Biometric and eddy-covariance based estimates of carbon fluxes in an age-sequence of temperate pine forests

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ABSTRACT

We present four years (2005–2008) of biometric (B) and eddy-covariance (EC) measurements of carbon (C) fluxes to constrain estimates of gross primary production (GPP), net primary production (NPP), ecosystem respiration (RE) and net ecosystem production (NEP) in an age-sequence (6-, 19-, 34-, and 69-years-old in 2008) of pine forests in southern Ontario, Canada. The contribution of individual NPP and respiration component fluxes varied considerably across the age-sequence, introducing different levels of uncertainty. Biometric and EC-based estimates both suggested that annual NPP, GPP, RE, and NEP were greatest at the 19-year-old site. Four-year mean values of NEP(B) and NEP(EC) were similar at the 6-year-old seedling (77 and 66 g C m⁻² y⁻¹) and the 69-year-old mature site (135 and 124 g C m⁻² y⁻¹), but differed considerably at the 19-year-old (439 and 736 g C m⁻² y⁻¹) and the 34-year-old sites (170 and 392 g C m⁻² y⁻¹). Both methods suggested similar patterns for inter-annual variability in GPP and NEP. Multi-year convergence of NEP(B) and NEP(EC) was not observed over the study period. Ecosystem C use efficiency was correlated to both forest NEP(EC) and NPP(B) suggesting that high productive forests (e.g. middle-age stands) were more efficient in sequestering C compared to low productive forests (e.g. seedling and mature stands). Similarly, negative and positive relationships of forest productivity with the total belowground C flux (TBCF) to GPP ratio and with the ratio of autotrophic to heterotrophic respiration (RA:RH), respectively, determined inter-annual and inter-site differences in C allocation. Integrating NEP across the age-sequence resulted in a total net C sequestration of 137 and 229 t C ha⁻¹ over the initial 70 years as estimated by the biometric and EC method, respectively. Total ecosystem C sequestered in biomass at the 69-year-old site suggested an accumulation of 160 t C ha⁻¹. These three estimates resulted in a mean C sequestration of 175 ± 48 t C ha⁻¹. This study demonstrates that comparing estimates from independent methods is imperative to constrain C budgets and C dynamics in forest ecosystems.

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1. Introduction

Forest ecosystems exchange large amounts of carbon dioxide (CO₂) with the atmosphere through photosynthetic uptake and respiratory losses (Dixon et al., 1994). The net balance between these two opposing fluxes determines the amount of carbon (C) that forest ecosystems sequester or lose within a certain time frame (Dixon et al., 1994; Gower, 2003). Generally, undisturbed forest ecosystems and afforested stands on formerly uncultivated or marginal agricultural land are a significant sink of atmospheric CO₂ (Goodale et al., 2002; Niu and Duiker, 2006). The quantification of forest ecosystem C exchange and productivity rates is therefore of major interest not only to forest industries but also to government policy makers with respect to environmental concerns about the rising concentrations of atmospheric CO₂.

On ecosystem level, forest net primary production (NPP) may be estimated with biometric measurements of changes in above-and belowground biomass, detritus production, and C losses via herbivory (Clark et al., 2001; Jenkins et al., 2001; Curtis et al., 2002). Carbon fluxes in the form of dissolved organic carbon (DOC) and volatile organic compounds (VOC) may be additional components of NPP but are usually ignored due to their small contribution to annual C balances (Curtis et al., 2002; Black et al., 2005). Based on biometric measurements, net ecosystem production (NEP) may further be derived by subtracting C losses via heterotrophic respiration (RH) from NPP. The sum of autotrophic respiration (RA) estimates and NPP results in estimates of gross primary production (GPP), while the sum of RA and RH represents ecosystem respiration (RE). Alternatively, stand level estimates of C exchanges may also be assessed by micrometeorological methods. As such, the eddy-covariance (EC) method has emerged as one of the most reliable measurement technique and essential tool in quantifying NEP in terrestrial ecosystems (Baldocchi, 2003; Luyssaert et al., 2007).
Nomenclature

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
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<tbody>
<tr>
<td>$B_T$</td>
<td>Aboveground tree biomass (foliage + living branches + stem) (gC m$^{-2}$)</td>
</tr>
<tr>
<td>$D_B$</td>
<td>Mass of dead branches attached to tree stem (gC m$^{-2}$)</td>
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<tr>
<td>$D_S$</td>
<td>Mass of dead standing tree stems (snags) (gC m$^{-2}$)</td>
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<tr>
<td>$G$</td>
<td>Ground vegetation biomass (height &lt;1.3m) (gC m$^{-2}$)</td>
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<tr>
<td>$H$</td>
<td>Herbivory loss (gC m$^{-2}$ y$^{-1}$)</td>
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<tr>
<td>$h$</td>
<td>Tree height (m)</td>
</tr>
<tr>
<td>$I_F$</td>
<td>Litterfall (&lt;1 cm) (gC m$^{-2}$ y$^{-1}$)</td>
</tr>
<tr>
<td>$I_B$</td>
<td>Branchfall (≥1 cm) (gC m$^{-2}$ y$^{-1}$)</td>
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<tr>
<td>$S$</td>
<td>Stem density (trees ha$^{-1}$)</td>
</tr>
<tr>
<td>$U$</td>
<td>Understorey biomass (DBH &lt;9 cm, height ≥1.3 m) (gC m$^{-2}$)</td>
</tr>
<tr>
<td>$V$</td>
<td>Stem volume (m$^3$)</td>
</tr>
<tr>
<td>BEF</td>
<td>Biomass expansion factor (t m$^{-2}$)</td>
</tr>
<tr>
<td>DBH</td>
<td>Diameter at breast height (cm)</td>
</tr>
<tr>
<td>ANPP</td>
<td>Aboveground net primary production (gC m$^{-2}$ y$^{-1}$)</td>
</tr>
<tr>
<td>BNPP</td>
<td>Belowground net primary production (gC m$^{-2}$ y$^{-1}$)</td>
</tr>
<tr>
<td>GPP</td>
<td>Gross primary production (gC m$^{-2}$ y$^{-1}$)</td>
</tr>
<tr>
<td>NEE</td>
<td>Net ecosystem exchange of CO$_2$ (µmol CO$_2$ m$^{-2}$ s$^{-1}$)</td>
</tr>
<tr>
<td>NEP</td>
<td>Net ecosystem production (gC m$^{-2}$ y$^{-1}$)</td>
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<tr>
<td>NPP$_{CR}$</td>
<td>Coarse root production (gC m$^{-2}$ y$^{-1}$)</td>
</tr>
<tr>
<td>NPP$_{FR}$</td>
<td>Net fine root litter production (gC m$^{-2}$ y$^{-1}$)</td>
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<tr>
<td>NPP</td>
<td>Net primary production (gC m$^{-2}$ y$^{-1}$)</td>
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<tr>
<td>$R_S$</td>
<td>Soil respiration (gC m$^{-2}$ y$^{-1}$)</td>
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<tr>
<td>$R_{HF}$</td>
<td>Heterotrophic respiration from forest floor (LFH-layer) (gC m$^{-2}$ y$^{-1}$)</td>
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<tr>
<td>$R_{M}$</td>
<td>Heterotrophic respiration from mineral soil (gC m$^{-2}$ y$^{-1}$)</td>
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<tr>
<td>RA</td>
<td>Autotrophic respiration (gC m$^{-2}$ y$^{-1}$)</td>
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<tr>
<td>RA$_R$</td>
<td>Autotrophic root respiration (gC m$^{-2}$ y$^{-1}$)</td>
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<tr>
<td>RA$_C$</td>
<td>Autotrophic canopy (foliage + living branches + stem) respiration (gC m$^{-2}$ y$^{-1}$)</td>
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<tr>
<td>RE</td>
<td>Ecosystem respiration (gC m$^{-2}$ y$^{-1}$)</td>
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<tr>
<td>RH</td>
<td>Heterotrophic respiration (gC m$^{-2}$ y$^{-1}$)</td>
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<tr>
<td>RH$_S$</td>
<td>Heterotrophic respiration from soil (gC m$^{-2}$ y$^{-1}$)</td>
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<tr>
<td>RH$_{WD}$</td>
<td>Heterotrophic respiration from aboveground woody debris (gC m$^{-2}$ y$^{-1}$)</td>
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<tr>
<td>TBCF</td>
<td>Total belowground carbon flux (gC m$^{-2}$ y$^{-1}$)</td>
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</tbody>
</table>

Subscript

| (B) | Biometric approach, e.g. NEP$_B$ |
| (EC) | Eddy-covariance approach, e.g. NEP$_{EC}$ |

EC-based estimates of NEP can be further partitioned into its component fluxes GPP and RE (Reichstein et al., 2005). Currently, more than 400 flux stations distributed around the world are collecting EC flux data (Baldocchi, 2008). Apart from site level studies, these fluxes are being used in large-scale synthesis and inverse modeling studies (Luysaert et al., 2007; Baldocchi, 2008; Thum et al., 2008). However, because EC measurements are not usually replicated and may have large uncertainties associated with various underlying methodological assumptions used for gap filling of missing data and flux partitioning procedures, cross-validation of EC derived C flux estimates with other methods such as the traditional biometric approach has been recommended (Curtis et al., 2002; Ehman et al., 2002; Baldocchi, 2003; Gough et al., 2008).

