Available online at www.sciencedirect.com
ScienceDirect
Geoderma 139 (2007) 79–89
GEODERMA
www.elsevier.com/locate/geoderma

Assessment of soil CO_2 efflux and its components using a process-based model in a young temperate forest site

Gustavo Saiz *, Kevin Black, Brian Reidy, Sandra Lopez, Edward P. Farrell

School of Biology and Environmental Science, University College Dublin, Belfield, Dublin 4, Ireland

Received 6 July 2006; received in revised form 9 December 2006; accepted 23 December 2006
Available online 20 February 2007

Abstract

It is crucial to advance the understanding of soil CO_2 efflux and its components for a better comprehension of carbon dynamics in terrestrial ecosystems. The process-based PATCIS model was applied to a first rotation young Sitka spruce stand in order to simulate the seasonal contribution of soil respiration components to the overall soil CO_2 efflux. We evaluated the performance of the model with observed measurements and compared it with empirically derived regressions. Once the model was parameterised, it explained 75% of the seasonal variation in total soil CO_2 efflux. Similar seasonal trends and annual estimates of soil CO_2 efflux were obtained with either empirical or the process-based PATCIS models. Heterotrophic and autotrophic respiration contributed almost equally to total CO_2 efflux during the early and late part of the year, while a larger contribution of autotrophic respiration to total CO_2 efflux occurred during the growing season. The overall annual contribution of autotrophic respiration to total soil CO_2 efflux was 54.7%. Most of root respiration took place in both the litter–humus layer and the A_1 horizon as a result of their large concentrations of fine roots. We observed an accumulation of organic matter in the litter–humus layer, and a net loss from the mineral soil, which had much larger organic matter content compared to the litter–humus layer. The organic matter turnover rate calculated for the mineral soil was 45 years (mean residence time).

The sensitivity analysis showed soil temperature as the most important factor controlling soil respiration. The influence of soil moisture was more variable and had an overall negative effect on soil respiratory rates, except for periods of low soil water content, such as summer drought. The episodic occurrence of very wet conditions at the deeper soil layers was responsible for their low contribution to total soil respiration. In general, gas transport within the soil was not an important constraint for soil CO_2 efflux since most of soil respiration was produced in the highly porous litter–humus and top mineral layers. The autotrophic component was more affected than heterotrophic respiration by changes in soil water content. Other factors such as changes in litterfall inputs were shown to have a more limited impact on soil CO_2 efflux. This work shows that the use of a process-based model to simulate soil CO_2 efflux may be a useful tool to separate soil respiration components.

Keywords: Afforestation; Autotrophic respiration; Gley soil; Heterotrophic respiration; PATCIS model; Sitka spruce; Soil respiration

1. Introduction

The relevance of soil CO_2 emissions in the global carbon budget has been pointed out in numerous studies (Houghton et al., 1998; Schlesinger and Andrews, 2000; IPCC, 2001). Poor knowledge of processes driving soil CO_2 efflux, insufficiency of experimental data, and weak geographical representation are among the main factors that make soil respiration to be considered a complex process (Stolbovoi, 2003). Soil respiration consists of CO_2 produced from biochemical processes associated with root activities (autotrophic respiration), and microbial organic matter decomposition (heterotrophic respiration) (Boone et al., 1998; Buchmann, 2000; Hanson et al., 2000). Soil CO_2 efflux is the combined result of production and gas transport (Šimunek and Suarez, 1993; Fang and Moncrieff, 1999).

There are many factors controlling soil CO_2 efflux in forest ecosystems. The main ones are soil temperature and soil water content (Davidson et al., 1998; Janssens et al., 2001). Soil respiration is influenced by the amount and quality of carbon stored in both the forest floor and the mineral soil (Klopatek, 2002). Jobbágy and Jackson (2000) suggested that more organic

* Corresponding author. School of Geography and Geosciences, University of St Andrews, St Andrews, Fife, Scotland, UK. Tel.: +44 1334 463936; fax: +44 1334 463949.
E-mail address: gustavo.saiz@st-andrews.ac.uk (G. Saiz).

0016-7061/$ - see front matter © 2007 Elsevier B.V. All rights reserved.
doi:10.1016/j.geoderma.2006.12.005

matter is available for decomposition in the upper part of a forest soil than in a grassland, as it was revealed by the relative shallower distribution of soil organic carbon observed in the top metre of the forest soil. Other important factors are carbon inputs rates to soil (Nadelhoffer and Raich, 1992), plant photosynthetic activity (Högberg et al., 2001; Kuzyakov and Cheng, 2001; Bhupinderpal-Singh et al., 2003), and plant root activities (Bowden et al., 1993). Additionally, soil physical and chemical properties (Borken et al., 2002), stand age (Irvine and Law, 2002; Saiz et al., 2006a), and forest management activities (Lytle and Cronan, 1998; Johnson et al., 2002) affect soil CO_2 efflux.

Extensive research has been carried out in order to quantify soil CO_2 efflux and study the factors that drive the emissions. The most common approach has been the development of empirical models based on the relationships between soil CO_2 efflux, soil temperature and soil water content (Davidson et al., 1998; Buchmann, 2000). While these models have been seen to produce reliable estimates of soil CO_2, they lack a biological framework, which makes it difficult to account for the role of the environment on soil respiration or carbon cycle in ecosystems (Fang and Moncrieff, 1999; Pumpanen et al., 2003). The main justification for the use of process-based models in soil respiration studies is that they can be used to perform simulations in which physiological properties and environmental regulations affecting soil respiratory processes are explicitly included. In general, process-based models have relatively complicated structure; however, they allow for more comprehensive analyses of ecological processes and they can also be used for making predictions on the response of soil respiration to warming scenarios. For the purpose of simulation, soil can be described as a multilayered structure where CO_2 is produced at various depths, and diffusion and convection transport the gas between the soil layers out of the soil (Pumpanen et al., 2003). PATCIS, which stands for production and transport of CO_2 in the soil, is a process-based model developed by Fang and Moncrieff (1999) that simulates both processes within the soil profile. Despite of its good performance in temperate forest ecosystems (Moncrieff and Fang, 1999; Hui and Luo, 2004), no attempt has been made to test the robustness of this model with regard to the simulation of autotrophic and heterotrophic respiration against periodic field observations of these components.

We conducted a study on a first rotation 15-year-old Sitka spruce stand (*Picea sitchensis* (Bong.) Carr.) located in Central Ireland. The objectives of our research were: 1) to parameterise the PATCIS model for the existing conditions, 2) to compare its performance against empirically derived regressions, and 3) to assess the relative contribution of soil respiration components calculated by PATCIS against observed heterotrophic and autotrophic respiration.

2. Materials and methods

2.1. Site description

The research was conducted on a 15-year-old Sitka spruce (*Picea sitchensis* (Bong.) Carr) first rotation plantation established on former grassland (afforestation site). The study site was located at the Dooary forest (52°57′N, 7°15′W) in the Irish midlands at an elevation of 260 m. Long-term mean annual temperature and average annual precipitation for the region are 9.3 °C and 804 mm, respectively. The seasonal variation of soil temperature and soil moisture for the year 2003 is shown in Fig. 1. The stand had a density of 2366 trees ha^{-1}, which had reached canopy closure and presented no understory or herbaceous vegetation. The stand had been established along ripped lines 1 m deep and 2 m apart. Surface drains across the ripped lines had been made at 50-m intervals. For a more detailed description of the site see Saiz et al. (2006a). The soil type was classified as low humic (mineral) gley. Table 1 shows the characteristics of the different soil horizons.

