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## Inventory and eddy covariance-based estimates of annual carbon sequestration in a Sitka spruce (*Picea sitchensis* (Bong.) Carr.) forest ecosystem

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**Abstract** A comparison was made of annual net ecosystem productivity (NEP) of a closed canopy Sitka spruce forest over 2 years, using either eddy covariance or inventory techniques. Estimates for annual net uptake of carbon (C) by the forest varied between 7.30 and 11.44 t C ha<sup>-1</sup> year<sup>-1</sup> using ecological inventory (NEP<sub>eco</sub>) measures and 7.69–9.44 t C ha<sup>-1</sup> year<sup>-1</sup> using eddy covariance-based NEP (-NEE) assessments. These differences were not significant due to uncertainties and errors associated with estimates of biomass increment (15–21%) and heterotrophic respiration (12–19%). Carbon-stock change inventory (NEP<sub>ΔC</sub>) values were significantly higher (27–32%), when compared to both NEP<sub>eco</sub>- and -NEE-based estimates. Additional analyses of the data obtained from this study, together with published data, suggest that there was a systematic overestimation of NEP<sub>ΔC</sub>-based assessments due to unaccounted decomposition processes and uncertainties in the estimation of soil-C stock changes. In contrast, there was no systematic difference between NEP<sub>eco</sub> and eddy covariance assessments across a wide range of forest types and geographical locations.

**Keywords** Carbon sequestration · Sitka spruce · Inventory · Eddy covariance

### Introduction

The net exchange of carbon (C) by a forest ecosystem over a given period of time is termed net ecosystem productivity (NEP). NEP captures a variety of processes and feedbacks associated with C cycling between the atmosphere, vegetation and soil pools. Long-term eddy covariance monitoring networks, such as CarboEurope-IP, have been established to assess biosphere-atmosphere net ecosystem CO<sub>2</sub> exchange (NEE) across a range of land-use categories. However, flux tower assessments of NEP (-NEE = NEP) need to be independently validated against bottom-up approaches before the data can be scaled up to the land-use level with confidence. Despite advances in micro-meteorological technology, national C-accounting methodologies for reporting to the International Panel on Climate Change and the Kyoto Protocol rely on forest inventory data and biometric approaches, that, in turn, require independent validation. Stand level C-stock changes are generally assessed using either ecological approaches (NEP<sub>eco</sub>), based on the estimation of net C balance from heterotrophic and autotrophic processes (Curtis et al. 2002; Ehman et al. 2002), or mass-balance (NEP<sub>ΔC</sub>) estimates of annual C gains and losses (Kolari et al. 2004; Curtis et al. 2002). The NEP<sub>eco</sub> approach includes an assessment of annual CO<sub>2</sub> losses from the ecosystem, via heterotrophic respiration as well as the net gain from autotrophic processes (Curtis et al. 2002; Ehman et al. 2002);

$$\text{NEP}_{\text{eco}} = \text{NPP} - \text{R}_h, \quad (1)$$

where NPP is the net primary productivity and R<sub>h</sub> is heterotrophic respiration due to microbial decomposition of soil-organic C, litter, above-ground detritus (AGD) and respiration by consumers;

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$$R_{h(\text{total})} = R_{h(\text{soil})} + R_{h(\text{AGD})} + R_{h(\text{consumers})}. \quad (2)$$

Generally, C stored as AGD includes decaying stumps and branches, which may be a particularly significant component in second rotation forests (Kolari et al. 2004) and natural unmanaged stands. In young unthinned afforested stands, the residual decay due to harvest or successional losses are small and AGD, in this case, can generally be defined as all dead branches that are attached to the tree.

Inventory-based estimates of NPP can be calculated as;

$$\text{NPP} = \Delta B + \Delta \text{AGD} + D_a + D_b + H + \text{VOC} \quad (3)$$

where  $\Delta B$  is the change in living biomass,  $\Delta \text{AGD}$  is the annual change in dead material still attached to the tree,  $D_a$  is the above-ground litterfall measured as the annual loss of live shoots or branches,  $D_b$  is the below-ground detritus, defined as all C transferred from roots and mycorrhizae to the soil through exudation and mortality and  $H$  is related to herbivore removal of biomass. Losses associated with the emission of volatile organic compounds (VOCs), such as monoterpenes, are not commonly accounted for and assumed to be small.

The more direct mass-balance inventory approach for estimating NEP ( $\text{NEP}_{\Delta C}$ ) is based on the change in C stocks in live ( $\Delta C_b$ ) and dead ( $\Delta C_{\text{dead}}$ ) biomass and soil ( $\Delta C_{\text{soil}}$ ), as described by Kolari et al. (2004):

$$\text{NEP}_{\Delta C} = \Delta C_b + \Delta C_{\text{dead}} + \Delta C_{\text{soil}}. \quad (4)$$

As  $\Delta C_{\text{soil}}$  is generally very small it is difficult to detect against the considerably higher background soil-C stock. An additional difficulty arises from the high spatial heterogeneity in soil-C stocks. In some cases,  $\Delta C_{\text{soil}}$  is not even measured or assumed to be zero (Kolari et al. 2004).

Theoretically, -NEE and inventory-based NEP measures both represent the difference between gross primary productivity (GPP) and total respiration, although they are independent assessments with unrelated errors. Therefore, such intercomparisons provide information on the causes of interannual and site-specific variations in NEP (Curtis et al. 2002; Falge et al. 2002). However, these assessments generally exclude an analysis of uncertainty associated with different NEP measures. In this paper, we report on an intercomparison of the use of the three procedures (-NEE,  $\text{NEP}_{\text{eco}}$  and  $\text{NEP}_{\Delta C}$ ), for assessing NEP of a closed canopy Sitka spruce stand, over a 2-year period. We also report on the sources of uncertainties and errors associated with the different approaches. By making a comparison between eddy covariance- and inventory-based NEP data, from this and other studies (Kolari et al. 2004; Curtis et al. 2002; Ehman et al. 2002), we examine whether any systematic differences between these independent assessments of C sequestration are associated with forest type, geographic location, disturbance or methodological differences.

## Materials and methods

### Study site

The research was conducted on a 14-year-old Sitka spruce forest growing on a wet mineral soil located in Co. Laois in the Irish midlands ( $\sim 52^\circ 57' \text{N}$ ,  $7^\circ 15' \text{W}$ , altitude of 260 m). The 30-year mean annual temperature was  $9.3^\circ \text{C}$ , with a mean rainfall of 850 mm. The site was previously an unmanaged grassland, now planted at a density of ca. 2,500 stem  $\text{ha}^{-1}$ , with a current leaf area index of  $8.7 \text{ m}^2 \text{ m}^{-2}$ .

### Meteorological measurements

Eddy covariance measurements of NEP (-NEE = NEP) were made over the period from February 2002 to February 2004 using the EdiSol system described in detail by Moncrieff et al. (1997). Fluxes of sensible heat, water vapour,  $\text{CO}_2$  and friction velocity (u-star) were calculated for 30 min periods using the EdiSol software (Moncrieff et al. 1997). The IRGA was calibrated every week by addition of  $\text{CO}_2$ , at a certified concentration of  $413 \mu\text{mol mol}^{-1}$  (BOC gases), to the main sample stream ( $6 \text{ l min}^{-1}$ ). A second IRGA (model EGM 3, PP systems) was used to sequentially measure the concentration of  $\text{CO}_2$  at six different levels in the canopy (0.5, 1, 2.8, 4.5, 6.2 and 10 m above the forest floor). The concentration change for storage of  $\text{CO}_2$  within the canopy profile was calculated every 30 min and added to the eddy flux observations to calculate -NEE (Wofsy et al. 1993).