Recently, a number of studies have compared NEP derived from biometric measurements and EC data. While the majority of these studies were conducted in deciduous forests (Barford et al., 2001; Curtis et al., 2002; Ehman et al., 2002; Gough et al., 2008; Kominami et al., 2008; Ohtsuka et al., 2009), less information is available for coniferous forests (Law et al., 2001; Black et al., 2005). The reported outcome in these studies also varied with often large discrepancies between biometric and EC estimates on annual scale (Curtis et al., 2002; Ehman et al., 2002; Black et al., 2005). Differences in temporal and spatial scales assessed by each method have been proposed as the primary reasons for these discrepancies (Curtis et al., 2002; Ehman et al., 2002). However, specific limitations associated with each methodology may furthermore hamper such comparison. For instance, the use of inadequate allometric equations and uncertainty in fine root litter production estimates have been suggested to potentially introduce significant error into biometric NPP estimates (Ketterings et al., 2001; Curtis et al., 2002; Black et al., 2005). In contrast, unaccounted C losses due to advective processes and uncertainties associated with the selection of the u-star (u) threshold and gap-filling procedures have been reported to considerably affect the accuracy of EC based C flux estimates (Moffat et al., 2007; Kominami et al., 2008; Keith et al., 2009). Furthermore, a time lag between photosynthetic C uptake and allocation to stem growth was suggested to cause discrepancies between biometric and EC measurements on annual scale (Gough et al., 2008). However, this lag effect may diminish over a longer time period as multi-year comparison studies suggested convergence of NEP estimates (Barford et al., 2001; Gough et al., 2008). In addition, the relative year-to-year changes in NEP have been reported to be comparable between both methods despite differences in absolute numbers (Ehman et al., 2002; Ohtsuka et al., 2005; Keith et al., 2009).

While previous studies have mostly focused on comparing biometric and EC-based NEP estimates, little information is available on the comparison of biometric and EC-based estimates of GPP and RE (Harmon et al., 2004; Keith et al., 2009). The comparison of these two component fluxes may provide further insight to identify the source of discrepancy reflected in biometric- and EC-based NEP estimates.

In this study, we compared biometric and EC-based estimates of all major components of C exchange (i.e. GPP, NPP, RE and NEP) in an age-sequence (6-, 19-, 34-, and 69-years-old in 2008) of four coniferous (eastern white pine) forests from 2005 to 2008. The main objectives were: (i) to compare annual C fluxes determined by each method, and (ii) to use both methods to constrain C budgets and C allocation across different stages of forest development.

2. Materials and methods

2.1. Site description

This study was conducted in an age-sequence (6-, 19-, 34-, and 69-years-old in 2008) of four eastern white pine (Pinus strobus L.) forests. These stands are part of the Turkey Point Flux Station located at the north shore of Lake Erie in Southern Ontario, Canada (42°7′N, 80°35′W). The two older forests were planted in 1939 (TP39) and 1974 (TP74) on cleared oak-savannah land, while the two younger stands were established on former agricultural lands in 1989 (TP89) and in 2002 (TP02). All four sites have generally similar soil conditions with little organic matter, low-to-moderate water holding capacity, and sandy to loamy sand soil texture (Peichl et al., 2009). However, the upper 20 cm soil layers at TP89 and TP02 have greater amounts of soil macronutrients (i.e. P, K, Ca, Mg) (Khomik, 2004) and trees at TP89 benefit from access to deep soil water due to a higher water table (Peichl et al., submitted for publication). The region has a temperate climate with a 30-year mean annual temperature of 7.8 °C and an annual precipitation of 1010 mm of which 438 mm fall from May to September (Environment Canada Norms from 1971 to 2000 at Delhi, Ontario). A more detailed description of soil and stand char-
characteristics is given by Peichl and Arain (2006) and Peichl et al. (2009).

2.2. Micrometeorological measurements

Continuous measurements of half-hourly net ecosystem exchange of CO₂ (NEE) were made at the oldest site TP39 using a closed-path eddy covariance system (IRGA model LI-7000, LI-COR Inc.; sonic anemometer model CSAT-3). A roving open-path eddy covariance system (IRGA model LI-7500; LI-COR Inc.; sonic anemometer model CSAT-3) was rotated on bi-weekly to monthly intervals among the three younger sites from 2005 to 2007. This methodology ensured the capture of about one month of fluxes during each season of the year at three younger sites. On average, 70, 72, and 74% of the annual datasets of 2005–2007 were gap-filled at TP02, TP89, and TP74, respectively. Since January and May 2008, continuous flux data have been collected at TP74 and TP02, respectively, using closed-path EC systems. This reduced the fraction of gap-filled data in 2008 to 17 and 57% at TP74 and TP02, respectively. Because the new EC system was installed at greater height (20 m vs. 16 m) at TP74, small changes in the flux contributing areas might have been introduced. Analytical footprint solution of the (20 m vs. 16 m) at TP74, small changes in the flux contributing areas might have been introduced. Analytical footprint solution of the two dimensional Eulerian advection–diffusion equation (Horst and Weil, 1994; Chen et al., 2008) suggested that 80% of fluxes originated within 400 and 500 m at 16 and 20 m measuring height, respectively. Flux measurements at TP89 were discontinued in January 2008.

Detailed descriptions of site set-up, instrumentation, data collection and processing, gap-filling, and flux partitioning of NEE into GPP and RE components are given in (Arain and Restrepo-Coupe, 2005) and Arain et al. (submitted for publication). In brief, site-specific logistic respiration functions based on the relationship between night-time RE and soil temperature at 5 cm depth as described by Arain and Restrepo-Coupe (2005) were used to fill gaps in night-time RE and to estimate day-time RE. Measured night-time fluxes were pooled from all years to develop a single and robust logistic respiration function separately for each of the three younger sites. GPP was determined by adding measured NEE to modelled day-time RE. Gaps in GPP were filled using a rectangular hyperbolic regression function that related maximum GPP to photosynthetic active radiation (PAR), modified by logistic scalars sensitive to soil temperature (Ts), soil moisture (SM) and vapour pressure deficit (VPD). In this study we use the term GPP equivalent to gross ecosystem production (GEP) ignoring possible re-absorption of respired CO₂ within the ecosystem (Stoy et al., 2006).

Air temperature (Ta), relative humidity (RH) and photosynthetic active radiation (PAR) above the canopy was continuously measured at all four sites. Soil temperature (Ts) was measured at 2, 5, 10, 20, 50, and 100 cm depth at two locations. Soil moisture (SM) was measured at the same two soil locations at 5, 10, 20, 50 cm depth at all four sites and additionally at 100 cm depth at TP39 and TP89. Precipitation (P) was measured at TP39 using an accumulation rain gauge and a heated tipping bucket rain gauge and a non-heated rain gauge at TP02. Data was cross-checked and gap-filled using data from a nearby weather station (Delhi Weather Station, Environment Canada). Further meteorological instrumentation details are given in (Arain et al., submitted for publication).

2.3. Biometric measurements

2.3.1. Aboveground net primary production (ANPP)

Aboveground net primary production (ANPP) was derived from annual aboveground biomass (B) and detritus (D) production, as well as herbivory loss (H) (Eq. (1)).

\[
\text{ANPP} = B + D + H
\] (1)

Aboveground biomass production (B) was estimated from the annual change in aboveground tree (\(B_T; \text{DBH} \geq 9 \text{ cm}\)), understory (\(U; \text{DBH} < 9 \text{ cm}\)), and ground vegetation (G) biomass (Eq. (2)).

\[
B = \Delta B_T + \Delta U + \Delta G
\] (2)

Aboveground tree biomass (\(B_T\)) at the three older sites was estimated with site-specific allometric biomass equations using the mean tree diameter at breast height (DBH; in cm) as input variable, multiplied with stem density (S) (Eq. (3a)).

\[
B_T(i) = c(D_{\text{base}}(i))^a \times S
\] (3a)

where \(c\) is biomass in kilograms (kg) of the aboveground tree component \(i\) (\(i = \text{foliage, stem wood, bark, living branches, and total aboveground}\)), the site and component specific allometric equation parameter \(c\) and \(a\) were previously determined by Peichl and Arain (2007).