2.2. Experimental design and measurement of soil CO_2 efflux

A stratified random sampling design for the measurement of soil CO_2 fluxes was put in place on the basis of the degree of disturbance made to the soil when trees were established. The study plot was placed at least 20 m apart from stand discontinuities or its boundaries. Within a 30 m × 30 m plot, a series of 30 PVC circular collars (16 cm in diameter) per stand were inserted into the soil to an average depth of 1.5 cm for measurements of total soil CO_2 fluxes. Collars set at this depth were stable and caused minimal disturbance to shallow fine roots. For investigation of heterotrophic respiration and next to the PVC collars, the same number of stainless steel pipes (16 cm in diameter) were driven 30 cm into the soil in order to exclude tree roots. In this study, measurements were not taken until 8 months after the collars had been installed. Subsequently, a correction was made to account for the overestimation in heterotrophic respiration produced by the decomposition of trenched roots (Saiz et al., 2006a).

Soil respiration measurements were carried out with a portable system on a monthly basis during 2003. This dataset was used both for fitting the empirical models and to allow for comparison with the simulated rates yielded by the PATCIS model. Soil respiration measurements were conducted for total

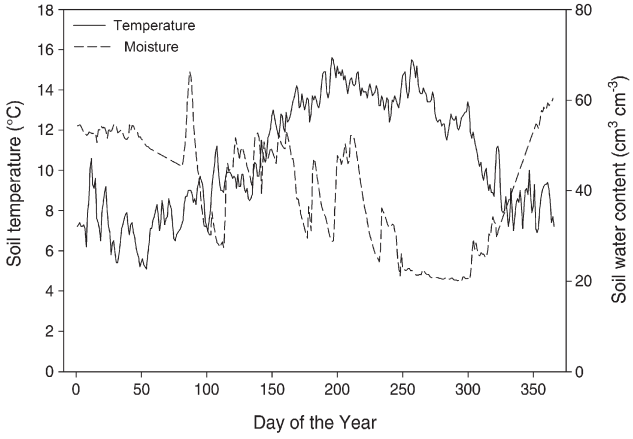

Fig. 1. Seasonal variation of soil temperature and soil moisture measured at 6 cm at the Dooary site for 2003.

Table 1
Soil characteristics of the Sitka spruce stand

Layer	Depth (m)	Organic matter pool (kg dry OM m^{-2})	Bulk density (g cm^{-3})	Nitrogen (%)	Phosphorous (mg/l available)	pH
Litter–humus	0.04	1.798±0.15	0.16±0.02	1.62	ND	ND
A_1	0.10	9.828±0.63	0.84±0.02	0.42	11.4	4.8
A_2	0.10	10.790±0.68	1.05±0.04	0.26	8.0	5.5
Bg	0.06	2.780±0.25	1.19±0.04	0.10	4.4	4.9

and heterotrophic respiration simultaneously at each of the paired sampling points using two portable infrared gas analysers connected to soil respiration chambers having a headspace volume of 2250 cm^3 (EGM-4 and enlarged SRC-1; PP Systems, Hitchin, UK). The measuring principle is a closed system that determines the increase in CO_2 concentration within the chamber over a 120-s period. The infrared gas analysers were calibrated before each sampling day against CO_2 with a nominal concentration of 409 μmol mol^{-1}. The chambers were fitted with a rubber-foamed ring cemented to a modified lip to ensure a tight seal with the soil collars. Root or autotrophic respiration was then calculated as the difference between total and heterotrophic readings. The temporal and spatial variability of the efflux at this ecosystem is analysed in detail in Saiz et al. (2006b). The use of portable soil respiration systems made possible sampling over many locations, thus increasing the confidence in the site mean estimate of soil respiration with respect to spatial heterogeneity (Savage and Davidson, 2003).

On the other hand, total soil CO_2 efflux was also monitored every 0.5 h using an automated open-top chambers system based on the design of Fang and Moncrieff (1998). The system was fitted with a parallel 4-way solenoid control system connected to four soil respiration chambers and a data logger (Goulden and Crill, 1997). In 2004, a total of 16 days of continuous measurements of total soil CO_2 efflux were randomly selected throughout the year to allow for the parameterisation of the PATCIS model. The automated soil respiration system installed at this site did not show significant diurnal variations in soil respiration (Black et al., in press). An inter-comparison between the automated and portable respiration systems showed that both devices yielded very similar soil CO_2 efflux readings (data not shown).

In July 2004, a total of twelve locations were used to assess the effect of soil layers removal on soil respiration rates. The litter–humus and root biomass found at the organic layer were carefully removed from four 30 cm × 30 cm locations. In other four locations both the litter–humus and the top mineral soil layer (A_1) were also removed. The same procedure was followed over the same number of locations where the litter–humus layer, and A_1 and A_2 mineral layers were also removed. Finally, four extra collars were set up over undisturbed ground to be used as controls to measure total soil respiration. All soil respiration collars were established 1 week before the measurements took place.

2.3. Measurement of environmental factors

An automatic weather station (Campbell Scientific Ltd., Shepshed, England, UK) placed at the study site recorded air and soil temperatures, soil moisture, and rainfall. Additionally, soil temperature at 2 and 10 cm depth was measured adjacent to each collar at the time of soil CO_2 efflux measurements (220 K temperature meter, Jenway, Essex, UK). Simultaneously, soil water content within every collar was determined using a moisture probe (ThetaProbe ML2x, Delta-T Devices, Cambridge, UK). In January 2004, half of the locations over which soil respiration measurements took place were sampled for determining the organic matter content and bulk density in each of the soil horizons (Table 1). The litter–humus layer was removed by hand from each sampling position, in order to be analysed for organic matter content. The organic matter in the soil samples was determined using loss on ignition. The Walkley–Black wet oxidation technique was also used over a number of subsamples to validate the estimates of soil organic matter. Soil bulk density was determined by retrieving undisturbed cores of known volume from each soil horizon to subsequently oven-dry the samples at 105 °C until constant weight was reached.

Root biomass determination was carried out over 15 sampling locations to a depth of 30 cm. The litter–humus layer and the different soil horizons were separated. All samples were then rinsed and sieved to detach roots from soil mineral particles. Samples were immediately stored at 4 °C until they were processed in the laboratory. Finally, washed roots were classified by diameter class and weighted after being oven-dried at 70 °C for 48 h to determine root biomass. Annual fine root biomass production was estimated using the in-growth core technique at the same locations employed for biomass determination (Janssens et al., 2002). Intact litter and soil columns were retrieved after 12 months. Roots were then processed and sorted into live and dead fractions. Aboveground litterfall was collected every month from January to December 2003 from ten litter traps (616 cm^2 section) randomly located within the 30 m × 30 m plot. Litter was then oven-dried to a constant mass.