An automatic weather station (Campbell Scientific Ltd, Shepshed, England) recorded additional meteorological data, including air temperature, relative humidity, wind speed and direction, net radiation, incident irradiance ( $I_0$ ), air temperature within the canopy at 0.5, 1, 2.8, 4.5, 6.2 and 10 m, air pressure, soil-heat flux, soil moisture, soil temperature and rainfall.

Footprint analysis, based on the model of Kormann and Meixner (2000), was used to identify the representative area of the stand with the greatest influence on a 30-min flux measurement. Half-hourly flux measurements were discarded when an area outside the target area accounted for more than 10% of the measured flux.

### Evaluation of errors associated with eddy covariance assessments of annual -NEE

The sources of error associated with annual estimates of  $\text{CO}_2$  exchange were divided into three categories (Goulden et al. 1996). First, uniform systematic errors caused by calibration errors of the IRGA were minimised by routinely calibrating the instrument. A standard error of estimate (% SEE) from the regression

based on the long-term energy balance (net radiation versus all other energy fluxes and stores, see Goulden et al. 1996) was used to determine the measurement error of the eddy covariance system. While the energy balance is used to directly assess errors associated with latent and sensible heat-flux estimates, this error can also be used to assess CO<sub>2</sub>-flux measurement errors (Goulden et al. 1996). This uncertainty analysis was based on the assumption that the characteristics of the co-spectra of vertical wind speed ( $w'$ ) and CO<sub>2</sub>'; and  $w'$  and air temperature ( $T'$ ) and  $w'$  and H<sub>2</sub>O' are similar under turbulent transport conditions (see Goulden et al. 1996). We assumed that data measured under non-turbulent conditions has been removed by low friction velocity ( $u$ -star) filtering. Surface energy budgets included half-hourly flux measurements of latent, sensible and soil-heat fluxes. Above-ground energy storage was calculated as a function of the rate of change in air temperature of a profile within the canopy and potential energy in the covalent bond of CO<sub>2</sub>, which is lost by the ecosystem during respiration and gained during C fixation (Goulden et al. 1996).

Second, microclimate-dependent systematic errors occur when atmospheric conditions influence the eddy covariance measurements, such as during periods with low  $u$ -star. Typically, these conditions occur at night resulting in an underestimation of nocturnal respiratory fluxes and a significant overestimation of long-term -NEE (Aubinet et al. 2002; Curtis et al. 2002). Night-time flux data were discarded when  $u$ -star was  $\leq 0.13 \text{ m s}^{-1}$ . The  $u$ -star threshold was based on an analysis of ecosystem respiration. A respiration rate at 10°C ( $R_{10}$ ) was calculated, using the respiration–temperature response function of Lloyd and Taylor (1994), for a range of  $u$ -star bins over the range 0–2.5  $\text{m s}^{-1}$ . For this analysis, the coefficient,  $E_0$  for respiration was kept constant (306 K) for the least squares non-linear optimisation of the respiration–air temperature response model. A  $u$ -star bin width of 0.1  $\text{m s}^{-1}$  was used with a minimum bin size of  $n=20$ . The threshold value selected was the mean  $u$ -star of the bin when  $R_{10}$  was stable and  $r^2$  for the observed and predicted -NEE values were  $>0.5$  ( $P < 0.05$ ).

Finally, sampling uncertainty errors were assessed. These are primarily caused by randomly distributed gaps in the data stream when estimating long-term -NEE. These gaps occur during unsuitable atmospheric conditions or because of instrument failure. These errors were determined as the standard error of the gap-filling models. For data gaps of less than 3 days, the mean diurnal variation (MDV) method was used to fill the gaps (Falge et al. 2001). For longer data gaps, due to instrument failure, semi-empirical models were used to generate missing data (Falge et al. 2001). Ecosystem night-time respiration ( $R_n$ ) was estimated using a temperature-dependent function based on night-time fluxes (Lloyd and Taylor 1994; Falge et al. 2001).

$$R_n = R_{10} e^{E_0[(1/(283.15-T_0)) - (1/(T-T_0))]} \quad (5)$$

where  $R_{10}$  is the respiration rate at 10°C,  $E_0$  is a derived coefficient for ecosystem respiration,  $T$  is the air temperature (K) at 13 m and  $T_0$  is a best-fit temperature value. Daytime respiration ( $R_d$ ) was calculated in a similar manner, but based on the corresponding daytime air temperatures. For filling long-term daytime-NEE data gaps, the non-linear regression relationship based on the response of -NEE to temperature and  $I_0$  (Falge et al. 2001) were used. The temperature dependence of GPP at an optimum irradiance ( $\text{GPP}_{\text{opt}}$ ) was determined using air temperature, and the energy of activation and deactivation, according to the equations described by Harley and Tenhunen (1991) and Falge et al. (2001). Separate values for  $\text{GPP}_{\text{opt}}$  and quantum (photon) yield ( $\phi_i$ ), based on  $I_0$ , were calculated for 3 K temperature classes. A light response equation was then used to describe ecosystem response to irradiance based on  $I_0$ ,  $\phi_i$ ,  $\text{GPP}_{\text{opt}}$  and  $R_d$ .

$$-\text{NEE} = [(\phi_i \times I_0 \times \text{GPP}_{\text{opt}}) / (\text{sqrt}((\text{GPP}_{\text{opt}})^2 + (\phi_i \times I_0)^2))] - R_d \quad (6)$$

Error assessments of the gap-filling procedures were based on a similar analysis to that of Falge et al. (2001), where artificial data sets were created with 10, 25, 35 and 45% of the missing data. The performance of the two models was assessed against a blind data set (data not included in the modelling data set). The unsigned SEE was used to estimate the model uncertainty associated with a gap-filled CO<sub>2</sub> flux (Falge et al. 2001).

## Inventory methods

### Annual surveys

The estimation of the change in living biomass ( $\Delta B$ ) was based on the relationships between tree biomass, stem diameter at 1.3 m (d.b.h., cm) and height (h, m), using an annual survey conducted in four 100 m<sup>2</sup> plots in the vicinity of the flux tower. Band dendrometers were installed to measure annual changes in the circumference of all of the trees in the sample plots. Tree height was estimated to the closest centimetre, in February of 2002, 2003 and 2004, using a laser hypsometer (Laser Technology Inc., Colorado, USA).

### Development of biomass models and estimation of NPP

Total biomass and its components (roots, stems, branches) were determined from harvested trees selected from five sites across a Sitka spruce chronosequence (9–45 years old). Stands represented the typical yield class (18–20 m<sup>3</sup> ha<sup>-1</sup> year<sup>-1</sup>) for Sitka spruce grown on wet mineral soils in Ireland. A total of six trees from the 14-year-old flux site, with a projected

yield class of  $24 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ , were also harvested. All biomass components were oven dried at  $70^\circ\text{C}$  and weighed after 3 days when the dry mass was constant (see Black et al. 2004). Carbon contents of the dried biomass, litter and soil samples were measured using a C–N analyser (Leco CSN-1000, Leco Corp., St. Joseph, MI, USA).

Biomass, d.b.h. and tree height data were used to derive total living and dead above-ground and below-ground biomass (phytomass and necromass, Eq. 7) and total phytomass functions (Eq. 8) for individual trees across the entire chronosequence.

$$\begin{aligned} &\text{Total dead and living biomass} \\ &= 0.1403 (\text{d.b.h.} \times h)^{1.23} \quad (r^2 = 0.97). \end{aligned} \quad (7)$$

$$\begin{aligned} &\text{Total living biomass} \\ &= 0.2667 (\text{d.b.h.} \times h)^{1.13} \quad (r^2 = 0.98). \end{aligned} \quad (8)$$

The change in living biomass ( $\Delta B$ ) was based on the relationship between d.b.h., height and total living biomass only (i.e. phytomass, Eq. 8), to account for potential changes in standing dead biomass ( $\Delta \text{AGD}$ ) over time. The total and living biomass models were validated against an independent Sitka spruce data set (Black et al. 2004) to assess the model error associated with the estimation of stand biomass. The % SEE of the regression line (measured versus predicted) was used to estimate the uncertainty range associated with the biomass estimates (Black et al. 2004; see Table 2).

