Soil carbon dynamics in a Sitka spruce (*Picea sitchensis* (Bong.) Carr.) chronosequence on a peaty gley

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Abstract

We investigated whether the establishment of forests on organic grassland soils leads to significant losses in soil carbon, due to the site preparation for the planting of trees and other disturbances. We also investigated whether subsequent biomass accumulation over two consecutive rotations separated by a clearfell leads to a recovery in the initial soil carbon losses.

Soil respiration, soil carbon stocks and annual litter fall were measured, while allometric equations were used for the estimation of above- and belowground biomass, in a replicated forest chronosequence of Sitka spruce (*Picea sitchensis*) on peaty gley soil, in Harwood Forest (NE England). The sites chosen were: 40-year-old first rotation stands, 12, 20 and a 30-year-old second rotation stands, one 18-month-old clearfelled site and unplanted natural grassland sites. The soil carbon stock of the first-rotation 40-year-old stands was $140 \pm 15$ t C ha$^{-1}$, far lower than in the surrounding unplanted grasslands ($274 \pm 54$ t C ha$^{-1}$), while clearfelling caused a further decline ($100 \pm 13$ t C ha$^{-1}$). Soil carbon accumulated again as the forest grew during the second rotation ($147 \pm 8, 181 \pm 17$ and $249 \pm 40$ t C ha$^{-1}$ at the 12, 20 and 30-year-old stands, respectively). Soil respiration was the highest at the grassland site ($14.2 \pm 3.1$ t C ha$^{-1}$ year$^{-1}$), possibly due to high respiration by the grasses. After forest establishment, soil respiration was: $2.3 \pm 0.9, 2.2 \pm 0.7, 5.4 \pm 0.7$ and $5.0 \pm 0.4$ t C ha$^{-1}$ year$^{-1}$ at the age of 12, 20, 30 and 40 years, while in the clearfelled site soil respiration was $5.6 \pm 1.6$ t C ha$^{-1}$ year$^{-1}$.

The inputs and outputs of carbon into the soil were combined to evaluate the long-term effects of forest management on soil carbon dynamics. It was concluded that the establishment of coniferous forests on peaty gley grassland soils in the uplands can lead to a net accumulation of soil carbon during the second rotation.

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1. Introduction

Globally, soils contain more than two-thirds of the total C stored in vegetation (Post et al., 1982; Eswaran et al., 1993) and almost twice the amount in the atmosphere (Schimel, 1995). Dixon et al. (1994)
estimated that forest ecosystems contain 1146 × 10^{15} \text{g C} while forest soils (including peaty soils) contain approximately 69\% of the total forest C pool.

The amount of C stored in the soil is the balance between inputs of organic material from the biota, which depends on the type of vegetation and its productivity at a particular site, and losses, primarily through soil respiration (Post et al., 1982). Forests continuously recycle C through photosynthesis and respiration; however, the net sequestration of C in vegetation and especially in soil can range over time periods from years to centuries, depending on the species, site conditions, disturbance regime and management practices (Dixon et al., 1994).

Currently, forest plantations globally occupy an area of 187 × 10^{6} \text{ha}; however, they account for less than 5\% of the global forest cover (FRA, 2000). Recent trends towards harvesting younger stands raise concerns about how such forest management will impact on soil processes and global carbon sequestration, as well as on site productivity and forest biodiversity (Harmon et al., 1990; Johnson, 1992). Forest plantations are usually planted in areas that did not have forest cover before (at least in temperate regions), such as grasslands or abandoned agricultural land. For forest establishment, site preparation often involves disturbing the soil, e.g. by the creation of drainage ditches or ploughing. These practices may accelerate organic matter decomposition by disturbing soil structure and breaking soil aggregates, thus leading to a loss of soil C (Turner and Lambert, 2000; Guo and Gifford, 2002).

Substantial losses of C from vegetation and soils can also be caused by harvesting (Houghton, 2003). Soil carbon storage is likely to initially decline after clearcutting, because C inputs from plant production are too low to counteract losses by soil respiration. Furthermore, intensive forest management may also lead to long term decreases in soil organic matter content (Harmon et al., 1990). On the other hand, regenerating forests and plantations may represent important carbon sinks as a result of carbon storage in both plant biomass and soils (IPPC, 2000). For a given site, forest management may thus result in net accumulation or loss of soil C, depending on the balance between net photosynthesis (of trees) and the various processes resulting in C export (Johnson et al., 1995). Carbon accumulation rates during afforestation depend on tree species and the length of the rotation (Thuille et al., 2000).

In Britain, about 315,000 ha of shallow peatlands (mainly peaty gleys) have been planted with coniferous forests, mostly Sitka spruce, mostly Sitka spruce (Picea sitchensis (Bong.) Carr) (Cannell et al., 1993). Afforestation on peaty soils may cause an increase in the rates of oxidation of the peat due to improved aeration by the drainage and the lowered water table under a maturing tree stand (King et al., 1986). Growing trees can sequester carbon in the above-ground biomass as well as in the litter layer and soil; however, whether or not afforestation will give a net benefit of C sequestration depends on the rate of peat oxidation.

