung stehenden Zeitrahmens.

Schließlich bestimmten wir die Temperaturabhängigkeit verschiedener Teilprozesse der Bodenatmung (autotroph und heterotroph). Dabei zeigten wurzelfreie Messpunkte eine geringere Temperaturabhängigkeit (Q_{10} etwa 1.9) als Messpunkte mit hoher Wurzelbiomasse (Q_{10} etwa 4.7). Außerdem schätzten wir mithilfe stabiler Isotope, dass in dem FACE-Experiment mit einer CO_2-Konzentration von 550 ppm etwa 70 % des im Boden veratmeten Kohlenstoffs aus rezenter Assimilation hervorgingen. Diese beobachtete Dominanz von erst kurz zuvor assimiliertem Kohlenstoff (der aus Wurzelaktivität stammt) sowie eine geringfügige Änderung des Kohlenstoff-Isotopenverhältnisses bei hoher CO_2-Konzentration (550 ppm) verstärkt die Unsicherheiten bezüglich der angestrebten Zunahme des Bodenkohlenstoffspeichers. Dies ist ein wichtiges Ergebnis angesichts der globalen Zunahme atmosphärischen Kohlendioxids und der Tatsache, dass die Rolle der Ökosysteme im globalen Kohlenstoffkreislauf noch nicht gänzlich verstanden ist.

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Publications

- Paper in review May 2003 (Plant and Soil): "Influence of elevated CO_2 on soil respiration and its partitioning into recently assimilated and older carbon sources", A. Søe, A. Giesemann, T. Anderson, H. Weigel, N. Buchmann.
- Paper in progress: "Spatial and temporal variation of soil respiration in relation to stand structure an unmanaged beech forest in Central Germany", A. Søe, N. Buchmann.
- Paper in progress: "Factors controlling soil respiration in an unmanaged beech forest in Central Germany", A. Søe, N. Buchmann.
- Paper in progress: "Respiration estimates based on soil chamber and eddy covariance measurements in an unmanaged beech forest", A. Søe, A. Knohl, N. Buchmann.
- Conference abstract:"Partitioning of root and microbial respiration in a FACE experiment" Soil Science Soiciety of Germany, Göttingen 2002.
- Conference abstract: "Temporal and spatial variability of soil respiration in beech forests" International association of Vegetation Science, Munich 2001.
- Masters thesis: The influence of Different Management Forms on the Regeneration of the Vegetation in an Industrially Polluted Grassland Ecosystem. Institute of Ecology, University of Jena. 92 pages. 1999.
- Bachelor thesis: Studies on a Forest Boundary on Maria Island. Parks and Wildlife Service, Tasmania, Australia. 45 pages. 1995.

Appointments and talks

- Reviewed paper for Global Change Biology (2002).
- Invited speaker at Risø, Denmark 2001: "Spatial and temporal variation in soil respiration in Central European Beech forest".
- Talk at a workshop by the German Soil Science Society, working group stable isotopes, Göttingen 2002:"Partitioning of root and microbial respiration in a FACE experiment".

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Curriculum vitae

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Jun. 2002	Participant in the summer school "Stable isotope ecology", University of Utah, Salt Lake City, USA.
Sep. 2001	Studies at University of Copenhagen and Risø (Denmark). Topic: "Spatial variability of soil CO_2 efflux in relation to the activity and diversity of the soil microbial community". Participation was sponsored by the European Science Fundation.
Apr. 2001	Participant in a spring school on "Stable isotopes in community and ecosystem ecology", Evora, Portugal. Sponsored by the European Science Foundation.
1998-1999	Master's degree project in Ecology, Friedrich-Schiller University, Jena, Germany. Topic: "Changes in flora by reestablishment of dry grassland after pollution with phosphate, fluorite and heavy metals". Supervisors: Dr. Winfried Voigt, Ecology, University of Jena, D. Dr. Finn Borchsenius, Botany, University of Aarhus, DK.
1997-1998	Minor subject in Comparative Religion at the University of Aarhus, DK.
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Jena, den 30. Mai 2003 (Astrid Søe)

Selbständigkeitserklärung

Ich erkläre hiermit, dass mir die geltende Promotionsordnung der Fakultät bekannt ist.

Hiermit versichere ich, die vorliegende Arbeit selbständig und ohne fremde Hilfe verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel verwendet zu haben.