Above-ground litterfall ( $D_a$ ) was collected every month over the 2-year period from ten 25-l plastic buckets, randomly located within one  $30 \text{ m} \times 30 \text{ m}$  plot. Litter was separated into green leaf, dead leaf, bud scale and woody components prior to oven drying to a constant mass. The green leaf and bud-scale components of litterfall ( $D_a$ ) were used in the NPP estimates (see Eq. 3).

Below-ground detritus production ( $D_b$ ) was determined as the product of fine-root biomass and the annual fine-root turn-over ratio. Annual fine-root biomass increment ( $< 5 \text{ mm}$ ) was estimated using the in-growth core technique (Janssens et al. 2002) for the 2003/2004 season only. A soil corer (8 cm inner diameter) was used to remove intact litter and soil columns up to a depth of 20 cm. A total of 17 in-growth samples were retrieved after 12 months. Roots were removed from cores and sorted into live and dead fractions (Janssens et al. 2002). Fine-root turn-over was determined as the ratio of the amount of fine-root production for 1 year over the total living fine-root biomass ( $< 5 \text{ mm}$ ), determined from soil cores.

The change in annual soil and associated litter C ( $\Delta C_{\text{soil}}$ ) content was estimated as the mean difference in soil-C content of the un-forested grassland (time zero) and 15-year-old (flux tower site) sites in the selected chronosequence. A total of 15 soil cores (10 cm diameter with a penetration depth of 30 cm) were collected over an area of  $900 \text{ m}^2$  during the 2003/2004 season for C and N analysis using the C–N analyser.

## Heterotrophic respiration models

All respiration measurements were conducted using a CIRAS 1 IRGA with a soil-respiration chamber (SRC1, PPsystems, Hitchin, Herts, UK). Estimates of heterotrophic respiration associated with AGD ( $R_{\text{h (AGD)}}$ ) were based on direct measurements on dead branches and needles and expressed on a mass basis. Attached dead branch and needle material was sampled from the site and placed in 10-cm diameter plastic tubes, which were sealed at one end, and incubated at 0, 3, 7, 10, 15, 20 and  $30^\circ\text{C}$  for 24 h before the respiration measurements were taken. A non-linear relationship between  $R_{\text{h (AGD)}}$  and temperature (Eq. 5) was used to calculate annual heterotrophic respiration, based on the air temperature 2 m above the forest floor and the total standing dead-branch biomass (Eqs. 7, 8). For this relationship ( $r^2 = 0.45$ ,  $P < 0.05$ ,  $n = 95$ ),  $R_{\text{h } 10 \text{ (AGD)}}$  is  $14.5 \text{ g C t}^{-1} \text{ h}^{-1}$ ,  $E_0$  is a coefficient for  $R_{\text{h (AGD)}}$  (1,218 K) and  $T_0$  is 168 K.

Soil respiration was measured on site under a variety of soil-temperature and -moisture conditions. The heterotrophic component of total respiration was assessed by making measurements on soils where stainless steel collars (16 cm diameter) had been inserted into the forest floor to a depth of 30 cm to exclude living roots. Respiration measurement were not taken until 4–6 weeks, after the collars had been inserted into the soil, to minimise the effects associated with root decomposition and disturbance. A modified model after Hanson et al. (1993) and Lloyd and Taylor (1994), based on site and laboratory respiration measurements, was used to estimate annual  $R_{\text{h (soil)}}$  as a function of soil temperature and soil-moisture content ( $M$ ,  $\text{m}^3 \text{ m}^{-3}$ ) at a depth from 0 to 10 cm.

$$\begin{aligned} R_{\text{h (soil)}} &= (R_{\text{h } 10 \text{ (soil)}} e^{E_0[(1/(283.15-T_0)) - (1/(T_s-T_0))]} \\ &\quad \times \left( \frac{M_{\text{opt}}}{M_{\text{opt}} - M} \right), \end{aligned} \quad (9)$$

$$r^2 = 0.61, P < 0.05, n = 636.$$

$R_{\text{h } 10 \text{ (soil)}}$  ( $0.89 \text{ CO}_2 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) is the respiration rate at  $10^\circ\text{C}$ ,  $E_0$  is the coefficient for  $R_{\text{h (soil)}}$  (316 K),  $T_s$  is the soil temperature at 10 cm in K and  $T_0$  is a best-fit value between 0 K and K at which respiration is 0 ( $230 \pm 19 \text{ K}$ ),  $M_{\text{opt}}$  is the soil-moisture content at which  $R_{\text{h } 10 \text{ (soil)}}$  was the highest and  $M$  is the soil-moisture content at the site. Independent sets of  $R_{\text{h (soil)}}$  measurements were made at the site to validate the soil model.

Total soil respiration was also measured, using an automated open-top chamber system based on the design of Fang and Moncrieff (1998), with a parallel four-way solenoid control system and data logger (Goulden and Crill 1997), in order to estimate the relative contribution of the heterotrophic fraction to total soil respiration. Continuous chamber respiration measurements were taken every half-an-hour for 120 days to assess the sampling resolution of the soil respiration model.



## Uncertainty analysis for inventory estimates

We examined potential uncertainties associated with the sampling, model and measurement errors of the inventory procedures. Sampling errors, in this case, represent the variability in the estimate due to measuring a subset of the population. Model errors, such as the allometric functions or respiration models, were estimated using % SEE from regression analysis of observed and predicted values (see Table 2). The only measurement errors assessed were the tolerances for d.b.h., using dendrometers (1 mm), and height (0.05 m). The total standard error for the inventory methods ( $\sigma_{\text{NEP}_{\text{eco}}}$  or  $\sigma_{\text{NEP}_{\Delta C}}$ ) were estimated as:

$$\sigma^2_{\text{NEP}_{\text{eco}}} = \sigma^2_{\Delta B} + \sigma^2_{D_a} + \sigma^2_{D_b} + \sigma^2_{R_h(\text{AGD})}, \quad (10)$$

or

$$\sigma^2_{\text{NEP}_{\Delta C}} = \sigma^2_{\Delta C_b} + \sigma^2_{C_{\text{dead}}} + \sigma^2_{C_{\text{soil}}}. \quad (11)$$

## Results

### Eddy covariance estimates

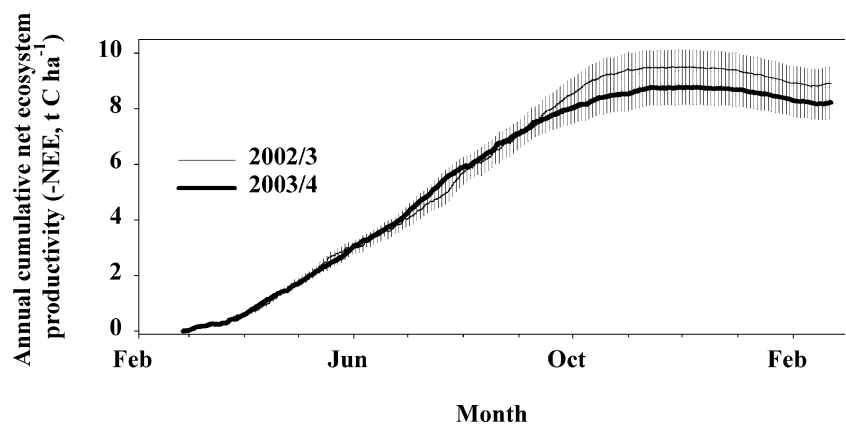
The site provided a fetch of 590 m in the SW direction and 1,420 m in the S direction, which were the dominant wind directions over the 2002–2004 measurement period. The fetch was 250 m in the N and 189 m in the E direction, but these wind directions were less frequent. Based on the footprint analysis, a total of 1.2% of all the half-hourly data was discarded when more than 10% of the measured flux came from outside the experimental site area. A total of 10% of the half-hourly flux data for 2002/2003 was discarded due to unsuitable atmospheric conditions with another 16% of the data missing due to instrument and/or power failure. In 2003/2004, slightly less data was discarded (8.5%), but there was more missing data (21%), primarily due to an 18-day gap caused by instrumentation failure.