2.4. Structure of the PATCIS model

PATCIS is a one-dimensional, process-based model developed by Fang and Moncrieff (1999) that simulates production and transport of CO_2 in soil. In the model, the production of CO_2 in the soil is the result of living roots respiration and decomposition of soil organic matter by microbes. Live and dead biomass, soil temperature, moisture content, and O_2 concentration in soil are considered as direct influencing factors on soil CO_2 production and transport. In the PATCIS model the effect of soil moisture on soil respiration and surface CO_2 efflux is simulated separately through its influence on microbial and root activities, and on gas diffusion in the soil. Although in this model the soil is divided into several layers, all layers are integrated into a system through their interactions with O_2 concentration (i.e. a change in one layer will affect

Table 2
Parameter values used for the PATCIS model

Parameter estimates	This study	Moncrieff and Fang (1999)	Hui and Luo (2004)
Activation energy >20 °C (Jul mol^{-1})	92 800	94 900	97 450[a]
Activation energy 10–20 °C (Jul mol^{-1})	82 200	79 300	82 150[a]
Activation energy <10 °C (Jul mol^{-1})	81 000	78 200	80 600[a]
Michaelis–Menten constant for O_2 (g O_2 m^{-3})	43 100	48 800	ND
Optimal organic matter decay rate (mg CO_2 g^{-1} dry matter s^{-1})	3.60×10^{-6}	3.73×10^{-7}	1.80×10^{-6}
Optimal litter decay rate (mg CO_2 g^{-1} dry matter s^{-1})	3.91×10^{-5}	3.85×10^{-6}	1.80×10^{-5}
Optimal dead root decay rate (mg CO_2 g^{-1} dry matter s^{-1})	3.91×10^{-5}	3.85×10^{-6}	1.80×10^{-5}
Optimal root respiration <3 mm (mg CO_2 g^{-1} dry matter s^{-1})	7.89×10^{-5}	4.30×10^{-5}	9.28×10^{-6}[b]
Optimal root respiration 3–10 mm (mg CO_2 g^{-1} dry matter s^{-1})	7.10×10^{-6}	5.07×10^{-6}	
Optimal root respiration >10 mm (mg CO_2 g^{-1} dry matter s^{-1})	1.10×10^{-6}	6.75×10^{-7}	
Moisture parameter *a* mineral	11.58	22.6	13[a]
Moisture parameter *c* mineral	0.11	0.11	0.11[a]
Moisture parameter *a* litter	4.58	7.5	6.25[a]
Moisture parameter *c* litter	0.15	0.15	0.135[a]

Values presented here have been compiled from the present study, Moncrieff and Fang (1999), and Hui and Luo (2004).

[a] In the study by Hui and Luo (2004), the activation energies and the moisture parameters were calculated separately for both the autotrophic and the heterotrophic components. The values presented here are the average calculated from both components.

[b] In the study by Hui and Luo (2004), optimal root respiration rates were presented for roots <1 mm, 1–2 mm, and >2 mm. The value included in this table is the average for all diameters, and it is presented for comparison purposes.

respirations in other layers). The reader is referred to Fang and Moncrieff (1999) for detailed explanation on the model functioning.

2.5. Parameterisation of the PATCIS model

A proper choice of model parameters is crucial for achieving a realistic simulation of soil CO_2 efflux. Parameters for the PATCIS model were determined from continuous total soil respiration data collected with the automated respiration system. A built-in multidimensional optimisation tool in PATCIS based on the Downhill Simplex method (Press et al., 1992) was used to determine values for model parameters, which follows work conducted by Moncrieff and Fang (1999). The method minimises the residual sum of squares between estimated and measured CO_2 fluxes with a pre-set convergence criteria. Parameter values are presented in Table 2.

2.6. Description of the empirical model

Using the data collected over the year, a two-parametric exponential function was used to describe the relationships between soil CO_2 fluxes and soil temperature. The formula is as follows:

$$y = ae^{bT} \quad (1)$$

where y is the measured soil CO_2 efflux rate, T is the measured soil temperature, being a and b the fitted parameters. Similarly, we developed an equation combining soil temperature and soil water content to explain the flux. The best fits were obtained using an equation of the form:

$$y = (ae^{bT})(c\mathrm{SWC} + d\mathrm{SWC}^2) \quad (2)$$

where y is total CO_2 efflux, T is soil temperature, and SWC is soil water content in the top 6 cm, and a, b, c and d are fitted parameters.

3. Results and discussion

3.1. Seasonal variation of soil CO_2 efflux and soil respiration

Simulated seasonal variation of soil CO_2 efflux followed that of soil temperature (Figs. 1 and 2). Total soil CO_2 efflux rates simulated with the process-based PATCIS model ranged from 33.3 mg C m^{-2} h^{-1} in late February to a maximum value of 148.0 mg C m^{-2} h^{-1} in late July (Fig. 2). In general, modelled soil CO_2 efflux using the PATCIS model compared well with observed measurements ($r^2=0.75$). However, there was a slight underestimation of the efflux following a very wet period in the summer, while the model tended to overestimate the efflux at the time of summer drought (Fig. 2). On the other hand, the model driven by temperature and moisture explained slightly less of the seasonal variation in soil CO_2 efflux ($r^2=0.71$), and although it did not accurately match the measured values observed at high and low contents of water in the soil during summer, it was more sensitive to these features (Fig. 2). The use

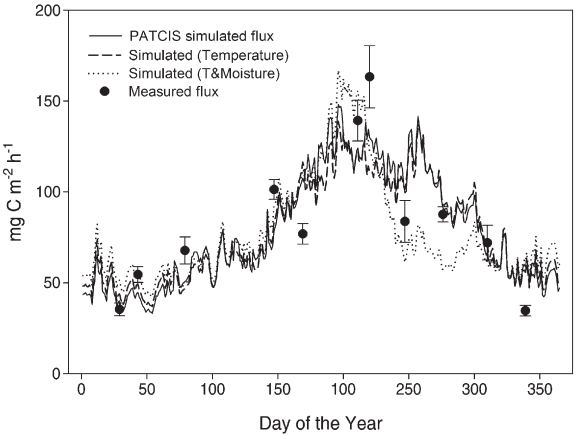

Fig. 2. Seasonal variation of soil CO_2 efflux modelled with PATCIS, with the model based on soil temperature: $y=21.96\exp^{(0.1262T)}$ ($r^2=0.65$); and with the model based on soil temperature and soil moisture combined: $y=-1.438\exp^{(0.1199T)}\times((-0.6372\mathrm{SWC})+(0.0048\mathrm{SWC}^2))$ ($r^2=0.71$). T is soil temperature (°C) and SWC is soil water content (cm^3 cm^{-3}). $P<0.05$ for both empirical models. Each measured value for soil CO_2 efflux is the mean of 30 measurements. Error bars are standard errors of the mean.

of temperature alone as the single variable to explain the flux yielded an even lower regression fit ($r^2=0.66$).

Mean modelled daily values were added up to obtain an annual estimate for soil CO_2 efflux. Similar annual estimates of soil CO_2 efflux were obtained using either the empirical or the process-based PATCIS model. An annual soil CO_2 efflux estimate of 691 g C m^{-2} $year^{-1}$ was obtained with the PATCIS model. Values of 677 and 686 g C m^{-2} $year^{-1}$ were obtained with the models driven by temperature and moisture, and temperature alone, respectively. Those values are within the summarised range reported for temperate forest ecosystems; i.e. 250 to 1255 g C m^{-2} (Raich and Schlesinger, 1992).

