Global Change Biology (2006) **12,** 1007–1020, doi: 10.1111/j.1365-2486.2006.01145.x

Stand age-related effects on soil respiration in a first rotation Sitka spruce chronosequence in central Ireland

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Abstract

The effect of stand age on soil respiration and its components was studied in a first rotation Sitka spruce chronosequence composed of 10-, 15-, 31-, and 47-year-old stands established on wet mineral gley in central Ireland. For each stand age, three forest stands with similar characteristics of soil type and site preparation were used. There were no significant differences in total soil respiration among sites of the same age, except for the case of a 15-year-old stand that had lower soil respiration rates due to its higher productivity. Soil respiration initially decreased with stand age, but levelled out in the older stands. The youngest stands had significantly higher respiration rates than more mature sites. Annual soil respiration rates were modelled by means of temperature-derived functions. The average Q_{10} value obtained treating all the stands together was 3.8. Annual soil respiration rates were 991, 686, 556, and 564 g C m^{-2} for the 10-, 15-, 31-, and 47-year-old stands, respectively. We used the trenching approach to separate soil respiration components. Heterotrophic respiration paralleled soil organic carbon dynamics over the chronosequence, decreasing with stand age to slightly increase in the oldest stand as a result of accumulated aboveground litter and root inputs. Root respiration showed a decreasing trend with stand age, which was explained by a decrease in fine root biomass over the chronosequence, but not by nitrogen concentration of fine roots. The decrease in the relative contribution of autotrophic respiration to total soil CO_2 efflux from 59.3% in the youngest stand to 49.7% in the oldest stand was explained by the higher activity of the root system in younger stands. Our results show that stand age should be considered if simple temperature-based models to predict annual soil respiration in afforestation sites are to be used.

Keywords: afforestation, autotrophic respiration, gley soil, heterotrophic respiration, Q_{10}, root biomass, sitka spruce, soil respiration, stand age

Received 2 May 2005; revised version received 26 July 2005; accepted 3 October 2005

Introduction

Forest ecosystems can act as a sink or as a source of atmospheric CO_2 on the basis of the difference between the two fluxes of photosynthesis and respiration. The impact of afforestation of former arable land on ecosystem carbon (C) dynamics needs to be better understood in order to maximize sequestration of atmospheric C. In forests, total ecosystem respiration tends to be dominated by soil respiration (Valentini *et al*., 2000). Soil respiration is the primary path by which CO_2 fixed by land plants returns to the atmosphere (Raich & Schlesinger, 1992; Janssens *et al*., 2001).

There is considerable interest in the effects of forest management on soil C balance and storage, specifically on the impact of stand age on soil CO_2 efflux (Irvine & Law, 2002). The influence of stand age on soil respiration varies among studies. Ewel *et al*. (1986a) suggested that soil respiration decreased with stand age in

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temperate forests, while it increased in tropical and subtropical forests. Soil respiration within a given stand is dependent upon both the amount of fine roots and quality of soil C pools. Therefore, soil respiration will differ according to the structure and age of the stand (Klopatek, 2002).

The production of CO_2 in the soil is primarily the result of the autotrophic respiration by live roots and their associated mycorrhizae, and heterotrophic respiration by microbes oxidizing plant detritus, root exudates and humified organic matter (Boone *et al*., 1998; Buchmann, 2000; Hanson *et al*., 2000). Temperature, together with soil moisture, are the main factors controlling soil respiration (Raich & Schlesinger, 1992; Kirschbaum, 1995; Davidson *et al*., 1998). Low or high soil water contents may limit soil respiration by either drought stress to microbial communities and root activities or by limiting oxygen availability due to reduced air diffusion for decomposition and root maintenance and growth (Rey *et al*., 2002). Soil respiration has also been described to be influenced by site fertility (Haynes & Gower, 1995; Maier & Kress, 2000; Butnor *et al*., 2003). The factors that control heterotrophic and autotrophic respiration will determine the contribution of each component to the total flux. Root respiration has been reported to be more temperature sensitive than heterotrophic respiration (Kirschbaum, 1995; Boone *et al*., 1998). In addition to temperature and moisture, root respiration is strongly influenced by plant photosynthetic activity (Högberg *et al*., 2001; Kuzyakov & Cheng, 2001; Bhupinderpal-Singh *et al*., 2003). The wide range of values reported (10–90%) on the relative contribution of the different soil components to the total soil efflux may be due to the type of ecosystem studied but also to the various methodologies used (Hanson *et al*., 2000).

The aim of the present work was to advance in the understanding of soil C dynamics in forests, in particular the effect that stand age poses on soil respiration. The specific objectives of our study were as follows: (1) to determine whether soil respiration varied with stand age and (2) to separate soil respiration components using the trenching methodology. In order to achieve the first objective, we conducted a study on a first rotation Sitka spruce (*Picea sitchensis* (Bong.) Carr.) replicated chronosequence comprising four age classes. The separation of soil respiration components was carried out over unreplicated age classes.

Materials and methods

Site characteristics

The forest stands in which the work was conducted are located in County Laois (52°57′ N, 7°15′W), in central Ireland, at an elevation of 260 m. All the stands were within a 5 km radius. Average annual precipitation and air temperature for the region are 804 mm and 9.3 °C, respectively (30 years average, Met Eireann, Irish Meteorological Service). During 2003, the year in which the study was carried out, the amount of rainfall was 772 mm and the average annual temperature 9.5 °C.

The study sites were pure Sitka spruce first generation plantations established on former agricultural land. All stands had reached canopy closure and were characterized by an almost total absence of understory or herbaceous vegetation. Together, they made up a chronosequence ranging from 10 to 47 years of age (Table 1), with the oldest stand being ready for harvest. Twelve forest stands were used for this study, three replicates per stand age. The four stands (1 per age class) over which total and heterotrophic respiration measurements took place are referred, hereafter, as core sites and all other sites as reference or replicate sites. These two additional sites per stand age had the same

Table 1 Characteristics of the Sitka spruce stands over which measurement of total and heterotrophic soil respiration took place (core sites)

Site	Age (years)	LAI ($m^2\,m^{-2}$)	Stem density (trees ha^{-1})	Basal area ($m^2\,ha^{-1}$)	Yield class	Litter-humus layer thickness (cm)	Soil organic carbon (%)	Nitrogen (%)	Phosphorous ($mg\,L^{-1}$ available)	Soil pH
Dooary 1	10	ND	2300	5.3	16–20	3.5 ± 0.2	6.96 ± 0.5[a]	0.627	11.2	4.5
Dooary 2	15	10.5	2366	34.4	20–24	4.1 ± 0.2	4.66 ± 0.4[b]	0.418	11.4	4.8
Dooary 3	31	7.2	1083	54.0	16–20	3.2 ± 0.2	7.10 ± 0.6[a]	0.599	9.4	4.1
Cullenagh	47	6.5	730	57.0	16–20	2.3 ± 0.1	6.86 ± 0.8[a]	ND	8.8	3.6