Soil carbon storage is an important factor in long-term ecosystem stability but slow changes in a large pool are difficult to detect, although even small changes in the soil carbon pool can result in relatively large changes in fluxes of CO_{2} to the atmosphere (Keith et al., 1997). Because of the difficulty in determining changes in large pools, the analysis of soil CO_{2} fluxes may be more informative.

Soils contribute about 50–76.5 × 10^{15} \text{g C year}^{-1} to the atmosphere through soil CO_{2} efflux (Raich and Schelesinger, 1992; Raich and Potter, 1995). True soil respiration under field conditions is unknown (Giaradina and Ryan, 2002). Different methods have been used to measure soil respiration, such as open dynamic chambers (Rayment and Jarvis, 1997), closed dynamic chambers (Rochette et al., 1991; Kim et al., 1992) and closed static chambers (Grahammer et al., 1991). The closed static chamber method has sometimes been criticised for underestimating the soil respiration fluxes, compared to the closed dynamic chamber method which has been shown to be more accurate for a wide range of flux rates (Healy et al., 1996; Jensen et al., 1996; Janssens et al., 2000). However, Rochette et al. (1997) found little difference in fluxes measured by either the closed dynamic or the static chamber method.

Soil respiration is a combination of biotic, chemical and physical processes. The two main sources of soil respiration are the heterotrophic (decomposition of organic compounds by soil microorganisms) and the autotrophic (respiration of plant roots and rhizomes), from different soil depths (Buchmann, 2000). Soil
respiration is a sensitive indicator of essential processes in ecosystems such as: metabolic activity of roots, mycorrhizae and other soil organisms, decomposition of plant residues in soil and conversion of soil organic carbon to atmospheric CO₂ (Ewel et al., 1987; Rochette et al., 1997). Several factors can affect soil respiration rate, the most important one being soil temperature (Loyd and Taylor, 1994; Kätterer et al., 1998).

Litterfall is the largest natural flow of C and nutrients to the forest floor (Berg and Meentemeyer, 2001). On a global scale, soil respiration increases systematically with litterfall in forest ecosystems (Raich and Nadelhoffer, 1989).

Roots play an important role in soil C cycling; stand age and disturbances due to forest management can affect the number and mass of roots present in the soil (Grier et al., 1981; Vogt et al., 1983) and thus can have a great impact on the C balance in the soil. A significant amount of C is allocated to fine roots annually, even though they comprise only a small fraction of the C content of forest trees (Gower et al., 1996). Accurate measurements of turnover of fine roots and mycorrhizae are essential for understanding and quantifying belowground carbon allocation (Nadelhoffer and Raich, 1992; Ryan et al., 1997; McDowell et al., 2001). However, this is the most difficult carbon flux to measure (Vogt et al., 1986).

Raich and Nadelhoffer (1989) used the conservation of mass approach in order to estimate the belowground carbon allocation for forest ecosystems globally. Total belowground carbon allocation (TBCA) is the sum of mycorrhizae and root (fine and coarse) production, respiration and exudates. All carbon that enters the soil must either leave the soil or increase soil carbon stocks. Raich and Nadelhoffer (1989) assumed that if the forest is near steady state, the change in soil carbon stock will be near zero and thus the main regulators of TBCA can be estimated from measurements of annual rates of soil respiration and aboveground litterfall. Many have followed their example (e.g. Ryan, 1991; Smith and Resh, 1999); however, this simple approach cannot be applied to aggrading or disturbed forests (Gower et al., 1996). A few studies have examined the TBCA patterns with age and the findings are not consistent. Ryan et al. (1997) concluded that TBCA may increase with stand age, while Smith and Resh (1999) estimated that TBCA declined with stand age in an age sequence of Lodgepole pine (Pinus contorta L.) stands and Giardina and Ryan (2002) concluded the same for Eucalyptus saligna stands. Although TBCA may be a large fraction of GPP (more than 30%, Gower et al., 1996) and it is the primary source of detrital C to the soil (Giardina and Ryan, 2002), the mechanisms that control the allocation of carbon belowground are still poorly understood.

The vital role of soils as a sink or source for C at the global scale and in offsetting atmospheric CO₂ concentrations (Johnson and Curtis, 2001) makes it important to evaluate accurately the effects of forest management on soil C storage.

Here we describe work in which we measured soil C stocks, aboveground litterfall and soil respiration, and estimated fine and coarse root production and TBCA along a Sitka spruce (P. sitchensis) chronosequence, from natural unplanted grassland to second rotation growth stands, in order to determine how stand age and management practices affect the soil C balance.

