

## 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  $175 \pm 48\ t\ C\ ha^{-1}$ . 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 ( $CO_2$ ) with the atmosphere via 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  $CO_2$  (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  $CO_2$ .

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; Luysaert et al., 2007).

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### Nomenclature

$B_T$	Aboveground tree biomass (foliage + living branches + stem) ( $\text{gC m}^{-2}$ )
$D_B$	Mass of dead branches attached to tree stem ( $\text{gC m}^{-2}$ )
$D_S$	Mass of dead standing tree stems (snags) ( $\text{gC m}^{-2}$ )
$G$	Ground vegetation biomass (height <1.3m) ( $\text{gC m}^{-2}$ )
$H$	Herbivory loss ( $\text{gC m}^{-2} \text{y}^{-1}$ )
$h$	Tree height (m)
$L_F$	Litterfall (<1 cm) ( $\text{gC m}^{-2} \text{y}^{-1}$ )
$L_B$	Branchfall ( $\geq 1$ cm) ( $\text{gC m}^{-2} \text{y}^{-1}$ )
$S$	Stem density (trees $\text{ha}^{-1}$ )
$U$	Understorey biomass (DBH <9 cm, height $\geq 1.3$ m) ( $\text{gC m}^{-2}$ )
$V$	Stem volume ( $\text{m}^3$ )
BEF	Biomass expansion factor ( $\text{t m}^{-3}$ )
DBH	Diameter at breast height (cm)
ANPP	Aboveground net primary production ( $\text{gC m}^{-2} \text{y}^{-1}$ )
BNPP	Belowground net primary production ( $\text{gC m}^{-2} \text{y}^{-1}$ )
GPP	Gross primary production ( $\text{gC m}^{-2} \text{y}^{-1}$ )
NEE	Net ecosystem exchange of $\text{CO}_2$ ( $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ )
NEP	Net ecosystem production ( $\text{gC m}^{-2} \text{y}^{-1}$ )
NPP <sub>CR</sub>	Coarse root production ( $\text{gC m}^{-2} \text{y}^{-1}$ )
NPP <sub>FR</sub>	Net fine root litter production ( $\text{gC m}^{-2} \text{y}^{-1}$ )
NPP	Net primary production ( $\text{gC m}^{-2} \text{y}^{-1}$ )
$R_S$	Soil respiration ( $\text{gC m}^{-2} \text{y}^{-1}$ )
RH <sub>LFH</sub>	Heterotrophic respiration from forest floor (LFH-layer) ( $\text{gC m}^{-2} \text{y}^{-1}$ )
$R_M$	Heterotrophic respiration from mineral soil ( $\text{gC m}^{-2} \text{y}^{-1}$ )
RA	Autotrophic respiration ( $\text{gC m}^{-2} \text{y}^{-1}$ )
RA <sub>R</sub>	Autotrophic root respiration ( $\text{gC m}^{-2} \text{y}^{-1}$ )
RA <sub>C</sub>	Autotrophic canopy (foliage + living branches + stem) respiration ( $\text{gC m}^{-2} \text{y}^{-1}$ )
RE	Ecosystem respiration ( $\text{gC m}^{-2} \text{y}^{-1}$ )
RH	Heterotrophic respiration ( $\text{gC m}^{-2} \text{y}^{-1}$ )
RH <sub>S</sub>	Heterotrophic respiration from soil ( $\text{gC m}^{-2} \text{y}^{-1}$ )
RH <sub>WD</sub>	Heterotrophic respiration from aboveground woody debris ( $\text{gC m}^{-2} \text{y}^{-1}$ )
TBCF	Total belowground carbon flux ( $\text{gC m}^{-2} \text{y}^{-1}$ )

#### Subscript

(B)	Biometric approach, e.g. NEP <sub>(B)</sub>
(EC)	Eddy-covariance approach; e.g. NEP <sub>(EC)</sub>

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 (Luyssaert et al., 2007; Baldocchi, 2008; Thum et al., 2008). However, because EC measurements are usually not 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°71'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-

acteristics 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 CO<sub>2</sub> (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 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 by 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 CO<sub>2</sub> 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. P 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)).

$$\text{ANPP} = B + D + H \quad (1)$$

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

$$B = \Delta B_T + \Delta U + \Delta G \quad (2)$$

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)).