The allometric equation developed for TP02 based on measurements made in 2004 (Peichl and Arain, 2007) was inadequate to determine changes in biomass of the seedling trees due to their rapid height growth (height tripled from 2004 to 2008). We therefore developed a new allometric equation for TP02 by adding biomass estimates of five randomly selected trees in 2007 into the destructive harvesting dataset collected in 2004. Biomass estimates of these additional trees were determined from stem volume measured in 2007 multiplied by site-specific biomass expansion factors (BEFs) (Peichl and Arain, 2007). From this dataset combining biomass of five trees harvested in 2004 and five estimated trees in 2007, we developed a new allometric equation (Eq. (3b)) relating biomass to diameter at tree base (\(D_{\text{base}}\)):

\[
B_T(i) = c(D_{\text{base}}(i))^a \times S
\] (3b)

where constant \(c\) and parameter \(a\) values were 0.011, 0.004, 0.006, 0.021 and 2.67, 2.76, 2.81, 2.73 for foliage, stem, living branches, and aboveground biomass, respectively. A comparison with inventory biomass estimates showed that this improved allometric equation was able to better predict annual tree biomass increments at this young seedling site.

The mean stand DBH (\(D_{\text{base}}\) at TP02) was determined in three (six at TP39) permanent inventory plots (plot size = 0.4 ha) at each site at the end of the growing season (throughout October) of each year (2004–2008) using a diameter measuring tape. The sample plots were located within the dominant fetch of the EC tower at each site. In addition, 15 white pine trees were equipped with band dendrometers at each of the three older sites. At TP39, where understorey trees have a more significant contribution to stand basal area (13% in 2008), additional dendrometers were installed on three oak (Quercus vultina) and three balsam fir (Abies balsamifera) understorey trees and the mean stand increment was determined as a weighted average based on the relative basal area of each species. Monthly dendrometer readings were taken at TP39 and TP74 in 2008 to estimate monthly tree biomass production (\(NP_{\text{tree}}\)). Mean tree height was determined in 2004 and 2007 at the three older sites using a Suunto clinometer, and annually at the seedling site TP02 using a measurement pole.

Forest floor (LHF-layer), woody debris, U and G were measured in 2004 (described by Peichl and Arain, 2006) and 2007 in the permanent sample plots following the National Forest Inventory (NFI) guidelines (NFI, 2003). The change in biomass of U and G over three years (2004 to 2007) was linearly interpolated and extrapolated to obtain annual production estimates for 2005 to 2008. At the seedling site TP02, biomass production and species composition of ground vegetation varied throughout the growing season due to
the seasonal occurrence of various herbs and weeds. The clipping of micro plots was therefore repeatedly conducted in early summer and at the end of growing season to determine the total annual production of G.

**Aboveground detritus production (D)** was calculated as the sum of litter-fall (<1 cm) (L<sub>L</sub>), branch-fall (≥ 1 cm) (L<sub>B</sub>), and the change in mass of dead standing tree (D<sub>D</sub>) and dead branches (D<sub>DB</sub>) still attached to the tree. Litter and branch-fall was collected using traps which were emptied seasonally (every three months; bi-weekly during peak litter-fall in autumn) in 2005 and 2006 and half-yearly (in May and November) in 2007 and 2008. The change in D<sub>DB</sub> was determined with site-specific allometric equations (Peichl and Arain, 2007). The change in D<sub>D</sub> was recorded over the four-year period as part of the NFI plot inventory.

**Herbivory loss (H)** was estimated as 0.7% of the annual needle biomass as previously suggested for pine forests (Larsson and Tenow, 1985).

### 2.3.2. Belowground net primary production (BNPP)

Belowground net primary production (BNPP) was calculated as the sum of coarse root (NPPCR; ≥ 2 mm) and net fine root production (NPPFR; < 2 mm) (Eq. (4)).

\[
BNPP = NPP_{CR} + NPP_{FR}
\]

(NPP<sub>CR</sub>) was determined from the annual increments in coarse root biomass (BR<sub>CR</sub>) using site-specific allometric biomass equations based on relationships between DBH (except D<sub>base</sub> at TP02) and root biomass (Peichl and Arain, 2007) (Eq. (5)):

\[
BR = c(DBH)^d \times S
\]

NPP<sub>FR</sub> was estimated by multiplying fine root biomass stock with a fine root turnover rate. Fine root mass within the upper 55 cm soil layer was determined in our previous study for each site (Peichl and Arain, 2006). Because fine root turnover rate estimates were found to vary depending on selected method (Vogt et al., 1998; Gough et al., 2008), we estimated fine root turnover rates as the average of three different estimates. The first estimate was based on the mass balance approach suggested by Raich and Nadelhoffer (1989) in which the fine root turnover rate results from the balance of heterotrophic soil respiration minus litter input divided by the standing fine root biomass stock. Secondly, turnover rate was estimated as a dependent of available nitrogen (N) from N mineralization as proposed by Aber et al. (1985). Net N mineralization rates were estimated in another ongoing study at our sites using the buried bag method which suggested available N of 52, 33, 20, and 16 kg N ha<sup>-1</sup> y<sup>-1</sup> at TP02, TP89, TP74, and TP39, respectively (Peichl et al., 2009). Total annual N deposition (dry and wet) in this region is approximately 7 kg N ha<sup>-1</sup> y<sup>-1</sup> (Environment Canada, 2004). In the third estimate, we assumed the turnover rate to be 0.60 yr<sup>-1</sup> as reported for ponderosa pine (Pinus ponderosa) stands by Law et al. (2001). The site-specific turnover rates as a mean of the three estimates and averaged for the four years ranged from 0.47 to 0.56 among our four study sites and were within the range of rates previously reported for pine forests (Aber et al., 1985; Vogt et al., 1998).

Total belowground carbon flux (TBCF) was determined from the sum of BNPP and autotrophic root respiration (R<sub>AR</sub>; see 3.4) assuming zero change in fine root C stocks during the study period, and ignoring C flux via root exudates and mycorrhizae (Liton et al., 2007). This may have introduced some error at the seedling site TP02 where a change in fine root C stock likely occurred throughout the study period.

### 2.3.3. Carbon content of biomass components and soil

We used compartment specific C concentrations as suggested for pine stands by Bert and Danjon (2006) to convert biomass of foliage (53.6% C), branches (53.4% C), bark (55.9% C), stem wood (53.3% C) and roots (51.7% C) to C per unit ground area. Litter-fall C concentration was determined as 53.1%. In a previous study, we determined C concentrations of herbs, moss, and woody debris to be 46, 47, and 53%, respectively (Peichl and Arain, 2006).

Soil sampling in 2004 at all four sites revealed that the distribution of soil C was highly heterogeneous (Peichl and Arain, 2006) which would have required a tremendous sample size beyond the scope of this study to detect significant changes in soil C. Gough et al. (2008) did not find any increase in soil C over a five years period. We therefore assume that soil C stock did not change significantly at our sites over the study period.

### 2.4. Autotrophic and heterotrophic respiration

Soil respiration (R<sub>S</sub>) was measured as part of a separate study across the Turkey Point age-sequenee stands as described in Khomik et al. (2009). In brief, R<sub>S</sub> and soil temperature was measured along a 50 m transect at each site on a bi-weekly to monthly basis, using a LI-6400 portable system (LI-COR Inc.) from 2004 to 2006. Soil heterotrophic (R<sub>H</sub>) and root autotrophic (R<sub>RA</sub>) respiration were determined at each site from measurements made during 2005 and 2006, using the trenched-plot technique (Hanson et al., 2000). At the three older stands, heterotrophic respiration from the LFH-layer (R<sub>HLFH</sub>) and from mineral soil (R<sub>HM</sub>) was determined as the difference between measurements in trenched plots from collars that had the LFH-layer present and those that had it removed. Based on soil temperature and respiration measurements, a model (gamma model) was developed to simulate time series of daily autotrophic and heterotrophic R<sub>S</sub> component fluxes (Khomik et al., 2009; Khomik and Arain, submitted for publication).

**Autotrophic aboveground canopy respiration (R<sub>AC</sub>; including foliage, branch, and stem respiration)** was derived by subtracting R<sub>RA</sub> from RA, with RA being the difference between GPP and NPP (see Section 2.5 below). This caused some autocorrelation between R<sub>AC</sub> and GPP, however, it ensured the closure of the biometric C budget. Aboveground heterotrophic respiration from decomposing woody debris and dead standing trees (R<sub>RWD</sub>) was calculated from debris stock mass multiplied by a decomposition rate. Annual decomposition rates for softwood debris have been reported in a range of 3–7% (Law et al., 2001; Black et al., 2005), we therefore applied a decomposition rate of 5% in our analysis. Total heterotrophic respiration (R<sub>H</sub>) was determined as the sum of R<sub>H</sub> and R<sub>RWD</sub>. The sum of RA and R<sub>H</sub> component fluxes resulted in a biometric estimate of ecosystem respiration (R<sub>EC</sub>).