2. Materials and methods

2.1. Site description

The study area is located in Harwood Forest, Northumberland, NE England (55°10′N, 2°3′W), 30 km inland from the North Sea coast. The size of the forest is approximately 4000 ha and its elevation varies from 200 to 400 m a.s.l. The average annual rainfall is about 950 mm. The establishment of the forest started in the 1930s and now Sitka spruce stands of several different ages dominate the area. The previous land cover was grassland (most abundant species: Calluna vulgaris, Festuca ovina, Eriophorum vaginatum, Deschampsia flexuosa). The forest is managed with rotations of about 40 years, the cycle being determined by the age at which risk of windthrow becomes unacceptably high (mean annual increment peaks at about 60 years of age). At this age a whole stand is clearfelled and replanting takes place after 2–3 years. Thinning in Harwood is extremely limited because of the risk of windthrow.

The dominant soil type is peaty gley, i.e., a seasonally waterlogged soil with a black-coloured,
organic O horizon, varying in depth between 15 and 40 cm. The experimental sites were identified from stock and soil maps. There was no understorey vegetation in the forest stands after canopy closure. After clearfelling, grasses (*Juncus* sp., *Deschampsia* sp., *Molinia caerulea*, *Holcus mollis*) invaded the site.

2.2. The chronosequence approach

The research was undertaken in stands of different ages, an area where a mature stand had been clearfelled, and areas under natural grassland that were representative of the land cover prior to any forest establishment. All stands were on peaty gley soil. The following stands were used in the study: three 40-year-old, three 30-year-old, three 20-year-old, and four 12-year-old. Two unplanted (grassland) areas were also used, together with a single clearfelled area, for which no comparable replicate was available.

In addition to comparisons made between stands of similar age, intra-stand variability in relation to soil carbon stocks and rates of litterfall were also investigated, by sampling in replicated plots for only one stand in each age class. Soil respiration studies made use of multiple replicate microsites, all falling within a radius of 15 m, within each of the investigated stands. Details of the sampling procedures are given in the relevant sections below.

2.3. Aboveground litter fall

To measure litterfall four circular traps (0.2 m²) were randomly placed within a 2 m radius north, east, south and west, respectively, from the centre of five random plots within each stand. Traps were constructed by using water-permeable, reusable acetate lining bags within frames made from 25 l plastic containers, and mounted on wooden pegs, so that the height of the trap opening was ca. 80 cm aboveground level. The traps were installed in the 12, 20, 30 and 40-year-old stands during May and June 2000. Litter was collected for the first time in October 2000, and then every 2 months from January 2001 until the end of September 2001. After collection, all litter was dried at 80 °C for 48 h and weighed. Average annual litter fall was then calculated. A C content of 50% was assumed for the litter.

2.4. Soil C stocks

2.4.1. Soil sampling

Soil sampling took place during the summer of 2000 and 2001. In summer 2000, a nested factorial design was used to investigate the within-stand variability (Anderson and McLean, 1974). Five plots were randomly selected in a single stand in each of four different ages (12, 20, 30 and 40-year-old, respectively), as well as in an unplanted control site (UN). All the sites (except the unplanted “control”) were part of a chronosequence selected for eddy covariance measurements (Kowalski et al., 2004). All the sites were in their second rotation, except for the 40-year-old one, which was in its first rotation. In each plot eight samples were taken from eight points at randomly selected distances from the centre of the plot in clockwise order and within a radius of 10 m from the centre. The samples were taken with a 45 cm long soil auger with a cross-section of about 2 cm diameter and were visually separated into three horizons: litter, organic and mineral. The samples were put in polyethylene bags and were stored in a cold room (4 °C) pending preparation and analysis.

During summer 2001, additional stands of each age were sampled (single, randomly selected plots in each stand). These were three additional 12-year-old stands, two additional for the 20, 30 and 40-year-old stands and one additional unplanted grassland area. Results were averaged with the corresponding stand mean obtained in 2000, to obtain the mean values for the age class. The new stands were chosen to be as close to each other as possible, in order to avoid topographic influences on soil C. A single clearfell area (clearfelled 18 months prior to sampling, referred to as CF from now on) was also sampled, but no further comparable areas were available.

The samples were taken using a manually driven soil corer (5.5 cm diameter) with a slide hammer attachment (Giddings Machine Company, Inc., U.S.), to a depth of about 50 cm. The samples were kept in the corer liners and were transferred to the laboratory, where the depth of the total core and each horizon (litter, organic and mineral) were measured and the layers separated. The samples were kept in polythene bags in a freezer (−4 °C) till further analysis when they were oven dried at 105 °C for 24 h (Jackson, 1958; Allen, 1989). Coarse fragments were removed.
by hand and the soil was ground to pass a 0.5 mm mesh.

2.5. Determination of C concentration

Two hundred and thirty samples from all layers were analysed both in a C/N analyser (Carlo-Erba, NA 2500) and by loss on ignition (LOI). Finely ground sub-samples of about 4 mg for the litter and the organic layer and 10 mg for the mineral layer were combusted in the C/N analyser, and their C concentration was determined. Total C was assumed to equal organic C as the samples did not come from a calcareous soil. Other sub-samples of approximately 1 g (Allen, 1989) were weighed and then ignited in a furnace at 500 °C, for 5 h. After burning the samples were weighed again and the percentage loss of mass (L, %) was calculated.