In general, the difference between simulated soil CO_2 production rates and simulated soil CO_2 efflux obtained using PATCIS was minimal (Fig. 3). The largest differences between both estimates occurred as a result of major rainfall events, being the largest difference of only about 1.3 mg C m^{-2} h^{-1} (Fig. 3). The minimal differences between soil CO_2 efflux and soil respiration obtained in this study, suggest that at this forest site there is little restriction on gas transport within the soil, which is also supported by the fact that most of CO_2 is produced in the highly porous upper soil layers (Fig. 4). By contrast, other studies applying the PATCIS model have shown slightly larger restrictions of CO_2 within the soil profile (Moncrieff and Fang, 1999; Hui and Luo, 2004). However, diffusivity experiments conducted at our site measuring soil CO_2 concentrations at different depths seem to confirm the low limiting conditions for the movement of gas throughout the soil profile (Black, unpublished data). Furthermore, the latter facts also suggest that there was little bias in measurements of soil CO_2 efflux carried out on most occasions, except perhaps on measurements

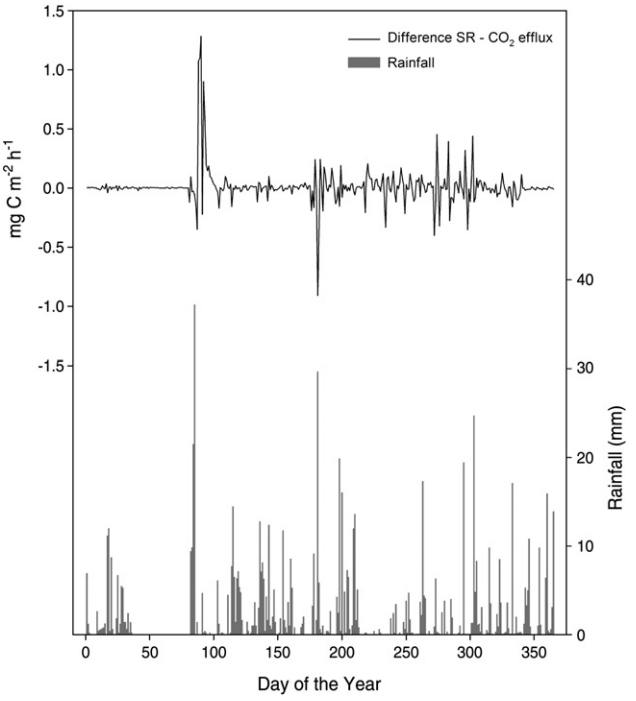

Fig. 3. Difference between simulated soil respiration (SR) and soil CO_2 efflux rates over the course of the year. The bar graph at the bottom shows the daily rainfall measured at the Dooary site for 2003.

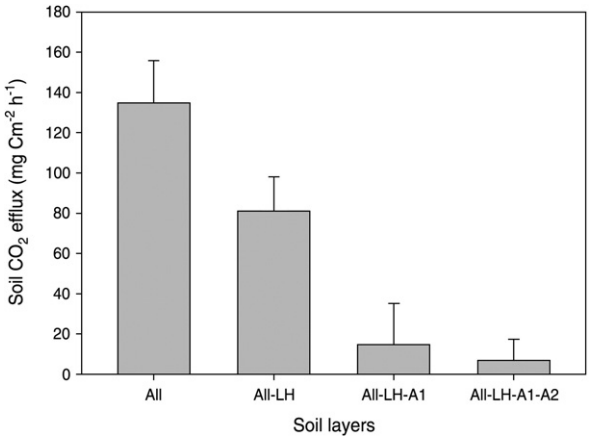

Fig. 4. Effect of soil layers removal on soil CO_2 efflux rates. LH stands for litter–humus layer. Error bars are standard deviation of the mean ($n=4$).

carried out immediately after heavy rainfall. Post-rainfall increases in soil CO_2 efflux are likely the result of the enhancement in the activity of the microbial community decomposing soil organic matter, in particular after long periods between rainfalls (Lee et al., 2002).

3.2. The effect of soil horizons removal on soil CO_2 efflux

The removal of soil layers had a strong negative impact on soil CO_2 efflux, which was most obvious with the exclusion of the upper soil layers (Fig. 4). The PATCIS model both confirmed such observation, while it also allowed for explaining the seasonal contribution of each soil layer to total soil respiration (Fig. 5). The largest contributors to total soil respiration were the litter–humus layer and the top mineral soil horizon (A_1) with an overall annual contribution of 32.9% and 54.4%, respectively (Table 3). The overall simulated contribution from deeper soil layers was significantly less, as it was also observed in the manipulation experiment (Fig. 4). Soil respiration in the A_2 horizon was very limited during winter time by the presence of high water contents (Fig. 5). As far as the Bg horizon is concerned, its lower porosity and the fluctuation of the water table following rainfall, created conditions of water saturation in

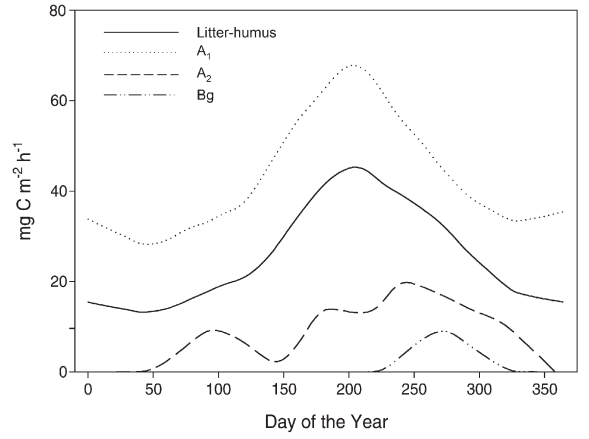

Fig. 5. Seasonal variation of simulated soil respiration with the PATCIS model at the different soil horizons.

Table 3
Contribution of heterotrophic and autotrophic components to total soil respiration for each soil layer

Horizon	Depth (m)	Total respiration (%)	Heterotrophic respiration (%)	Autotrophic respiration (%)
Litter–humus	0.04	32.9	9.2	23.7
A_1	0.10	54.4	33.8	20.6
A_2	0.10	10.9	2.1	8.8
Bg	0.06	1.8	0.2	1.6
Total	0.30	100	45.3	54.7

this layer for most of the year. This fact is interpreted as "zero" production by the PATCIS model, although some respiration can still take place, as it was proved by Magnusson (1993). However, the overall production may be rather modest, and consequently the underestimation of the efflux may be relatively small.

3.3. Heterotrophic and autotrophic soil respiration

The separation of soil respiration into its heterotrophic and autotrophic component allowed us to test the performance of the process-based PATCIS model in predicting the seasonal contribution of each component to the overall efflux. Fig. 6a shows the simulated seasonal variation in both heterotrophic and autotrophic soil respiration. The contribution of both components to the total soil CO_2 efflux varied over the year. Both heterotrophic and autotrophic respiration contributed almost equally to total CO_2 efflux during the early and latter part of the year, while a larger contribution of autotrophic respiration to total CO_2 efflux occurred during the growing season (Fig. 6a). Measured soil heterotrophic rates ranged from as high as 68.0±10.1 mg C m^{-2} h^{-1} during mid summer, to as low as 18.4±2.5 mg C m^{-2} h^{-1} recorded in late January. Similarly, maximum autotrophic respiration rates were also observed in mid summer with a highest rate of 95.3 mg C m^{-2} h^{-1} while the lowest value was 17.0 mg C m^{-2} h^{-1} calculated in late January. The process-based model simulated well actual measurements at low to medium rates. However, there was a larger degree of scatter at higher rates (Fig. 6b). The model explained 64% and 74% of heterotrophic and autotrophic soil respiration, respectively.

Around day 210 (late July) there was a significant reduction in modelled autotrophic respiration as a result of the large amount of soil water content following rainfall in deep soil layers (Fig. 6a). The explanation for such a larger reduction of the autotrophic component as compared to the heterotrophic one is similar to that reported by Moncrieff and Fang (1999). The conditions of saturation in the A_2 horizon affected more significantly to root respiration since its contribution was higher than that of microbial respiration for that depth (Table 3). Another significant reduction in autotrophic respiration occurred around day 240, partially due to a drop in soil temperature of about 3 °C (Fig. 1), but also as a result of summer drought, which is a feature that has been previously described (Burton et al., 1998). Microbial respiration was also limited during this period (Fig. 6a), which is probably attributable to the restriction of soluble organic substrates (Epron et al., 1999; Rey et al., 2002).

