Biogeochemistry (2005) 75: 479–506
DOI 10.1007/s10533-005-3690-9

Subsurface CO_2 dynamics in temperate beech and spruce forest stands

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Received 18 June 2004; accepted in revised form 11 March 2005

Key words: CO_2 efflux, Soil carbon turnover, Soil respiration, Temperate forest, Temperature

Abstract. Rates of soil respiration (CO_2 effluxes), subsurface pore gas CO_2/O_2 concentrations, soil temperature and soil water content were measured for 15 months in two temperate and contrasting Danish forest ecosystems: beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* [L.] Karst.). Soil CO_2 effluxes showed a distinct seasonal trend in the range of 0.48–3.3 μmol CO_2 m^{-2} s^{-1} for beech and 0.50–2.92 μmol CO_2 m^{-2} s^{-1} for spruce and were well-correlated with near-surface soil temperatures. The soil organic C-stock (upper 1 m including the O-horizon) was higher in the spruce stand (184 ± 23 Mg C ha^{-1}) compared to the beech stand (93 ± 19 Mg C ha^{-1}) and resulted in a faster turnover time as calculated by mass/flux in soil beneath the beech stand (28 years) compared to spruce stand (60 years). Observed soil CO_2 concentrations and effluxes were simulated using a Fickian diffusion-reaction model based on vertical CO_2 production rates and soil diffusivity. Temporal trends were simulated on the basis of observed trends in the distribution of soil water, temperature, and live roots as well as temperature and water content sensitivity functions. These functions were established based on controlled laboratory incubation experiments. The model was successfully validated against observed soil CO_2 effluxes and concentrations and revealed that temporal trends generally could be linked to variations in subsurface CO_2 production rates and diffusion over time and with depths. However, periods with exceptionally high CO_2 effluxes (>20 μmol CO_2 m^{-2} s^{-1}) were noted in March 2000 in relation to drying after heavy rain and after the removal of snow from collars. Both cases were considered non-steady state and could not be simulated.

Introduction

Boreal and temperate forest ecosystems are important components of the global carbon (C) cycle and account for roughly 25% of the global terrestrial ecosystem C (IPCC 2001). These ecosystems show consistent net ecosystem C uptake on the order of 200–300 g C m^{-2} yr^{-1} (Wofsy et al. 1993; Janssens et al. 2001). This storage capacity depends on tree production and the turnover time of C in soil. About 55% of the total amount of C being fixed during photosynthesis is released as carbon dioxide (CO_2) from the soil and forest floor (Janssens et al. 2001). Thus, the CO_2 release represents one of the major fluxes of carbon to the atmosphere (Raich and Schlesinger 1992).

In forest ecosystems, CO_2 effluxes primarily result from near-surface respiration in living roots (Billings et al. 1998) and the decomposition of litter, dead roots

and soil organic matter by heterotrophic soil microbes and fungi (Hanson et al. 2000). The decomposition of soil organic matter is sensitive to several site-specific environmental conditions including the quality and quantity of C substrates and climatic factors, in particular soil temperature and water content (Kirschbaum 1995; Fang and Moncrieff 2001). Availability of oxygen, type of microbes present as well as faunal abundance and activity are additional factors influencing soil microbial respiration processes (Lomander et al. 1998).

Despite the complexity of soil organic matter decomposition the net result may be quantified as an overall turnover time (mass/flux) of soil organic carbon (SOC). In temperate forests, the turnover time has been reported to range between 23 and 29 years (Raich and Schlesinger 1992). However, this mean turnover time is the result of a turnover time of 2–5 years for surface litter, 5–10 years for root litter, 40–100 years for low-density humified organic matter and more than 100 years for SOC associated with clay minerals (Gaudinski et al. 2000). The net results given by the SOC balance must be taken into consideration when determining the ability of forest ecosystems to sequester carbon (Borken et al. 2002).

Modelling the temporal and spatial variation in CO_2 efflux from the soil surface has lead soil ecologists to investigate rate functions, stability and resilience of soil organic matter. However, soil effluxes have proved difficult to use directly to evaluate subsurface CO_2 production due to the complex nature of the soil system and the net result of interacting CO_2 production and transport processes (Fang and Moncrieff 1999; Moncrieff and Fang 1999).

Subsurface CO_2 production results in gas-filled pores in soils which have CO_2 concentrations that are typically 10–100 times higher than concentrations in the atmosphere (Welles et al. 2001). This results in a net CO_2 flux from the soil to the atmosphere driven by the concentration gradient. The transport of near-surface gases such as CO_2 has long been considered to be mainly a diffusion process (e.g. Lundegärdh 1927; De Jong and Schappert 1972). This means that the presence of continuous air-filled soil pores becomes crucial for the soil diffusivity which again is closely related to the water content (Millington 1959). Assuming steady state conditions and neglecting the effect of water movement, the relationship between one-dimensional diffusion and production of CO_2 in soils may be described by Fick's second law:

$$\frac{\mathrm{d}}{\mathrm{d}x}\left(D_{\mathrm{e}}\frac{\mathrm{d}C}{\mathrm{d}x}\right)+R=0 \tag{1}$$

where C is the CO_2 concentration, x is the depth, D_{e} is the effective diffusion coefficient, and R is the CO_2 production rate per unit volume of soil. In addition to Fickian diffusion, also Knudsen diffusion, multicomponent molecular diffusion (Thorstenson and Pollock 1989a,b) as well as liquid phase diffusion (Fang and Moncrieff 1999) may play minor roles in the total gas transport. For the purpose of this study, only Fickian diffusion is considered. This simplification is consistent with other research (Fang and Moncrieff 1999; Hirano et al. 2003). Assuming that one-dimensional diffusion dominates the

subsurface CO_2 transport, then CO_2 concentration profiles rather than CO_2 effluxes should be analysed in order to improve the understanding of the depth-dependent CO_2 production.

The spatial and temporal variability of D_e and R under field conditions results in substantial variations in total soil CO_2 production and effluxes between vegetation types. Furthermore, this variation is strongly influenced by land use type and practice. In contrast to soil CO_2 effluxes, soil CO_2 concentration profiles reflect the depth of biological activity and are relevant for improving the understanding of spatial and temporal trends in subsurface CO_2 production and corresponding estimates of depth-related soil organic carbon turnover times. Several studies have reported CO_2 concentrations in forest soils (e.g., Winston et al. 1997; Certini et al. 2003). Piñol et al. (1995) and Billings et al. (1998) estimated CO_2 effluxes using CO_2 concentration profiles from forest soils; Gaudinski et al. (2000) used subsurface CO_2 gradients to calculate CO_2 production profiles and Fang and Moncrieff (1999) and Moncrieff and Fang (1999) simulated soil CO_2 profiles using diffusion models. However, little research has been conducted (e.g. Hirano et al. 2003) relating the vertical distribution of soil respiration (CO_2 production rates) to seasonal trends in soil CO_2 levels and the resulting soil CO_2 efflux using diffusion-reaction models. This, despite the relevance for improving the understanding and the quantification of vegetation-specific soil CO_2 dynamics, including the source of CO_2 released to the atmosphere and the availability of CO_2 gas for weathering and acidification processes within the soil.

The present study aims to evaluate CO_2 effluxes and CO_2 concentration profiles to assess soil CO_2 dynamics, and to use annual soil organic matter mineralisation rates to discuss forest soil carbon budgets associated with two contrasting tree species. Two forest stands, beech (*Fagus sylvatica* L.) and spruce (*Picea abies* [L.] Karst.), were selected due to the similarity between the soil properties, drainage conditions and climate at the study site. Contrasts between the two forest ecosystems are emphasized by Borken et al. (2002) who reported significantly lower annual soil respiration rates for spruce compared to beech sites and Heinze et al. (2001), who noted that soils under beech trees tend to be looser, less acidic and richer in nutrients than soils under spruce forest.

Materials and methodology

Study site

The study site is located near Nødebo in the north of Zealand (55° N, 12° E), Denmark. Two contrasting forest stands located within 2 ha of each other were selected: deciduous beech (*Fagus sylvatica* L.) and coniferous common or Norway spruce (*Picea abies* [L.] Karst.). The beech forest stand was planted in 1977 and has been growing at a rate of 8–9 $m^3\ ha^{-1}\ yr^{-1}$ to an average height of 9 m (2003). The spruce forest was planted in 1959 and has been growing at a

rate of 16–17 m^3 ha^{-1} yr^{-1} to an average height of 23 m. The current live aboveground volume of beech and spruce wood has been estimated to be 145 and 387 m^3 ha^{-1}, respectively (personal comm. with forest ranger S. Løw 2003). The forest is a production forest where 10–20% of the above ground biomass is cut every 4–5 years. Under-storey vegetation is scarce in both forest stands. No fertilizer has been used.