$$B_{T(i)} = c(\text{DBH})^a \times S \quad (3a)$$

where  $B_T$  is biomass in kilograms (kg) of the aboveground tree component  $i$  ( $i$ =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 ( $D_{\text{base}}$ ):

$$B_{T(i)} = c(D_{\text{base}})^a \times S \quad (3b)$$

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 understory 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*) understory 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 ( $\text{NPP}_{\text{tree}}$ ). 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 (LFH-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) ( $L_F$ ), branch-fall ( $\geq 1$  cm) ( $L_B$ ), and the change in mass of dead standing tree ( $D_S$ ) and dead branches ( $D_B$ ) 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  $D_B$  was determined with site-specific allometric equations (Peichl and Arain, 2007). The change in  $D_S$  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 (NPP<sub>CR</sub>;  $\geq 2$  mm) and net fine root production (NPP<sub>FR</sub>; <2 mm) (Eq. (4)).

$$\text{BNPP} = \text{NPP}_{\text{CR}} + \text{NPP}_{\text{FR}} \quad (4)$$

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

$$B_R = c(\text{DBH})^a \times S \quad (5)$$

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 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 (RA<sub>R</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 (Litton 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 ( $R_S$ ) was measured as part of a separate study across the Turkey Point age-sequence stands as described in Khomik et al. (2009). In brief,  $R_S$  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 (RH<sub>S</sub>) and root autotrophic (RA<sub>R</sub>) respirations 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 (RH<sub>LFH</sub>) and from mineral soil (RH<sub>M</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  $R_S$  component fluxes (Khomik et al., 2009; Khomik and Arain, submitted for publication).

Autotrophic aboveground canopy respiration (RA<sub>C</sub>; including foliage, branch, and stem respiration) was derived by subtracting RA<sub>R</sub> from RA, with RA being the difference between GPP and NPP (see Section 2.5 below). This caused some autocorrelation between RA<sub>C</sub> and GPP, however, it ensured the closure of the biometric C budget. Aboveground heterotrophic respiration from decomposing woody debris and dead standing trees (RH<sub>WD</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 (RH) was determined as the sum of RH<sub>S</sub> and RH<sub>WD</sub>. The sum of RA and RH component fluxes resulted in a biometric estimate of ecosystem respiration (RE<sub>(B)</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 net 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

**Table 1**  
(a) Mean annual (A) and growing season (GS; DOY 92–305) air temperature ( $T_a$ , °C) and precipitation ( $P$ ; mm) from 2005 to 2008 with 30-year normal for  $T_a$  and  $P$ , and (b) growing season means of soil temperature at 5 cm depth ( $T_s$ ; °C), volumetric soil water content (VWC) in 0–20 cm soil depth, and photosynthetically active radiation (PAR;  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) at the four age-sequence sites from 2005 to 2008; N.A. not available.

Year	$T_a$		$P$									
	A	GS	A	GS								
(a)												
2005	9.1	16.6	862	477								
2006	9.8	15.6	1187	777								
2007	8.5	15.6	705	436								
2008	7.9	14.6	1021	503								
30-year normal	7.8	13.2	1010	606								
Year	$T_s$				VWC				PAR			
	TP02	TP89	TP74	TP39	TP02	TP89	TP74	TP39	TP02	TP89	TP74	TP39
(b)												
2005	20.2	11.5	15.2	14.4	0.10	0.11	0.10	0.11	460	427	438	459
2006	19.0	11.6	14.9	14.2	0.12	0.13	0.12	0.11	404	390	405	413
2007	19.2	12.4	14.9	14.4	0.10	0.12	0.09	0.09	453	425	445	461
2008	17.5	N.A.	14.2	13.4	0.10	N.A.	0.09	0.12	460	N.A.	433	453

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 ( $\text{NEP}_{(B)}$ ) was calculated from  $\text{NPP}_{(B)}$  minus C losses via RH. Half-hourly NEE from EC measurements was summed up and converted to annual NEP estimates ( $\text{NEP}_{(EC)}$ ; 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  $\text{GPP}_{(EC)}$ ,  $\text{RE}_{(EC)}$  and  $\text{NEP}_{(EC)}$ . Based on the site-specific gap frequency, gap length and flux magnitude, the average (2005–2008) uncertainty of  $\text{NEP}_{(EC)}$  was estimated as  $\pm 29$ , 56, 85, and  $40 \text{ g C m}^{-2} \text{ y}^{-1}$  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 ( $\sigma_{LB}$ ) was computed from (a) the error in annual DBH increment estimates ( $\sigma_D$ ), (b) the error of the allometric biomass equation ( $\sigma_{EQ}$ ), 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 ( $\sigma_{DBH}$ ), mean tree height ( $\sigma_H$ ), and stem density ( $\sigma_{SD}$ ) resulting from differences among sample plots. The propagation of these error terms resulted in an estimate of  $\sigma_{LB}$  (Eq. (6)).