The contribution of both heterotrophic and root respiration to total soil CO_2 efflux was calculated by means of integrating the different components of soil respiration at different depths throughout the year. Consequently, annual contribution of autotrophic respiration to total soil CO_2 efflux was 54.7% (Table 3), which compares well with the estimated autotrophic contribution calculated for this forest stand that accounted for 56.7% (Saiz et al., 2006a). The litter–humus layer and the top mineral soil horizon were the largest contributors to total soil respiration (87.3%). Most of the microbial respiration was produced in the top layer of mineral soil, which had together with the A_2 horizon the largest organic matter pools (Table 1). On the other hand, a large proportion of root respiration (81%) took place in both the litter–humus layer and the A_1 horizon, which appreciably had the largest concentrations of fine roots (<3 mm) (Fig. 7). Small roots have higher specific respiration rates than larger root structures (Pregitzer et al., 1998; Widén and Majdi, 2001). In addition to it, root respiration has been reported to decline with soil depth as a result of possible effects

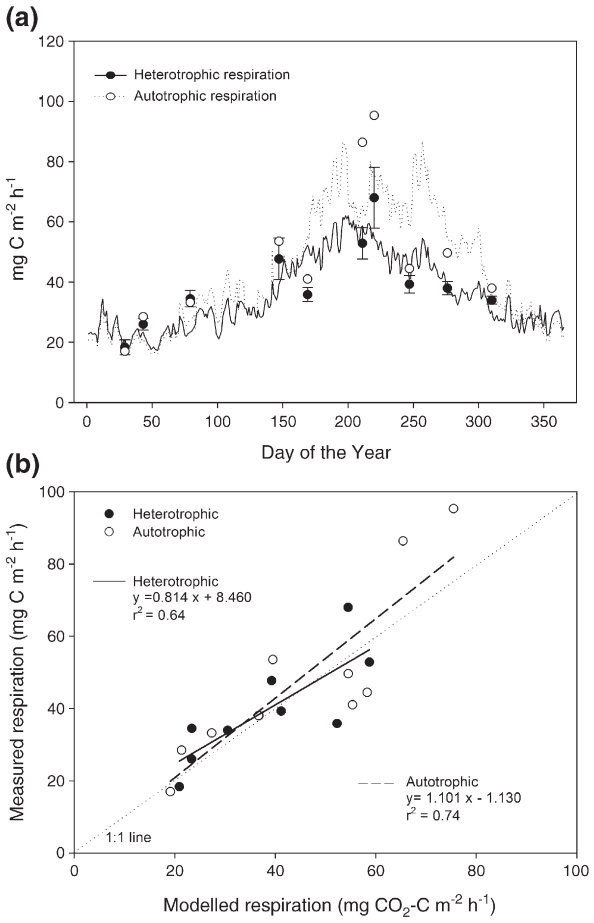

Fig. 6. (a) Simulated seasonal variation in heterotrophic and autotrophic soil respiration with the PATCIS model. Each measured heterotrophic CO_2 flux is the mean of 30 measurements per sampling date. Error bars in heterotrophic measurements are standard errors of the mean. (b) Comparison of modelled components of soil respiration with observed measurements.

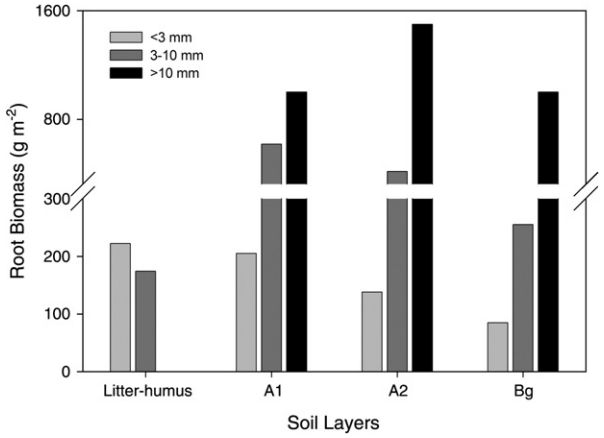

Fig. 7. Distribution of the different root diameter classes in the soil profile.

of variation of root functions (Pregitzer et al., 1998). As far as the annual fine-root increment is concerned, we calculated a rate of 52 g C m^{-2} $year^{-1}$, which falls within the lower range of published values (15–360 g C m^{-2} $year^{-1}$) reported for temperate coniferous forests (Breymeyer et al., 1996). A study conducted under similar environmental conditions also showed a low annual fine-root production rate for Sitka spruce growing on wet mineral soils (Nieuwenhuis et al., 2003).

3.4. Parameter values and soil carbon flows

Table 2 shows both the parameter values calculated for the present work, and those estimated in two other studies that are shown for reference. A comparison between these studies reflects that parameter values calculated in this study are not too different from those published in previous research work. With all, direct comparisons of parameter values with other studies is difficult given that parameters show potential values rather than actual decomposition or respiration rates (Moncrieff and Fang, 1999). However, the fact that we obtained good regression fits between modelled and observed data sets for autotrophic and heterotrophic respiration (r^2=0.64 and 0.74, Fig. 6b) added extra confidence to the parameterisation of the model performed for this forest ecosystem.

Optimal root respiration rates at 10 °C were set at 7.89×10^{-5}, 7.10×10^{-6}, and 1.10×10^{-6} mg CO_2 g^{-1} dry matter s^{-1} for roots <3 mm, 3–10 mm and >10 mm, respectively. The simulated respiration rate using those values was 0.37 g (dry mass) g^{-1} (dry mass) $year^{-1}$ for all roots in the whole soil profile. This value compares well with the range calculated for total root respiration of 0.32–0.44 g (dry mass) g^{-1} (dry mass) $year^{-1}$ based on the annual estimate of 389 g C m^{-2} $year^{-1}$ of autotrophic respiration obtained for this forest ecosystem (Saiz et al., 2006a). We have preferred to report a range as opposed to an individual value, since these results should be treated as a coarse estimation of root respiration. Moreover, values may be very influenced by the inclusion or not in the calculations of very thick structural roots (>20 mm), which could not be sheared with the stainless steel pipes at the time of root trenching.

With regard to simulation of organic matter decomposition, optimal decomposition rates at 10 °C were set at 3.60×10^{-6}, 3.91×10^{-5}, and 3.91×10^{-5} mg CO_2 g^{-1} dry matter s^{-1} for decomposition of soil organic matter, litter–humus, and fine root detritus, respectively. Simulation results showed a turnover rate for the litter–humus layer of 13 years, which was calculated by comparing the modelled annual rate of carbon emitted as heterotrophic respiration with the amount of carbon actually measured for this upper layer. The turnover rate simulated for this layer compares well with research conducted on Sitka spruce by Miller et al. (1996), that observed turnover times for litter–humus decomposition of above 13 years in forest stands across Scotland and Northern England. Litter decomposition is critical to the production of future soil carbon pools and is strongly influenced by plant detritus lignin content, as well as by other factors such as nitrogen content in litter (Melillo et al., 1982; Berg, 2000). Indeed, the high value of lignin content in needles that we observed in our study (41.7%), may be an important factor influencing the apparently low litter–humus turnover rate simulated in our study. This rate of lignin content in needles is in the upper end of summarised average values (31.7–42.7%) that have been observed in European coniferous forests (Berg and Meentemeyer, 2002). Simulated turnover rate of organic matter in the mineral soil was 45 years (mean residence time), which falls well within the 36- to 56-year range reported in other temperate forest ecosystems (Ewel et al., 1986). Moreover, and based on the annual estimate of 297 g C m^{-2} $year^{-1}$ for heterotrophic respiration obtained at this forest ecosystem (Saiz et al., 2006a), a turnover rate of 38 years was calculated for total soil organic matter (including the litter–humus fraction), which was almost identical to the annual turnover rate simulated with the PATCIS model (37 years). However, these turnover estimates should be treated with caution because they may be an overestimation of the actual rates, given that only organic matter present in the first 30 cm of soil was considered for the calculations.