Ferner versichere ich, dass ich diese Dissertation noch an keiner anderen Universität eingereicht habe, um ein Promotionsverfahren eröffnen zu lassen

Jena, den 30. Mai 2003

Astrid Søe

Thesen zur Doktorarbeit:

Steuerungsgrößen, Skalierungsfragen und Zusammensetzung der Bodenatmung

vorgestellt von cand. scient. (M. Sc.) Astrid R. B. Søe

Bodenatmung stammt aus autotropher Wurzelatmung und heterotropher mikrobieller Atmung im Boden und im Wurzelraum. Da Bodenatmung einer der Hauptflüsse in terrestrischen Ökosystemen ist, können kleine Veränderungen in der Größe dieses Flusses große Auswirkungen auf die Konzentration von CO_2 in der Atmosphäre haben. Die im Boden ablaufenden Prozesse sind jedoch sehr komplex und noch nicht ausreichend verstanden. Deshalb wurden detaillierte Untersuchungen der Bodenatmung und der mit ihr verknüpften Parameter in einem stark heterogenen Laubwald im Nationalpark Hainich (West-Thüringen, Deutschland) sowie im Rahmen eines Hoch-CO_2-Experiments auf einer landwirtschaftlichen Fläche in der Nähe von Braunschweig (Deutschland) durchgeführt.

Die zeitliche Variabilität der Bodenatmung hängt von der Bodentemperatur und der Bodenfeuchte ab

- Die Bodenatmung zeigte einen deutlichen jahreszeitlichen Verlauf mit Flussraten von 0.4 - 11.0 µmol CO_2 m^{-2} s^{-1}.
- Im Jahresverlauf waren die Bodenatmungsraten stark mit der Bodentemperatur korreliert (r^2 = 0.68 - 0.95). Dagegen konnte die Bodenatmung im Jahr 2001 (mit einer ausgeprägten Trockenperiode) statistisch besser durch Einbeziehung des Bodenwassergehalts in das deskriptive Modell beschrieben werden.

Die räumliche Variabilität der Bodenatmung kann nicht alleine durch die Bodentemperatur erklärt werden

- Die Schwefelkonzentration des Oberbodens war der am stärksten mit der Bodenatmung korrelierte Parameter (p < 0.001; r^2 = 0.61), der seinerseits in hohem Maße mit den Kohlenstoff- und Stickstoffkonzentrationen des Bodens zusammenhing.
- Feinwurzelbiomasse, Feinwurzel-Stickstoff, Mächtigkeit der Auflage und des A-Horizonts, mikrobielle Biomasse und einige strukturelle Parameter waren positiv mit der Bodenatmung korreliert, während Bodendichte und Bodenfeuchte negativ mit den Atmungsraten korreliert waren.

- Das beste Modell zur Beschreibung der Muster der Bodenatmung erklärte 77 % der räumlichen Variation der Bodenatmungsraten im Sommer. Dieses Modell enthielt folgende Faktoren: Schwefelkonzentration, große Bäume nahe des Messpunkts, Feinwurzelbiomasse und Bodenfeuchte.
- Das Muster hoher und niedriger Atmungsraten blieb während der Vegetationsperiode und von Jahr zu Jahr konstant.

Die räumliche Variabilität hat einen starken Einfluss auf die Hochrechnung der Bodenatmung von Einzelwerten auf die Ökosystemebene.

- Die räumliche Variabilität der Temperaturabhängigkeit (Q_{10}) der Bodenatmung konnte teilweise durch die Feinwurzelbiomasse erklärt werden.
- Die hohe räumliche Variabilität der Bodenatmungsraten bewirkte eine Streuung der jährlichen Flussraten von 500 bis 1500 g C m^{-2} a^{-1} in Abhängigkeit von der Größe und der Lage des Messpunkts.
- Berechnungen ergaben, dass etwa 20 Messpunkte nötig waren, um eine Genauigkeit von 10 - 20% des gesamten Populationsmittels bei einem Vertrauensbereich von 95 % zu erreichen.
- Die Messung an diesen 20 Punkten in der Nähe eines Eddy-Kovarianz-Turms ergab, dass Bodenatmung 79 – 85 % der Ökosystematmung (Boden-, Stamm-, Ast- und Blattatmung) ausmachte.