Artificial gaps in the remaining, measured, data set were created to evaluate the performance of the MDV

and non-linear regression gap-filling procedures. The mean percentage absolute error for the combined gap-filled data over the 2-year period was 9.8%. The annual absolute error associated with the gap-filling procedures was considerably less because of the low frequency of missing data over the whole period.

The estimation of uncertainty, for the measured flux data, was problematic since these errors are likely to involve numerous sources of uncertainty. In this study, we assessed the error using an energy-balance regression analysis (Goulden et al. 1996). As with most flux studies, there was a general underestimation of latent heat fluxes, due to damping, high frequency fluctuations (see Goulden et al. 1996) and storage of water within the canopy profile (unmeasured). The latent energy flux was increased by 20% to account for this underestimation resulting in a good long-term energy balance closure (Goulden et al. 1996). The removal of unsuitable data, where  $u^*$  was below the selected threshold, significantly improved the energy-balance closure correlation with  $r^2$  increasing from a value of 0.57 to 0.78 and the slope from 0.64 to 0.95. The overall error of uncertainty was calculated for each measured or gap-filled half-hourly flux, using either an absolute gap-filling model SEE, or the SEE of the long-term energy-balance regression, expressed as a percentage. The mean annual errors of the -NEE estimate were 6.4 and 7.1% of the cumulative flux for 2002/2003 and 2003/2004, respectively (Fig. 1). Daily -NEE was positive between March and October for both the 2002/2003 and 2003/2004 seasons. The decline in the cumulative -NEE during the winter months was associated with a net daily loss of C (Fig. 1), primarily due to longer nights and a lower daily insolation (data not shown). While there was a loss of C from the system over the winter months, there was still a significant uptake of C during the day, suggesting that photosynthesis occurred throughout the year. There was no significant difference in the cumulative annual flux for 2002/2003 (8.9 t C ha<sup>-1</sup>) when compared to 2003/2004 (8.3 t C ha<sup>-1</sup>).

**Fig. 1** Seasonal changes in cumulative -NEE (t C ha<sup>-1</sup>) for 2002/2003 and 2003/2004. The error bars represent the cumulative estimate of uncertainty



**Table 1** An intercomparison of inventory ( $NEP_{eco}$ ,  $NEP_{AC}$ ) and eddy covariance-based estimates (-NEE) of net ecosystem productivity in a Sitka spruce forest for 2002/2003 and 2003/2004

Carbon store	Symbol or formula	Mean and range for 95% confidence limits (t C ha <sup>-1</sup> year <sup>-1</sup> )	
		2002/2003	2003/2004
Living biomass increment	$\Delta B$	10.51 (8.91–12.11)	10.30 (8.1–12.5)
Dead-branch biomass increment	$\Delta AGD$	1.37 (1.29–1.44)	1.71 (1.62–1.83)
Litterfall, green shoots and bud scales	$D_a$	0.19 (0.17–0.21)	0.22 (0.15–0.29)
Net fine = root production <sup>a</sup>	$D_b$	0.43 (0.35–0.51)	0.43 (0.35–0.51)
Herbivory	$H$	nd	nd
Volatile organic compound emissions	VOC	nd	nd
NPP	$\Delta B + D_a + D_b + H + VOC + \Delta AGD$	12.49 (10.89–14.10)	12.65 (10.37–14.92)
Heterotrophic soil respiration	$R_{h(soil)}$	2.85 (2.55–3.14)	3.18 (2.56–3.80)
Heterotrophic wood-debris respiration	$R_{h(AGD)}$	0.09 (0.08–0.10)	0.09 (0.08–0.11)
Herbivore respiration	$R_{h(consumer)}$	nd	nd
Total heterotrophic respiration <sup>b</sup>	$R_h$	2.94 (2.62–3.32)	3.27 (2.65–3.89)
Total living biomass increment	$\Delta C_b = \Delta B$	10.51 (8.91–12.11)	
Dead-branch increment	$\Delta C_{dead} = \Delta AGD$	1.37 (1.29–1.44)	
Soil-C change <sup>c</sup>	$\Delta C_{soil}$	1.15 (0.70)	
Ecological inventory	$NEP_{eco} = NPP - R_h$	9.52 (7.89–11.16)	9.38 (7.30–11.44)
Stock-change inventory <sup>d</sup>	$NEP_{AC} = \Delta C_b + \Delta C_{dead} + \Delta C_{soil}$	13.02 (11.30–14.75)	nd
Eddy covariance	-NEE	8.90 (8.39–9.44)	8.31 (7.69–8.91)
$NEP_{eco}$ to -NEE ratio	$NEP_{eco}/-NEE$	1.07	1.13
$NEP_{AC}$ to -NEE ratio	$NEP_{AC}/-NEE$	1.46	

Values represent a mean and range, based on the SE at 95% confidence interval for individual components and different C sequestration estimates

<sup>a</sup>Fine-root production (total - dead fine roots) was determined for 1 year only (2003/2004)

<sup>b</sup>Heterotrophic estimates were based on validated models

<sup>c</sup>Soil-C stock changes were based on a chronosequence comparison

<sup>d</sup>When fine-root C increment was included in the  $\Delta C_b$  estimate,  $NEP_{AC} = 13.46 (\pm 1.79) \text{ t C ha}^{-1} \text{ year}^{-1}$

## Net primary productivity

Values for contributing components of the  $NEP_{eco}$  inventory method and ranges of the estimates are shown in Table 1. The C content of the different biomass components (0.49 g C g<sup>-1</sup> d.wt) was similar and did not vary by more than  $\pm 0.87\%$  (see Table 2). The mean C content (0.49 g C g<sup>-1</sup> d.wt) and net fine-root production was only estimated for the 2003/2004 season and assumed to be the same for the previous season. No fine roots were detected at a soil depth of > 15 cm. The total living fine-root stock, in terms of C biomass (< 5 mm diameter) in 2003, was  $3.5 \pm 0.084 \text{ t C ha}^{-1}$  and the mean annual living fine-root production was  $0.43 \pm 0.08 \text{ t C ha}^{-1} \text{ year}^{-1}$ . The fine roots isolated from the in-growth cores were less than 2 mm in diameter and the mean fine-root turn-over ratio for this diameter class was  $0.22 \text{ year}^{-1}$ , indicating a mean lifespan of ca. 4.5 years.

Cross-validation of the biomass models with an independent data set indicated that the biomass estimates were robust with a small SEE of < 8%. The error estimates for living and dead biomass increment were based on the combined errors associated with sampling, model predictions and estimates of C content (Tables 1, 2). The largest uncertainties regarding estimates of  $\Delta B$  were associated with model errors (SEE = 8%) and variations in stand density (SE = 4.8%) and tree biomass (SE of 12.0%, Table 2). The uncertainty and absolute cumulative errors associated with the estimation of  $\Delta B$

for 2002/2003 ( $\pm 1.60 \text{ t C ha}^{-1} \text{ year}^{-1}$ ) and 2003/2004 ( $\pm 2.19 \text{ t C ha}^{-1} \text{ year}^{-1}$ ) was larger than any of the other ecosystem-component errors for NPP (Tables 1, 2).