Based on the comparison between the annual litter–humus decomposition rate simulated for this young ecosystem, and the annual aboveground and belowground organic matter inputs to this most superficial layer, we summarised that there was an accumulation of organic matter in the litter–humus layer. On the other hand, and applying the same argument as above, we observed an overall loss of organic matter from the mineral soil that was not compensated by belowground detritus. The initial loss of organic matter in the mineral soil following afforestation is a feature that has been previously described in studies looking at changes of organic carbon of former arable land using a chronosequence approach (Vesterdal et al., 2002). Furthermore, the significant contribution of mineral soil to total soil respiration found in our simulation study has been observed in other research works (Mallik and Hu, 1997; Buchmann, 2000). The large contribution of mineral soil horizons to total soil respiration observed in our study may be expected given the limited accumulation of organic matter in the litter–humus layer (Table 1), which is the result of the short period of time (15 years) that the forest floor has been developing.

3.5. Sensitivity analysis

A sensitivity analysis was performed on the parameters and factors driving soil respiration by applying separately a ±10% over their actual values. Results of the sensitivity analysis are presented in Table 4. Parameters and values are ranked by order of decreasing relevance of their influence on annual soil CO_2 efflux.

The most important factor controlling soil respiration was soil temperature (Table 4). This factor had a more marked impact on soil respiration during the summer (Fig. 8a), which agrees well with previous studies (Moncrieff and Fang, 1999; Hui and Luo, 2004). The sensitivity analysis of soil CO_2 efflux to a change in soil temperature showed that each soil horizon had slightly different sensitivities, which were higher with increasing soil depth. For instance, with a 10% increase in soil temperature, the heterotrophic component of soil respiration showed an annual increment of 12.8%, 13.9%, 14.1% and 15.1% in the litter–humus, A_1, A_2 and Bg horizons, respectively. Furthermore, we observed the same trend in our field experiment; Table 5 shows the fits and temperature sensitivity indexes (Q_{10} values) for non-linear regressions functions performed between measured soil CO_2 efflux and soil temperatures taken at 2 and 10 cm depth. These depths were chosen because they corresponded to the litter–humus layer and the top mineral soil horizon (A_1). In all treatments, respiration rates were more sensitive to temperature in the A_1 horizon than in the litter–humus layer as proved by the higher annual Q_{10} observed at 10 cm. The increase in the temperature sensitivity of soil respiration with soil depth has been previously reported, and it has been attributed to three potential causes affecting microbial decomposition. These causes, which are still treated as hypothesis, may be the different microbial community compositions observed at different soil depths, a decrease in carbon quality with soil depth, and finally, the positive feedback between CO_2 production and mineralization of nutrients other than carbon (Fierer et al., 2003).

The influence of soil moisture on soil respiration was more variable than that of soil temperature throughout the year. An increase in soil moisture had an overall negative effect on soil respiratory rates (Table 4), in particular during periods in which the soil was close to saturation as a result of high rainfall and high water table (Fig. 8b). A reduction in soil moisture would have an overall positive influence on soil respiration over the year, with the exception of periods in which low soil water content limited soil respiration, such as late summer (Fig. 8b). It is worth pointing out the negative response of the model to an increase in soil moisture during the period in which the upper mineral layers presented the lowest water content during the year (around day 275). The explanation for this is that, while an increase in soil moisture resulted in an enhancement of soil

Table 4
Sensitivity analysis of annual soil CO_2 efflux to a ±10% change in parameter values and model inputs

Variable or parameter	+10%	−10%
Soil temperature	+14.3	−12.5
Total porosity in mineral soil	+9.5	−6.7
Optimal root respiration rate	+5.4	−5.4
Live root biomass <3 mm	+4.5	−4.5
Optimal organic matter decomposition rate	+3.0	−4.3
Soil moisture	−2.4	+4.1
Soil organic matter (in all layers)	+3.5	−3.5
Activation energy	+1.6	−1.3
Live root biomass 3–10 mm	+0.8	−0.8
Live root biomass >10 mm	+0.2	−0.2
Aboveground litterfall	+0.1	−0.1
Dead root inputs	+0.0	−0.0
Total porosity in litter–humus layer	+0.0	−0.0

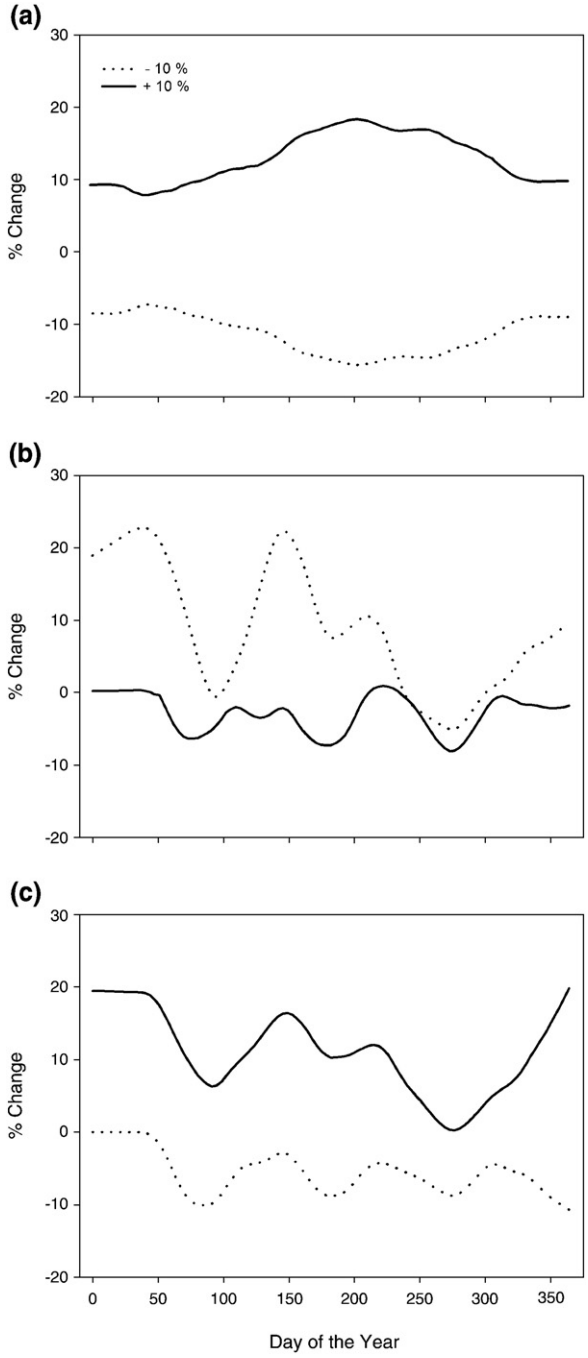

Fig. 8. Sensitivity of modelled soil CO_2 efflux to a ±10% change in: (a) soil temperature, (b) soil water content, and (c) total soil porosity.