LAI denotes leaf area index. Yield Class represents a potential maximum mean annual aboveground increment in $m^3\,ha^{-1}$. Soil organic carbon (Mean values ± SE), Nitrogen, Phosphorous, and pH (pooled samples) measured for A_1 soil horizon 8–10 cm thickness ($n = 15$). Different letters between the stands denote significantly different SOC rates ($P < 0.05$). Soil organic carbon content was analysed by LOI. For more details see (Green *et al*., submitted). Soil nitrogen content was analysed using the Dumas method. Phosphorus was determined by the Olsen method, and soil pH was analysed in a 1 : 2 soil–water slurry with an automated system.

characteristics for forest management, tree age, soil type, tree establishment, and yield class as their core site (with the exception of the 15-year-old core site, which had a higher yield class than the others). Neither fertilisation nor drainage works had been carried out since tree establishment in any of the stands (Coillte Teoranta, the Irish Forestry Board, pers. comm.). Since the 10- or 15-year-old stands had not yet reached thinning stage, stem density was greater than in the older stands (Table 1). The thickness of litter-humus layers varied over the sites as it is shown in Table 1.

The soil was classified as low humic (mineral) gleys in the 10-, 15-, and 31-year-old stands, and as a gleyic brown earth in the 47-year-old stand. Analyses of their chemical properties are presented in Table 1.

The two youngest stands had been established along ripped lines 1 m deep with a separation of 2 m between them. This technique consists on a ripper mounted on the tool bar of a tractor that is pulled through the ground in order to shatter heavy soils and/or break subsurface pans to improve drainage and tree root penetration. Surface drains were also created every 50 m across the ripped lines. The older stands were ploughed at 1.7 m intervals, following the contour lines of the slope. At the plot level, this created a series of topographical variations in the form of ridges, furrows, and undisturbed grounds.

Experimental design

Soil respiration measurements were carried out in three stands of each age class. Within 30 m × 30 m plots, a series of 30 PVC circular collars (16 cm 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. 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. Collars were proportionally distributed to the area occupied by furrows, ridges and undisturbed grounds to account for morphologically driven differences in soil respiration since preliminary studies showed that CO_2 emissions were higher from furrows (data not shown). For investigation of heterotrophic respiration, at one of the 10-, 15-, 31- and 47-year-old stands and next to the PVC collars, the same number of stainless steel pipes (16 cm diameter) were driven 30 cm into the soil in order to exclude tree roots. The first measurements were not taken until eight 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. Root density within the collars was assumed to be the same as the average calculated for each stand. To calculate the flux resulting from roots left within the pipes, a decay constant of 0.2 $year^{-1}$ was applied based on Silver and Miya (2001). However, and as a result of using such constant for decomposition of trenched roots, there may be a bias on the seasonal contribution of heterotrophic and autotrophic respiration. At the end of the experiment, root exclusion collars were retrieved and examined. No root regrowth was observed underneath these structures.

Soil CO_2 flux measurements

Soil respiration measurements were carried out during 2003 on a monthly basis at all core sites and bimonthly at the replicate sites. At the core sites, soil respiration measurements were carried out for total and heterotrophic respiration 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). They were fitted with a rubber-foamed ring cemented to a modified lip of the chamber to ensure a tight seal with the soil collars. Measurements of total (R_{TOT}) and heterotrophic (R_H) respiration were carried out simultaneously. The measuring principle is a closed system which determines the increase in CO_2 concentration within the chamber over time. The system was calibrated before each sampling day against CO_2 with a nominal concentration of 409 μmol mol^{-1}.

In order to minimize the diel variation in soil respiration, measurements were made between 10:00 and 16:00 hours. On two occasions, 24 h measurements were carried out. The average values obtained for the 10:00 and 16:00 hours did not differ significantly from the other 18 h period in both days where the 24 h measurements were taken. Furthermore, an automated soil respiration system installed at the end of this study did not show any significant diurnal variations in soil respiration either (data not shown).

Soil temperature and moisture measurements

Soil temperature at different depths was measured adjacent to each collar (220 K temperature meter, Jenway, Essex, UK). The probe was sequentially inserted into soil depths of 2, 6, and 10 cm. In addition, soil temperature was continuously monitored in the 15-year-old stand using soil temperature probes set up at ground level, 5, 10, and 30 cm depth (T107 Campbell Scientific Ltd, Loughborough, UK). The system was set up to record 30 min average temperatures. Site-specific temperatures were achieved by means of linear regressions

performed between the temperature taken at the time of measurements in the different stands and the ones simultaneously recorded by the automatic system. Giving the physical proximity among all the stands, regressions were highly correlated (data not shown).

Soil water content within every collar was determined using a moisture probe (ThetaProbe ML2x, Delta-T Devices, Cambridge, UK).

Relationships between soil temperature, soil moisture, and soil respiration

A two parametric exponential function was used to describe the relationships between soil CO_2 fluxes and soil temperature. The formula is as follows:

$$y = ae^{bT},$$

where y is the measured soil CO_2 efflux rate, T the measured soil temperature, being a and b the fitted parameters obtained using least squares nonlinear regressions with SigmaPlot V.8.02.

The Q_{10} values were calculated as follows:

$$Q_{10} = \mathrm{e}^{10b},$$

Standard error for Q_{10} was calculated as: SE $(Q_{10}) = Q_{10} \times 10 \times$ SE (b).

The response of R_{TOT} to soil water content was modelled using a polynomial function of the form $R_{TOT} = y_0 + ax + bx^2$, where R_{TOT} is total CO_2 efflux, x is soil water content in the top 6 cm, and a and b are fitted parameters.

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: $R_{TOT} = (a \times e^{b \times y}) \times (cz + dz^2)$, where R_{TOT} is total CO_2 efflux, y is soil temperature, and z is soil water content in the top 6 cm; a, b, c, and d are fitted parameters.

Root biomass

In May 2003, between 7 and 15 soil cores per stand age were retrieved to a depth of 30 cm at the four core sites with the aid of a root auger (4 cm radius). Beyond this depth only occasional thick structural roots with a small number of fine roots were found. Soil samples were immediately stored at 4 °C and processed within 4 days of their collection. For this, the different soil horizons were separated and fine roots were washed and sieved – using whole sampling material – to detach them from soil mineral particles. Roots were sorted into three diameter classes (<1 mm, 1–2 mm and 2–5 mm). Finally, washed roots were weighed after being oven-dried at 70 °C for 48 h to determine fine root biomass. The C and nitrogen (N) concentration of roots <1 mm were determined in a Vario El-III C/N analyzer (Elementar Americas, Inc. Mt. Laurel, NJ, USA).

The entire root system of six trees per stand age was excavated to determine coarse root biomass (>5 mm diameter). Subsequently, root subsamples were taken to determine dry weight.