The C (%) obtained from the C/N analyser and the mass loss (L, %) obtained from the LOI were found to be significantly related to each other. Also a significant effect of soil layer was found (data not shown). Therefore separate regression equations were calculated for each layer and were used to estimate the C (%) for the remaining samples on the basis of the LOI method only. The regression equations used were:

\[
\text{C}(\%) = 0.513L(\%) - 0.092, \\
R^2 = 0.99 \text{ for the litter layer},
\]

(1)

\[
\text{C}(\%) = 0.542L(\%) + 0.184, \\
R^2 = 0.99 \text{ for the organic layer},
\]

(2)

\[
\text{C}(\%) = 0.533L(\%) - 0.700, \\
R^2 = 0.99 \text{ for the mineral layer}.
\]

(3)

2.6. Soil respiration measurements

Soil respiration was measured weekly or biweekly, from July 2001 to October 2002, in the 40-year-old stand, while in the CF, 20 and 30-year-old stands measurements were taken biweekly or once a month. In the 40-year-old stand and in a recently clearfelled site soil respiration was measured using two methods. With the first method, 10 collars (diameter = 10 cm, height = 5 cm) were permanently inserted to a depth of approximately 3 cm. A visual examination confirmed that no roots were cut. Soil respiration was measured with a portable, dynamic closed chamber system (EGM-3, SCR-1, PP-Systems, Hitchin, UK), equipped with a portable infrared gas analyser (IRGA), with a slightly modified chamber to obtain an effective gas seal. A small, low-speed fan inside the chamber ensured mixing of air during the measurements while a mesh at the bottom of the chamber eliminated potential Venturi effects. Fan speed tests showed very small pressure differentials (±0.1 Pa) at the mesh.

The second method employed was the static closed chamber (CC) technique. Twelve chambers consisting of PVC cylinders (inside diameter = 40 cm and height 20 = cm) open at the top and the bottom were inserted into the soil to a depth of about 5 cm to create a gas tight seal. An aluminium sheet with a foam rubber sealing ring on the under side acted as a lid on the top of the chamber during the period of the measurement. The chambers were left permanently in the field in order to minimise the effects of disturbance caused by their insertion in the soil. After taking an initial sample of ambient air, the chambers were kept closed for 1 h. At the end of this period air samples from inside the chambers were taken with 60 ml syringes. The samples were transferred to the laboratory and gas chromatographic analysis (Perkin Elmer gas chromatograph fitted with a thermal conductivity detector) was used for determination of CO₂ within 24 h of their collection. The CO₂ concentrations in the chambers showed an almost linear increase over time.

Soil respiration at the other sites was measured with the CC method on 8–16 chambers (of diameter 20–40 cm). To allow a comparison between C stocks and CO₂ efflux measurements at all sites, we also estimated the annual respiration flux at the 12-year-old stand from a relationship obtained between annual litterfall and annual soil respiration (\(R^2 = 0.93, n = 4\)).

Soil temperature was measured with a digital temperature probe (Fisher Scientific) inserted adjacent to each collar and chamber, to 5 cm depth, every time a measurement of soil CO₂ efflux was taken.

2.7. Root biomass

Fine root biomass, \(M_{FR}\) (t ha\(^{-1}\)) was estimated from the equation:

\[
M_{FR} = -0.12 \text{ age} + 7.23,
\]

(4)
where \( M = d \) was estimated by the difference in C stocks between fine and coarse roots.

Coarse root biomass was estimated from empirical allometric equations (Dimitriadis, 2000):

\[
M_{CR} = 0.0149 \times d_0^{2.3302},
\]

(5)

where \( M_{CR} \) is the coarse root biomass.

\[
d_0 = -2.4 + 6.9 \times 0.85^{DBH} + 1.4DBH \]

(6)

and DBH is the tree diameter at breast height (1.33 m).

Annual changes in fine and coarse root biomass were estimated from the same allometric equations, while the change in DBH was estimated from measured annual mean growth data for each age class (Van Der Eb, 2002). Root biomass (fine and coarse) was assumed to be 50% C.

2.8. Total belowground carbon allocation (TBCA)

Total belowground allocation (TBCA) was estimated by using a conservation of mass approach as in Giardina and Ryan (2002), where outputs from the belowground system must equal inputs minus any change in storage over a defined time period:

\[
F_S + F_E = TBCA + F_A - (\Delta C_S + \Delta C_R)/\Delta t,
\]

(7)

where \( F_S \) is the soil respiration, \( F_E \) the export of C (CH\(_4\) flux or erosion or leaching), TBCA the total of root respiration, carbohydrates used for mycorrhizae or exudates and production of fine roots, \( F_A \) the aboveground litterfall, \( \Delta C_S \) the change is soil C stock, \( \Delta C_R \) the change in C stored in roots (fine and coarse) and \( \Delta t = 1 \) year for this study. All the components are expressed in t C ha\(^{-1}\) year\(^{-1}\).