The forest is situated on ice marginal hills and sandy ground moraine from the Weichel ice age. Soils in the forest stands have been classified as Typic Udorthents according to Soil Taxonomy (Soil Survey Staff 1997) and the texture is predominantly loamy sand and stones of varying sizes are present in the soil.

Fieldwork

Fieldwork was initiated in December 1999 and included measurement of soil CO_2 effluxes, soil CO_2 concentrations, soil temperatures (to a depth of 60 cm), and soil water contents (to a depth of 120 cm). Measurements were made one to two times a week for a period of 15 months from March 2000 to June 2001 (apart from two short interruptions). CO_2 efflux measurements were made using LiCor infrared (non-dispersive) gas analysers (LiCor 6400-09 Soil CO_2 Flux Chamber, LiCor, Lincoln, USA) with the procedure described in Elberling (2003), which is similar to the procedure used by Buchmann (2000). The procedure has been tested and found to provide fairly accurate and consistent results when the LiCor-6400 system is shielded from direct sunlight and strong winds (Healy et al. 1996; Welles et al. 2001). Measurements were made on 15–18 replicate collars installed along diagonals in each of the two forest systems. Collars were reinserted every three weeks, to avoid the creation of a microclimate within collars. Measurements were made at approximately the same time of day starting at 10–12.00 AM. Based on repeated measurements over 24 h, rates have been adjusted to represent daily fluxes by multiplying observed fluxes by 0.96–0.99.

Soil gas was withdrawn from pre-installed passive gas samplers inserted at 10, 20, 40, 60, 90 and 260 cm depths in the beech stand and 9, 13, 24, 34, 60, 91, 124 and 280 cm in the spruce stand. Gas samplers, with a volume of 250 ml, were inserted into the walls of soil pits and then connected to the surface with copper tubes (2 mm inner diameter). Pits were back-filled after installation. The concentrations of CO_2/O_2 were measured using a PCO4/10 Portable Carbon Dioxide and Oxygen Analyser (Gas Data Ltd., 1998) with a resolution 0.01% CO_2 and 0.1% O_2 and an accuracy of 2% of full scale for both gases. With a flow rate of 30 ml min^{-1} the extracted volume of gas represents about 20% of the total gas volume in the gas sampler and tube. The set-up has previous been described by Elberling (2003, 2005).

The volumetric soil water content was monitored using an Athom Time Domain Reflectometry method (Topp et al. 1980) and measurements were

conducted using a Tektronix model 1502 B/C cable tester (Tektronix Inc., Beaverton, Oregon, USA) connected to two probes installed at each of the following depths: 20, 40, 60, 80 and 120 cm. The PC program AUTOTDR3 (The Danish Institute of Plant and Soil Science in Foulum, Denmark) was used to calculate the water contents in depth intervals. Additional manual readings (at least 3 replicates) of near-surface water contents (0–5 cm) were made concurrently with soil CO_2 efflux measurements using a Theta Probe, Soil Moisture sensors, ML2x (Delta-T Devices Ltd., Cambridge, UK). Air temperatures in the beech plot and ground temperatures at 6 depths at one site in each of the tree stands were logged on an hourly basis using TinyTag loggers (Gemini Data Loggers Ltd., Chichester, UK). Manual temperature readings were made adjacent to the collars simultaneously to LiCor measurements using the soil temperature thermocouple attached to the LiCor.

Intact depth-specific and volume-specific (100 cm^3) soil samples (3–5 replicates) were collected in June, October and March 1999 and October 2000, at 5 cm depth intervals within each horizon to a depth of 1 m. Soil samples were kept cold and dark until analysed. Root sampling was undertaken at the beech site only, using sequential soil coring up to 85 cm depths. Root samples were taken in June 2000 ($n = 5$ profiles), July 2000 ($n = 3$), April 2001 and May 2001 ($n = 2$). Litter fall was collected in the beech stand from the September 29, 2000 until December 5, 2000 using plastic covers ($n = 3$) placed between trees and sampled on a weekly basis. Litter fall data from a 3-year period were available for beech and Norway spruce stands which were planted nearby in 1966 (Bastrup-Birk et al. 2003).

Laboratory analyses

Soil pH was measured in distilled water (1:2.5) and the grain size distribution obtained by sieving. Bulk density was determined based on the weight of dried volume-specific soil cores.

Roots were removed from the soil after soaking the samples overnight in water and gently stirring to separate mineral material from roots and organic debris. Roots were manually sorted into three classes according to diameter (<1, 1–3 and 3–10 mm) and viability. Dead roots were identified by appearance, strength and colour: dead roots being black/dark brown, brittle and often hollow as described by Leuschner et al. (2004). After sorting, the roots were dried at 65 °C for 24 h, weighed and analysed for C. Also litter samples were dried at 65 °C, and weighed and analysed for C.

All other chemical soil analyses were made using only the soil fraction finer than 2 mm. Total inorganic carbon (TIC) and total organic carbon (TOC) were measured after acidification using the dry combustion method at 1250 °C on an Eltra SC-500 analyser, with an accuracy of $\pm 0.2\%$. Total nitrogen was analysed using dry combustion and infrared detection of N using a LECO FP-428, version 2.03 apparatus. Exchangeable cations (Ca, Mg, K and Na) were

extracted with 1 M NH_4OAc at pH 7 and determined by atomic absorption spectrophotometry. Exchangeable acidity (H^+ and Al^{3+}) was extracted with 1 M KCl and determined by titration with NaOH (Sims 1996). The effective cation exchange capacity (ECEC) was determined as the sum of exchangeable cations and exchangeable acidity.

Soil respiration and CO_2 release experiments in the laboratory

Basal soil respiration rates (BSR) were measured in the laboratory using soil samples stored in polyethylene bags at 0–2 °C for a maximum of 3 days. Prior to measurements, soil samples were carefully split to remove roots and stones. After pre-incubation (minimum 48 h), weighed soil samples (equivalent to 2–3 g dry soil) were transferred to 12 ml Venoject tubes and purged with CO_2-free air. Soil respiration in depth-specific soil samples was subsequently measured by monitoring the linear ($r^2 > 0.95$) increase in headspace CO_2 concentrations over 6–8 h by gas chromatography. Pre-incubation and measurements were made at constant temperatures at 0, 7, 21, 26 and 32 °C (± 0.5 °C).

Additional experiments made with samples after various degrees of sample mixing indicated that splitting the sample had little influence on CO_2 production rates whereas mixing increased rates by up to 20% and up to 50% in near-surface layers. However, tests revealed that by applying a consistent and very gentle mixing procedure, the effects of mixing could be reduced to about 10% for all horizons.

BSR measurements of temperature and water content dependency were made on samples which had been air-dried for a few hours, sieved (2 mm) and subsequently rewetted and thoroughly mixed to ensure homogenous samples. The temperature dependence of BSR in beech horizons was further investigated by incubating Venoject tubes with soil (equivalent to 2–3 g dry soil) in a stable (± 0.3 °C) thermoblock consisting of an insulated solid aluminium block of 1.85 m length (Isaksen et al. 1994) at 21 temperatures between 0 and 25 °C. This temperature range corresponds to another experiment investigating of the temperature dependence above and below freezing for different soil types (Elberling and Brandt 2003). The temperature dependence of BSR on samples collected at various seasons during 1999–2001 was studied at 0, 7 and 21 °C only. Control incubations with empty Venoject tubes showed that CO_2 diffusion into the tubes was negligible. Repeated incubation experiments revealed that the BSR result was independent of the running time of the experiment.

Calculations

All soil samples were analysed for total volume, weight, and solid bulk density in order to calculate soil diffusivity and element stocks. Based on total porosity (ϕ) and air-filled porosity (a) the effective soil diffusion coefficient (D_e) was calculated using the following equation:

$$D_e = \frac{D_a a^{10/3}}{\phi^2} \quad (2)$$

where D_a is the diffusivity in free air [equal to $0.139 \times (T/273)^2$ cm^2 s^{-1}; where T is the temperature (K) reported by De Jong and Schappert (1972)]. Equation (2) was originally suggested by Millington (1959) for describing the relationship between the effective diffusion in soil to the fraction of 'continuous' air-filled pore volume. The equation was later shown to be suitable for a variety of soils (Jin and Juri 1996).

The total porosity was calculated using the observed bulk density and a weighted average of the particle density, assuming an organic matter density of 1.3 g cm^{-3} and a soil mineral density of 2.65 g cm^{-3}. The air-filled porosity was calculated as the difference between total porosity and volumetric water content measured in the field.

Soil organic carbon contents were calculated by multiplying C concentrations with soil density. For mineral soil layers, the fraction >2 mm was neglected (Homann et al. 1995). The soil C stock to a depth of one meter was estimated by depth-integrating the C content in soil layers.