Statistical analysis

Data sets were tested for normal distribution by the Kolmogorov–Smirnov test. Correlation analyses were used to examine relationships between soil respiration rates and soil temperature and soil moisture. A one-way repeated-measures ANOVA was performed to compare soil respiration rates between stands for each stand age. *Post hoc* comparisons using Tukey HSD test were conducted to find out which of the sites differed. The same statistical procedure was used to compare soil respiration rates as well as root biomass between different stand ages. SPSS 12.0 (SPSS Inc. Chicago, IL, USA) was used for all statistical analyses.

Results

Annual variation of soil temperature and soil water content

No significant differences in mean annual soil temperature, taken at a depth of 2 cm, were found among stands or treatments ($P > 0.05$). The mean annual soil temperature at 2 cm depth ranged from 9.1 °C (31-year-old stand) to 10.1 °C (47-year-old stand). Consistently for all stand ages, maximum soil temperatures coincided with minimum soil water contents during the summer (Fig. 1). In contrast, minimum soil temperatures were normally accompanied by the highest soil water contents occurring in the year. Volumetric water contents determined in the first 6 cm of the soil profiles averaged about 36%, and showed no significant differences among three of the four stands over the course of the year ($P > 0.05$). However, the 31-year-old stand had 22% mean soil water content that was significantly lower in comparison with the rest of the stands. Neither soil temperature nor soil volumetric water content differed significantly in stands of the same age ($P > 0.05$), nor there were significant differences in soil temperatures or soil water contents between total soil respiration and heterotrophic soil respiration treatments.

Relationships between total soil respiration and stand age

Soil respiration rates measured at the core sites were compared with the ones obtained at their reference sites by means one-way repeated-measures ANOVA (Table 2).

There were no significant differences ($P > 0.05$) among core sites and their correspondent references in the 10-, 31-, and 47-year-old stands. In the 15-year-old stands, the core site had significantly lower soil respiration rates than one of the reference sites (Table 2).

To test for differences in total soil respiration with stand age, stands of the same age that showed no significant differences between them were pooled. The statistical analyses carried out over the different age classes consistently showed that 10-year-old sites had significantly higher respiration rates than 31- and 47-year-old sites (Table 2). The significance of the results did not change with the exclusion or inclusion of any of the 15-year-old stands. Older stands did not show significant differences between them (Table 2).

Total soil respiration (R_{TOT})

In all core sites, R_{TOT} showed a pronounced seasonal variation which followed that of soil temperature (Fig. 1). R_{TOT} values were at their lowest during winter time. By contrast, values of soil respiration peaked in late July or early August in all the stands. Subsequently, soil respiration rates showed a steady decline towards the end of the year, with the exception of sites where low soil water content during late summer acted as a limiting factor for soil CO_2 efflux (Fig. 1).

There was a decrease in R_{TOT} with stand age (Table 3). An analyses of the monthly values obtained at the core sites showed that only the youngest stand (10-year-old) was significantly higher ($P < 0.05$) than the 15-, 31-, and 47-year-old stands, whose mean soil respiration rates were not significantly different from each other ($P > 0.05$) (Table 3).

For each core site, an exponential model was fitted with soil respiration rates and soil temperatures at depths of 2, 6, and 10 cm. The temperature depth used in the regressions was 2 cm (Fig. 2) because it produced the best fit for the models among all depths. All relationships were highly significant ($P < 0.0001$). Models fitted for the core sites explained more of the annual variation in those stands less limited by soil water content with r^2 values of 0.77, 0.66, 0.56, and 0.79 for

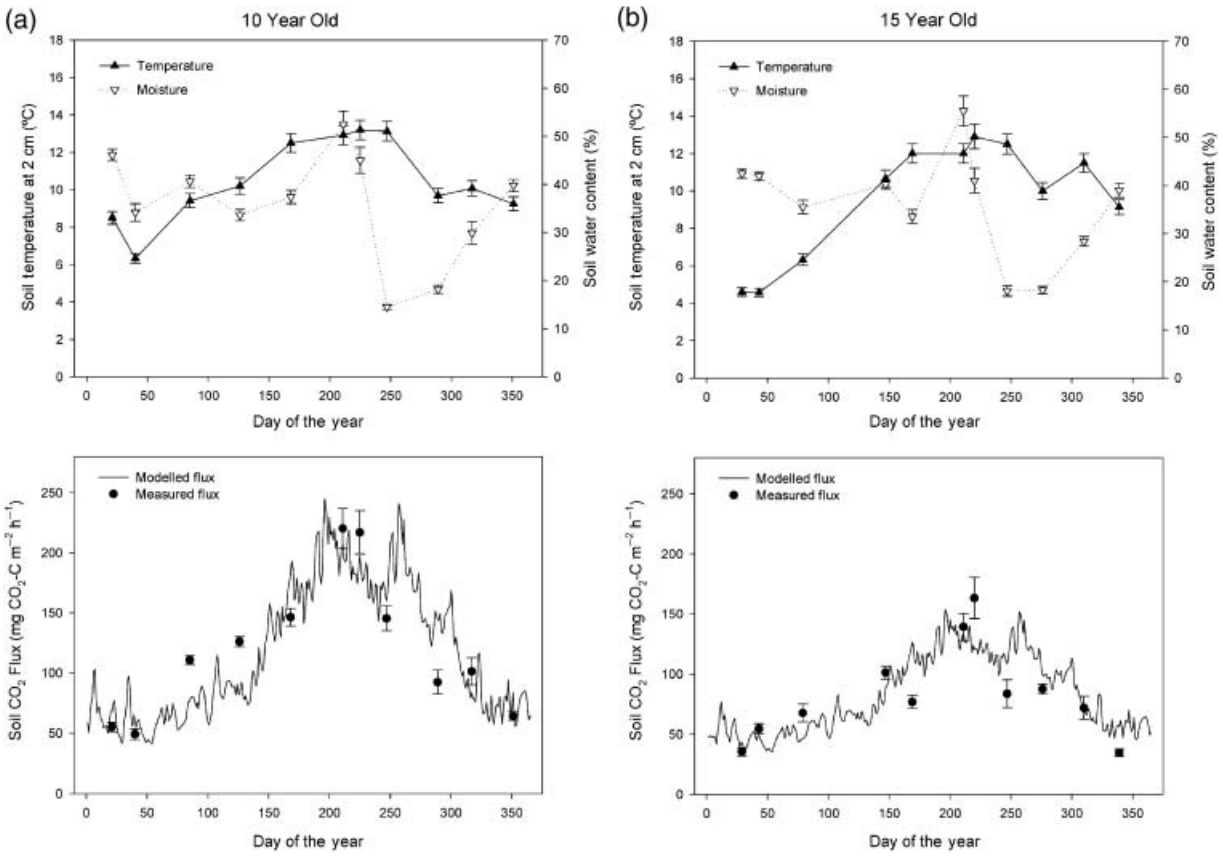

Fig. 1 Seasonal variation of soil CO_2 flux, soil temperature and soil water content in the different stand ages. Each measured value for temperature, water content and soil CO_2 flux is the mean of 30 measurements. Error bars are standard errors of the means. The continuous line represents the modelled flux based on the exponential functions fitted for each stand that are shown in Table 4.