Thereafter, TBCA can be expressed by difference by measuring fluxes out of the soil \( (F_S \) and \( F_E \)), into the soil \( (F_A) \) and any change in the C storage 

\[
TBCA = F_S + F_E - F_A + (\Delta C_S + \Delta C_R)/\Delta t.
\]

(8)

The fluxes of C in leaching, runoff and erosion were ignored, but these are probably minor in most closed canopy forests (Raich and Nadelhoffer, 1989). The annual soil CH\(_4\) flux in the 40-year-old stand was 0.05 ± 0.03 t C ha\(^{-1}\) year\(^{-1}\) (Zerva et al., 2003), and because it was so low it was assumed to be zero in the estimation of TBCA. For the first rotation, the \( \Delta C_S \) was estimated by the difference in C stocks between the first rotation 40-year-old stand and the unplanted grassland site, divided by the period length, while for second rotation the \( \Delta C_S \) was estimated by the difference in C stocks between different age classes divided by the period length, and with starting value the C stock in the clearfelled site.

The variance in the TBCA was estimated from the sum of the variances of the other components, with the exception of \( \Delta C_R \), since this term was estimated from an allometric equation. However, compared to the other fluxes, \( \Delta C_R \) is a very small component in the TBCA equation therefore variance was assumed to be negligible and was ignored.

2.9. Statistical analysis

Because of the lack of stand replication, the significance of the differences in soil respiration or litterfall among stands of different age could not be tested. However, the means for the replicate plots within each stand and the standard errors were calculated. For the soil C stocks, means for each stand were similarly calculated and in turn averaged to give means for each age class. One-way ANOVA was then used to test for significant differences among age classes.

3. Results

3.1. Components of the TBCA budget

3.1.1. Litterfall

Mean annual litterfall mass ranged from 1.1 to 1.9 t C ha\(^{-1}\) year\(^{-1}\) (Table 1). The litterfall was almost the same in the 12 and 20-year-old stands (1.1 ± 0.2 and 1.1 ± 0.3 t C ha\(^{-1}\) year\(^{-1}\), respectively) and it increased as the stands grew older to 1.7 ± 0.3 t C ha\(^{-1}\) year\(^{-1}\) in the 30-year-old and 1.9 ± 0.2 t C ha\(^{-1}\) year\(^{-1}\) in the 40-year-old stand.

3.1.2. Soil C stocks

Soil C stocks across the chronosequence are shown in Fig. 1. The planting of trees led to a decrease in soil C stocks from 274 ± 54 t C ha\(^{-1}\) in the unplanted sites (UN) to 140 ± 15 t C ha\(^{-1}\) \((P < 0.001)\) in the first rotation 40-year-old stands. Clearfelling at the end of first rotation led to a further decrease in soil C to
Soil started accumulating C again during the second rotation, with soil C stocks of 147±8, 181±17, and 249±40 t C ha⁻¹ in the 12, 20 and 30-year-old stands, respectively. The soil C stocks in the 30-year stands were similar to that in the UN site (P>0.05).

### 3.1.3. Soil respiration

For the two sites where respiration was measured with both methods, the two series were linearly correlated (CO₂(PP-Systems) = 1.77 × CO₂(CC), R² = 0.84, Fig. 2). Further comparisons of the two methods by using a soil monolith in a controlled environment indicated that the static closed chamber method underestimated the soil respiration fluxes (Zerva, 2004) and the above relationship was used to adjust the CC soil respiration values to those given by the dynamic closed chamber system (PP-Systems) method. All values cited below are in terms of those given by the dynamic closed chamber method.

Annual soil respiration ranged from 2.2±0.7 to 14.2±3.1 t C ha⁻¹ year⁻¹, with the lowest value in the 20-year stand and the highest in the UN (Table 1). The CF had similar soil respiration rates to the mature (40-year-old) stand, 5.6±1.6 and 5.0±0.4 t C ha⁻¹ year⁻¹, respectively. Soil respiration was 2.3±0.9 t C ha⁻¹ year⁻¹ in the 12-year-old, and 2.2±0.7 t C ha⁻¹ year⁻¹ in the 20-year-old, but more than doubled to 5.4±0.7 t C ha⁻¹ year⁻¹ in the 30-year-old and 5.0±0.9 t C ha⁻¹ year⁻¹ in the 40-year-old stand. As mentioned before, annual soil respiration was linearly related to annual litterfall (R² = 0.93, n = 4) for the four stands for which measurements were available.

Soil respiration showed a strong seasonal trend at all sites, with higher fluxes during the summer and low fluxes during the winter (Fig. 3).