There was no significant difference in the increment of  $\Delta B$  in 2002/2003, compared to 2003/2004 (Table 1). Dead needle and branch C-stores were significantly lower in 2002/2003, compared to the 2003/2004 season, possibly due to the onset of canopy senescence (K. Black et al., unpublished data). This was consistent with an increase in total litterfall from 6.7, in 2002/2003, to  $7.2 \text{ t C ha}^{-1} \text{ year}^{-1}$ , in 2003/2004 (data not shown). AGD ( $D_a$ ) production was ca. 3% of the total litter fall over the 2 years, and was included in NPP as an estimate of above-ground loss of living biomass.

## Heterotrophic respiration

Decomposition of previously fixed C in soils and dead-branch material ( $R_{het}$ ) accounted for a 23–25% loss of the C accumulated in biomass and other pools (NPP). The decomposition of dead woody material, such as dead branches, represented a decay rate of 5–7%, which is consistent with values (10%) reported by Ehman et al. (2002). Decomposition of soil C accounted for most (95%) of the total heterotrophic loss of C from the ecosystem (Table 1). The higher  $R_{h(soil)}$  efflux in 2003/2004, compared to 2002/2003 (Table 1, Fig. 2), was associated with lower soil-moisture contents and higher

**Table 2** Summary of the sources of error and uncertainty for  $NEP_{eco}$  estimates during 2002/2003

Parameter	Source of error	Unit	Mean	Absolute SE	% SE or SEE <sup>a</sup>	% Cumulative error <sup>b</sup>	% Total cumulative error
$\Delta B$	Model	kg tree <sup>-1</sup>	8.272		7.97		
	Carbon content	g g <sup>-1</sup>	0.490	0.004	0.87		
	Tree increment	kg tree <sup>-1</sup> year <sup>-1</sup>	8.771	1.050	12.00		
	Planting density	tree ha <sup>-1</sup>	2445	117	4.81		
		t C ha <sup>-1</sup> year <sup>-1</sup>	10.511	1.599 <sup>c</sup>		15.22	
$\Delta AGD$	Model	kg tree <sup>-1</sup>	1.149		2.54		
	Carbon content	g g <sup>-1</sup>	0.490	0.004	0.87		
	ADW increment	kg tree <sup>-1</sup> year <sup>-1</sup>	1.145	0.011	0.98		
	Planting density	tree ha <sup>-1</sup>	2445	117	4.81		
		t C ha <sup>-1</sup> year <sup>-1</sup>	1.371	0.0767 <sup>c</sup>		5.60	
$D_a$	Carbon content	g g <sup>-1</sup>	0.480	0.002	0.57		
	Needles per m <sup>2</sup>	kg tree <sup>-1</sup> year <sup>-1</sup>	0.039	0.004	10.31		
$D_b$		t C ha <sup>-1</sup> year <sup>-1</sup>	0.191	0.019 <sup>c</sup>		10.46	
	Carbon content	g g <sup>-1</sup>	0.485	0.003	0.73		
$R_{het}$	Roots per m <sup>2</sup>	kg tree <sup>-1</sup> year <sup>-1</sup>	0.089	0.017	18.56		
		t C ha <sup>-1</sup> year <sup>-1</sup>	0.432	0.080 <sup>c</sup>		18.57	
$NPP = \Delta B + \Delta AGD + D_a + D_b$		t C ha <sup>-1</sup> year <sup>-1</sup>	12.494	1.602 <sup>d</sup>			12.83
$R_{het (soil)}$	Model	t C ha <sup>-1</sup> year <sup>-1</sup>	2.855	0.294	10.30		
$R_{het AGD}$	Model	t C ha <sup>-1</sup> year <sup>-1</sup>	0.094	0.005	5.12		
	AGD	t C ha <sup>-1</sup> year <sup>-1</sup>	4.650	0.099	2.15		
$R_{het NEP_{eco}} = NPP - R_{het}$		t C ha <sup>-1</sup> year <sup>-1</sup>	2.973	0.347 <sup>c</sup>		11.7	
		t C ha <sup>-1</sup> year <sup>-1</sup>	9.52	1.630 <sup>d</sup>			16.39

<sup>a</sup>The standard error (SE) was used for measured data and the standard error of estimate (SEE) for the modelled data

<sup>b</sup>The cumulative error was determined using squared the sum of the % SE or SEE, where % cumulative error =  $\sqrt{n_1^2 + n_2^2 + \dots + n_v^2}$

<sup>c</sup>The absolute cumulative SE for each parameter = mean  $\times$  (% cumulative error/100)

<sup>d</sup>The cumulative error for NPP,  $R_{het}$  and  $NEP_{eco}$  was determined directly from the squared sum of the SE of component parameters

soil temperatures, particularly from August to October 2003 (Fig. 2).

A comparison between continuous total soil-respiration data and an  $R_{h (soil)}$ -model estimates suggested that the heterotrophic component accounted for  $41 \pm 26\%$  of the total respiratory efflux during June and July (Fig. 3). Hanson et al. (2000) showed that  $R_{h (soil)}$  flux represented 50% of the total soil-CO<sub>2</sub> efflux from an oak forest. Although there was generally a good agreement between the predicted and observed  $R_{h (soil)}$  rates in 2003/2004 (Fig. 2c), the soil-respiration model only accounted for 61% of the observed variation in measured values. Comparisons of the  $R_{h (soil)}$ -model estimates with the automated soil-respiration measurements also suggested that the temporal resolution of the  $R_{h (soil)}$  model could be improved by accounting for the influence of rainfall events (Fig. 3a, b). This is manifested by the large fluctuations in measured soil-respiration rates during and after major rainfall events, which was not evident from the predicted  $R_{h (soil)}$  data (Fig. 3a, b).

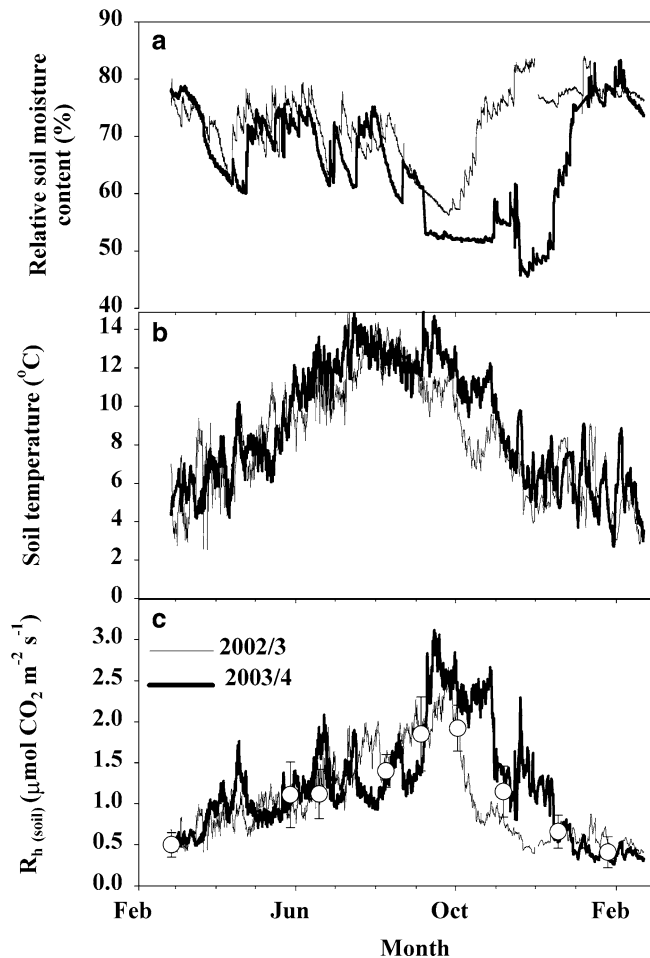
#### Mass-balance inventory estimates ( $NEP_{AC}$ )