Die Trennung in autotrophe und heterotrophe Atmungsflüsse ist für die Vorhersage von Kohlenstoffflüssen und -vorräten essentiell

- Die Bodenatmung war in einer Periode hoher pflanzlicher Aktivität unabhängig von der Höhe der Stickstoffdüngung an Messpunkten mit erhöhter atmosphärischer CO_2-Konzentration (Free Air Carbon dioxide Enrichment, FACE; 550 ppm) deutlich höher als an den Kontrollpunkten, die mit Luft aus der unmittelbaren Umgebung begast wurden.
- Die Verwendung stabiler Kohlenstoffisotope bei der Begasung im FACE-Experiment ergab, dass bei erhöhter CO_2-Konzentration (550 ppm) etwa 70 % des im Boden veratmeten Kohlenstoffs aus rezenter Assimilation stammten.
- Das Vorherrschen der Wurzelatmung, die Zunahme der Veratmung rezenten Kohlenstoffs sowie eine geringfügige Abreicherung des Kohlenstoff-Isotopenverhältnisses im Oberboden bei erhöhter CO_2-Konzentration (550 ppm) erschwert die zukünftige Abschätzung der Bodenkohlenstoff-Vorräte.

Theorems to the Dissertation:

Controlling factors, scaling issues and partitioning of soil respiration

Presented by cand.scient. (M.Sc.) Astrid R. B. Søe

Soil respiration (soil CO_2 efflux) originates from autotrophic root respiration and heterotrophic microbial respiration in the bulk soil and in the rhizosphere. Since soil respiration is one of the major fluxes in terrestrial ecosystems, small changes in the magnitude of this flux could have large effects on the concentration of CO_2 in the atmosphere. However, processes in the soil are highly complex and many aspects are still poorly understood. Therefore, detailed studies on 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 experiment in an agricultural field close to Braunschweig, Germany.

Temporal variation in soil respiration depends on soil temperature and moisture

- Soil respiration showed a clear annual cycle (0.4 – 11.0 µmol CO_2 m^{-2} s^{-1}).
- Over the year, soil respiration rates were highly correlated with soil temperature (r^2 =0.68 – 0.95). However, in 2001 (with a pronounced drought period) respiration was statistically better described by including the soil water content in the descriptive model.

Spatial variation in soil respiration cannot be explained by soil temperature alone

- The parameter most highly correlated with soil respiration was the sulfur concentration in the top soil ($p < 0.001$; $r^2 = 0.61$), which was also strongly related to the concentrations of nitrogen and carbon.
- Fine root biomass, fine root N per m^2 ground, depth of litter and A-horizon, microbial biomass and some stand structural parameters were positively correlated with soil respiration, while soil bulk density and soil moisture were negatively correlated with soil respiration rates.
- The best model for describing patterns of soil respiration explained 77% of the spatial variation in soil respiration rates in summer. This model contained the following parameters: concentration of sulfur, large trees close to the measurement location, fine root biomass, and soil moisture.
- The pattern of high and low respiration rates stayed remarkably constant during the growing season and from year to year.

Spatial variability has pronounced effects for scaling of soil respiration measurements from chamber to ecosystem level

- Spatial variability of the temperature sensitivity (Q_{10}) of soil respiration could partly be explained by fine root biomass.
- The high spatial variability in soil respiration rates resulted in estimates of an annual efflux that could vary from 500 to 1500 g C m^{-2} yr^{-1} depending on the plot size and location.
- Calculations showed that about 20 sampling locations were needed at our study site in order to achieve a precision in the soil respiration estimate of 10 to 20% of the full population mean at a confidence level at 95%.
- Using these 20 locations in the main source area of an eddy covariance tower resulted in an estimate where soil respiration constituted 79 – 85% of the ecosystem respiration (soil, leaf, stem and branch respiration).

Separation of the individual autotrophic and heterotrophic respiration fluxes is essential for predictions of carbon fluxes and pools

- Soil respiration was considerably higher (34%) in the plots with elevated CO_2 concentration (Free Air Carbon dioxide Enrichment with 550 ppm) than in the control plots (fumigated with ambient air) during a period of high plant activity, independent on levels of N fertilization.
- Using the stable carbon isotopes provided by the fumigation gas in the Free Air Carbon dioxide Enrichment experiment it was estimated that about 70% of the soil-respired carbon originated from recent assimilation in the plots with elevated CO_2.
- The observed dominance of root respiration together with an observed increase of carbon losses from recently assimilated carbon and a minute depletion in the carbon isotope ratio of the top soil under high CO_2 (550 ppm) adds major uncertainties to the anticipated increase of soil carbon storage in the future.