**Table 1**

<table>
<thead>
<tr>
<th>Stand age (years)</th>
<th>Fₛ (t C ha⁻¹ year⁻¹)</th>
<th>Fₐ (t C ha⁻¹ year⁻¹)</th>
<th>M_FR (t C ha⁻¹)</th>
<th>M_CR (t C ha⁻¹)</th>
<th>ΔCₘ₟(F + C) (t C ha⁻¹ year⁻¹)</th>
<th>ΔCₛ (t C ha⁻¹ year⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>UN</td>
<td>14.2 (3.1)</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>40, first rotation</td>
<td>5.0 (0.4)</td>
<td>1.9 (0.2)</td>
<td>2.4</td>
<td>56.3</td>
<td>1.2</td>
<td>–3.4 (1.4)</td>
</tr>
<tr>
<td>CF</td>
<td>5.6 (1.6)</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>12</td>
<td>2.3 (0.9)</td>
<td>1.1 (0.2)</td>
<td>5.8</td>
<td>11.1</td>
<td>0.5</td>
<td>3.9 (1.3)</td>
</tr>
<tr>
<td>20</td>
<td>2.2 (0.7)</td>
<td>1.1 (0.3)</td>
<td>4.8</td>
<td>24.0</td>
<td>0.9</td>
<td>4.3 (1.1)</td>
</tr>
<tr>
<td>30</td>
<td>5.4 (0.7)</td>
<td>1.7 (0.3)</td>
<td>3.6</td>
<td>27.1</td>
<td>0.8</td>
<td>6.8 (1.4)</td>
</tr>
</tbody>
</table>

Fₛ is the soil respiration, Fₐ the litterfall, M_FR the fine root biomass, M_CR the coarse root biomass, ΔCₘ₟(F + C) the change in root biomass (fine plus coarse) over a year and ΔCₛ the change in soil C stocks over a year. The numbers in the brackets represent the standard error of the mean.
Soil respiration data combined for all forest stands and all seasons was strongly related to soil temperature, with an exponential relationship:

\[ R_S = 0.50 e^{0.25T_5} \]

\[ (R^2 = 0.56, \text{apparent } Q_{10} = 13.3), \]

where \( R_S \) is soil respiration (g CO\(_2\) m\(^{-2}\) day\(^{-1}\)) and \( T_5 \) is the soil temperature at 5 cm depth (°C). Most of the variability around this relationship was accounted for by the differences across stands and age classes (Zerva, 2004).

3.1.4. Root biomass

Modelled fine-root biomass decreased from 5.8 t ha\(^{-1}\) in the 12-year to 2.4 t ha\(^{-1}\) in the 40-year stand (Table 1). In contrast coarse root mass increased from 11.1 t ha\(^{-1}\) at the 12-year to 56.3 t ha\(^{-1}\) in the 40-year (Table 1).

3.1.5. Total belowground carbon allocation (TBCA)

Fig. 4 gives all the values employed to calculate TBCA for the four studied age classes. The values of some additional parameters are listed in Table 1. TBCA was found to range from 1.0 ± 0.9 t C ha\(^{-1}\)

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Fig. 2. Linear relationship between soil respiration (g CO\(_2\) m\(^{-2}\) day\(^{-1}\)) measured with the static closed chamber method and the dynamic closed chamber method (PP-Systems) in the 40-year-old stand and a recently clearfelled site. The regression was forced through the origin.

Fig. 3. Monthly soil respiration (t C ha\(^{-1}\)) in the chronosequence. Soil respiration follows the same seasonal trend at all sites. Values calculated using the dynamic closed chamber method. The vertical bars represent the standard error of the mean.
11.3 ± 1.2 t C ha⁻¹ year⁻¹, in the 30-year-old stand second rotation.

Soil respiration was the largest flux contributing to TBCA, for the 40-year-old stands, while ∆Cₘ/Δt was the largest flux for the second rotation stands, 12, 20 and 30-year-old and stands (Fig. 4).

4. Discussion

4.1. Litterfall

The aboveground litterfall values in this study (1.1–1.9 t C ha⁻¹ year⁻¹) are within the range of 0.57–3.48 t C ha⁻¹ year⁻¹ for temperate forests, referred to by Gower et al. (1996). The values increased with age, but this trend could not be tested statistically because of the absence of stand replication. Litterfall values are also similar to those measured by Pedersen and Bille-Hansen (1999) in 35 years old Sitka spruce and Norway spruce on poor soil in Denmark during 6 years.

4.2. Soil C stocks

The unplanted grassland (UN) in the forest area contained 274 ± 54 t C ha⁻¹, which agrees with the estimation by Cannell et al. (1993) of soil C in the range of 200–240 t C ha⁻¹ in shallow peat (peats and peaty ironpan soils) in Britain. However, soil C stocks in the 40-year-old stands were only 140 ± 15 t C ha⁻¹, suggesting a major decrease following afforestation, possibly due to the accelerated decomposition of soil organic matter caused by improved aeration, initially by drainage for the planting of trees and then by a natural lowering of the water table under the trees, as observed in the nearby Kielder Forest by King et al. (1986). The loss due to the conversion of grassland to forest corresponds to a decrease of about 2.7 t C ha⁻¹ year⁻¹, which agrees with the estimate made by Armentano and Menges (1986), of 2.81 t C ha⁻¹ year⁻¹ in the temperate region.