The total C-stock changes ( $NEP_{AC}$ ) were estimated for 2002/2003 because soils samples were only taken in June 2002. The total living biomass increment, or  $\Delta C_b$  in this case, was calculated as the sum of above-ground, coarse

root and stump biomass increment ( $\Delta B$ , Table 1). Uncertainty and errors associated with the estimation of  $\Delta C_b$  were larger than other stock-change estimates because of the larger coefficients of variance for  $\Delta B$ . The fine-root C increment was initially excluded from this assessment so that comparisons could be made with other reported  $NEP_{AC}$  estimates (Fig. 4a, b). However, this pool ( $D_b$ ) was included in the  $\Delta C_b$  pool since  $D_b$  was not zero (see Curtis et al. 2002) and can account for 3–33% of NPP (Table 1, Janssens et al. 2002). The change in dead-wood biomass C stock only included the increment in dead branches and needles, which were attached to the tree ( $\Delta AGD$ ). There was no significant dead-wood biomass on the forest floor in this afforested stand. Soil-C storage was estimated to be  $1.15 \text{ t C ha}^{-1} \text{ year}^{-1}$ , but we were only able to provide a sampling error estimate and no values for errors associated with the chronosequence approach or historical disturbance events were available. The range of the estimated values for soil-C stock change was  $0.45\text{--}1.85 \text{ t C ha}^{-1} \text{ year}^{-1}$ .

#### Intercomparison of different NEP estimates

Based on eddy covariance measurements (-NEE), the uptake of C by the forest was  $8.9$  and  $8.3 \text{ t C ha}^{-1} \text{ year}^{-1}$  for 2002/2003 and 2003/2004, respectively. The extent of any difference between eddy covariance- and inventory-based assessments of NEP varied depending on the type



**Fig. 2** Seasonal variations in relative soil-moisture content at 0–10 cm (a), soil temperature at 10 cm (b) and, predicted and observed heterotrophic respiration rates from the soil ( $R_{h(\text{soil})}$ , c) for 2002/2003 and 2003/2004. The white circular symbols and error bars represent the mean measured  $R_{h(\text{soil})}$  rates and standard deviation ( $n = 15$ ) for 2003/2004

of inventory procedure used. Although the inventory-based  $\text{NEP}_{\text{eco}}$  estimates were 7 and 13% higher than the cumulative -NEE, this was not significant due to the large cumulative errors associated with biometric, ecophysiological and modelled estimates. However, the  $\text{NEP}_{\Delta C}$  estimate was significantly higher (ca. 40%), when compared to the  $\text{NEP}_{\text{eco}}$  and -NEE measures (Table 1). When the fine-root C increment was included in the  $\Delta C_b$  estimate ( $\Delta B + D_b$ ), the difference between  $\text{NEP}_{\Delta C}$  and the other NEP assessment was even larger (41–51%, Table 1).

## Discussion

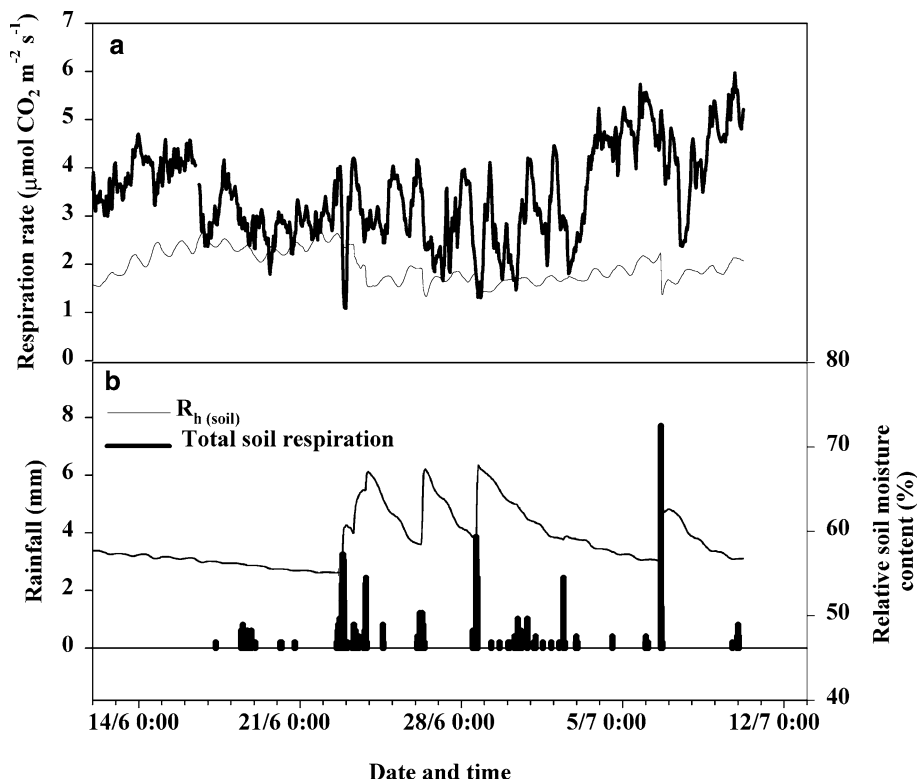
A comparison of inventory-based approaches with eddy covariance (-NEE) assessments of NEP, from this and other studies (Kolari et al. 2004; Curtis et al. 2002; Ehman et al. 2002), shows that there may be discrepancies between the different estimates of NEP (Fig. 4). While

there is often a good agreement between the  $\text{NEP}_{\text{eco}}$  and  $\text{NEP}_{\Delta C}$  estimates (Fig. 4a, Curtis et al. 2002), inclusion of annual fine-root C increment in the  $\text{NEP}_{\Delta C}$  assessment, results in a systematic overestimation of annual C storage, when compared to  $\text{NEP}_{\text{eco}}$  and -NEE estimates (Fig. 4a, b). Clearly, the fine-root C increment represents a significant C-stock change, which cannot be excluded from living  $\text{NEP}_{\Delta C}$  assessments. Curtis et al. (2002) report annual fine-root increments ranging from 1.4 to 4.9 t C ha<sup>-1</sup> year<sup>-1</sup>, but excluded this C pool from their  $\Delta C_b$  estimate. The  $\text{NEP}_{\Delta C}$  values reported by Kolari et al. (2004) did not include fine root or  $\Delta C_{\text{soil}}$  estimates. Based on soil-C stock data, from the 0-, 12- and 75-year-old stands reported by Kolari et al. (2004), we estimated the integrated annual  $\Delta C_{\text{soil}}$  to be 0, -0.61 and -0.35 t C ha<sup>-1</sup> year<sup>-1</sup>, respectively (sites 8a, b, c; Fig. 4b). We suggest that the overestimation of NEP, based on the  $\text{NEP}_{\Delta C}$  method, is associated with unaccounted soil decomposition losses (Kolari et al. 2004). Alternatives to the chronosequence approach, such as the application of soil carbon balance models, may provide a better insight in to how soil C stocks may changes over time.