Total soil CO_2 respiration observed as an efflux is the result of both root and microbial respiration. In this study, microbial respiration was assumed to be 54% of total soil respiration in accordance with previous estimates from deciduous and coniferous forest (Edwards and Harris 1977; Hanson et al. 2000). In a review, Hanson et al. (2000) reported variable contributions of roots to total soil respiration, but in most forest studies the contribution ranged between 40 and 60% root contribution and on average 45.8%. In order to relate observed soil CO_2 effluxes in the beech stand to CO_2 production and CO_2 concentration profiles, basal soil respiration measurements as observed in the laboratory were used as a measure of the relative depth-distribution of microbial CO_2 production. While the total annual root respiration was fixed to 46% of the total soil respiration observed, seasonal changes in the depth-integrated root respiration were simulated in steps as suggested by Moncrieff and Fang (1999) with increasing amounts of live roots during spring time, reaching a peak level during summer and declining to a minimum in autumn and winter. The fluctuating root respiration rates are consistent with Rasse et al. (2001) who reported a net root production in the spring and summer and net root death during winter based on model results using TRAP for a beech stand in Belgium. Thus, seasonal soil respiration rates were allowed to vary from a constant maximum value in June and July, decrease linearly over the period August to October to minimum values in November to February and increase linearly thereafter to maximum values in June. The amplitude of the step function was determined by the observed change in mass of live roots from early pre-foliation period (mean of April and May 2001, $n = 4$) and mid-summer (July 2000, $n = 3$). The average distribution of observed live roots (<10 mm) with depth was used as a measure of the vertical CO_2 production due to root respiration. Finally, the vertical soil respiration was calculated

according to Fang and Moncrieff (1999) assuming that effects of water and temperature are multipliable and that the influence of these two factors is similar for both root and microbial respiration.

Soil C turnover time (= mass/flux), denotes the average time required for the organic C in soil to replace itself. Turnover time was estimated from the SOC content of the soil and the microbial soil respiration. The SOC content was estimated to 1-m depth as suggested by Raich and Schlesinger (1992) as well as SOC plus forest floor (O-horizon), dead roots and litter fall as described by Davidson and Trumbore (1995).

Diffusion and production model

Gas dynamics in most soil systems ought to be considered in three-dimensions, but the use of one-dimensional models is generally accepted (De Jong and Schappert 1972; Cerling 1984; Fang and Moncrieff 1999; Moncrieff and Fang 1999). Assuming steady state conditions, both diffusion and chemical reactions will determine the CO_2 gradient as described by Fick's Second Law (Equation (1)). Depth variations of D_e and R prevent an analytical solution, thus Equation (1) has been solved numerically using a control volume approach as described by Berg et al. (1998). The soil columns were divided into N horizontal layers each with a grid point located in the center. The numerical solution calculates the CO_2 concentration for each grid point and the fluxes across each boundary between the horizontal layers based on known or estimated values of D_e and R. Based on the numerical model, the spatial distribution of soil CO_2 concentrations was simulated using the depth-distribution of soil respiration calculated as the sum of root and microbial respiration as described above. The model was calibrated by fitting the depth-integrated sum of microbial and root respiration (absolute soil CO_2 production rates) to observed CO_2 effluxes in March 1–18 (2000) assuming steady state conditions. Subsequently, seasonal trends in soil CO_2 concentrations were simulated for 1 year and compared to observed CO_2 concentrations to validate the model. The assumption of steady state conditions was tested by comparing the depth-integrated CO_2 production to observed soil CO_2 effluxes. The model has been used previously with success to simulate subsurface gas dynamics (Berg et al. 1998; Elberling and Damgaard 2001; Elberling 2003).

Results

Soil characteristics in Nødebo

Results of the soil analysis (Table 1) reveal that soil bulk densities are low in the top layers of both soils corresponding to a high organic carbon content (Figure 1). Furthermore, the bulk densities increase and porosities decrease

Table 1. Mean physical and chemical properties of the beech and spruce forest soils (n = 4, standard deviation <10%).

Horizon	Depth, cm	% clay	Soil bulk density, g cm^{-3}	ECEC, $mol(+)kg^{-1}$	% Base saturation	Porosity, %	pH (H_2O)
Beech							
O	2–0	–	0.17	–	–	–	3.2
A	0–10	10.9	0.84	5.06	17.0	63	3.7
E	10–20	10.7	1.22	5.92	26.0	51	4.0
B_1	20–37	11.5	1.06	5.99	19.7	56	4.5
B_2	37–57	10.0	1.26	3.36	27.1	51	4.8
C_1	57–65	9.5	1.37	3.01	25.2	46	4.9
C_2	65–100	9.0	1.28	2.71	34.8	51	5.1
Spruce							
O	8–0	–	0.28	–	–	–	3.7
A	0–3	8.2	0.95	3.91	7.2	50	3.7
E	3–11	8.2	1.20	3.71	7.6	51	3.8
B_1	11–29	8.3	1.14	3.96	6.4	54	4.2
B_2	29–43	6.2	1.18	4.25	5.9	54	4.4
C_1	43–85	8.3	1.48	2.31	10.0	43	4.5
C_2	85–100	14.1	1.60	2.52	9.41	39	4.4

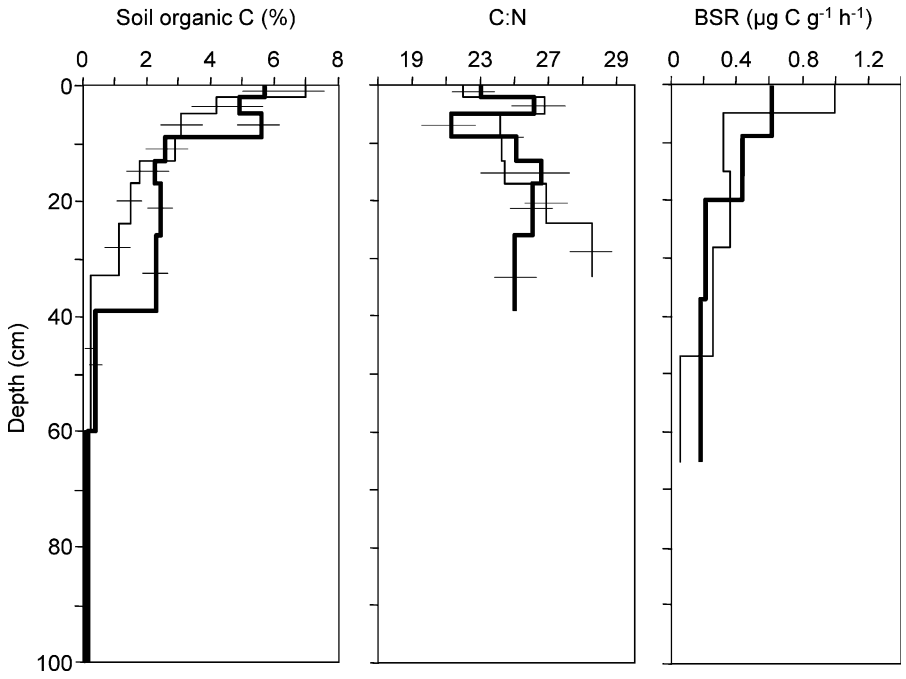

Figure 1. Soil profiles for the two forest sites; spruce shown with thick lines and beech shown with thin lines. Profiles include the soil organic C (SOC, %), C:N ratio and basal soil respiration (BSR) at 7 °C (one standard deviation are shown by horizontal lines).

with depth. An increase in soil bulk density at 57–65 cm (in the beech stand) corresponds to an observed compacted layer. Both soils are acidic with pH-values between 3.2 and 5.1, and with lowest pH in the top layers. The spruce forest soil is slightly more acidic than the beech forest soil which is consistent with a lower effective cation exchange capacity in spruce soil and a lower base saturation (Table 1). Calcium is the dominant exchangeable base cation in both soils (about 50%).

Carbon (C) measurements revealed no significant differences between total carbon (TC) and total organic carbon (TOC), which suggests that all C stored in the soil is organic. This is consistent with the low soil pH. The C content was highest in the topsoil in both forest soils and decreased with depth (Figure 1). Small pieces of charcoal (<2 mm) were found in the upper 15 cm of the beech profile and had a C content of $62 \pm 4\%$ ($n = 9$).

The nitrogen content in the soil showed the same variation with depth as the C content. The C:N relationship varied between 21 and 29 within the upper 45 cm in the two soils (Figure 1) although no significant variations between the two stands. Below 45 cm, the N contents were very low, less than 10 times the detection limit of the analysis thus, these values are somewhat unreliable. At these depths the C:N relationship reached 38. The C:N ratio of charcoal was greater than 95.