Table 5
Temperature dependence on soil respiration rates (mg CO_2–C m^{-2} h^{-1}) and its components at 2 and 10 cm depth based on $n=11$ sampling dates in which an average of 30 points per treatment were sampled

Treatment	T_2		T_{10}	
	r^2	Q_{10}	r^2	Q_{10}
Total	0.66	3.5±1.1	0.65	3.8±1.2
Heterotrophic	0.71	2.7±0.5	0.66	2.8±0.7
Autotrophic	0.67	3.5±1.6	0.65	3.7±1.3

All relationships were highly significant ($P<0.0001$). A two-parametric exponential function of the form, $y=ae^{bT}$, was used to describe the relationships between soil CO_2 fluxes and soil temperature. Q_{10} values calculated from the exponential equation ($Q_{10}=e^{10b}$); Q_{10} standard errors were calculated as follows: $Q_{10}\times SE(b)\times 10$.

respiration in the upper soil mineral layers, the deepest mineral layer got saturated, and consequently the overall response of the model became negative (Fig. 8b). This latest fact is further justified by the model's response to changes in soil porosity during those days (Fig. 8c). This is the only period throughout the year in which an increase of 10% in total soil porosity had almost negligible effects on soil CO_2 efflux, which further points out the limiting effect that soil water had on soil respiration at that time. The sensitivity analysis showed that soil porosity had a larger effect on the annual soil respiration than that of soil moisture. However, both factors had the same seasonal pattern of soil respiration (Fig. 8c). The large values of sensitivity of soil CO_2 efflux to an increase in total soil porosity shows the importance of air space in the soil as a critical factor determining soil respiration, especially during very wet or close to saturation soil water conditions.

There was a larger sensitivity of soil CO_2 efflux to optimal root respiration rate than to the optimal organic matter decomposition (Table 4), which suggests a larger contribution of the autotrophic component to the total annual soil CO_2 efflux than the contribution made by the heterotrophic component, as it is also shown in Table 3. Similarly, the sensitivity of the efflux to both the initial conditions of fine root biomass (<3 mm) and organic matter present in the soil profile, confirmed the autotrophic component as a larger contributor to soil respiration as compared to microbial decomposition (Table 4). On the other hand, the sensitivity analysis showed other factors such as activation energy, thicker roots, aboveground litterfall and dead root inputs as factors with a more limited role on soil CO_2 efflux (Table 4).

4. Conclusions

Similar seasonal trends and annual estimates of soil CO_2 efflux were obtained with either empirical or the process-based PATCIS models. The parameterisation of the PATCIS model for this forest ecosystem was validated against observed measurements of total soil respiration. The model explained 75% of the seasonal variation in soil CO_2 efflux. Furthermore, the heterotrophic and autotrophic components of soil respiration were determined at the site, which allowed confirming the good performance of the process-based model in predicting the seasonal contribution of each component to the overall efflux. The overall annual contribution of autotrophic respiration to total soil CO_2 efflux was 54.7%, which compared well with previous research work. Heterotrophic and autotrophic respiration contributed almost equally to total CO_2 efflux during the early and late part of the year, while a larger contribution of autotrophic respiration to total CO_2 efflux occurred during the growing season. Most of autotrophic respiration took place in both the litter–humus layer and the A_1 horizon as a result of their large concentrations of fine roots.

We observed an accumulation of organic matter in the litter–humus layer, and a net loss from the mineral soil, which had much larger organic matter content compared to the litter–humus layer. The soil carbon dynamics observed in this young afforested ecosystem reflect the relative short time elapsed since the trees were established, yet this compartment is prone to undergo significant changes in such carbon flows as the ecosystem matures. The arguments in support of this latest statement are the expected changes in soil organic inputs as a result of stand development, as well as changes in both soil respiration rates and in the contribution of autotrophic and heterotrophic respiration observed in a chronosequence study conducted at this ecosystem (Saiz et al., 2006a). The present work shows that the use of process-based models to simulate soil CO_2 efflux may be a useful tool to separate soil respiration components, which is essential if a better comprehension of the carbon balance in forest ecosystems is to be achieved.

Model simulation of soil respiration may bear great uncertainty. In addition to the inherent structure of the model and the accuracy of the measuring system, the other two great sources of uncertainty come from a non appropriate selection of parameters and from the temporal and spatial variability in the respiratory flux. In spite of its good performance, additional model testing over more years is needed to further assess how robust are the fitted parameters for simulation of soil CO_2 efflux at this forest ecosystem.

Acknowledgements

We gratefully thank Dr Changming Fang for providing us the PATCIS model and for his generous help and advice. We acknowledge Dr Viorel Blujdea and Dr Brian Tobin for his valuable work in fine root processing, and Dr Carly Green and Valerio Avitabile for soil carbon analyses. We thank (COFORD) The Irish Council for Forestry Research and Development for provision of funds, and Coillte Teoranta, the Irish Forestry Board for allowing the use of its site.

References

Berg, B., 2000. Litter decomposition and organic matter turnover in northern forest soils. Forest Ecology and Management 133, 13–22.

Berg, B., Meentemeyer, V., 2002. Litter quality in a north European transect versus carbon storage potential. Plant and Soil 242, 83–92.

Bhupinderpal-Singh, Nordgen, A., Ottosson Löfvenius, M., Högberg, M.N., Mellander, P.-E., Högberg, P., 2003. Tree root and soil heterotrophic respiration as revealed by girdling of boreal Scots pine forest: extending observations beyond the first year. Plant, Cell and Environment 26, 1287–1296.

Black, K., Bolger, T., Davis, P., Neuwenhuis, M., Reidy, B., Saiz, G., Tobin, B., Osbone, B., in press. Inventory and eddy covariance based estimates of annual carbon sequestration in a Sitka spruce forest ecosystem. European Journal of Forestry. doi:10.1007/s10342-005-0092-4.

Boone, R.D., Nadelhoffer, K.J., Canary, J.D., Kaye, J.P., 1998. Roots exert a strong influence on the temperature sensitivity of soil respiration. Nature 396, 570–572.

Borken, W., Xu, Y.-J., Davidson, E.A., Beese, F., 2002. Site and temporal variation of soil respiration in European beech, Norway spruce, and Scots pine forests. Global Change Biology 8, 1205–1216.

Bowden, R.D., Nadelhoffer, K.J., Boone, R.D., Melillo, J.M., Garrison, J.B., 1993. Contributions of aboveground litter, belowground litter, and root respiration to total soil respiration in a temperate mixed hardwood forest. Canadian Journal of Forest Research 23, 1402–1407.

Breymeyer, A.I., Berg, B., Gower, S.T., Johnson, D., 1996. Carbon budget: temperate coniferous forests. In: Breyermeyer, A.I., Hall, D.O., Melillo, J.M., Ågren, G.I. (Eds.), Global Change: Effects on Coniferous Forests and Grasslands. Wiley, New York, pp. 41–67.

Buchmann, N., 2000. Biotic and abiotic factors controlling soil respiration rates in *Picea abies* stands. Soil Biology & Biochemistry 32, 1625–1635.

Burton, A.J., Pregitzer, K.S., Zogg, G.P., Zak, D.R., 1998. Drought reduces root respiration in sugar maple forests. Ecological Applications 8, 771–778.

Davidson, E.A., Belk, E., Boone, R.D., 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. Global Change Biology 4, 217–227.

Epron, D., Farque, L., Lucot, É., Badot, P.-M., 1999. Soil CO_2 efflux in a beech forest: dependence on soil temperature and soil water content. Annals of Forest Science 56, 221–226.

Ewel, K.C., Cropper, W.P., Gholz, H.L., 1986. Soil CO_2 evolution in Florida slash pine plantations: II. Importance of root respiration. Canadian Journal of Forest Research 17, 330–333.

Fang, C., Moncrieff, J.B., 1998. An open-top chamber for measuring soil respiration and the influence of pressure difference on CO_2 efflux measurements. Functional Ecology 12, 319–325.