The magnitude and the sign of the difference between NEP and -NEE-based assessments also varied depending on the type, age and topography of forest stands (Fig. 4a, b). For example, there were no clear trends in the differences between inventory and eddy covariance measures of NEP in coniferous stands in northern Europe (sites 8a, b, c, Fig. 4b) including the site in Ireland (sites 6a, b). Data from second rotation Norway spruce stands in Finland suggested that there was a systematic overestimation of  $\Delta C$  in the young stand (4-year-old, site 8a) and an underestimation of  $\Delta C$  in older (12–75-year-old, sites 8b, c) stands (Fig. 4b, Kolari et al. 2004). However, these inventory-based estimates did not include changes in fine-root biomass (see Kolari et al. 2004), which could increase with stand age. Analyses of AMERIFLUX data also showed that there were discrepancies between different NEP estimates, but these differences showed no clear trends (Curtis et al. 2002). For example,  $\text{NEP}_{\text{eco}}$  estimates were 50% higher than -NEE estimates from an 80-year-old mixed deciduous forest in Indiana (site 2, Fig. 4). Conversely, inventory estimates were 56% lower than -NEE measurements from a 50–120-year-old oak-dominated forest, located on a topography represented by ridges and valleys in southern Tennessee (site 1, Fig. 4, Curtis et al. 2002). The larger eddy covariance estimate in site 1 (Fig. 4a) is possibly due to the fact that there was no correction for low u-star and advection due to unsuitable atmospheric conditions and sloping topography, resulting in an overestimation of long-term -NEE fluxes (Aubinet et al. 2002; Curtis et al. 2002). A possible reason for the larger discrepancies between inventory and eddy covariance-based measures in natural mixed deciduous forests may include the introduction of larger biomass modelling errors due to the use of generalised allometric functions for broadleaf trees (Ehman et al. 2002).



**Fig. 3** A comparison between predicted soil heterotrophic respiration ( $R_{h(\text{soil})}$ ) and measured total soil-respiration rates (a), and changes in relative soil-moisture content (line plot) and rainfall (histograms) during June and July (b)

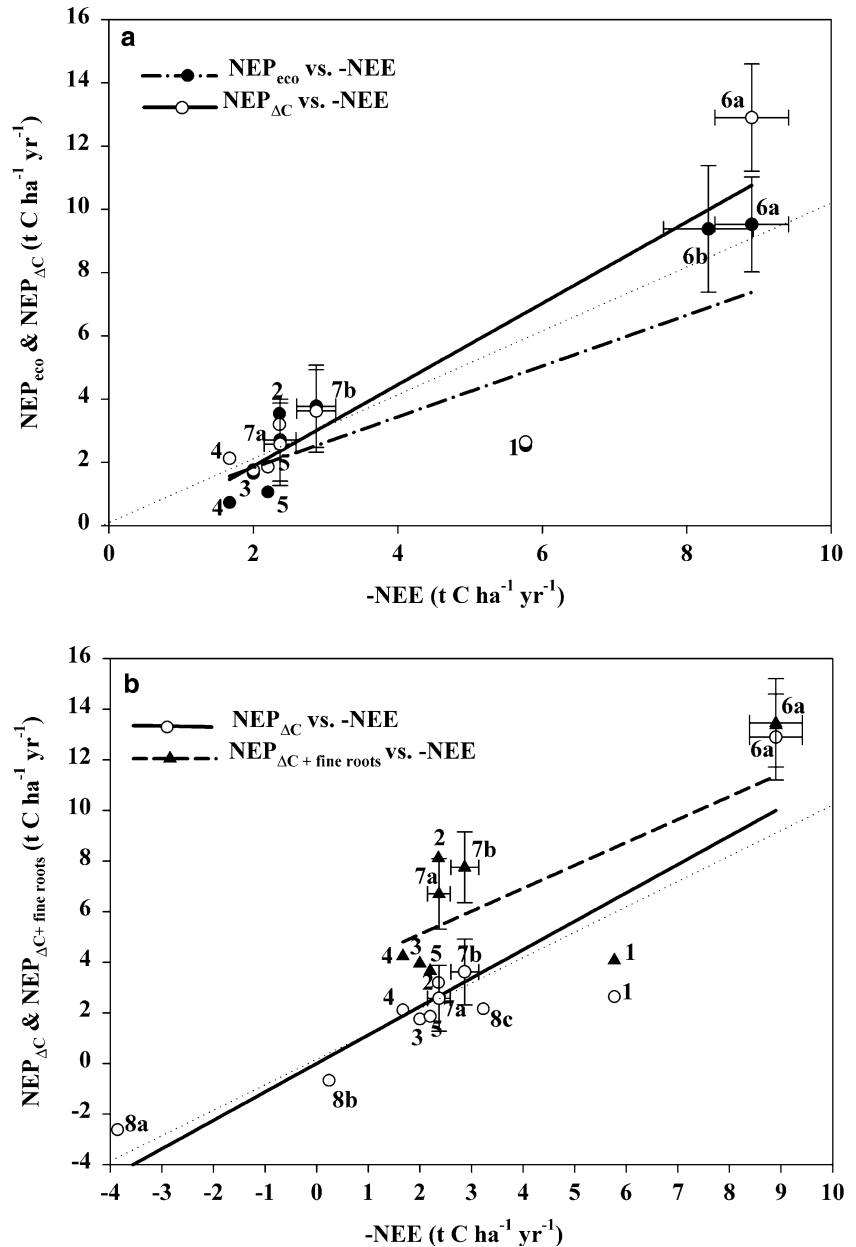


It was evident from this analysis that the  $\text{NEP}_{\text{eco}}$  inventory method did not exclude any major C fluxes and that there were no systematic differences between  $\text{NEP}_{\text{eco}}$  and  $-\text{NEE}$  estimates across the sites investigated (Fig. 4a). We suggest that the  $\text{NEP}_{\text{eco}}$  method produces a more representative estimate of NEP than  $\text{NEP}_{AC}$ , but could be difficult to apply using conventional inventory data without a better understanding of below-ground C processes, particularly fine-root production or heterotrophic respiration. Difficulties in assessing heterotrophic respiration are related to the problems associated with both the measurement and modelling methodologies. The use of solid-root exclusion pipes, as in this study, may lead to errors in estimating heterotrophic respiration, including unaccounted losses due to the metabolism of root exudates, the input of dead fine-root material and mycorrhizal respiration. While the proportion of heterotrophic to total soil respiration (Figs. 2, 3) appears to be consistent with previous reports (Hanson et al. 2000) and our heterotrophic soil-model estimates appear to be as robust as those reported by Ehman et al. (2002) and Curtis et al. (2002), there is a need to develop mechanistic process-based models. Based on the observation that soil-temperature and moisture only accounted for 61% of the observed variation in  $R_{\text{het}(\text{soil})}$  in the current study, empirical models may fail to fully capture the temporal variability in respiration. In addition, the sharp decrease in soil-C efflux during and after rainfall events (Fig. 3) highlights the importance of accounting for transport processes through the soil profile, such as the diffusion of  $\text{CO}_2$  out

of, and  $\text{O}_2$  into, the soil column (Fang and Moncrieff 1999; Moncrieff and Fang 1999). Difficulties in assessing annual fine-root production are illustrated by the large range of reported values in this and other studies (see Janssens et al. 2002; Curtis et al. 2002). While our reported annual fine-root increment values are considerably lower than those reported by Curtis et al. (2002), they do fall within the lower range of published values ( $0.15\text{--}3.6 \text{ t C ha}^{-1} \text{ year}^{-1}$ ) for temperate coniferous forests (Breymeyer et al. 1996). Regardless of the methodology used, measurements of fine-root production are associated with large errors (see Janssens et al. 2002), which may partially contribute to the wide range reported in the literature. However, fine-root growth and distribution is inherently variable due to numerous factors including soil texture and structure, nutrient status and hydrology (Xu et al. 1997). The lower reported annual fine-root production of Sitka spruce on wet mineral gley soils (Nieuwenhuis et al. 2003; Table 1) may be associated with a higher bulk density as well as the effects of anoxia under these conditions (Coutts 1982; Faulkner and Malcolm 1972). The lower production and slower turn-over rates of fine roots in our site is also consistent with the observed reduction in soil respiration at high soil-moisture contents (Fig. 3).