Root characteristics and distribution in the beech stand

The total live root biomass to a depth of 80 cm in the beech stand is summarized in Table 2. The average total root biomass (<10 mm) was 16.6 ± 7.8 Mg ha^{-1} (equal to 1660 g m^{-2}, averaged from 4 dates) of which live roots account for 9.6 ± 4.2 Mg dry root ha^{-1} (58%). Roughly twice as many live roots (weight per area) were observed in the samples collected in the middle of the growing season (July 2000) as compared to samples collected in the early part of the season (April and May 2001). This variation is used in the following as the maximum variation in the absolute root respiration over a year. The root density showed an exponential decrease with soil depth in all profiles and for all size-classes (Figure 2). About 80% of all roots were found within the upper 50 cm of

Table 2. Root biomass estimates (tonnes dry root ha^{-1}) in the beech stand at four different times from June 2000 to May 2001 (only roots finer than 10 mm are considered).

Sampling date	June 1, 2000[a]	July 27, 2000	April 4, 2001	May 31, 2001
No of cores (n)	5	3	2	2
Total live roots	–	14.49 ± 4.95	7.69 ± 0.91	6.75 ± 0.45
Total dead roots	–	12.37 ± 3.68	9.95 ± 1.69	1.76 ± 1.17
Total root biomass	13.56	26.86 ± 7.03	17.64 ± 0.78	8.51 ± 1.61
% live roots <1 mm		30.1	34.7	39.4

[a]Averages of 5 collars but pooled prior to analyses. Results from other dates are reported $\pm$ one standard deviation.

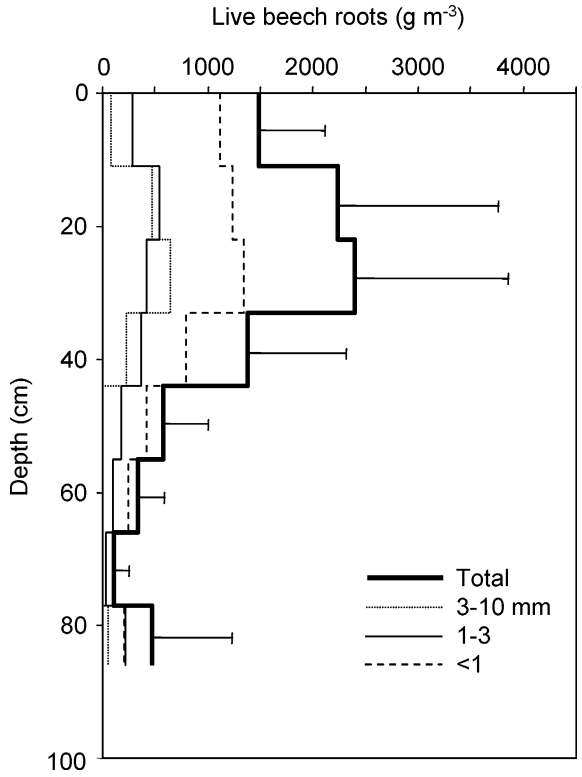

Figure 2. The vertical distribution of living roots separated into three size classes. The profiles represent the average values for soil samples taken in 2 or 3 replicates 4 times over a year in the beech stand (one standard deviation are shown by horizontal lines).

the soil, an observation which is consistent with Bille-Hansen and Hovmand (1987) who found that 90% or more of the roots in all size classes were located within the upper 50 cm. The vertical distribution of living roots was similar to that reported by Leuschner et al. (2004) who found a mean fine root (<2 mm) biomass of 320–470 g m^{-2} to a depth of 40 cm in an older beech forest stand.

The carbon content in the fine roots (<3 mm) varied from 42 to 45% depending of the depth of sampling. The nitrogen content in the live roots varied more than the carbon content resulting in C:N ratios from 24 to 35 in roots finer than 1 mm and up to 53 in larger roots.

Litter distribution and characteristics for the beech stand

The observed foliation period in the study area was from May 1 until June 1, 2000 and defoliation occurred between September 10 and November 14, 2000. A total of 0.24 ± 0.04 kg dry weight m^{-2} was collected from September until November 2000. The litter consisted mainly of leaves but also twigs and beech

nuts. There is some uncertainty associated with the value of autumn litter fall as a storm in October may have dispersed litter away from the collection sites. Investigations of a similarly aged beech stand in Denmark found that the autumn litter constitutes 83% of the total annual litter fall (Bastrup-Birk et al. 2003) which was used to calculate an annual litter fall of 2.9 ± 0.4 t ha^{-1} yr^{-1} (equal to 290 g m^{-2} yr^{-1}) for the Nødebo site. Other reports on litter fall from temperate deciduous forests range from 2 to 6.5 t ha^{-1} yr^{-1} (Waring and Schlesinger 1985). Branches and fallen logs on the forest floor represent additional C-sources. These were noted at the beech stand, but not quantified although coarse woody debris has been reported to range from 20 to 90% of total litter fall in 10 predominantly deciduous forest sites (Raich and Nadelhoffer 1989).

The carbon content in the litter fall was about 48% regardless of time of collection, and therefore was used to convert total mass of litter to a total mass of C. The nitrogen content in the leaves from autumn 2000 was less than the nitrogen content in leaves from the previous year thus reducing the C:N ratio from 34 to 25.

Controls on soil CO_2 production as observed in the laboratory

The temperature-dependent microbial soil respiration was investigated in soil samples from each of the main horizons identified (A, B, C) in the beech forest. An exponential increase in soil respiration with increasing temperature was observed, consistent with most other studies and commonly described using an Arrhenius-type equation (Fang and Moncrieff 2001). The increase in reaction rate per 10 °C (Q_{10}) is often used to characterise the temperature dependence of soil respiration in various soil types and at temperature ranges above freezing (Kirschbaum 1995; Fang and Moncrieff 2001). Q_{10} equalled 2.7 ($r^2 = 0.99$ based on 21 temperatures) for the A-horizon for the entire temperature range shown (Figure 3). For the temperature range most relevant for this study (0–10 °C), the Q_{10} equalled 2.9. Deviation from these Q_{10} values with respect to season or depth could not be documented based on soil samples collected during summer, autumn and late winter and from the three main horizons.

In contrast to the temperature dependency, respiration experiments investigating the dependence of microbial respiration at 7 °C on water content (expressed as percentage of water per volume to match field observations) revealed distinct differences between horizons. Results for the three horizons indicated a strong positive correlation between microbial respiration and water content in samples with a water content less than 10% per volume. At water contents ranging between 10 and 35% per volume, microbial respiration appeared to be independent of the availability of water (Figure 3). In samples with more than 35% water per volume, the microbially-driven CO_2 production gradually decreased with increasing water content. This negative correlation was noted for the B-horizon at water contents $> 40\%$ per volume.

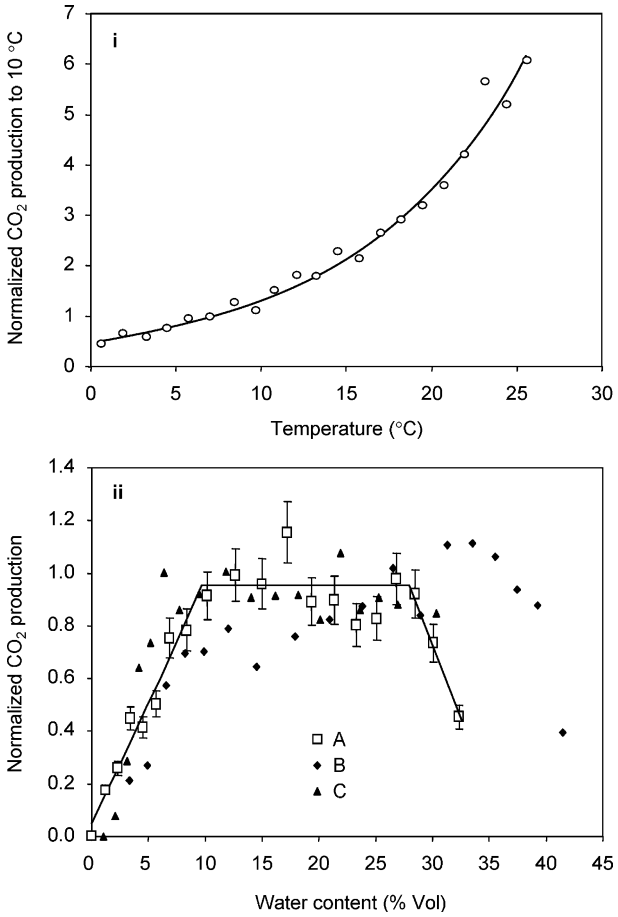

Figure 3. Laboratory data on the sensitivity of CO_2 production in beech soil samples (A, B, and C horizons) as a function of temperature and the water content. The temperature data are fitted by an exponential function ($0.4845e^{0.0993T}$, $Q_{10} = 2.7$, $r^2 = 0.94$) and water content data by step-wise linear fits, which for the A horizon at low water contents (shown as open squares) equals $9.1757W + 0.0489$ ($r^2 = 0.95$).