Soil C stocks in the CF site were considerably lower than in the 40-year-old stand. Although the difference in the soil C cannot be definitely related to clearfelling, as only the one clearfell site was available for sampling, there is evidence from other work that increased decomposition and the cessation of litter inputs after clearfelling may lead to such a decrease. Ballard (2000) indicated that clearfelling changes the soil temperature regime, which is likely to be significant in contributing to increased biological activity and increased rates of organic matter decomposition. Smethurst and Nambar (1990) found that clearfelling of a Pinus radiata plantation caused a decrease in the soil C of about 14 t C ha⁻¹ during the first 3 years after planting on sandy podzol soil in south-eastern Australia, while Knoepp and Swank
(1997) found that soil C declined slightly in the 0–10 cm depth following clearfelling in a white pine plantation in the southern Appalachians in the USA. Although several other authors have indicated that clearfelling may not cause large declines in soil C stocks (Johnson and Curtis, 2001; Johnson, 1992; Pennock and van Kessel, 1997), in Hardwood clearfelling is accompanied by additional soil disturbances which may stimulate C loss, e.g., restoration of the ditches to re-activate drainage channels, and mounding, a technique by which about 10–15% of the soil surface to about 30 cm depth is turned over in patches of about 0.5 m² each to create elevated mounds, on which the new transplants (1 + 1) are planted.

The increase of soil C stocks in the stands growing in second rotation indicates that soil C stocks can recover towards the end of this second cycle to values approaching those prevailing before the initial planting, some 75 years earlier. Wilde (1964) found that soil organic matter concentration (%) at a depth of 15 cm increased linearly with stand age (13–48 years) in red pine plantations in Wisconsin. He also found a faster increase with age (12–30 years) in the soil organic matter content in a jack pine plantation in the same area. Black and Harden (1994) studied the soil carbon storage in a mixed conifer chronosequence in California and found an initial loss of about 15% (30 t ha⁻¹) of organic C from the soil within 1–7 years after harvesting. The loss continued until the forest was 17 years old (another 15%). The carbon accumulation rates exceeded rates of loss after 80 years of re-growth, but carbon storage had declined and it was not likely to recover to pre-harvest levels.

On the other hand, Boone et al. (1988) estimated that it took more than 100 years for the organic layer in a Tsuga mertensiana (Bong.) Carriere forest to recover to the pre-disturbance values in thickness and carbon storage in Oregon, USA. Switzer et al. (1979) found a steady state in the organic layer carbon pools after about 70 years of old field succession to oak–hickory–pine forests in eastern Mississippi, USA.

4.3. Soil respiration

The annual $F_S$ in the UN site was far higher compared to the $F_S$ from forest stands or the CF site. This is in agreement with Raich and Tufekcioglu (2000) who reported consistently greater soil respira-

tion rates in grasslands than in forests under similar conditions, world-wide. This appears to be because grasses, with virtually no allocation of C to wood production, may have more photosynthes available to allocate belowground than trees do (Raich and Tufekcioglu, 2000).

The annual $F_S$ fluxes in the forest stands were much lower (about a third to one-half) than the mean rates for temperate coniferous forests reported by Raich and Schelesinger (1992) and those estimated by Law et al. (1999), in mixed age stand of ponderosa pine in Oregon. On the other hand, our measured fluxes are similar to those reported by Wingate (2003) for a similar Sitka spruce stand in Griffin (Scotland).

Rates of $F_S$ at the clearfell site were similar to those in the 40-year-old (first rotation) stand. Londo et al. (1999) reported higher soil respiration rates in a clearfelled bottomland hardwood forest in Texas between 6 and 22 months after clearfelling. They also reported vigorous vegetation recovery in the first growing season following harvesting from rapid invasion of herbaceous species. However, Striegl and Wickland (1998) found that clearfelling of a boreal jack pine (Pinus banksiana Lamb.) forest in Canada reduced soil respiration to about 40% of that in an uncut stand of similar age (60–90-year-old), in the first season following harvest. They attributed the major part of this reduction to destruction of near-surface soil autotrophic and heterotrophic respiration and to tree-root die-off. At our site, colonisation by grasses and shrubs is generally vigorous after about one or two years since harvesting. The data reported here are for the third year after clearfelling.