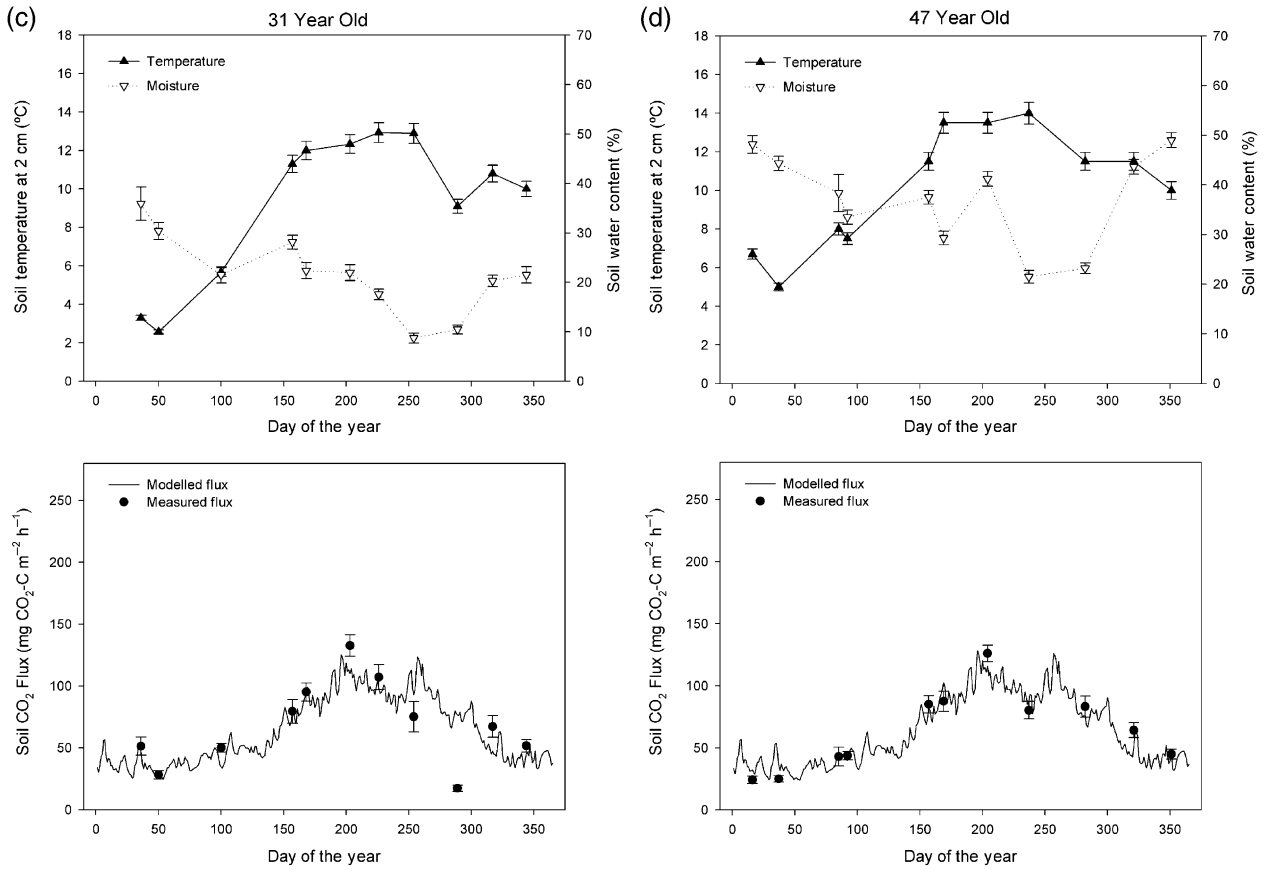

Fig. 1 Continued

Table 2 Mean soil respiration rates (mg CO_2-C m^{-2} h^{-1}) and standard errors for core and reference sites in each stand age

	Sites			
Stand Age	Core (A) ($n = 6$)	Reference B ($n = 6$)	Reference C ($n = 6$)	Pooled sites ($n = 18$)
10-year old	132.4 ± 22.4^{a}	124.2 ± 26.6^{a}	124.1 ± 28.2^{a}	126.9 ± 24.7^{A}
15-year old	80.8 ± 18.1^{a}	109.8 ± 17.8^{ab}	136.2 ± 39.9^{b}	$123.0 \pm 24.9^{AB*}$
31-year old	59.9 ± 17.8^{a}	81.0 ± 24.5^{a}	69.8 ± 21.7^{a}	71.1 ± 16.7^{B}
47-year old	60.1 ± 14.5^{a}	65.5 ± 12.3^{a}	54.9 ± 17.7^{a}	60.7 ± 14.0^{B}

*In this case $\underline{n} = 12$ since the 15-year-old core site was significantly different and was not pooled.
Different superscripts in small letters denote significant differences in soil respiration rates between reference and core sites ($P < 0.05$). Different superscripts in capital letters indicate significant differences between age classes ($P < 0.05$). Data was pooled from stands of the same age to allow for comparisons between different stand ages.

the 10-, 15-, 31-, and 47-year-old stands, respectively (Table 4).

The polynomial function was found to provide the best fit for the relationship between total soil CO_2 efflux and soil water content in this study. The resultant fits were low, with r^2 ranging from 0.18 to 0.41. However, none of the relationships was significant ($P > 0.2$ in all cases). The combined use of soil temperature and soil water content functions did not improve our capability to better explain soil CO_2 efflux compared with regressions based on temperature only, and are not reported here.

Daily mean soil temperatures were used to simulate daily soil CO_2 efflux. The mean modelled daily values were then added up to obtain the annual estimate for soil CO_2 efflux in each stand. Those values were 991, 686, 556, and 564 g C m^{-2} yr^{-1} for the 10-, 15-, 31-, and 47-year-old stands, respectively (Table 4). A further

Table 3 Mean soil respiration rates (mg CO_2–C m^{-2} h^{-1}) and standard errors for each treatment in the four core sites of the chronosequence

Treatment	*n*	10-year old	15-year old	31-year old	47-year old
Total	11	111.1 ± 16.4[a]	83.3 ± 13.2[b]	68.7 ± 10.3[b]	68.8 ± 11.1[b]
Heterotrophic	11	48.5 ± 5.3[a]	36.6 ± 3.5[b]	30.1 ± 5.5[b]	35.1 ± 5.2[b]
Autotrophic	11	62.6 ± 11.2[a]	46.7 ± 7.8[b]	38.6 ± 6.0[b]	33.7 ± 5.1[b]

Means and standard errors for the different stand ages are based on $n = 11$ sampling dates in which an average of 30 points per treatment were sampled. Different letters within the same treatment denote significantly different soil respiration rates ($P < 0.05$).