### 2.5. Net primary production (NPP), gross primary production (GPP), and net ecosystem production (NEP)

**Net primary production from biometric measurements (NPP<sub>(B)</sub>)** was calculated as the sum of ANPP and BNPP. Eddy-covariance based NPP<sub>(EC)</sub> was determined from the sum of RH and the annual net ecosystem production (NEP<sub>(EC)</sub> = − NEE; see Section 2.2). Assuming NPP as a constant fraction (47%) of gross primary production (GPP) on annual scale as suggested for coniferous forests by Waring et al. (1998), we estimated GPP<sub>(B)</sub> = NPP<sub>(B)</sub> × 2.13 (see Section 2.6 for an estimate of uncertainty introduced by this simplified relationship).

In this study, we did not account for additional C fluxes via dissolved organic carbon (DOC) and volatile organic compounds (VOC). A previous study at the Turkey Point sites estimated an annual DOC export (leaching loss minus input via precipitation) of 6, 3, 2, and 1 g DOC m<sup>-2</sup> y<sup>-1</sup> at TP02, TP89, TP74 and TP39, respectively (Peichl et al., 2007). Annual C losses via VOC were estimated to be between 0.01 and 0.27% of assimilated C in conifer
forests (Street et al., 1996). Thus, C losses via DOC and VOC fluxes were presumably very small and together may have accounted for <1.5% of NPP in this study. 

Net ecosystem production from biometric measurements (NPP) was calculated from NPP minus C losses via RH. Half-hourly NEE from EC measurements was summed up and converted to annual NEP estimates (NPP, with positive NEP indicating C uptake). 

Biometric estimates of tree biomass and detritus production spanned the biological year from November to October (e.g. year 2005 = November 1 of 2004 to October 31 of 2005). Therefore, annual sums of soil respiration component fluxes and annual EC fluxes were also computed for the same time period. However, we also present EC-based NEP determined over the calendar year (1 January to 31 December) for further reference.

2.6. Uncertainty in EC and biometric estimates of C exchange

Mean average error (MAE) and bias errors (BE) introduced by the gap-filling models were determined at each site for periods in which measured data was available and integrated over the respective annual number of missing data points to estimate the uncertainty of annual GPP, RE, and NPP. Based on the site-specific gap frequency, gap length and flux magnitude, the average (2005–2008) uncertainty of NPP was estimated as ±29, 56, 85, and 40 g C m⁻² y⁻¹ at TP02, TP89, TP74, and TP39, respectively. We did not apply any correction for the lack of energy balance closure to annual totals presented in this study. The average annual energy balance closure at the four sites during the study period was 73, 76, 72, and 78% at TP02, TP89, TP74, and TP39, respectively (Restrepo-Coupe, 2005).

The uncertainty in biometric estimates of annual tree biomass increments (σNBP) was computed from (a) the error in annual DBH increment estimates (σDBH), (b) the error of the allometric biomass equation (σEQ), and (c) the within-stand spatial variability (SV). The error in annual DBH increment estimates was determined from the regression error of DBH increments measured with the diameter tape against increments measured with the band dendrometers on the same trees. Uncertainty in stand biomass caused by within-stand SV was derived from the standard deviation (SD) around the mean tree diameter (σDBH), mean tree height (σH), and stem density (σSD) resulting from differences among sample plots. The propagation of these error terms resulted in an estimate of σNBP (Eq. (6)).

Uncertainty of NPP (σNPP) was estimated as the propagated sum of σNBP, the SV of the changes in the amount of dead standing trees (σDBH) and understorey/green vegetation biomass (σEQ), the SV of annual litter-and branch-fall (σL), and the uncertainty around net fine root production (σNFR) (Eq. (7)). Estimates of σNFR were derived from the SD around the mean of the three different approaches estimating NPPFR.

\[
\sigma_{LB} = \sqrt{\sigma_{DBH}^2 + \sigma_{EQ}^2 + \sigma_{L}^2 + \sigma_{SD}^2}\]

(6)

\[
\sigma_{NPP} = \sqrt{\sigma_{DBH}^2 + \sigma_{EQ}^2 + \sigma_{L}^2 + \sigma_{SD}^2}\]

(7)

The uncertainty of the annual RHS (σRHS) and RA (σRA) was determined from the mean square error given by the model output for the respective respiration model. Uncertainty of RHWD (σRHD) was determined from SV of woody debris stock mass. The propagated sum of σRHD and σRHS resulted in an uncertainty estimate for RH (σRH). Finally, the uncertainty in biometric NEP estimates (σNEP) was calculated from the propagation of σNPP and σRH (Eq. (8)).

\[
\sigma_{NEP} = \sqrt{\sigma_{NPP}^2 + \sigma_{RHS}^2}\]

(8)

To account for possible deviations of the NPP/GPP ratio from the assumed constant ratio of 0.47, we applied a 20% error on the annual GPP as proposed by Delucia et al. (2007). Because of the dependency of RA on GPP, we also assumed a 20% error for RA (σRA). The uncertainty of RE was calculated from the error propagation of σRH and σRA.

3. Results

3.1. Climate and environmental conditions

A comparison of annual mean air temperature (Ta) and precipitation (P) over the study period (2005–2008) to 30-year normals identified 2005 as hot and dry, 2006 as hot and wet, 2007 as warm and dry, and 2008 as a normal year Table 1. Average growing season soil temperature (Tg) was highest at the seedling site TP02 and lowest in the dense stand TP89, with considerable inter-annual variation occurring at TP02 only (Table 1b). Growing season soil moisture (SM) in the upper 20 cm soil layer was low and similar among sites and years. Mean growing season photosynthetically

### Table 1

(a) Mean annual (A) and growing season (GS; DOY 92–305) air temperature (Ta), precipitation (P), and volumetric soil water content (VWC) in 0–20 cm soil depth, and photosynthetically active radiation (PAR; μmol m⁻² s⁻¹) at the four age-sequence sites from 2005 to 2008; N.A. not available.

(b) Mean average error (MAE) and bias errors (BE) introduced by the gap-filling models were determined at each site for periods in which measured data was available and integrated over the respective annual number of missing data points to estimate the uncertainty of annual GPP, RE, and NPP.
active radiation (PAR) was lowest for the wet growing season of 2006 and similar among the other three years.

3.2. Ecosystem C pools and component fluxes across the age-sequence

Aboveground tree and root biomass were the two largest C pools at each site and increased with stand age (Table 2). Understorey and woody debris C pools also increased with age. The total amount of C stored in above and belowground biomass pools increased from 9.2 t C ha$^{-1}$ at the seedling site TP02 to 61, 75 and 160 t C ha$^{-1}$ at TP89, TP74 and TP39, respectively.

Both biometric and EC-based estimates suggested that mean annual NPP, GPP, RE, and NEP were greatest at TP89 and lowest at TP02 (Table 3). ANPP and its components tree biomass and litter-fall production followed the same age-related pattern. Among the four years, highest and lowest NPP fluxes were observed in 2007 and similar among the other three years.

The greatest variation amongst RE component fluxes were observed for RA$_C$ ranging from 14% at TP02 to 53% at TP89 (Fig. 1c). While belowground respiration dominated RE at TP02 (85%), its contribution decreased to 45–60% in the three older stands.

3.3. Comparison of biometric and EC-based estimates of annual GPP, RE, and NEP

Biometric and EC-based estimates of GPP agreed reasonably well at TP02 (except in 2008), TP74 and TP39 (Table 3, see also Fig. 3). However, GPP$_{EC}$ exceeded GPP$_{B}$ at TP89. RE$_{B}$ and RE$_{EC}$ were similar at TP39 and initially at TP02, although divergence occurred at TP02 throughout the study period ending with a large mismatch in 2008. In contrast, RE$_{EC}$ was considerably greater than RE$_{B}$ at TP89, whereas RE$_{EC}$ was smaller than RE$_{B}$ at TP74. NEP$_{B}$ and NEP$_{EC}$ agreed well at TP02 and TP39 in 2005 and 2006 but slightly diverged in 2007 and 2008. NEP$_{EC}$ exceeded NEP$_{B}$ at TP89 whereas NEP$_{B}$ exceeded NEP$_{EC}$ at TP74.