Uncertainty of NPP ( $\sigma_{NPP}$ ) was estimated as the propagated sum of  $\sigma_{LB}$ , the SV of the changes in the amount of dead standing trees ( $\sigma_{DB}$ ) and understorey/ground vegetation biomass ( $\sigma_{UG}$ ), the SV of annual litter- and branch-fall ( $\sigma_L$ ), and the uncertainty around net fine root production ( $\sigma_{FR}$ ) (Eq. (7)). Estimates of  $\sigma_{FR}$  were derived from the SD around the mean of the three different approaches estimating  $\text{NPP}_{FR}$ .

$$\sigma_{LB} = \sqrt{\sigma_D^2 + \sigma_{EQ}^2 + \sigma_{DBH}^2 + \sigma_H^2 + \sigma_{SD}^2} \quad (6)$$

$$\sigma_{NPP} = \sqrt{\sigma_{LB}^2 + \sigma_{DB}^2 + \sigma_{UG}^2 + \sigma_L^2 + \sigma_{FR}^2} \quad (7)$$

The uncertainty of the annual  $\text{RH}_S$  ( $\sigma_{RH_S}$ ) and  $\text{RA}_R$  ( $\sigma_{RA_R}$ ) was determined from the mean square error given by the model output for the respective respiration model. Uncertainty of  $\text{RH}_{WD}$  ( $\sigma_{RH_{WD}}$ ) was determined from SV of woody debris stock mass. The propagated sum of  $\sigma_{RH_{WD}}$  and  $\sigma_{RH_S}$  resulted in an uncertainty estimate for RH ( $\sigma_{RH}$ ). Finally, the uncertainty in biometric NEP estimates ( $\sigma_{NEP}$ ) was calculated from the propagation of  $\sigma_{NPP}$  and  $\sigma_{RH}$  (Eq. (8)).

$$\sigma_{NEP} = \sqrt{\sigma_{NPP}^2 + \sigma_{RH}^2} \quad (8)$$

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  $\text{GPP}_{(B)}$  as proposed by DeLucia et al. (2007). Because of the dependency of  $\text{RA}_C$  on  $\text{GPP}_{(B)}$ , we also assumed a 20% error for  $\text{RA}_C$  ( $\sigma_{RA_C}$ ). The uncertainty of  $\text{RE}_{(B)}$  was calculated from the error propagation of  $\sigma_{RH}$  and  $\sigma_{RA}$ .

## 3. Results

### 3.1. Climate and environmental conditions

A comparison of annual mean air temperature ( $T_a$ ) and precipitation ( $P$ ) over the study period (2005–2008) to 30-year norms identified 2005 as hot and dry, 2006 as hot and wet, 2007 as warm and dry, and 2008 as a normal year Table 1a. Average growing season soil temperature ( $T_s$ ) 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 2**  
Carbon pools ( $\text{tC ha}^{-1}$ ) at the four age-sequence sites in 2007.

Carbon pool	TP02	TP89	TP74	TP39
Aboveground tree	5 ± 0.9	41 ± 5	56 ± 7	112 ± 19
Understorey <sup>a</sup>	0	2 ± 0.7	2 ± 0.4	5 ± 0.5
Ground vegetation <sup>b</sup>	0.9 ± 0.4	0.1 ± 0.05	0.2 ± 0.2	0.3 ± 0.2
Coarse roots (>2 mm)	2 ± 0.5	9 ± 2	10 ± 2	28 ± 4
Woody debris <sup>c</sup>	0.4 ± 0.2	1.3 ± 0.3	2.9 ± 1.8	6.2 ± 2.7
Forest floor (LFH-layer)	0.9 ± 0.3	7.2 ± 0.9	4.1 ± 0.7	8.5 ± 2.0
Total	9.2 ± 1.2	61 ± 5.5	75 ± 7.6	160 ± 20

<sup>a</sup> Understorey includes all trees with DBH < 9 cm.