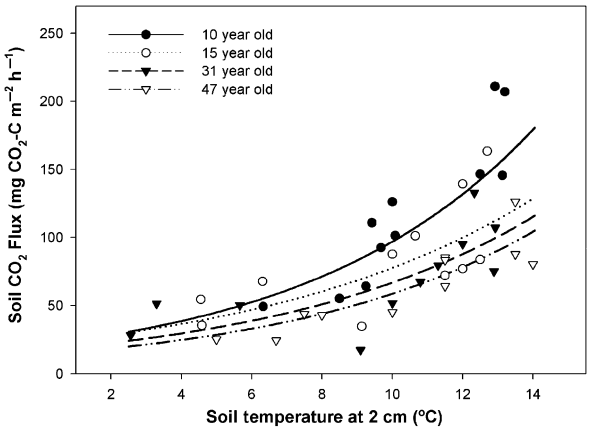

Fig. 2 Relationships between total soil CO_2 fluxes and soil temperature measured at 2 cm for the core Sitka spruce stands. Each point is the mean of 30 sampling points made per sampling day. The exponential functions are shown in Table 4.

estimate of annual R_{TOT} at each stand age was calculated by interpolating measured soil respiration between sampling dates for every day of the year and then computing the sum to obtain the annual value (Table 4).

Calculated Q_{10} values ranged from 3.5 (15-year-old) to 4.6 (10-year-old). The average Q_{10} value, calculated by pooling the core stands, was 3.8. Q_{10} values calculated for 6 and 10 cm depth were slightly higher (data not shown).

Heterotrophic soil respiration (R_H)

The youngest stand (10-year-old) had significantly higher rates of R_H ($P < 0.05$) than any of the other age classes, which showed no significant differences between them ($P > 0.05$) (Table 3). Temperature-based regressions had the lowest fit in the cooler and apparently more water-limited 31-year-old stand ($r^2 = 0.27$). Models in other stands explained better the annual variation with r^2 around 0.72 (Table 4). The resultant Q_{10} values for this treatment ranged from 2.4 to 3.3. Likewise, values very close to the ones calculated by interpolation were obtained by applying models to estimate annual R_H. Estimates of the decomposition of roots killed by trenching were made as previously described for each core site (Table 4).

Autotrophic respiration (R_A)

Root or autotrophic respiration (R_A) was calculated as the difference in daily mean respiration rates between total and heterotrophic plots. Our reference to autotrophic respiration includes that of live roots, mycorrhizae and rhizosphere microbial respiration. Soil temperatures used for this treatment are the means of total and heterotrophic plots. In all the stands, R_A rates peaked around mid summer, and reached minimum values during winter.

Over the year, measured mean R_A rate in the youngest stand was significantly higher ($P < 0.05$) than R_A rates obtained in the older stands. Thus, there was a decrease in R_A with stand age (Table 3). However, R_A rates in the older stands were not statistically different from each other ($P > 0.05$).

Following the same procedure as for the other treatments, exponential functions were fitted for each age class in the chronosequence. Temperature-based models could in general explain the annual variation of R_A quite well (Table 4). The contribution R_A to R_{TOT} varied throughout the year as shown in Fig. 3. According to the variation in the modelled components of soil respiration, the biggest R_A contribution to total CO_2 fluxes occurred during the growing season, reaching up to a contribution of 64% in the 10-year-old stand in late July. However, during winter time the contribution by R_H and R_A were about the same. The contribution of R_A to R_{TOT} for the whole year was calculated by means of comparing the modelled annual estimates for total and heterotrophic respiration. Annual contributions of R_A to R_{TOT} ranged from 59.3% for the youngest stand to 49.7% calculated for the oldest stand (Table 4).

Root biomass and N concentration

There was a decreasing trend in root biomass <1 mm diameter over the chronosequence (Table 5). The oldest

Table 4 Relationships between soil respiration rates (mg CO_2–C m^{-2} h^{-1}) and soil temperature (°C) measured at 2 cm depth based on $n = 11$ sampling dates in which an average of 30 points per treatment were sampled

	10-year old			15-year old			31-year old			47-year old		
Treatment	r^2	a	b	r^2	a	b	r^2	a	b	r^2	a	b
Total	0.77	20.84	0.1537	0.66	21.96	0.1262	0.56	17.11	0.1362	0.79	13.85	0.1442
Heterotrophic	0.72	13.69	0.1197	0.71	14.03	0.0998	0.27	11.04	0.1065	0.70	9.37	0.1200
Autotrophic	0.77	9.41	0.1729	0.67	12.74	0.1242	0.66	8.80	0.1391	0.70	5.46	0.1628

Treatment	Q_{10}	Interp	Modelled	Q_{10}	Interp	Modelled	Q_{10}	Interp	Modelled	Q_{10}	Interp	Modelled
Total	4.6 ± 1.5	1013	991	3.5 ± 1.1	692	686	3.9 ± 1.9	559	556	4.2 ± 1.4	577	564
Heterotrophic	3.3 ± 0.9	439	403 (434)	2.7 ± 0.5	328	297 (329)	2.9 ± 1.9	263	240 (267)	3.3 ± 1.1	296	284 (294)
Autotrophic	5.6 ± 2.1	574	588 (557)	3.5 ± 1.6	364	389 (357)	4.0 ± 1.8	296	316 (289)	5.1 ± 2.7	281	280 (270)
Autotrophic contribution	—	—	59.3%	—	—	56.7%	—	—	56.8%	—	—	49.7%

For all r^2 values, $P < 0.0001$. 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; a and b parameters are shown. Q_{10} values calculated from the exponential equation ($Q_{10} = e^{10b}$). For calculation of Q_{10}'s standard errors see text. Interpolated and modelled annual fluxes (g C m^{-2}) calculated for each treatment over the different stand ages. In brackets are the annual estimates before being corrected for decomposition of trenched roots. Autotrophic contribution is calculated from the difference between annual estimates of total soil respiration and heterotrophic respiration after correcting for the decomposition of trenched roots.

site had significantly lower values of fine root biomass in all categories <5 mm, but showed the highest biomass of roots >5 mm. Fine roots were concentrated close to surface horizons, especially in the litter-humus layer. N concentration in roots <1 mm showed no significant differences among all stand ages (Table 5).