Measurements of the microbial respiration of charcoal from beech profiles revealed CO_2 production rates close to the detection limit (about 1% of BSR of C-horizon in beech). Thus, the total amount of charcoal contributed less than 10^{-4}% to the total respiration of the soil and was therefore neglected.

Depth-specific soil respiration rates

The laboratory basal soil respiration measurements from various horizons show the importance of the upper soil layers (Figure 1). The respiration rate

was highest in the O-horizon from the beech site (not shown in Figure 1 because data are out of scale), but due to its limited thickness, the contribution of O-horizon to the total respiration was between 4 and 12% depending on its thickness. The combined effect of O- and A-horizons in the beech stand ($n = 10$) was between 30 and 40%, except at one site where the O- and A-horizons contributed 53% of the total soil respiration. For the spruce forest, basal soil respiration measurements revealed that CO_2 production rates per volume material collected from the O-horizon were on average 45% compared to the beech stand and significantly lower than the beech ($p < 0.05$). However, due to the thicker O-horizon in the spruce stand (on average 8) the contribution from the O-horizon was on average 37% of the total respiration observed in the spruce stand.

These laboratory observations provide only a snapshot of a relative CO_2 production profile at constant temperatures. The importance of near-surface layers increases during summer months where the near-surface layer warms more rapidly than deeper layers, while it cools more rapidly in the winter. Due to effects of the disturbance of the soil systems and soil samples prior to measurement, laboratory results on microbial respiration should not be compared directly to field measurements of total soil respiration (Thierron and Laudelot 1996). Instead, laboratory microbial respiration results were used as a measure of the relative contribution of each soil layer to total microbial respiration.

Seasonal trends in field observations

Soil temperatures throughout the study period are shown for beech (Figure 4) and for spruce (Figure 5) locations. A typical seasonal soil temperature pattern was observed corresponding to air temperatures. Maximum temperatures were generally the same in the two stands, whereas minimum temperatures were lower in the beech stand at all depths, probably due to the bare canopy in the beech stand during winter.

The soil water content also showed a seasonal variation which correlated fairly well with precipitation events. In particular, the water content in near-surface layers was well correlated with precipitation events, and water contents were lowest during the dry summer months. In the beech stand, the 40–60 cm layer had a higher water content than both the 20–40 cm layer and the 60–80 cm layer, probably as a result of stowed water above a compacted layer at 60 cm. During short periods in the spring time, the water content was high enough to limit CO_2 production in the A-horizon and low enough to limit CO_2 production in the C-horizon at 60–80 cm (Figures 3ii and 4iii). Seasonal variations at the spruce location were similar, although the water contents were slightly lower. However, mean values observed in the spruce location were often within the standard deviation of values observed in the beech location.

The subsurface spatial distribution of CO_2 reveals that CO_2 concentrations in general and at both locations increased with depth (Figures 4–6). Soil CO_2

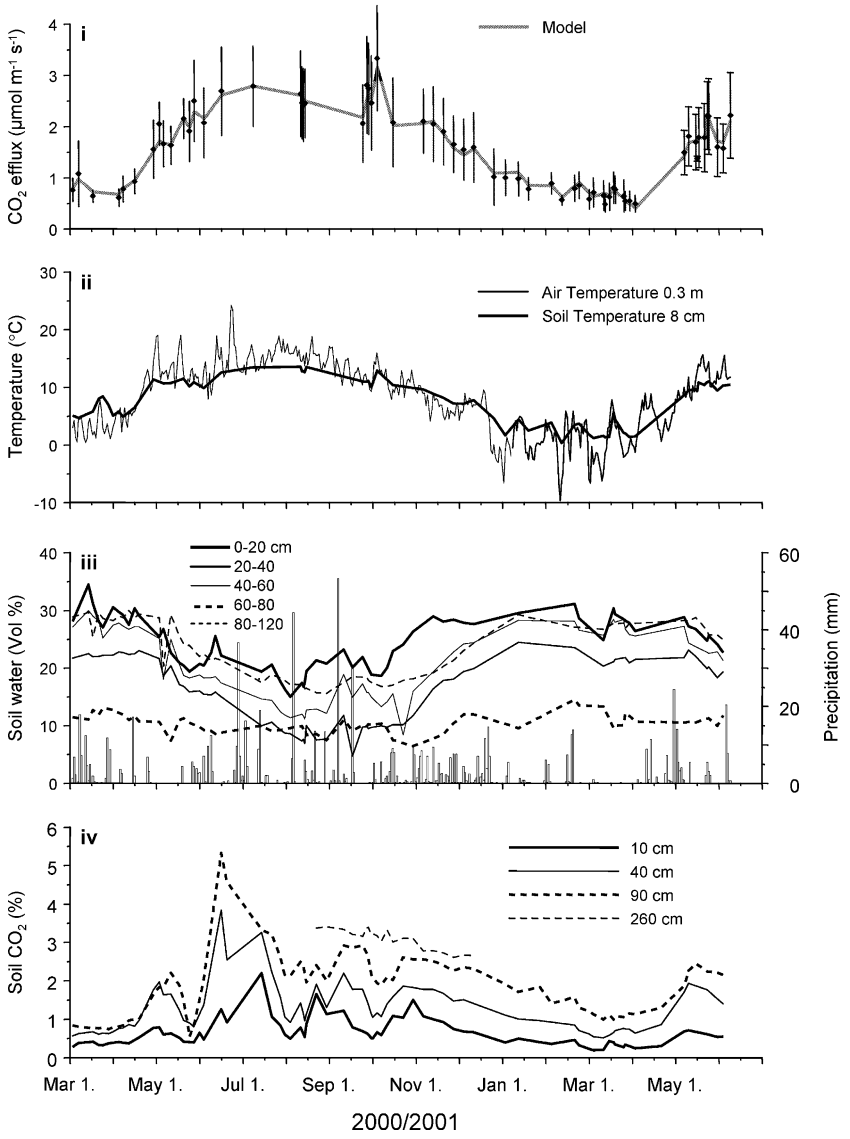

Figure 4. Seasonal variations in the beech stand including observed and simulated for soil CO_2 effluxes and seasonal, and spatial variations in temperatures, precipitation, soil water contents, and soil CO_2 concentrations.

concentrations started to rise in early April at both forest stands and maximum concentrations were noted in June–July. In the beech stand, the CO_2 concentrations increased again in the upper soil layers in mid August while concentrations remained stable below 90 cm. From early September, the CO_2 concentration decreased in the topsoil (10 cm), but increased at greater depths.