<sup>b</sup> Ground vegetation is the sum of shrubs and trees with height < 1.3 m, herbs, and moss.

<sup>c</sup> Woody debris includes fine, small, coarse woody debris and standing dead trees.

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  $9.2 \text{ tC ha}^{-1}$  at the seedling site TP02 to 61, 75 and  $160 \text{ tC ha}^{-1}$  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 2008 and 2005, respectively. Mean  $\text{NPP}_{\text{CR}}$  was greater in the two younger stands compared to the two older stands. However, BNPP peaked at TP74 due to greater  $\text{NPP}_{\text{FR}}$ . Whereas heterotrophic respiration component fluxes  $\text{RH}_5$  and  $\text{RH}_{\text{WD}}$  both increased with stand age, RA peaked at TP89 due to greatest  $\text{RA}_{\text{C}}$ . Mean  $\text{RA}_{\text{R}}$  was slightly higher in the two younger sites compared to the two older sites.

The relative contribution of stem wood production to total tree biomass production increased with stand age from 27% at TP02 to 55% at TP39, whereas the contribution of foliage production decreased with stand age from 34% at TP02 to 2% at TP39 (Fig. 1a). Branch biomass production was considerable at the two middle-aged stands TP89 (33%) and TP74 (27%). The relative contribution of  $\text{NPP}_{\text{CR}}$  ranged from 16% at TP74 to 28% at TP39.

The contribution of aboveground tree biomass production to NPP decreased with stand age from 51% at TP02 to 21% at TP39

(Fig. 1b). Ground vegetation growth at TP02 (30% of NPP), litter-fall at the three older sites (25–46% of NPP), and  $\text{NPP}_{\text{FR}}$  at TP74 (29% of NPP), were additional important components of NPP. The relative contribution of  $\text{NPP}_{\text{CR}}$  decreased from 17% at TP02 to <10% at the two oldest forest stands.

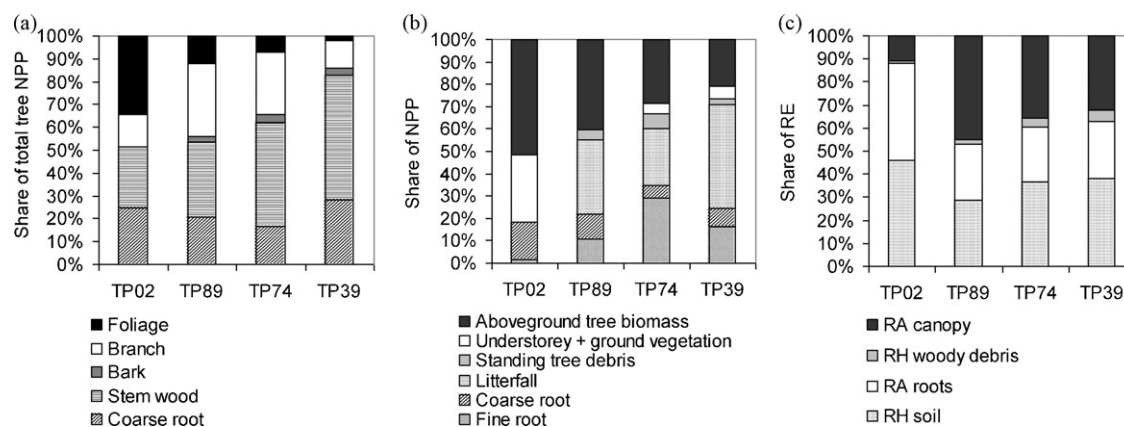
The greatest variation amongst RE component fluxes were observed for  $\text{RA}_{\text{C}}$  ranging from 14% at TP02 to 53% at TP89 (Fig. 1c). While belowground respiration dominated RE at TP02 (85%), its contribution decreased to 45–60% in the three older stands.