Ratios of NEP$_{B}$/NEP$_{EC}$ suggested discrepancies ranging from 32 to 78% after one year and 9 to 56% after converging four years of measurements (Table 4). Although a slight increase of NEP$_{B}$/NEP$_{EC}$ with time towards unity occurred at TP74, overall we did not observe multi-year convergence of NEP$_{B}$ and NEP$_{EC}$.

A strong correlation between annual NEP$_{EC}$ and stem volume increment was observed within the three younger sites ($R^2 = 0.94$) and within the mature site ($R^2 = 0.97$) implying that approximate estimates of annual NEP in these stands could be efficiently derived from tree diameter increment measurements only (Fig. 2).
Table 3
Biometric (B) and eddy-covariance (EC) based estimates of annual above- and below-ground C fluxes (g C m\(^{-2}\) y\(^{-1}\)) at the four Turkey Point pine forest ecosystems.

<table>
<thead>
<tr>
<th>Site</th>
<th>TP02</th>
<th>TP89</th>
<th>TP74</th>
<th>TP39</th>
</tr>
</thead>
<tbody>
<tr>
<td>Foliage</td>
<td>53</td>
<td>82</td>
<td>78</td>
<td>151</td>
</tr>
<tr>
<td>Living branches</td>
<td>21</td>
<td>34</td>
<td>33</td>
<td>64</td>
</tr>
<tr>
<td>Stem bark</td>
<td>N.A.</td>
<td>N.A.</td>
<td>N.A.</td>
<td>N.A.</td>
</tr>
<tr>
<td>Stem wood</td>
<td>39</td>
<td>64</td>
<td>63</td>
<td>125</td>
</tr>
<tr>
<td>Aboveground tree</td>
<td>112</td>
<td>178</td>
<td>172</td>
<td>338</td>
</tr>
<tr>
<td>Understory (U) + Ground veg. (G)</td>
<td>82</td>
<td>101</td>
<td>120</td>
<td>125</td>
</tr>
<tr>
<td>Herbivory (H)</td>
<td>0.5</td>
<td>1.0</td>
<td>1.6</td>
<td>2.6</td>
</tr>
<tr>
<td>Coarse root (&gt;2 mm)</td>
<td>38</td>
<td>58</td>
<td>56</td>
<td>108</td>
</tr>
<tr>
<td>Standing woody debris</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Litterfall (L + L)</td>
<td>195</td>
<td>280</td>
<td>294</td>
<td>466</td>
</tr>
<tr>
<td>ANPP</td>
<td>43</td>
<td>64</td>
<td>61</td>
<td>114</td>
</tr>
<tr>
<td>BNPP</td>
<td>322</td>
<td>359</td>
<td>332</td>
<td>421</td>
</tr>
<tr>
<td>NPP_{EC}</td>
<td>238</td>
<td>344</td>
<td>355</td>
<td>579</td>
</tr>
<tr>
<td>Gross primary production</td>
<td>195</td>
<td>280</td>
<td>294</td>
<td>466</td>
</tr>
<tr>
<td>GPP_{EC}</td>
<td>195</td>
<td>280</td>
<td>294</td>
<td>466</td>
</tr>
<tr>
<td>Ecosystem respiration</td>
<td>195</td>
<td>280</td>
<td>294</td>
<td>466</td>
</tr>
<tr>
<td>Net ecosystem production</td>
<td>195</td>
<td>280</td>
<td>294</td>
<td>466</td>
</tr>
</tbody>
</table>

\(a\) Measured in 2004 and 2007 and linearly interpolated for other years at TP89, TP74 and TP39.

\(b\) Calculated for the biological year (November 1 to October 31).

\(c\) Calculated for the EC year (January 1 to December 31) \((\text{Arain et al., submitted for publication})\).
3.4. Inter-annual variability in GPP, RE, and NEP

For the two oldest sites TP74 and TP39, the biometric and EC methods produced comparable patterns for inter-annual differences in GPP suggesting reduced assimilation in the warm and dry years 2005 and 2007 of about 150–300 g C m\(^{-2}\) y\(^{-1}\) compared to 2006 and 2008. (Fig. 3, upper row panels). Whereas the biometric method suggested a similar pattern for TP89, the EC method produced the highest \(G_{\text{PP(EC)}}\) estimate for 2007 at that site (\(G_{\text{PP(EC)}}\) for 2008 was not measured at TP89). At TP02, biometric and EC methods both suggested a somewhat steady increase in GPP over the four years masking inter-annual effects from climatic variations.

Inter-annual patterns in RE\(_{(B)}\) suggested a reduction in RE of about 50 to 150 g C m\(^{-2}\) y\(^{-1}\) in the warm and dry years 2005 and 2007 compared to 2006 and 2008 (Fig. 3, middle row panels). This inter-annual pattern was also observed for RE\(_{(EC)}\) at TP39 but not at TP89 and TP74, where elevated RE\(_{(EC)}\) values occurred in 2007 and 2008, respectively. At the seedling site TP02, RE\(_{(B)}\) showed a continuous increase whereas RE\(_{(EC)}\) remained similar throughout the study period.

Inter-annual patterns in NEP\(_{(B)}\) and NEP\(_{(EC)}\) agreed well at TP74 and TP39 suggesting a reduction in NEP of about 50 to 150 g C m\(^{-2}\) y\(^{-1}\) in the warm and dry years 2005 and 2007 compared to 2006 and 2008 (Fig. 3, bottom row panels). Greater NEP in 2006 and 2008 resulted from greater increases in GPP compared to smaller increases in RE. While this inter-annual pattern was also observed for NEP\(_{(B)}\) at TP89, NEP\(_{(EC)}\) at that site was highest in 2007. At TP02, both NEP\(_{(B)}\) and NEP\(_{(EC)}\) increased throughout the study period masking inter-annual effects from climatic variations. Overall, both biometric and EC-based estimates suggested that age-related differences in GPP, RE, and NEP among sites exceeded inter-annual variations.

A negative correlation of both NPP\(_{(B)}\) and NEP\(_{(EC)}\) to mean growing season air temperature observed at each site may explain inter-annual differences to some extent (Fig. 4). Between the years 2005 and 2006, which had similar growing season air temperature, higher productivity in 2006 coincided with greater precipitation.
Table 5
Ratios of plant C use efficiency (CUE(P) : NPP:GPP), ecosystem C use efficiency (CUE(E) : NEP:GPP), efficiency of C uptake (NEP:RE), soil C gain/loss (RH:NPP), RA:RH, TBCF:GPP(EC), and ANPP:BNPP based on biometric (B) and eddy-covariance (EC) measurements at the four age-sequence sites from 2005–2008.