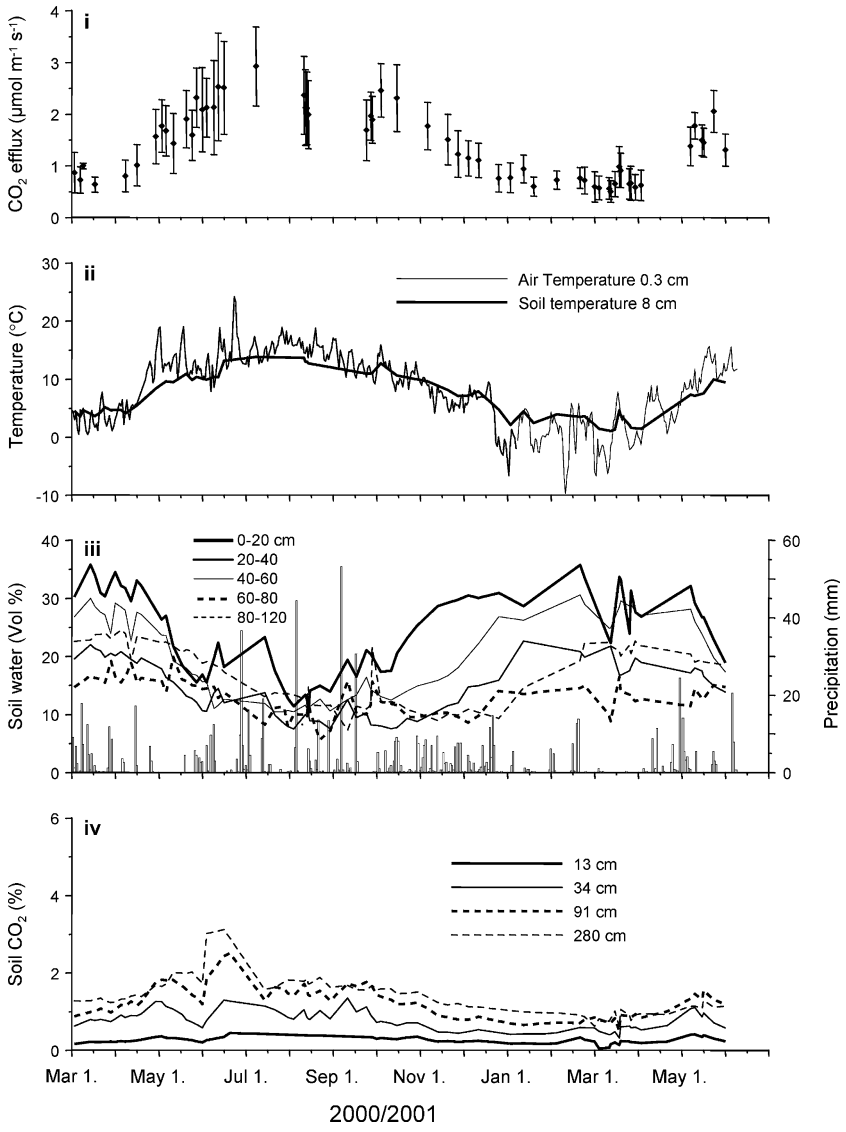

Figure 5. Seasonal and spatial variations observed in the spruce stand including the soil CO_2 efflux, temperatures, precipitation, soil water contents and soil CO_2 concentrations.

After October, the CO_2 concentrations decreased in all layers and reached minimum concentrations in March. In the spruce stand, a minor peak was observed in September in the lower soil layers, but not in the upper layers. In general the spruce stand revealed lower soil CO_2 concentrations than the beech stand (Figures 4 and 5).

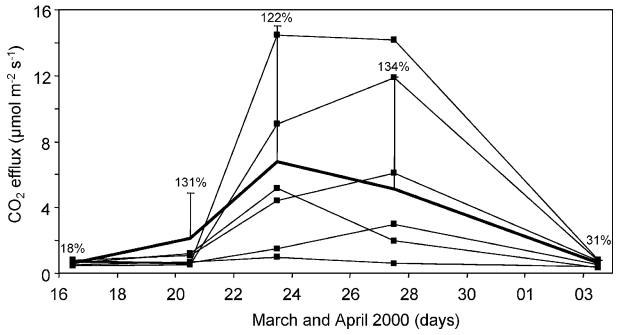

Figure 6. Extreme soil CO_2 effluxes measured between March 16 and April 4, 2000 during a period after heavy rain and subsequently warming. Temporal variations in effluxes are shown for 6 individual collars with thin lines and the mean efflux evaluated based on 17 collars is shown as a thick line. The standard deviations of the mean effluxes ($n = 17$) are shown with bars and reported in percentage.

The concurrent oxygen concentration profiles were found to decrease with depth but not below 18% suggesting aerobic soil conditions year round (Figure 6). The sum of CO_2 and O_2 partial pressures remained fairly constant over time and depth.

Seasonal trends in soil CO_2 effluxes at the beech (Figure 4) and spruce stands (Figure 5) show a similar, distinct seasonal variation, with the lowest fluxes occurring during winter and highest fluxes occurring during summer. Effluxes were well correlated to observed near-surface soil temperatures (8 cm) and revealed Q_{10} values of 3.73 ($r^2 = 0.88$) and 3.45 ($r^2 = 0.96$) for beech and spruce locations, respectively. The soil CO_2 efflux from the spruce forest (0.50–2.92 μmol CO_2 m^{-2} s^{-1}) was slightly lower than fluxes observed in the beech forest (0.48–3.33 μmol CO_2 m^{-2} s^{-1}). At 10 °C (R_{10} value) the average efflux was 1.7 μmol CO_2 m^{-2} s^{-1} at the spruce location and 1.8 μmol CO_2 m^{-2} s^{-1} at the beech location. The largest differences in the soil CO_2 effluxes between the two locations were observed in autumn and winter, where soil CO_2 effluxes in the spruce stand were 0.7–0.8 times effluxes observed in the beech stand. In early spring, there seems to be a tendency towards a relatively larger efflux from the soils in the spruce forest. In April 2001, the spruce forest CO_2 efflux was about 1.2 times the beech forest CO_2 efflux.

Cumulative soil respiration rates ranged from 2.18 kg CO_2 m^{-2} yr^{-1} in the spruce stand to 2.37 kg CO_2 m^{-2} yr^{-1} in the beech stand. These values correspond to 595 and 646 g C m^{-2} yr^{-1}, respectively, and lie within reported ranges. Janssens et al. (2001) reported soil respiration rates from 18 forest ecosystems in Europe (EUROFLUX) to be 760 ± 340 g C m^{-2} yr^{-1}. Borken et al. (2002) observed cumulative soil respiration rates at beech and spruce stands varying from 594 to 587 g C m^{-2} yr^{-1} in sandy sites to 489–532 g C m^{-2} yr^{-1} at silty sites, whereas the corresponding spruce sites were 420–396 and 512–508 g C m^{-2} yr^{-1}. Other studies confirm these ranges

(Ewel et al. 1987; Borken et al. 1999). The standard deviations calculated based on replicate collars installed in the two forest stands are similar and about 33 and 32% of the average CO_2 efflux in the beech and spruce stand, respectively. The standard deviations generally corresponded to the same percentage of the observed mean efflux throughout the year. Scott-Denton et al. (2003) concluded the same and found that variations between points could be related to organic layer thickness, ammonium concentration, water content and the microbial and soil soluble C-pools.

Extremely high fluxes from some collars were measured on March 20, 23, and 27, 2000 (Figure 6; not shown in Figures 4 and 5). Mean ($\pm$ one standard deviation) CO_2 effluxes in the beech stand during these days were 2.1 ± 2.7, 6.8 ± 8.2 and 5.1 ± 6.8 μmol CO_2 m^{-2} s^{-1}. The large standard deviations (120–140%) were consistent with the high fluxes that were observed for some collars (up to 26 μmol CO_2 m^{-2} s^{-1}) while the fluxes measured at other collars remained at the same level observed prior and after the high fluxes (around 0.6 ± 0.1 μmol CO_2 m^{-2} s^{-1}). The variability in the fluxes measured at different collars (Figure 6) indicates that maximum fluxes were observed at different days for different collars. The high effluxes were seen after a period with several days with heavy rain (8–16 mm day^{-1}) and temperatures fluctuating around freezing (± 5 °C). The near-surface water content decreased from about 36 to 30% by volume from 18 to 28 March and near-surface CO_2 concentrations fluctuated between 0.3 and 0.4% without revealing any significant increase. Similar, although less pronounced patterns were observed for the spruce stand (mean CO_2 effluxes during the same days were 1.1, 2.5 and 2.2 μmol CO_2 m^{-2} s^{-1}).

Regular efflux measurements on March 30, 2000 were difficult to make as snowfall 2 days prior had buried the collars. Wet snow was removed from collars, and immediately afterwards the effluxes were high, although they reached normal levels within few hours (Figure 7).

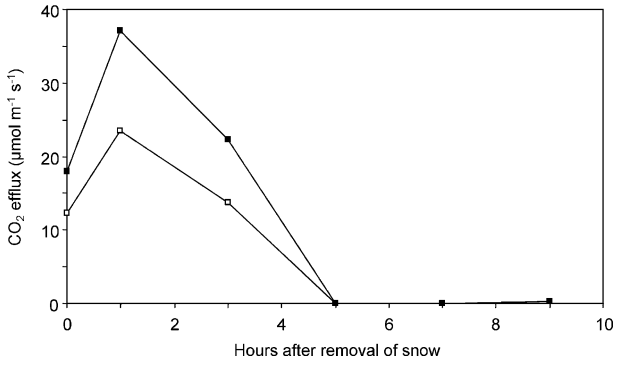

Figure 7. Extreme soil CO_2 effluxes measured on March 30, 2000 after wet snow was removed from two collars placed in the beech stand.