In this study, there was good agreement between eddy covariance and  $\text{NEP}_{\text{eco}}$ -based estimates, however, the small discrepancy between the values could be due to numerous factors including incomplete accounting, scaling up errors and inherent systematic errors. Our eddy covariance estimates are higher than previously

**Fig. 4** Different inventory-based estimates of NEP compared to eddy covariance (-NEE) measures for various forest sites across Europe and the USA. The *solid* and *dashed lines* represent the linear relationships between  $NEP_{eco}$  and -NEE (a),  $NEP_{AC}$  and -NEE (a and b) and  $NEP_{AC} + \text{fine roots}$  and -NEE (b). The *dotted line* represents the 1:1 slope of the relationship. Different numbered symbols represent data from different sites. Sites 1–5 are deciduous forests in the USA (Curtis et al. 2002) Walker Branch, Tennessee (1), Morgan Monroe State Forest, Indiana (2), Harvard Forest, Massachusetts (3), University of Michigan Biological Station, Michigan (4) and Willow Creek, Wisconsin (5). Site 6 is a Sitka spruce forest in Co Laois, Ireland, based on 2002/2003 (6a) and 2003/2004 (6b) data. Site 7 is also for Morgan Monroe State Forest, Indiana (see 2), but based on different estimates for 1998 (7a) and 1999 (7b) reported by Ehman et al. (2002). Sites 8a, b and c are 0- (a), 12- (b) and 75-year-old (c) second rotation Norway Spruce stands in Southern Finland (Kolari et al. 2004). The *error bars* represent SE of -NEE,  $NEP_{eco}$  and  $NEP_{AC}$  means for sites 6 and 7. The errors associated with  $NEP_{eco}$  and  $NEP_{AC}$  for site 7 were determined from the literature, using the same procedure outlined in Table 2



reported -NEE ranges ( $-2$  to  $7.9$  t C ha<sup>-1</sup> year<sup>-1</sup>) for FLUXNET (Baldocchi et al. 2001; Falge et al. 2002) and EUROFLUX (Aubinet et al. 2002; Kolari et al. 2004) conifer forests. This may be associated with the higher productivity of Sitka spruce when grown in wet mineral soils in Ireland (Joyce and O'Carroll 2002), in part due to the continuous uptake of C throughout the year under these mild climatic conditions (Fig. 1). To our knowledge, the current study represents the only assessment performed on an afforested conifer stand, where NEP may be higher than similar-aged second rotation stands due to minimal decay from harvest residues. A possible reason for the slight differences in eddy covariance, compared to  $NEP_{eco}$  estimates, is that not all C fluxes have been accounted for when both methodologies are used. The -NEE

assessment does not include VOC and methane fluxes, or losses due to run-off of dissolved and particulate soil-organic matter. Losses of C, as dissolved organic C, via run-off, may represent between  $0.05$  and  $0.5$  t C ha<sup>-1</sup> year<sup>-1</sup>, depending on the climate, hydrology and forest species (Gödde et al. 1996). Emissions of VOCs, which are not captured using eddy covariance, may also represent a small C loss of  $\sim 0.2$  t C ha<sup>-1</sup> year<sup>-1</sup> (Ciccoilli et al. 2003). In this study,  $NEP_{eco}$ -based measurements could be incomplete due to unaccounted pool changes associated with herbivore activity. A previous study indicated that herbivore activity only accounted for 1% of total NPP (Ehman et al. 2002). It could be argued, however, that herbivore activity in Sitka spruce forests, that are not native to

Ireland, are negligible because of the absence of many natural consumers or pests.

Until now, only Ehman et al. (2002) has attempted to determine the significance of the differences between inventory and eddy covariance-based estimates. Generally, the cumulative standard errors were smaller for eddy covariance (5–10%, Ehman et al. 2002; Goulden et al. 1996), when compared to  $NEP_{eco}$  methods (~20%, Ehman et al. 2002; this study). However, it should be noted that uncertainty estimates for  $CO_2$  flux, based on single eddy covariance tower measurements, and for inventory estimates, based on a limited number of sample plots, may not be directly comparable because they represent different ecosystem components with different replication and different spatial resolutions. Therefore, the mean and variance of annual NEP estimates could be different because they reflect different spatial scales and/or experimental approaches. The question also arises as to whether the different measures are directly comparable because of the different temporal dynamics of top-up and bottom-down methodologies. For example, litter turn-over and heterotrophic respiratory losses may lag behind C inputs, particularly in colder climates (see Curtis et al. 2002), or where high soil-moisture contents may slow down the efflux of  $CO_2$  from soils (Fig. 2). While leaf turn-over and litter inputs can be estimated with relative ease in deciduous forests (Curtis et al. 2002; Ehman et al. 2002), assessments of above-ground litter inputs and living above-ground biomass for conifer species are confounded by the slower turn-over rates of needles (up to 7 years, see Norman and Jarvis 1974) and the longer residence time of dead needles attached to branches. Differences in the temporal dynamics of live biomass accumulation and detritus production in conifer forests may lead to an overestimation of NPP. As far as estimates of uncertainty in the -NEE measurements are concerned, these are problematic, since there are a number of unknown systematic errors from a variety of sources, even after u-star filtering. The combined effect of random errors on the annual sum of -NEE is difficult to assess due to mutual cancellation of errors. Clearly, additional evaluation of the errors associated with these approaches to estimate NEP, should be an important component of future work.

Although there were no significant inter-annual changes in either inventory or eddy covariance-based estimates of NEP (Fig. 1, Table 1), further comparative assessments may provide some insight into how the ecosystem processes may influence net ecosystem exchange. Based on the results from the inventory method, inter-annual differences in NEP may be driven by differences in soil respiration and to a smaller extent by a change in the ratio of dead to living biomass. The lower cumulative NEP, based on -NEE fluxes in 2003/2004, compared to 2002/2003 (Fig. 1), may be associated with an increase in heterotrophic soil respiration, due to lower soil-moisture contents (Fig. 2). In contrast to

other studies on soil respiration (Lee et al. 2004), the efflux of  $CO_2$  from the wet mineral clay soils at our forest site is reduced under high soil-moisture contents, possibly due to a decrease in  $CO_2$  transport and the creation of oxygen-deficient conditions. Ehman et al. (2002) also showed that inter-annual variations in both  $NEP_{eco}$  and -NEE measurements (sites 7a, b, Fig. 4a) were associated with variations in  $R_h$  (soil). Alternative explanations for the decrease in -NEE and  $NEP_{eco}$  at our site in 2003/2004 include an increase in dead-branch biomass (Table 1), lower soil-moisture contents and a higher midday VPD (data not shown), all of which could potentially reduce GPP.

There is generally a good agreement between eddy covariance and  $NEP_{eco}$  inventory-based estimates of annual C storage across forests representing various species, disturbance events and geographical locations (Ehman et al. 2002; Curtis et al. 2002). However, both methodologies are associated with significant uncertainties that, in most cases, have not been quantified. While not specifically identifying the best procedure for estimating the C- stock changes, this study provides insights into the advantages and uncertainties of both approaches and how different components may influence C storage at the ecosystem level.

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