<table>
<thead>
<tr>
<th>Ratio</th>
<th>TP02</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NPP(B) : GPP(EC)</td>
<td>0.55</td>
<td>0.56</td>
<td>0.50</td>
<td>0.84</td>
<td>0.61</td>
<td>0.33</td>
<td>0.36</td>
<td>0.30</td>
<td>N.A.</td>
<td>0.34</td>
<td>0.46</td>
<td>0.51</td>
<td>0.52</td>
<td>0.53</td>
<td>0.50</td>
<td>0.41</td>
</tr>
<tr>
<td>NEP(B) : GPP(B)</td>
<td>-0.15</td>
<td>0.06</td>
<td>0.06</td>
<td>0.24</td>
<td>0.05</td>
<td>0.23</td>
<td>0.26</td>
<td>0.22</td>
<td>0.27</td>
<td>0.25***</td>
<td>0.07</td>
<td>0.16</td>
<td>0.12</td>
<td>0.18</td>
<td>0.13***</td>
<td>0.03</td>
</tr>
<tr>
<td>NEP(B) : RE(B)</td>
<td>-0.13</td>
<td>0.06</td>
<td>0.06</td>
<td>0.32</td>
<td>0.30</td>
<td>0.30</td>
<td>0.34</td>
<td>0.29</td>
<td>0.38</td>
<td>0.33***</td>
<td>0.07</td>
<td>0.19</td>
<td>0.13</td>
<td>0.22</td>
<td>0.15**</td>
<td>0.03</td>
</tr>
<tr>
<td>RH:NPP(B)</td>
<td>1.31</td>
<td>0.86</td>
<td>0.86</td>
<td>0.47</td>
<td>0.87</td>
<td>0.48</td>
<td>0.43</td>
<td>0.49</td>
<td>0.39</td>
<td>0.45**</td>
<td>0.78</td>
<td>0.60</td>
<td>0.68</td>
<td>0.55</td>
<td>0.65***</td>
<td>0.83</td>
</tr>
<tr>
<td>EC</td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NPP(EC) : GPP(EC)</td>
<td>0.47</td>
<td>0.54</td>
<td>0.67</td>
<td>0.68</td>
<td>0.59</td>
<td>0.45</td>
<td>0.48</td>
<td>0.46</td>
<td>N.A.</td>
<td>0.46</td>
<td>0.70</td>
<td>0.74</td>
<td>0.71</td>
<td>0.62</td>
<td>0.69</td>
<td>0.43</td>
</tr>
<tr>
<td>NEP(EC) : GPP(B)</td>
<td>-0.26</td>
<td>0.28</td>
<td>0.26</td>
<td>0.28</td>
<td>0.07</td>
<td>0.28</td>
<td>0.32</td>
<td>0.30</td>
<td>0.30</td>
<td>0.32</td>
<td>0.30</td>
<td>0.40</td>
<td>0.32</td>
<td>0.29</td>
<td>0.33</td>
<td>0.05</td>
</tr>
<tr>
<td>NEP(EC) : RE(EC)</td>
<td>-0.20</td>
<td>0.05</td>
<td>0.28</td>
<td>0.38</td>
<td>0.13</td>
<td>0.40</td>
<td>0.45</td>
<td>0.44</td>
<td>0.44</td>
<td>0.44</td>
<td>0.67</td>
<td>0.48</td>
<td>0.38</td>
<td>0.49</td>
<td>0.05</td>
<td>0.10</td>
</tr>
<tr>
<td>RH:RE</td>
<td>1.54</td>
<td>0.96</td>
<td>0.65</td>
<td>0.58</td>
<td>0.92</td>
<td>0.36</td>
<td>0.32</td>
<td>0.32</td>
<td>N.A.</td>
<td>0.33***</td>
<td>0.51</td>
<td>0.42</td>
<td>0.49</td>
<td>0.47</td>
<td>0.47***</td>
<td>0.80</td>
</tr>
<tr>
<td>RA:RH</td>
<td>0.9</td>
<td>1.3</td>
<td>1.3</td>
<td>2.4</td>
<td>1.5</td>
<td>2.2</td>
<td>2.5</td>
<td>2.1</td>
<td>2.7</td>
<td>2.4***</td>
<td>1.3</td>
<td>1.7</td>
<td>1.5</td>
<td>1.8</td>
<td>1.6***</td>
<td>1.2</td>
</tr>
<tr>
<td>TBCF:GPP(EC)</td>
<td>0.74</td>
<td>0.59</td>
<td>0.47</td>
<td>0.61</td>
<td>0.60</td>
<td>0.22</td>
<td>0.21</td>
<td>0.18</td>
<td>N.A.</td>
<td>0.20</td>
<td>0.42</td>
<td>0.38</td>
<td>0.39</td>
<td>0.35</td>
<td>0.39</td>
<td>0.32</td>
</tr>
<tr>
<td>ANPP:BNPP</td>
<td>4.5</td>
<td>4.4</td>
<td>4.8</td>
<td>4.1</td>
<td>4.4</td>
<td>3.7</td>
<td>3.9</td>
<td>3.3</td>
<td>3.6</td>
<td>3.6</td>
<td>1.6</td>
<td>2.0</td>
<td>2.0</td>
<td>2.1</td>
<td>1.9</td>
<td>3.8</td>
</tr>
</tbody>
</table>

* / ** / *** indicate increase / decrease with stand age among the three older stands TP89, TP74, TP39 with * < ** < ***.

Italic numbers: A change in footprint size in 2008 may have affected EC measurements compared to previous years at TP74.

* Because of the assumption GPP(B) = 2.13 × NPP(B), GPP(EC) was used to estimate the biometric plant C efficiency ratio.

3.5. Ecosystem C use efficiency and C allocation
Biometric and EC-based estimates of plant C use efficiency CUE(P) (determined from the ratio of NPP:GPP) agreed reasonably well at TP02, TP89, and TP39 but disagreed considerably at TP74 (Table 6). Averaged over four years, mean CUE(P) ranged between 0.33–0.54 and 0.42–0.69 based on the biometric and EC estimates, respectively, across the four stands (Table 5). No effect of stand age was apparent in these ratios.

Ecosystem C use efficiency (CUE(E) = NEP:GPP) and the efficiency of C uptake (NEP:RE) decreased with stand age among the three oldest stands based on the biometric estimates, but peaked at TP74 based on the EC estimates (Table 5). Both methods suggested similar inter-annual patterns for the three older sites with higher CUE(E) and NEP:RE ratios during years with sufficient rainfall (2006 and 2008) compared to the dry and warm years 2005 and 2007. This inter-annual pattern may have been caused by a positive correlation of CUE(E) with forest productivity (for both NPP and NEP) observed across the age-gradient (Fig. 5a). A similar positive correlation was observed between NEP(RE) and forest productivity (data not shown).
The mean ratio of RA:RH increased from 1.5 at TP02 to a maximum of 2.4 at TP89 and subsequently decreased with increasing stand age to 1.4 at TP39 (Table 5). Lower annual RA:RH ratios occurred in the dry years of 2005 and 2007 compared to 2006 and 2008. Inter-annual and inter-site differences in annual RA:RH were likely caused by a positive correlation of RA:RH to forest productivity (NPP, NEP) (Fig. 5c). Conversely, the allocation of assimilated C to belowground production, expressed as the ratio of TBCF:GPP, was greatest for the lowest productive site (TP02) and year (2005) and lowest for the highest productive site (TP89) and year (2008) (Table 5) due to a negative correlation with forest productivity (NPP, NEP) (Fig. 5d). No inter-annual pattern was observed for ANPP:BNPP which, however, was greater in the two younger stands compared to the two older stands indicating enhanced contribution of belowground production to NPP in the older forests (Table 5).

### Seasonal variation in C allocation

Monthly GPP\(_{(EC)}\) and RE\(_{(EC)}\) peaked at each of the two older sites in the growing season of 2008, although a temporal shift occurred between peaks at TP74 (in June) and TP39 (in July; Fig. 6). The difference in timing of maximum GPP\(_{(EC)}\) was likely related to greater contribution from broadleaf understory growth at TP39 (broadleaf trees account for 1.5% and 9% of basal area at TP74 and TP39, respectively), as dendrometer data suggested maximum broadleaf tree growth in July/August but maximum pine growth in June (data not shown). At both sites, monthly tree biomass production (NPP\(_{\text{tree}}\))
peaked in June and maximum monthly NEP\textsubscript{(EC)} occurred in May when soil temperature and therefore RE\textsubscript{(EC)} was still low. At both sites, NPP\textsubscript{tree} was about 50% of GPP\textsubscript{EC} in June suggesting that tree growth accounted for close to 100% of NPP during this month (assuming that NPP is ∼50% of GPP) (Fig. 6). Small contributions of NPP\textsubscript{tree} to GPP during April/May may have been related to greater contribution from other NPP components (e.g., ground vegetation and/or fine root growth) or a temporal delay in the onset of stem radial growth. Little allocation of GPP to NPP\textsubscript{tree} in October (when allocation to other NPP components can be expected to be negligible) at both sites indicated that most assimilates may have been either allocated to storage (as reserve for tree growth in the spring of the following year) rather than being invested in tree growth, or lost as root exudates within the current month.

3.7. Aggregated C sequestration estimates across the age-sequence

Linear interpolation and integration of annual NEP across the age-sequence resulted in a total C sequestration of 137 and 229 t Ch\textsubscript{-1} over the initial 70 years estimated by the biometric and EC method, respectively. The total ecosystem C sequestered in biomass pools at TP39 as of 2007 suggests an accumulation of 160 t Ch\textsubscript{-1} (assuming no change in mineral soil C pool). The mean C sequestration over 70 years based on these three estimates resulted in 175 ± 48 t Ch\textsubscript{-1}, suggesting a mean annual sequestration rate of 2.5 t Ch\textsubscript{-1} y\textsuperscript{-1}.

3.8. Uncertainty in C flux estimates

Uncertainty of tree biomass production estimates was the greatest error source of the total uncertainty of NPP\textsubscript{B} (σ\textsubscript{NPP}) at all sites, except at TP74, where the uncertainty around NPP\textsubscript{B} estimates was the greatest contributor to σ\textsubscript{NPP} (Table 6). The relative σ\textsubscript{NPP} ranged from ±14% at TP89 to ±28% at the oldest site TP39 and increased with stand age among the three older sites. The four-year mean values of uncertainty in NEP\textsubscript{B} estimates relative to their annual totals (i.e., annual uncertainty/annual NEP\textsubscript{B}) was ±28, 21, 24, and 32% for TP02, TP89, TP74 and TP39, respectively, which was overall comparable to ±24, 8, 21, and 32% determined for NEP\textsubscript{(EC)} at TP02, TP89, TP74 and TP39, respectively.