### 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,  $\text{GPP}_{\text{EC}}$  exceeded  $\text{GPP}_{\text{B}}$  at TP89.  $\text{RE}_{\text{B}}$  and  $\text{RE}_{\text{EC}}$  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,  $\text{RE}_{\text{EC}}$  was considerably greater than  $\text{RE}_{\text{B}}$  at TP89, whereas  $\text{RE}_{\text{EC}}$  was smaller than  $\text{RE}_{\text{B}}$  at TP74.  $\text{NEP}_{\text{B}}$  and  $\text{NEP}_{\text{EC}}$  agreed well at TP02 and TP39 in 2005 and 2006 but slightly diverged in 2007 and 2008.  $\text{NEP}_{\text{EC}}$  exceeded  $\text{NEP}_{\text{B}}$  at TP89 whereas  $\text{NEP}_{\text{B}}$  exceeded  $\text{NEP}_{\text{EC}}$  at TP74.

Ratios of  $\text{NEP}_{\text{B}}:\text{NEP}_{\text{EC}}$  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  $\text{NEP}_{\text{B}}:\text{NEP}_{\text{EC}}$  with time towards unity occurred at TP74, overall we did not observe multi-year convergence of  $\text{NEP}_{\text{B}}$  and  $\text{NEP}_{\text{EC}}$ .

A strong correlation between annual  $\text{NEP}_{\text{EC}}$  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).



**Fig. 1.** Relative contribution of (a) individual tree component biomass production to total tree NPP ( $\text{NPP}_{\text{tree}}$ ) and (b) NPP component fluxes to NPP, and (c) ecosystem respiration component fluxes to  $\text{RE}_{\text{B}}$  at the four age-sequence sites TP02, TP89, TP74, and TP39 as a mean of four years (2005 to 2008).

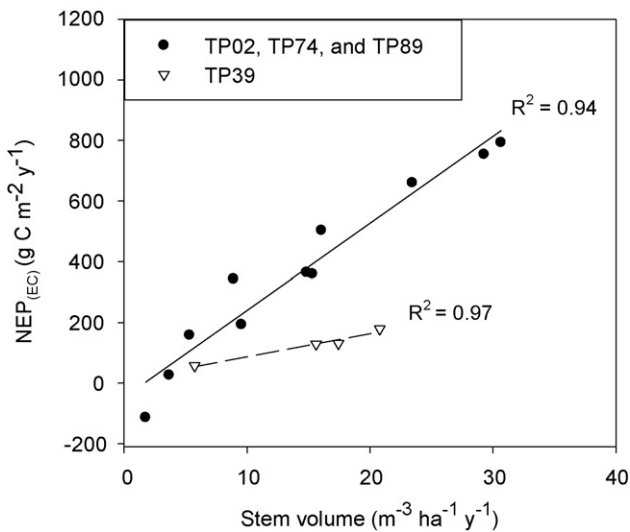
**Table 3**  
Biometric (B) and eddy-covariance (EC) based estimates of annual above- and below-ground C fluxes ( $\text{g C m}^{-2} \text{y}^{-1}$ ) at the four Turkey Point pine forest ecosystems.