Discussion

Relationships between soil respiration and stand age

The analysis of the different stands showed a decrease of total soil respiration with stand age, which was significant between the youngest stands (10-year-old) and the 31- and 47-year-old stands (Table 2). Soil respiration rates levelled out in the older stands. The observed decreasing trend in soil respiration with stand age has also been reported in a Douglas fir plantation, where a 20-year-old stand had significantly higher soil respiration rates than a 40-year-old site, although the latter was not significantly different from an old-growth stand (Klopatek, 2002). Furthermore, consistently higher soil respiration rates were observed in younger stands than in old ones in a ponderosa pine ecosystem in Oregon (Law *et al.*, 1999). By contrast, soil respiration has been reported to increase with stand maturation in a loblolly pine chronosequence ranging from 1- to 25-year-old (Wiseman & Seiler, 2004). In a study by Irvine and Law (2002), contrasting soil respiration patterns between forest stands hindered attempts to explain the influence of stand age on soil CO_2 efflux. Moreover, the same fact prevented the use of a simplified single model to account for seasonal soil respiration at these sites. For the present study, before direct intercomparisons among stands of different ages were made, care was taken to assure that all the study sites had similar seasonal respiration patterns.

Stands of the same age showed no significant differences in total soil respiration among them, except for the case of 15-year-old sites (Table 2). An analysis of the inequality observed in the 15-year-old stands shows that compared with the reference sites, the core site had lower soil respiration rates than expected for this forest age. This particular stand had greater productivity than all the sites under investigation (Table 1). Moreover, this stand had the highest soil phosphorous concentration, though C:N ratios were in a range comparable with those observed at the other sites (Table 1). While on a global scale it is widely accepted that there is a strong positive correlation between plant productivity and soil respiration (Janssens *et al.*, 2001; Davidson *et al.*, 2002), within a given ecosystem, belowground C allocation is inversely related to aboveground productivity and nutrient availability (Haynes & Gower, 1995). There are several studies reporting that closed canopy forests have lower soil CO_2 emissions on sites with high fertility than on sites with more restricted nutrient availability (Haynes & Gower, 1995;

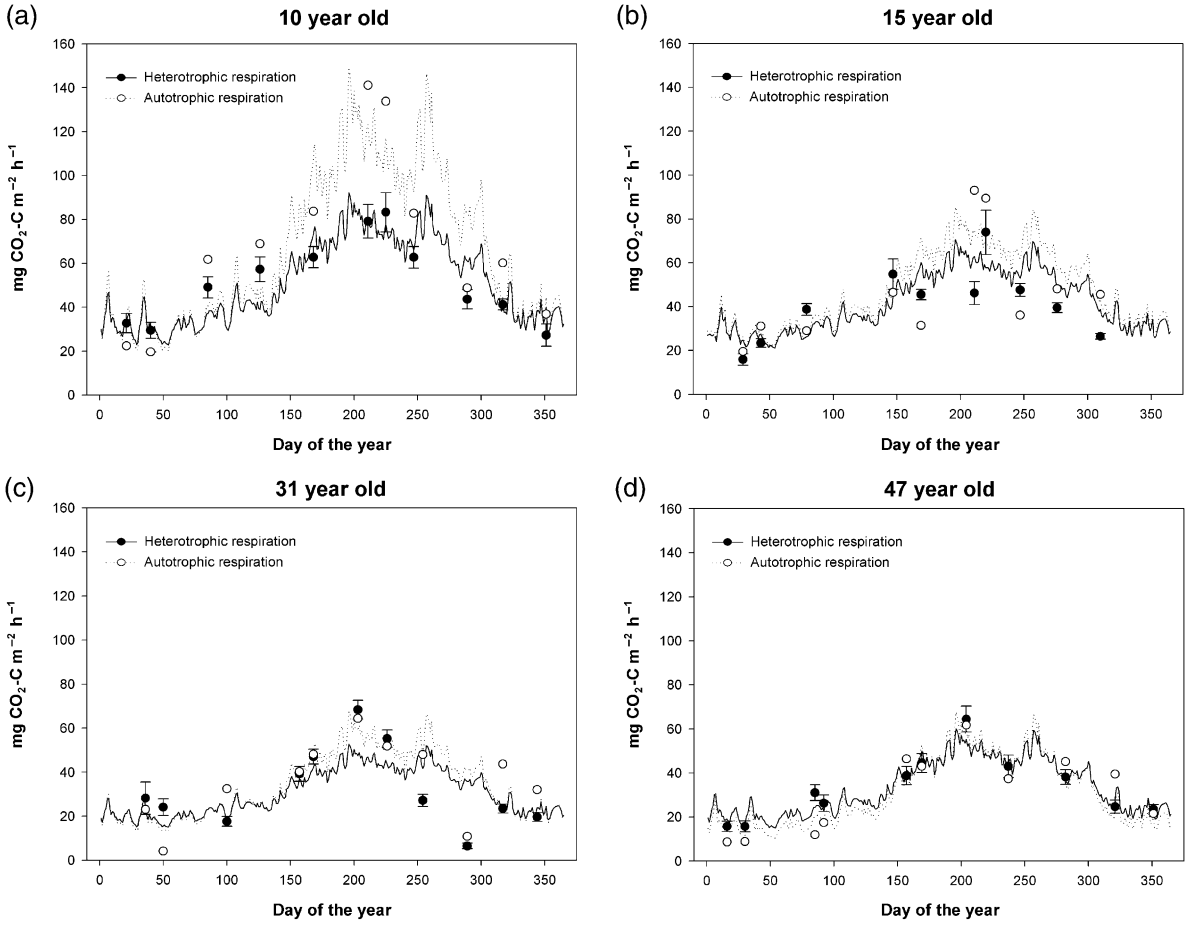

Fig. 3 Seasonal variation of heterotrophic and autotrophic soil CO_2 flux measured in the different stand ages. Each measured heterotrophic CO_2 flux is the mean of 30 measurements per sampling date. Error bars are standard errors of the means. The lines represent the modelled fluxes based on the exponential functions fitted for each stand and treatment that are shown in Table 4.

Maier & Kress, 2000; Butnor *et al*., 2003). For the differences between the 15-year-old stands in our study, we hypothesize that higher productivity is the most likely cause for the apparent low soil CO_2 efflux at this particular site. Additionally, other research work carried out over this chronosequence showed that the biomass and allocation pattern of this highly productive site (yield class 20–24) was similar to that of a less productive stand (yield class 18–20) which was five years older (Black *et al*., 2004). In other words, soil respiration in this core site would be equivalent to that of an older but less productive stand. This is in agreement with the observed decreasing trend in soil respiration and highlights the confounding effect that site productivity may exert on the influence of stand age on soil respiration. Furthermore, it supports the idea that with increasing soil fertility, soil respiration will be reduced and the productivity of the growing stock increased. Reduced soil fertility has been reported to limit C sequestration (Butnor *et al*., 2003) and fertilisation of nutrient poor sites has been reported to decrease the time for a young plantation to change from a C source to a C sink (Maier & Kress, 2000).

Total soil respiration

An important fraction of the annual variation in soil respiration was explained by soil temperature (Table 4). Soil respiration was strongly influenced by soil moisture when soil water content approached or dropped below 20% (day of year 235–280) (Fig. 1). The limiting effect that drought exerts on soil respiration is a feature well documented in forest ecosystems (Davidson *et al*., 1998; Rey *et al*., 2002). There was generally a good agreement between measured respiration rates obtained over the different sampling dates and the fitted exponential equations used with mean daily soil temperatures (Fig. 1). Regression fitness invariably increased if drought related measurements were discarded from the analysis. Measurements carried

out during this period were too sparse to infer a model based on significant limiting soil water content.