4. Discussion

4.1. NPP component fluxes and associated uncertainties

Our estimates of ANPP (309–654 g Ch\textsubscript{-1} y\textsuperscript{-1}) and BNPP (71–205 g Ch\textsubscript{-1} y\textsuperscript{-1}) were well within and at the lower end, respectively, compared to the range (ANPP = 56–1490 g Ch\textsubscript{-1} y\textsuperscript{-1}; BNPP = 150–566 g Ch\textsubscript{-1} y\textsuperscript{-1}) previously reported for temperate pine forests (Aber et al., 1985; Vogt, 1991; Law et al., 2001; Harmon et al., 2004; Litton et al., 2007). Total NPP estimates (379–1135 g Ch\textsubscript{-1} y\textsuperscript{-1}) were within the range of 150–400 g Ch\textsubscript{-1} y\textsuperscript{-1} for recently initiated stands (Law et al., 2003; Schwalm et al., 2007) and 400 to 2400 g Ch\textsubscript{-1} y\textsuperscript{-1} for maturing temperate conifer forests reported by previous studies (Vogt, 1991; Waring et al., 1998; Pregitzer and Euskirchen, 2004; Schwalm et al., 2007).

Compared to a 13% error estimate of NPP reported for a 14-year-old spruce forest (Black et al., 2005), our uncertainty estimate of NPP at TP89 (14%) was similar, but greater at our other three sites (21–28%). The varying contribution of individual C fluxes to total NPP among the chronosequence stands introduced various levels of uncertainty to the NPP estimates depending on forest development stage. For instance, the uncertainty associated with NPP\textsubscript{FR} estimates became critical at TP74 where NPP\textsubscript{FR} accounted for 30% of total NPP, whereas uncertainty related to tree biomass estimates was of greater importance in the low-productive seedling and mature stands than in the two high-productive middle-age stands. Thus, varying contribution of NPP component uncertainty at different forest development stage should be considered in the design of NPP census. Understanding error sources and magnitude in biometric NPP estimates is imperative since most regional and global C-budget estimations from terrestrial ecosystem models are validated by global NPP datasets (e.g. Olson et al., 2001).

4.2. Biometric and EC-based estimates of GPP, RE and NEP

The range of biometric and EC-based four-year mean estimates of RE (∼549–1717 g Ch\textsubscript{-1} y\textsuperscript{-1}) and GPP (∼610–2445 g Ch\textsubscript{-1} y\textsuperscript{-1}) at our sites was comparable to other temperate conifer forests (∼700 to 1600 and 700 to 2100 g Ch\textsubscript{-1} y\textsuperscript{-1} for RE and GEP, respectively) (Law et al., 2002), although both RE\textsubscript{(EC)} and GPP\textsubscript{(EC)} were exceptionally high at TP89. Similarly, NEP at our sites (∼114 to 793 g Ch\textsubscript{-1} y\textsuperscript{-1}) spanned the entire range (∼105 to 707 g Ch\textsubscript{-1} y\textsuperscript{-1}) previously reported for young and mature temperate conifer forests (Law et al., 2002; Pregitzer and Euskirchen, 2004).

The consistent offset between biometric and EC-based estimates for GPP at TP89 and RE at TP74 and TP74 may have resulted from either incorrect census of one or more biometric component fluxes or from errors associated with the EC flux partitioning procedure (e.g., effect of u-threshold, etc.). At TP74, RE\textsubscript{(EC)} of <800 g Ch\textsubscript{-1} y\textsuperscript{-1} may be an underestimation considering that RE\textsubscript{(EC)} at the three older sites and RE\textsubscript{(EC)} at TP89 and TP39 were consistently above 1000 g Ch\textsubscript{-1} y\textsuperscript{-1}. At TP89, we suspect that lower GPP\textsubscript{(EC)} and RE\textsubscript{(EC)} compared to GPP\textsubscript{(EC)} and RE\textsubscript{(EC)} resulted from the fact that the allometric biomass equation with DBH as single input variable may not have been able to adequately account for the considerable tree height growth (∼1 m per year) therefore underestimated tree NPP and RA\textsubscript{B}.

Previous comparison studies have primarily focused on forest NPP to evaluate the agreement between biometric and EC estimates (Curtis et al., 2002; Ehman et al., 2002; Gough et al., 2008) whereas comparisons of biometric and EC-based GPP and RE estimates are sparse (Harmon et al., 2004; Keith et al., 2009). However, the comparison of GPP and RE offers the possibility to detect the sources of divergence in NPP estimates. In the specific case of our TP74 site, the poor agreement between NEP\textsubscript{B} and NEP\textsubscript{(EC)} resulted primarily from a good agreement in GPP estimates while RE\textsubscript{(EC)} exceeded RE\textsubscript{B}. In contrast, reasonable agreement between NEP\textsubscript{B} and NEP\textsubscript{(EC)} may be achieved if both GPP\textsubscript{B} and RE\textsubscript{(EC)} differ from GPP\textsubscript{(EC)} and RE\textsubscript{B} in similar magnitude and essentially outweighed each other, thereby producing similar NPP estimates. Thus, biometric and EC methods may fail in producing similar estimates of the independent component fluxes (GPP and RE) but coincidently result in similar net estimates (NEP) thereby simulating good agreement, whereas in other cases both methods may agree on one of the two component fluxes but consequently produce different NPP estimates. It is therefore important to consider the agreement in GPP and RE estimates besides NEP when evaluating the biometric and EC methods in estimating forest C exchange and to detect method-specific weaknesses in these techniques.

The observed correlation between NEP and stem volume increment may have been possible because heterotrophic respiration, fine root production and litter-fall provided rather constant C fluxes on annual scale among years within each site. Variations in NEP therefore scaled primarily with changes in tree biomass production as the driving component of NPP. Similar to our findings, Ohtsuka et al. (2009) and Arneth et al. (1998) reported a conservative relationship between NEP\textsubscript{(EC)} and woody tissue NPP. This relationship could therefore provide an efficient way to determine approximate annual NPP estimates on regional scales from existing forest.
Uncertainty (σ) of biometric NPP components in g C m⁻² y⁻¹ and in % of total NPP as a mean of years (2004–2008). Uncertainty of biometric NPP, RH and NEP shown as coefficient of variation (CV); Numbers in parentheses indicate SD from inter-annual variability; √V = within-stand spatial variability.

<table>
<thead>
<tr>
<th>Source of uncertainty</th>
<th>Symbol</th>
<th>TP02</th>
<th>TP09</th>
<th>TP74</th>
<th>TP39</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>g C m⁻² y⁻¹</td>
<td>% of NPP</td>
<td>g C m⁻² y⁻¹</td>
<td>% of NPP</td>
</tr>
<tr>
<td>Tree biomass production</td>
<td>σLb</td>
<td>69 (29)</td>
<td>20 (5)</td>
<td>104 (22)</td>
<td>12 (2)</td>
</tr>
<tr>
<td>SV of detritus production</td>
<td>σLb</td>
<td>N.A.</td>
<td>N.A.</td>
<td>21 (4)</td>
<td>3 (1)</td>
</tr>
<tr>
<td>SV of understory/ground vegetation production</td>
<td>σLc</td>
<td>40 (7)</td>
<td>11 (2)</td>
<td>1 (N.A.)</td>
<td>&lt;1</td>
</tr>
<tr>
<td>SV of litter production</td>
<td>σL</td>
<td>N.A.</td>
<td>N.A.</td>
<td>51 (10)</td>
<td>6 (1)</td>
</tr>
<tr>
<td>Fine root production</td>
<td>σRb</td>
<td>1 (&lt;1)</td>
<td>26 (7)</td>
<td>3 (1)</td>
<td>82 (4)</td>
</tr>
<tr>
<td>NPP</td>
<td>σNPP</td>
<td>23 (1)</td>
<td>14 (1)</td>
<td>21 (2)</td>
<td>28 (6)</td>
</tr>
<tr>
<td>RH</td>
<td>σRH</td>
<td>16</td>
<td>15</td>
<td>13</td>
<td>14</td>
</tr>
<tr>
<td>NEP</td>
<td>σNEP</td>
<td>28</td>
<td>21</td>
<td>24</td>
<td>32</td>
</tr>
</tbody>
</table>

a σNPP = \sqrt{NPPb^2 + σLb^2 + σRb^2 + σDB^2 + σUG^2 + 2 \times σLb \times σNPPb + 2 \times σRb \times σNPPb + 2 \times DB \times σNPPb + 2 \times UG \times σNPPb + 2 \times LB \times σNPPb + 2 \times 2 \times DB \times σNPPb}

b σRH = \sqrt{LB^2 + LB^2 + σDB^2 + σUG^2 + 2 \times LB \times σRHb + 2 \times DB \times σRHb + 2 \times UG \times σRHb + 2 \times LB \times σRHb + 2 \times 2 \times DB \times σRHb}

c σNEP = \sqrt{σNPPb^2 + σRHb^2 + 2 \times σLb \times σNEPb + 2 \times σRb \times σNEPb + 2 \times DB \times σNEPb + 2 \times UG \times σNEPb + 2 \times LB \times σNEPb + 2 \times 2 \times DB \times σNEPb}

d Measured in 2004 and 2007 and linearly interpolated for other years.

inventory data. However, more research is required to confirm this observation in other forest ecosystems.