Fang, C., Moncrieff, J.B., 1999. A model for soil CO_2 production and transport: 1. Model development. Agricultural and Forest Meteorology 95, 225–236.

Fierer, N., Allen, A.S., Schimel, J.P., Holden, P.A., 2003. Controls on microbial CO_2 production: a comparison of surface and subsurface soil horizons. Global Change Biology 9, 1322–1332.

Goulden, M.L., Crill, P.M., 1997. Automated measurements of CO_2 exchange at moss surface of a black spruce forest. Tree Physiology 17, 537–542.

Hanson, P.J., Edwards, N.T., Garten, C.T., Andrews, J.A., 2000. Separating root and soil microbial contributions to soil respiration: a review of methods and observations. Biogeochemistry 48, 115–146.

Högberg, P., Nordgren, A., Buchmann, N., 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. Nature 411, 789–792.

Houghton, R.A., Davidson, E.A., Woodwell, G.M., 1998. Missing sinks, feedbacks, and understanding the role of terrestrial ecosystems in the global carbon balance. Global Biogeochemical Cycles 12, 25–34.

Hui, D., Luo, Y., 2004. Evaluation of soil CO_2 production and transport in Duke Forest using a process-based modeling approach. Global Biogeochemical Cycles 18, GB4029. doi:10.1029/2004GB002297.

IPCC, 2001. Climate Change 2001. The Scientific Basis. Cambridge University Press. 881 pp.

Irvine, J., Law, B.E., 2002. Contrasting soil respiration in young and old-growth ponderosa pine forests. Global Change Biology 8, 1183–1194.

Janssens, I.A., Lankreijer, H., Matteucci, G., Kowalski, A.S., Buchmann, N., Epron, D., Pilegaard, K., Kutsch, W., Longdoz, B., Grünwald, T., Montagnani, L., Dore, S., Rebmann, C., Moors, E.J., Grelle, A., Rannik, Ü., Morgenstern, K., Oltchev, S., Clement, R., Guðmundsson, J., Minerbi, S., Berbigier, P., Ibrom, A., Moncrieff, J., Aubinet, M., Bernhofer, C., Jensen, N.O., Vesala, T., Granier, A., Schulze, E.-D., Lindroth, A., Dolman, A.J., Jarvis, P.G., Ceulemans, R., Valentini, R., 2001. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. Global Change Biology 7, 269–278.

Janssens, I.A., Sampson, D.A., Curiel-Yuste, J., Carrara, A., Ceulemans, R., 2002. The carbon cost of fine root turnover in a Scots pine forest. Forest Ecology and Management 168, 231–240.

Jobbágy, E.G., Jackson, R.B., 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecological Applications 10, 423–436.

Johnson, D.W., Knoepp, J.D., Swank, W.T., Shan, J., Morris, L.A., Lear, D.H.V., Kapeluck, P.R., 2002. Effects of forest management on soil carbon: results of some long-term resampling studies. Environmental Pollution 116, 201–208.

Klopatek, J.M., 2002. Belowground carbon pools and processes in different age stands of Douglas-fir. Tree Physiology 22, 197–204.

Kuzyakov, Y., Cheng, W., 2001. Photosynthesis controls of rhizosphere respiration and organic matter decomposition. Soil Biology & Biochemistry 33, 1915–1925.

Lee, M.-S., Nakane, K., Nakatsubo, T., Mo, W., Koizumi, H., 2002. Effects of rainfall events on soil CO_2 flux in a cool temperate deciduous broad-leaved forest. Ecological Research 17, 401–409.

Lytle, D.E., Cronan, C.S., 1998. Comparative soil CO_2 evolution, litter decay, and root dynamics in clearcut and uncut spruce-fir forest. Forest Ecology and Management 103, 121–128.

Magnusson, T., 1993. Carbon dioxide and methane formation in forest mineral and peat soils during aerobic and anaerobic incubations. Soil Biology & Biochemistry 25, 877–883.

Mallik, A.U., Hu, D., 1997. Soil respiration following site preparation treatments in boreal mixedwood forest. Forest Ecology and Management 97, 265–275.

Melillo, J.M., Aber, J.D., Muratore, J.F., 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63, 621–626.

Miller, J.D., Cooper, J.M., Miller, H.G., 1996. Amounts and nutrient weights in litterfall, and their annual cycles, from a series of fertilizer experiments on pole-stage Sitka spruce. Forestry 69, 289–302.

Moncrieff, J.B., Fang, C., 1999. A model for soil CO_2 production and transport: 2. Application to a Florida *Pinus elliotte* plantation. Agricultural and Forest Meteorology 95, 237–256.

Nadelhoffer, K.J., Raich, J.W., 1992. Fine root production estimates and belowground carbon allocation in forest ecosystems. Ecology 73, 1139–1147.

Nieuwenhuis, M., Wills, J., Gardiner, J., Sunström, E., Keane, M., 2003. The effect of soil cultivation methods on rooting depth of young Sitka spruce (*Picea sitchensis* (Bong.) Carr.) trees on wet mineral soils in Ireland. Forestry 76, 465–477.

Pregitzer, K.S., Laskowski, M.J., Burton, A.J., Lessard, V.C., Zak, D.R., 1998. Variation in sugar maple root respiration with root diameter and soil depth. Tree Physiology 18, 665–670.

Press, W.H., Teukolsky, S.A., Vetterling, W.T., Flannery, B.P., 1992. Numerical Recipes in C: The Art of Scientific Computing, Second edition. Cambridge University, pp. 408–412.

Pumpanen, J., Ilvesniemi, H., Hari, P., 2003. A process-based model for predicting soil carbon dioxide efflux and concentration. Soil Science Society of America Journal 67, 402–413.

Raich, J.W., Schlesinger, W.H., 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus 44B, 81–89.

Rey, A., Pegoraro, E., Tedeschi, V., De Parri, I., Jarvis, P.G., Valentini, R., 2002. Annual variation in soil respiration and its components in a coppice oak forest in Central Italy. Global Change Biology 8, 851–866.

Saiz, G., Byrne, K.A., Butterbach-Bahl, K., Kiese, R., Blujdea, V., Farrell, E.P., 2006a. Stand age-related effects on soil respiration in a first rotation Sitka spruce chronosequence in central Ireland. Global Change Biology 12, 1007–1020.

Saiz, G., Green, C., Butterbach-Bahl, K., Kiese, R., Avitabile, V., Farrell, E.P., 2006b. Seasonal and spatial variability of soil respiration in four Sitka spruce stands. Plant and Soil 287, 161–276.

Savage, K.E., Davidson, E.A., 2003. A comparison of manual and automated systems for soil CO_2 flux measurements: trade-offs between spatial and temporal resolution. Journal of Experimental Botany 54, 891–899.

Schlesinger, W.H., Andrews, J.A., 2000. Soil respiration and the global carbon cycle. Biogeochemistry 48, 7–20.

Šimunek, J., Suarez, D.L., 1993. Modelling of carbon dioxide transport and production in soil: 1. Model development. Water Resources Research 29, 487–497.

Stolbovoi, V., 2003. Soil respiration and its role in Russia's terrestrial C flux balance for the Kyoto baseline year. Tellus. Series B, Chemical and Physical Meteorology 55, 258–269.

Vesterdal, L., Ritter, E., Gundersen, P., 2002. Change in soil organic carbon following afforestation of former arable land. Forest Ecology and Management 169, 137–147.

Widén, B., Majdi, H., 2001. Soil CO_2 efflux and root respiration at three sites in a mixed pine and spruce forest: seasonal and diurnal variation. Canadian Journal of Forest Research 31, 786–796.