The observed decreasing trend in soil respiration with stand age was well captured by the nonlinear regressions (Fig. 2). Q_{10} values in this study ranged from 3.5 to 4.6, and they are well within the range (2.0–6.3) reported for other temperate forest ecosystems (Kirschbaum, 1995; Davidson *et al*., 1998). A mean Q_{10} value of 2.72 was reported for four Norway spruce stands in Germany (Buchmann, 2000). However, this study was carried out during the growing season only, and a comparison of Q_{10}'s obtained at different time scales may be biased.

Annual Q_{10} of soil respiration is a measure of temperature sensitivity that may mask a combination of several factors such as plant phenological patterns, moisture conditions, and perhaps other unknown variables (Curiel Yuste *et al*., 2004). However, seasonal changes in Q_{10} do not significantly alter the accuracy of an annual simulated flux (Janssens & Pilegaard, 2003). Annual parameterized models cannot be applied with confidence over shorter periods because other factors may be the main drivers of soil CO_2 efflux during such periods (Davidson *et al*., 1998; Janssens & Pilegaard, 2003). Temperature-derived functions calculated in the core sites provided reasonably good annual estimates of soil respiration compared with interpolated measurements (Table 4). Our annual estimates fall well within the summarized values for temperate forest ecosystems, which range from 250 to 1255 $g\,C\,m^{-2}$ (Raich & Schlesinger, 1992). By contrast, in a recent study carried out in Sitka spruce in N. England (Zerva *et al*., 2005), values reported were generally much lower than the ones obtained in our research because of the wet, far less productive sites.

Heterotrophic respiration

Soil CO_2 efflux measured at the trenched (unreplicated) plots had consistently lower rates than the observed total measurements but showed the same, though less marked, seasonal pattern, indicating the importance of temperature on microbial activities (Fig. 3). Microbial activity was probably limited by the restriction of soluble organic substrates during summer drought, which is a feature that has been widely reported (Fahey *et al*., 1988; Epron *et al*., 1999a; Rey *et al*., 2002).

Calculated Q_{10} functions (Table 4) agreed well with the Q_{10} value of 3.1 at 10 °C obtained in an incubation experiment using soil from a Sitka spruce plantation (Fang & Moncrieff, 2001). In common with other studies, calculated Q_{10} values for heterotrophic respiration were consistently lower than the Q_{10}'s obtained for total respiration which may indicate a lower sensitivity of microbial respiration to temperature (Kirschbaum, 1995; Boone *et al*., 1998). However, the use of different temperature sensitivities for the different soil respiration components has been challenged by recent findings that attribute this observed difference in field-based studies to plant photosynthetic activity (Bhupinderpal-Singh *et al*., 2003; Bååth & Wallander, 2003).

The youngest site had significantly greater decomposition rates than the other stand ages. This site together with the 15-year-old stand showed the highest pH values (Table 1), which is a factor that may have enhanced microbial decomposition (Dilly & Munch, 1996). Furthermore, these sites presented the thickest litter-humus layers of all stands studied. These thick layers contain a large pool of easily decomposable organic matter. Additionally, annual litter inputs over the chronosequence showed a decreasing trend with stand age, while microbial biomass determined by the fumigation–extraction procedure appeared to be higher in the youngest stand (B. Reidy, unpublished data). This latest fact together with the greater availability of organic C in the topsoil of the 10-year-old stand (Table 1) may explain its significantly higher microbial respiration as compared with the rest of stands (Table 3). The relative increase in heterotrophic respiration observed at the 47-year-old site is probably due to the accumulation of organic matter inputs over the years, mostly in the litter-humus layer and upper soil horizons. The decomposition trend observed in this chronosequence perfectly matches the initial loss and subsequent recovery of soil organic C following afforestation reported in several studies (Vesterdal *et al*., 2002; Zerva *et al*., 2005). Moreover, a study on soil C stocks carried out in this chronosequence confirms the same trend as described above (Green *et al*., submitted).

Autotrophic respiration

The difference between total and heterotrophic respiration was used to estimate root or autotrophic respiration. Rates of root respiration varied seasonally as a result of fine root activity. Earlier studies on Sitka spruce stands in Great Britain indicated that fine root growth increased with increasing temperatures and that this relationship could be altered by soil moisture effects (Deans, 1979). Effectively, the highest rates of root respiration obtained in our study were consistently observed at a time of high temperature when soil moisture was at its highest. In contrast, root respiration rates declined due to soil water deficits during a period of relatively high summer temperatures. The effect of drought on root respiration has been documented (Burton *et al*., 1998). During the drought period, autotrophic respiration rates remained higher than heterotrophic

Table 5 Categories of root biomass, fine root nitrogen concentration and fine root carbon content (<1 mm) for the different stand ages

Stand age	*N*	<1 mm (g m^{-2})	1–2 mm (g m^{-2})	2–5 mm (g m^{-2})	>5 mm (g m^{-2})	Nitrogen concentration (%)	Carbon content (%)
10-year old	7	335.9 ± 30.3^{a}	33.9 ± 15.2^{ab}	376.1 ± 150.4^{a}	663 ± 74^{a}	1.005 ± 0.02	44.97 ± 0.8
15-year old	15	316.0 ± 35.4^{a}	98.8 ± 20.0^{bc}	437.9 ± 128.3^{b}	4785 ± 587^{b}	1.020 ± 0.06	47.52 ± 0.2
31-year old	7	263.5 ± 31.1^{b}	120.1 ± 26.7^{c}	610.7 ± 189.0^{b}	5518 ± 945^{b}	1.100 ± 0.07	46.80 ± 0.4
47-year old	7	100.4 ± 11.5^{c}	11.1 ± 5.2^{a}	12.4 ± 12.4^{c}	12500 ± 785^{c}	1.003 ± 0.09	48.74 ± 0.3

Mean values ± SE. Different letters within the same root category denote significantly different biomass rates ($P<0.05$). Roots <5 mm were measured up to 30 cm depth.

ones in all the stands, although differences were observed between sites in the relative reduction of each flux component compared with mid-summer fluxes (Fig. 3).

Root respiration rates decreased as the plantations developed. The significantly greater root respiration rates observed in the youngest stand are in agreement with the observations by Ohashi *et al*. (2000), whereby the root system in a young plantation (10-year-old) may have greater activity than a mature forest where soil organic C is in dynamic equilibrium. Rates of fine root respiration are correlated with fine root N content (Ryan *et al*., 1996; Pregitzer *et al*., 1998; Widén & Majdi, 2001), although we found no significant variation in fine root N concentrations over the stands of the chronosequence (Table 5).