4.3. Biometric and EC-based inter-annual variability

Similar to our study, consistency in the relative inter-annual change was reported by previous comparison studies (Ehman et al., 2002; Ohtsuka et al., 2009). Highest forest productivity during normal years (as suggested by both methods for 2008 in this study) might be the result of an adaptation process in which forest ecosystems adjust their optimum productivity to the respective normal regional climate conditions. The observed negative response of NPP to air temperature is reverse to the common understanding of forest NPP-climate response (Luyssaert et al., 2007) and may have been caused by drought and/or heat stress limiting NPP during the warmer years (Ciais et al., 2005; Arain et al., submitted for publication). For similar reasons we may have obtained a negative relationship of NEP with growing season temperature, while other studies have reported a positive (Curtis et al., 2002) or no relationship (Law et al., 2002; Luyssaert et al., 2007).

Autocorrelation effects between RAEC and GPP[J] may explain why inter-annual patterns in RE(J) followed patterns in GPP[J]. In contrast, RE(EC) estimates were rather constant among years, likely because soil temperature showed little inter-annual variation. Inter-annual variation in NEP[J] was driven by tree NPP because RH was little affected by climate variability in our study, which is similar to findings by Ohtsuka et al. (2009). In contrast, Ehman et al. (2002) reported that differences in heterotrophic soil respiration were responsible for inter-annual changes in NEP.

4.4. Multi-year convergence of biometric and EC-based NEP estimates

Previous comparison studies using multi-year data observed convergence of biometric and EC-based NEP estimates over several years (Barford et al., 2001; Gough et al., 2008). These and other studies (Curtis et al., 2002; Keith et al., 2009) argue that assimilates obtained in autumn and used for stem growth during spring of the following year cause discrepancies between NEP[J] and NEP(EC) estimates on annual basis. Similar observations at our two oldest sites showing little tree growth relative to total ecosystem C assimilation during October support this idea. The discrepancy of about ±50 g between GPP and tree NPP in October could possibly explain annual differences in NEP[J] and NEP(EC) at our mature site.

At the two middle-age stands however, our study suggests a somewhat constant offset between NEP[J] and NEP(EC) rather than convergence over four years. Similarly, Ehman et al. (2002), Keith et al. (2009) and Black et al. (2005) reported annual NEP[J] to exceed NEP(EC) in both years of their 2-year comparisons. Kominami et al. (2008) and Curtis et al. (2002) found poor agreement between both methods over three or more years. Ohtsuka et al. (2009) did not observe any convergence over eight years. Error due to method-specific issues in either the biometric (e.g. choice of allometric biomass equation, indirect estimate of NPPFC) or EC method (e.g. choice of u-threshold, advection loss etc) may therefore likely exceed errors from the lag in C allocation and therefore be primarily responsible for constant differences between NEP[J] and NEP(EC).

4.5. Ecosystem C use efficiency and C allocation

Our estimates of CUE(J) based on NPP[J]:GPP(EC) and NPP(EC):GPP(EC) were within the commonly reported range of 0.40–0.70 (Waring et al., 1998; Litton et al., 2007), except for TP89, where low CUE(J) may have resulted from an underestimation of NPP[J] or overestimation of GPP(EC).

The range of CUE(J) observed in our study (−0.26 to 0.40) is consistent with the range of −0.20 to 0.45 reported for other conifer forests (Law et al., 2002). The age-related decrease of CUE(J) and NEP:RE, as well as the increase of RH:NPP across the three older age-sequence sites may be primarily controlled by differences in site productivity. It suggests that the C sequestration potential in both soil and aboveground forest ecosystem decreased following the initial two decades of stand establishment in our age-sequences stands. In contrast, Schwalm et al. (2007) found a continuous increase of CUE(J) and NEP:RE, and a decrease of RH:NPP over the initial 50 years in a Douglas-fir chronosequence. Besides site productivity as controlling factor, differences in the temporal development of these ratios between our and their study may also be related to contrasting stand establishment regimes (afforestation of agricultural land vs. regeneration of a clear-cut in a commercial forest). In addition, lower CUE(J) and higher RH:NPP in the two oldest stands during dry and warm years compared to years with sufficient water availability implies that the net C sequestration potential was sensitive to changes in temperature and precipitation patterns and their effects on forest productivity.
The observed increase of RH across our age-sequence is in contrast to findings by Pregitzer and Euskirchen (2004) who reported a decrease in RH with stand age in temperate forests. Smaller initial woody debris pools in our afforestation stands compared to forests regenerating after natural disturbance or harvest may explain these contrasting findings on the successional development of RH.

Greater TBCF in less productive years and forest stands as observed in our study is consistent with previous studies suggesting a dependency of the TBCF:GPP ratio on resource (water and nutrient) availability (Litton et al., 2007; Keith et al., 2009).

4.6. Successional variation in NEP and C sequestration potential

A peak of NEP in middle-age stands with a subsequent decrease with stand age as suggested by both methods in our study is well documented by previous studies (Pregitzer and Euskirchen, 2004; Baldocchi, 2008). The peak in annual NEP at the 19-year-old site (TP89) in our age-sequence may be the result of either a stand age effect and/or greater site quality at this particular site as further discussed in Peichl et al. (submitted for publication).

Our estimated mean C sequestration over 70 years (175 t C ha\(^{-1}\)) is considerably larger compared to 21 t C ha\(^{-1}\) reported over a 56-year-rotation in a clear-cut Douglas-fir chronosequence (Schwalm et al., 2007), demonstrating the large C sequestration potential of afforestation projects. For further comparison, Pregitzer and Euskirchen (2004) suggested a mean of 106 t C ha\(^{-1}\) sequestered in maturing (31–70 years old) temperate forests, while Hooker and Compton (2003) suggested 150 t C ha\(^{-1}\) accumulating over 70 years in biomass and soil of a white pine chronosequence. The discrepancies among method-specific C sequestration estimates over the forest maturing phase in our study highlight the importance of constraining C budget estimates using independent methods.

5. Conclusions

We determined biometric (B) and eddy-covariance (EC) estimates of C fluxes in an age-sequence (6-, 19-, 34-, and 69-years-old in 2008) of pine forests over a period of four years (2005–2008) to compare biometric and EC-based estimates of gross primary production (GPP), net primary production (NPP), ecosystem respiration (RE) and net ecosystem productivity (NEP), and to constrain C allocation dynamics and C budgets across the age-sequence. Based on our findings, we conclude:

- The contribution of individual NPP and respiration component fluxes varied considerably across the age-sequence and thereby introduced various levels of uncertainty into NPP and NEP estimates depending on forest development stage. A good understanding of uncertainties in biometric NPP estimates is necessary for validation of terrestrial ecosystem models to estimate regional and global C-budgets.

- NEP(B) and NEP(EC) were similar at the seedling and the mature site, but differed by a constant offset in the two middle-age stands. In these cases, method-specific issues in either the biometric (e.g. choice of allometric equation, uncertainty of net fine root production estimates) or EC method (e.g. choice of u-threshold, unaccounted advective processes and uncertainty due to gap-filling, etc.) may have affected the comparison. Inter-comparison of the component fluxes GPP and RE offered the possibility to detect sources of divergence in NEP estimates. Overall, no multi-year convergence of NEP(B) and NEP(EC) occurred over the four-year study period.

- Biometric and EC estimates agreed reasonably well on inter-annual changes in GPP and NEP suggesting highest forest productivity and net C sequestration rates in years with normal climate conditions, and lowest rates in warm and dry years.

- Correlations of NEP-GPP, RH-NPP, RA:RH and TBCF-GPP ratios to forest productivity resulted in inter-annual and age-related patterns across the age-sequence sites suggesting that C sequestration potentials in both soil and aboveground forest ecosystem where greater in higher productive years and stands. We therefore conclude that climate and stand age effects on forest productivity may cause considerable alterations of forest C allocation patterns.

- Aggregated C sequestration across the age-sequence (over 70 years) differed considerably between the biometric and EC-based estimates. Cross-validation of individual methods is therefore imperative to constrain C budget estimates on ecosystem and regional to global scale.

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