Simulated subsurface CO_2 levels

The observed subsurface CO_2 concentrations were simulated based on CO_2 production profiles, calculated as a sum of depth-specific microbial and root respiration, and soil diffusivity characteristics (Figure 8). Microbial respiration was estimated from basal soil respiration measurements (Figure 1). Root respiration was estimated by the vertical distribution of live roots (Figure 2). Soil diffusivity was calculated based on water content measurements (Figures 4 and 5). The root distribution observed in the beech stand was used for simulating CO_2 concentrations in the soil at the spruce stand knowing that the distribution of roots in the spruce forest may be significantly different from beech. The model was calibrated by matching the depth-integrated subsurface CO_2 production to measured soil CO_2 effluxes observed the same days at the two stands (from December 14, 1999 to March 18, 2000) and finally validated for 1 year (April 2000–March 2001). The deviations between simulated and observed subsurface CO_2 concentrations (Figure 9) show that more than 92% of the annual and spatial variation within the upper one meter could be described by the model. The corresponding predicted soil CO_2 effluxes are shown (Figure 4) and reveal a fair match ($r^2 = 0.90$) but little improvement compared to simulations based on near-surface temperatures alone ($r^2 = 0.88$). However, the consistency in observed and simulated soil CO_2 effluxes shows that subsurface CO_2 production and transport may be reasonably well predicted using Fickian

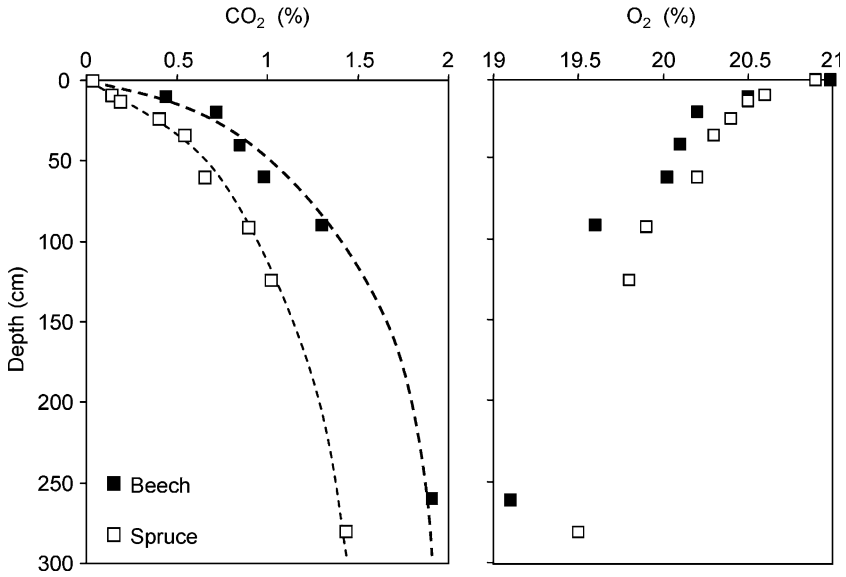

Figure 8. Observed O_2 and CO_2 concentration profiles at the beech and spruce stands measured in December 1999. Simulated CO_2 concentration profiles are shown as dashed lines.

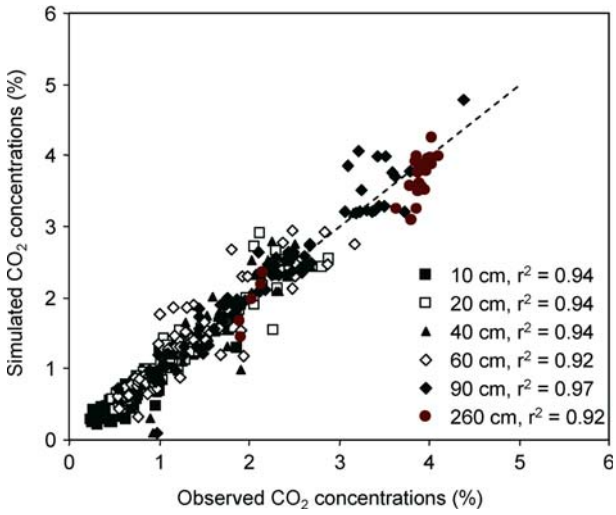

Figure 9. Observed and simulated CO_2 concentrations at the beech stand. The 1:1 relationship is shown by a dashed line.

diffusion theory and consistently linked to net output as represented by soil CO_2 effluxes.

Forest soil C turnover

Based on the results reported, organic C budgets were determined for the two forest stands (Table 3). The above-ground biomass in beech and spruce forests were estimated to be 39 and 71 Mg C ha^{-1}, respectively and are a function of the age of the two forests and forestry practices. Excluding the O-horizon, the SOC equals 88 and 137 Mg C ha^{-1} for beech and spruce, respectively. Including the O-horizon, SOC stocks increase to 93 and 184 Mg C ha^{-1}, respectively. Calculating the turnover time according to the method of Raich and Schlesinger (1992) which excludes the O-horizon, results in an average C turnover time for at the beech location of 25 years which is significantly faster than an average turnover time at the spruce location of up to 43 years ($p < 0.05$). If the turnover time is calculated according to the method suggested by Davidson and Trumbore (1995), which includes the O-horizon as well as dead roots and litter fall, the values increase to 28 and 60 for the beech and spruce locations, respectively.

Integration of the vertical variation in soil microbial respiration for the validation year resulted in the following average carbon turnover times in the soil beneath the beech forest: 8.7 years for carbon stored in the O-horizon, 23.4 years for carbon in the A-horizon and 60 years for carbon stored in layers below the A-horizon. The same calculations could not be made for the spruce

Table 3. Carbon stocks and turnover at the two forest stands in Nødebo.

	Beech	Spruce
Above-ground live biomass, Mg C ha^{-1}	39.0	70.6
Annual litterfall, Mg C ha^{-1} yr^{-1}	1.4 ± 0.1 (1.9 ± 0.4)[a]	(2.1 ± 0.8)[a]
O-horizon C stock, Mg C ha^{-1}	5.6 ± 1.5	47.3
Live roots biomass, Mg C ha^{-1}	4.2 ± 1.9	–
Dead roots biomass, Mg C ha^{-1}	3.5 ± 2.5	–
SOC (upper 1 m), Mg C ha^{-1}	88 ± 19	137 ± 23
Total soil respiration observed, Mg C ha^{-1} yr^{-1}	6.46	5.90
[b]Turnover time, yr	25	43
[c]Turnover time, yr	28	60[d]

[a]Mean values (1994–1997) reported by Bastrup-Birk (2003).
[b]Mean residence time as suggested by Raich and Schlesinger (1992): SOC divided by the microbial soil respiration, representing 54% of total respiration observed by chamber measurements (Hanson et al. 2000).
[c]Turnover estimated as suggested by Davidson and Trumbore (1995): microbial soil respiration divided by the total carbon pool consists of soil organic matter, carbon content of the O-horizon, dead roots and litter.
[d]Assuming the same amount of dead roots as observed in the beech stand.

stand. However, the average turnover time in the O-horizon at the beech location may be compared to the spruce stand by assuming that 37% of the total soil respiration observed at the spruce location is due to CO_2 produced within the O-horizon. This results in an average turnover of 21.5 years for the O-horizon under the spruce stand and thus, a significantly longer, roughly 2.5 times longer turnover time, compared to the beech soil.

Discussion

Changes in root biomass and root respiration over time

Roots in the root size fraction <1 mm are the fraction most likely to show seasonal cycles of growth and death; with increasing biomass during spring and gradually decrease during autumn (Gholz et al. 1985; Santantonio and Grace 1987; Olsthoorn and Tiktak 1991; Rasse et al. 2001). Due to the low spatial and temporal sampling density of soil cores in this study, it was not possible to estimate a fine root production from the root samples. Uncertainty in this study is related to field observations indicating that the total mass of live roots was highest in July, 2000 and almost a factor of two higher than in April 2001 and May 2001. This is in contrast to the observation that the percentage of live roots in the finest size class (<1 mm) increased by 4.6% of total root biomass from late summer (June 27, 2000) to spring (April 4, 2001) and by a further 4.7% to early summer (May 31, 2001). This latter increase in the proportion of very fine roots compared to total live roots is believed to be the result of spatial variability rather than temporal trends within the stand. Thus, for the purpose

of simulating subsurface CO_2 dynamics, it was assumed that the mean annual root respiration accounted for 46% of the total annual efflux, which equals 0.81 g C m^{-2} day^{-1} for beech (and 0.75 g C m^{-2} day^{-1} for spruce) and that the annual fluctuation in live root biomass can be simulated using a step function from a minimum value of 0.72 kg dry mass m^{-2} to a maximum value of 1.45 kg dry mass m^{-2}. These values deviate from those used by Moncrieff and Fang (1999) for similar modelling using PATCIS. Moncrieff and Fang (1999) used a minimum value of 0.92 and a maximum value 1.2 kg m^{-2} for a slash pine plantation in Florida. However, when the average C-content in fine roots is taken into account, values used in the present study are within the range of fine root production summarized for temperate forest ecosystems (Rasse et al. 2001). The importance of microbial versus root respiration is further complicated by the presence of an intermediate respiration compartment consisting of specific rhizosphere respiration which may vary between tree species and soil types. This rhizosphere respiration can be defined as soil respiration under the influence of roots, which contains a relatively large microbial community living off root-derived organic substrate (Kelting et al. 1998). The simulation of subsurface CO_2 levels was repeated in order to evaluate the model sensitivity with respect to the part of the total annual efflux related to root respiration of (46% used). No significant effects ($p < 0.05$) were noted for values between 37 and 55%.