Fine root biomass in coniferous forests has been reported to range from 100 to 1260 g m^{-2}, with a mean of 500 g m^{-2} (Fogel, 1983). Moreover, Ford and Deans (1977) measured a fine root biomass of 353 g m^{-2} in a young Sitka spruce stand. The decreasing trend in fine root biomass <1 mm diameter with stand age (Table 5) has also been reported in other studies (Vanninen & Mäkelä, 1999; Zerva *et al*., 2005). From the point of view of root dynamics, the most active fraction corresponds with roots <1 mm diameter. Large roots have low respiration rates consistent with structural and transport functions rather than with active nutrient uptake and assimilation (Pregitzer *et al*., 1998). A coarse root density of 2.5 kg m^{-2}, reported for a 16-year-old Sitka spruce stand by Deans (1981), compares well with coarse root biomass (>5 mm diameter) observed in our study (Table 5).

The different root respiration rates observed among the stands may be explained on the basis of the relationship between fine root biomass (<1 mm diameter) and mean autotrophic respiration rates (Fig. 4). Linear relationship of fine root biomass and soil respiration has already been reported (Pregitzer *et al*., 2000). However, in our study such linearity was impeded by the oldest stand that had significantly lower fine root biomass

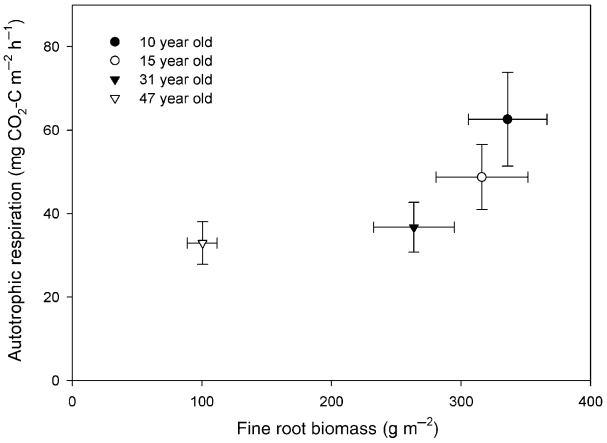

Fig. 4 Relationships between mean autotrophic respiration and fine root biomass (<1 mm diameter) determined in May 2003. Error bars are standard errors of the means.

(Fig. 4). As this mature stand has a significantly different root size distribution with the minimum amount of fine roots (<5 mm) and the maximum amount of coarse roots (>5 mm diameter), we believe that a large proportion of autotrophic respiration in this stand must be related to respiration of coarse roots. With all, an unambiguous linear relationship between fine root biomass and soil respiration rates could not be fully proved.

The highest Q_{10} for root respiration (5.6) was found at the 10-year-old stand, which had higher fine root biomass and quite likely higher root exudation than any of the other sites. In contrast, lower Q_{10} values for root respiration were obtained at sites where root respiration was more limited during summer drought (Table 4). This could be explained by the presence of a maintenance respiration, less dependent on temperature than root growth respiration, occurring during those periods (Burton *et al*., 1998). Girdling experiments have shown that the major C output from the root system is in the form of respiration as opposed to growth (Högberg *et al*., 2001; Bhupinderpal-Singh *et al*., 2003). The fact

that photosynthesis co-varies with temperature explains the high Q_{10}'s for root respiration obtained in this and in other field-based studies (Bååth & Wallander, 2003; Bhupinderpal-Singh *et al*., 2003).

Contribution of autotrophic and heterotrophic respiration to total CO_2 efflux

In all stand ages, the relative contribution of heterotrophic and autotrophic respiration to total soil CO_2 efflux varied over the year. The largest contribution of root respiration to total soil flux was during the summer, up to 64% of total flux in the 10-year-old stand, and reducing during the early and later part of the year (Fig. 3). The relative contribution of root respiration to the total soil efflux was 60% in a beech forest in France (Epron *et al*., 1999b). A value of 62% was reported for a 29-year-old Florida slash plantation (Ewel *et al*., 1986b). An apparent low value, 23%, has been reported by Rey *et al*. (2002), attributing the small contribution of roots to the coppicing performed the year previous to the experiment. A recent experiment in which the soil was not disturbed, showed that root respiration was about 50% of the total respiration and it accounted for up to 65% during the summer (Bhupinderpal-Singh *et al*., 2003). A similar value (51%) was reported in a 80-year-old forest (Nakane *et al*., 1983). Additionally, the same author concluded that when soil organic C is in dynamic equilibrium in the forest ecosystem, the relative contribution of root respiration to soil respiration may converge at approximately 50%, which is almost the value we obtained in the oldest stand that had reached such equilibrium in soil organic C.

Our results show that there is an age-related effect on the relative contribution of heterotrophic and autotrophic respiration over the chronosequence. Comparison of annual estimates calculated for the different components of the flux revealed a decreasing trend in the contribution of autotrophic respiration to total soil CO_2 efflux, ranging from 56.6% in the youngest stand to as low as 47.9% in the oldest site (Table 4). Similarly, in an experiment conducted over a boreal black spruce fire chronosequence, where root trenching was also used to partition soil respiration components, the highest autotrophic contribution was observed in 12–20-year-old stands, with lower contributions being reported in older stands (Bond-Lamberty *et al*., 2004).

Interestingly, the models showed that calculated root respiration exceeded heterotrophic respiration later in the year with increasing stand age (Fig. 3). These differences are likely due to the differential age-related effects on heterotrophic and autotrophic respiration. However, due to our inability to account for seasonal changes on the decomposition of roots left within the pipes, the seasonal contribution of heterotrophic and autotrophic respiration may be biased.

Conclusions

Our results show that afforestation of Sitka spruce on former agricultural land leads to an initial large soil CO_2 efflux that decreases as the stand matures, showing little change in the later stages prior to felling. Soil respiration rates were significantly higher in the younger stands as a result of both the larger availability of soil organic matter, and the greater activity of their root system as compared with more mature stands. Autotrophic respiration decreased with stand age. Soil C dynamics throughout the chronosequence levelled out with stand maturation, as evidenced by the similar respiration rates in the 31- and 47-year-old stands. The smaller root respiration observed in the oldest stand was compensated for by a higher microbial decomposition activity due to accumulated organic inputs. The relative contribution of root respiration to total CO_2 efflux decreased with stand age.

Temperature-based models used to predict annual mean soil respiration in afforestation sites should consider the age of the stand. Within a given ecosystem, site productivity may confound the effects of stand age on soil respiration. Further research over longer periods and on different ecosystems is required to validate and assess the importance of stand age on afforestation sites.

Acknowledgements

We thank Mr. Javier Cubillo and Mr. Ray Byrne for their help in setting-up the sites, Mr. Brian Tobin and Ms. Carly Green for providing coarse root data and nutrient analyses, and Dr. Kevin Black for provision of climatic data. We gratefully acknowledge (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 sites.

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