4.4. Roots

Our estimations of fine root biomass in the chronosequence (except for the 40-year-old stand) are within the range of 3.5–11 t ha⁻¹, as estimated by Fogel (1985) for coniferous forests. The estimation of fine root biomass with Eq. (4) gives results in agreement with Deans (1981), who estimated fine root biomass (<2 mm) of 5.2 t C ha⁻¹ for a 16-year-old Sitka spruce plantation. If this age is used in the above equation we obtain 5.3 t C ha⁻¹. Fine root biomass was estimated to decrease with stand age; this was similar to the trend observed by John et al. (2001) in Pinus kesiya stands in north east India. Vanninen
and Makela (1999) studied fine root biomass in Scots pine (Pinus sylvestris) stands of different ages in poor and fertile stands in Finland. They found that fine root biomass increased with age at the poor site, while root biomass decreased with stand age at the fertile sites. Vogt et al. (1983) found that fine root biomass decreased after canopy closure in a Douglas fir (Pseudotsuga menziesii) chronosequence in Washington.

Coarse root mass was estimated to increase with stand age, as expected, since coarse roots primarily serve a support function and need to increase with stand size and age (Giardina et al., 2003). Such an increase in coarse root biomass with age was also shown by John et al. (2001) for Pinus kesiya.

4.5. Total belowground carbon allocation (TBCA)

The TBCA in this study for the stands growing in second rotation is within the range of 2.33–10.13 t C ha\(^{-1}\) year\(^{-1}\) for temperate forests referred to by Gower et al. (1996), and the global range of 2.6–11 t C ha\(^{-1}\) year\(^{-1}\) by Raich and Nadelhoffer (1989). However, Raich and Nadelhoffer (1989) only estimated TBCA in near-steady-state forests; the chronosequence in this study cannot considered to be steady state, since it is probably still affected by the land use change which took place between 40 and 70 years ago.

TBCA increased with stand age in stands growing in second rotation from 12 to 30 years old. However, Giardina and Ryan (2002) found a linear decline with age in TBCA in a Eucalyptus saligna stand over a period of 4 years, from 0.224 t C ha\(^{-1}\) year\(^{-1}\) in year 1 to 0.161 t C ha\(^{-1}\) year\(^{-1}\) in year 4. Similarly Smith and Resh (1999) found a decline of TBCA with age in lodgepole pine (Pinus contorta) stands in Wyoming.

As a further check, we compared our estimated rates of TBCA with values of GPP measured with eddy covariance. This comparison showed that between 33 and 57% of GPP was allocated belowground in the 20 and 30-year stands at our sites (Clement et al., 2003; Kowalski et al., 2004). Law et al. (1999) found that about 61% of GPP was allocated belowground in a ponderosa pine (Pinus ponderosa) forest in Oregon, which consisted of old (250-year-old), young (45-year-old) and mixed-aged stands, whereas Giardina et al. (2003) estimated that TBCA was about 50% of GPP in a Eucalyptus saligna plantation during 4 years of measurements. Therefore, our comparison suggested that the rates of carbon flowing belowground estimated from eddy covariance estimates of productivity and the TBCA calculated using a carbon balance approach agreed to a considerable extent.

Total belowground carbon allocation has been reported to increase with increased litterfall (Raich and Nadelhoffer, 1989). Although this report was for closed canopy forests near steady state, the trend matched that observed for our stands growing in a second rotation, despite the fact that litterfall was not the main factor contributing to TBCA.

Accurate estimations of TBCA depend on measuring the annual fluxes of inputs, outputs and changes in soil C stock and root mass with a reasonable precision. Since \(F_S\) and \(\Delta C_S\) are the major fluxes controlling TBCA they have the greatest potential contribution to the error in the estimation of TBCA. Different methods for measuring \(F_S\) can give different values and a correction factor may be needed (Norman et al., 1997). In this study, \(F_S\) was measured with static closed chambers for most of the sites, and a correction factor using the dynamic closed chamber method was required. Also the \(F_S\) in the 12-year stand had to be estimated, as no soil respiration measurements were available at this site.

\(\Delta C_S\) can be negative during the first rotation due to decomposition of the drying peat and positive during second rotation when C starts accumulating again as the trees produce more and more litter. Measurements at smaller time intervals would be required in order to determine changes in the storage of soil C more accurately.

In summary, average estimates of TBCA suggest fairly high rates of C storage belowground as a result of the high productivity of plantations of Sitka spruce in the British Isles. However, our estimates of soil respiration appear lower than equivalent estimates for temperate coniferous forests. The resulting substantial rates of C accumulation in the soil of second rotation forests found in this study are remarkable, but similar to values found for Sitka spruce stands in Ireland (K. Byrne, personal communication).

5. Conclusions

The establishment of Sitka spruce forests on previous grassland on peaty gley soils may lead to
a decrease in soil C during the first rotation but also to net accumulation of soil carbon during a second rotation, bringing the soil C stock back to a similar level to that prevailing in the grassland prior to afforestation. When the standing tree biomass is also taken into account, a mature second rotation forest system with a restored level of soil C will have more total C than the grassland and thus constitute a substantial C sink.

Also, C accumulation in the soil occurring during the second rotation was probably caused by fairly high rates of C storage belowground, coupled to low rates of soil respiration.

A more intensive investigation of C efflux and storage in the chronosequence over a longer period is required to better understand the soil C balance of these forests.

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