Finally, the temperature dependency of root respiration was simulated using a value observed for microbial respiration despite some indications of that 'rhizosphere respiration' has a higher Q_{10} value than microbial respiration alone (Boone et al. 1998; Epron et al. 2001). This may explain the greater Q_{10} value determined from field observations (microbial and root respiration) compared to laboratory observations (microbial respiration only). On the other hand, simulations using a Q_{10} value of 3.7 in stead of 2.7 for root respiration did not improve model results.

The present study assumed a fixed distribution of fine roots among soil layers. This is based on model predictions for beech stands suggesting that the distribution of fine roots changes rapidly for young beech trees but remain fairly unchanged for trees 40 years old and older (Rasse et al. 2001). Because of these uncertainties, a fairly successful simulation of subsurface CO_2 concentrations in this study should not be seen as an improvement or validation of the general understanding of soil root dynamics in beech forests. This simply requires a more extensive soil core sampling strategy as shown by Makkonen and Helmisaari (1999).

Soil CO_2 dynamics and controls in the beech stand

Soil temperatures have long been considered among the most important parameters controlling soil respiration (Kirschbaum 1995; Raich and Tufekciogul 2000; Fang and Moncrieff 2001). In the present study, a Q_{10} value

equal to 2.9 was estimated for temperatures between 0 and 10 °C, which is slightly higher than Q_{10} values estimated for higher temperatures. An increase in Q_{10} at low temperatures is consistent with Fang and Moncrieff (2001) and higher winter Q_{10} values compared to summer Q_{10} values in a Danish beech forest (Janssens and Pilegaard 2003). However, such seasonal trends could not be confirmed in the present study based on field observations of near-surface temperatures and CO_2 effluxes. Constant Q_{10} values over time and depths have been reported previously in studies of Arctic soils (Oberbauer et al. 1996).

The dominance of temperature as the controlling parameter on observed soil CO_2 in the field period may not be representative for all years. Data from Danish Meteorological Institute (www.dmi.dk) revealed that the summer precipitation observed in Nødebo in June, July and August (2000) was about 245 mm, which is higher than average values of 190 mm (1900–2000) and 175 mm (1980–1990). Thus, the unusually moist conditions in the summer 2000 may have prevented the soil respiration from becoming water-limited. Despite the moist conditions in Summer 2000, the water contents at some depths were close to the critical 10% water content per volume (see Figures 3 and 4). Therefore, it is likely that a low water content may be critical for summer respiration in dryer years. In the period 1980–2000, the total June, July and August precipitation was less than 150 mm three times, thus the annual soil respiration reported in the present study may be higher than the average summer soil respiration over the previous 20 years. Further complications arise because dry years also tend to be warmer. Pilegaard et al. (2001) investigated CO_2 eddy-flux measurements over a Danish beech forest and found higher soil respiration rates during a warm (and dry) summer in 1997 compared to a more 'normal' year (1996). In contrast, Borken et al. (2002) could not document any significant interannual variations in soil CO_2 effluxes from beech forest stands comparing two contrasting years (1998–1990). Undoubtedly, forest soil respiration predictions over decades need to take into account interannual variations in precipitation as well as temperature.

Extreme events characterised by unusually high effluxes that decrease to normal rates were observed in association with drying after heavy rain (Figure 6) and after the removal of snow (Figure 7). In both cases, it is likely that the soil system was isolated from the atmosphere for a short period of time, causing the soil CO_2 effluxes to decrease to a lower level, while the continuous subsurface production of CO_2 resulted in an increase in subsurface CO_2 concentrations. A slow response (over days) was noted in relation to a natural drying of leaves and possible melting (Figure 6) while a more rapid response (over hours) was noted after an artificial removal of snow from collars (Figure 7). During a period of isolation and subsequent high effluxes, the soil–atmosphere system is in a non-steady state condition; whereas diffusion may still be the dominant transport mechanism, it was not possible to simulate the situation using a steady state model. The importance of the non-steady state periods during the period of investigation is likely small, as the amount of CO_2 released during the two events accounted for less than 1% of the total annual

soil respiration. However, in other years with freezing soil and thick snow during a longer period (in Denmark seldom more than a month) the conditions may be similar to winter conditions in cold climates. In particular, snow fall may insulate the ground from cooling, thus relatively high soil temperatures (between 0 and 10 °C) may be combined with a freezing top soil, freezing wet litter layer and snow/ice layers which may act as an effective diffusion barrier for gas exchange between the soil and the atmosphere (Winston et al. 1997; Fahnestock et al. 1998, 1999; Elberling 2003; Elberling and Brandt 2003). Subsequent thaw conditions may lead to pronounced non-steady state conditions.

Excluding the extreme events, the diffusion-reaction model used in this study has proven to be suitable to provide insight into the interacting processes of subsurface CO_2 production, CO_2 transport and the net result in terms of soil CO_2 effluxes. This is in agreement with the results of Hirano et al. (2003). Due to the lack of root data for the spruce stand, it was only possible to validate the model for the beech stand.

Tree-specific differences in turnover times

Soil temperatures were generally the same during late spring (after bud break), summer and autumn at the two forest stands. In winter and early spring, the temperature amplitude was largest in the beech stand, due to lack of canopy cover. Soil water content was approximately equal in the two stands (Figures 4 and 5). Thus, the difference in soil CO_2 effluxes between the forest stands is neither due to temperature nor soil water content. Differences in substrate quality and the size and activity of microbial communities could be part of the explanation. The C:N ratio for the organic matter stored below the O-horizon is almost equal for the two stands. In contrast, the C:N ratio of litter fall collected in 1994 at a nearby site (Bastrup-Birk et al. 2003) reveals that beech litter had a significantly lower C:N ratio (37) compared to spruce (42) and consequently is likely more easily degraded. Similar observations have been made of the forest floor chemistry under similarly-aged beech and spruce along a soil fertility gradient in Denmark (Vesterdal and Raulund-Rasmussen 1998). The acidic conditions observed in both forest stands indicate an incomplete decomposition. The thicker O-horizon (mor-layer), slightly lower pH-values, and lower base cation saturation levels in the spruce stand compared to the beech stand may partly explain the faster accumulation of organic matter near the surface of the spruce stand and consequently the slower turnover time in the spruce compared to the beech stand (in general and for O-horizon material only). Further, earthworms were occasionally observed in the beech forest, and not in the spruce forest. These observations are in agreement with observations of the influence tree species on soil and soil solution properties in two mixed spruce–beech stands in Germany (Rothe et al. 2002) and observations by Borken et al. (2002) and Heinze et al. (2001). In combination, the observations

from Nødebo indicate that organic matter in the beech forest is decomposed more rapidly than in the spruce forest, and that the almost equal annual effluxes observed are related to the larger amount of less reactive SOC stored in the spruce stand.

Conclusions

Soil temperatures were noticed to be the dominating parameter affecting fluctuation in observed soil CO_2 effluxes which were measured for 15 months in two temperate and contrasting Danish forest ecosystems: beech and spruce. The soil organic C-stock (upper 1 m including the O-horizon) beneath the spruce stand was significantly higher compared to the beech stand and consistent with a significantly faster turnover time for beech soils as compared to spruce soils. Based on O-horizons, the organic C turnover time at the spruce location was more than twice as long as for the beech location. Despite differences in forest type and turnover times of soil organic carbon, the soil CO_2 fluxes in the field were surprisingly similar. The similarity is believed to be due to the current conditions in the spruce stand where there is more soil organic carbon stored, although it is less reactive. Temporal trends in soil CO_2 effluxes could be successfully linked to variations in subsurface CO_2 production rates and diffusion over time and with depth. Periods with extremely high fluxes were noted after heavy rain and after removal of snow. These periods were considered non-steady state situations and could not be simulated. Excluding these non-steady state periods, the overall relationship between soil CO_2 effluxes and soil CO_2 concentration profiles provide a better understanding of the links between the depth of biological activity, the source of CO_2 released to the atmosphere, as well as the depth-dependent residence time of SOC. The results of the study further highlight the importance of incorporating the soil component in future climate models aiming to predict the interaction of greenhouse gas, climate and vegetation.

Acknowledgements

The project was financed by the Danish Natural Science Research Council (1235) and Danish Agricultural and Veterinary Research Council (23-03-0195). Thanks to students at the Institute of Geography, University of Copenhagen, particularly M.-B. Petersen and M.H. Simonsen for participating in the field work. Also thanks to the staff at the Department of Microbial Ecology, University of Aarhus, Denmark, in particular to S.P. Andersen and P.G. Sørensen for help with thermoblock measurements. Many thanks are extended to two BIOG reviewers for a thorough review with many helpful suggestions.

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