Site	TP02					TP89					TP74					TP39				
	2005	2006	2007	2008	Mean	2005	2006	2007	2008	Mean	2005	2006	2007	2008	Mean	2005	2006	2007	2008	Mean
<i>Net primary production</i>																				
Foliage	53	82	78	151	91	47	56	48	66	54	10	18	14	18	15	1	5	3	5	3
Living branches	21	34	33	64	38	117	143	133	182	144	36	65	52	67	55	7	31	20	32	23
Stem bark	N.A.	N.A.	N.A.	N.A.	N.A.	10	11	8	12	10	6	10	3	7	7	3	6	2	11	5
Stem wood	39	64	63	125	72	133	154	126	172	146	74	132	65	105	94	39	132	72	163	101
Aboveground tree	112	178	172	338	200	293	345	297	406	335	128	228	137	199	173	50	173	97	209	132
Understorey (U) + Ground veg. (G) <sup>a</sup>	82	101	120	125	107	0.4	0.4	0.4	0.4	0.4	25	25	25	25	25	32	32	32	32	32
Herbivory (H)	0.5	1.0	1.6	2.6	1.4	3.8	4.2	4.5	5.0	4.4	2.1	2.2	2.3	2.4	2.2	2.4	2.4	2.3	2.2	2.3
Coarse root ( $\geq 2$ mm)	38	58	56	108	65	79	95	84	115	93	25	44	27	39	34	17	71	45	74	52
Fine roots (<2 mm)	6	6	6	6	6	87	81	100	87	89	177	172	167	170	171	89	110	101	83	96
Standing woody debris ( $D_B + D_S$ )	0	0	0	0	0	32	37	45	37	38	15	28	58	61	40	30	16	8	12	17
Litterfall ( $L_F + L_B$ )	N.A.	N.A.	N.A.	N.A.	N.A.	282	288	253	281	276	143	143	161	154	150	290	229	271	310	275
ANPP	195	280	294	466	309	612	675	601	729	654	313	425	383	441	391	404	452	409	564	457
BNPP	43	64	61	114	71	166	175	184	197	181	202	216	194	197	202	107	180	144	149	145
TBCF	322	359	332	421	358	494	494	482	401	468	476	486	435	421	454	394	467	403	366	407
NPP <sub>(B)</sub>	238	344	355	579	379	778	850	785	926	835	515	641	577	638	593	511	632	554	713	603
NPP <sub>(EC)</sub>	202	328	471	470	368	1059	1142	1205	N.A.	1135	784	929	791	766	818	532	602	614	629	594
<i>Gross primary production</i>																				
GPP <sub>(B)</sub>	523	733	756	1232	811	1655	1808	1671	1971	1776	1095	1364	1228	1383	1268	1088	1345	1178	1517	1282
GPP <sub>(EC)</sub> <sup>b</sup>	435	610	706	688	610	2339	2359	2637	N.A.	2445	1122	1261	1116	1237	1184	1238	1457	1371	1561	1407
<i>Ecosystem respiration</i>																				
R <sub>S</sub>	600	591	577	578	587	704	682	683	563	658	678	657	632	582	637	710	706	690	614	680
R <sub>LH</sub>	N.A.	N.A.	N.A.	N.A.	N.A.	134	134	140	132	135	97	98	101	93	97	137	139	142	133	138
R <sub>M</sub>	312	296	307	270	296	242	229	246	227	236	306	290	291	265	288	287	280	290	264	280
R <sub>AR</sub>	278	295	271	307	288	328	319	298	204	287	274	269	241	224	252	287	287	258	217	262
R <sub>AC</sub>	7	94	130	346	144	549	639	588	840	654	306	454	410	496	416	290	426	366	587	417
R <sub>A</sub>	285	388	401	653	432	877	958	886	1044	941	580	723	651	720	668	576	713	624	804	679
R <sub>H<sub>S</sub></sub>	312	296	307	270	296	376	363	386	359	371	403	388	391	358	385	423	418	432	397	418
R <sub>H<sub>WD</sub></sub>	5	6	7	7	6	23	25	27	29	26	37	38	41	44	40	52	52	53	53	53
R <sub>H</sub>	316	302	313	277	302	399	388	412	388	397	441	426	432	402	425	475	471	485	450	470
RE <sub>(B)</sub>	601	690	714	930	734	1276	1346	1298	1432	1338	1021	1149	1083	1122	1094	1052	1184	1109	1254	1150
RE <sub>(EC)</sub> <sup>b</sup>	558	565	579	495	549	1671	1657	1823	NA	1717	782	753	763	920	814	1159	1294	1214	1379	1263
<i>Net ecosystem production</i>																				
NEP <sub>(B)</sub>	-78	42	42	302	77	379	462	373	539	438	74	215	145	236	167	36	161	69	263	132
NEP <sub>(EC)</sub> <sup>b</sup>	-114	26	158	193	66	660	754	793	NA	736	343	503	359	364	392	57	131	129	179	124
NEP <sub>(EC)</sub> <sup>c</sup>	-126	34	164	184	64	684	708	826	NA	739	346	511	366	296	380	36	148	120	177	120

<sup>a</sup> Measured in 2004 and 2007 and linearly interpolated for other years at TP89, TP74 and TP39.

<sup>b</sup> Calculated for the biological year (November 1 to October 31).

<sup>c</sup> Calculated for the EC year (January 1 to December 31) (Arain et al., submitted for publication).



**Fig. 2.** Relationship between  $NEP_{(EC)}$  and annual stem volume increments ( $m^{-3} ha^{-1} y^{-1}$ ).

**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  $150\text{--}300\text{ g C m}^{-2} y^{-1}$  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 GPP estimate for 2007 at that site ( $GPP_{(EC)}$  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.

**Table 4**

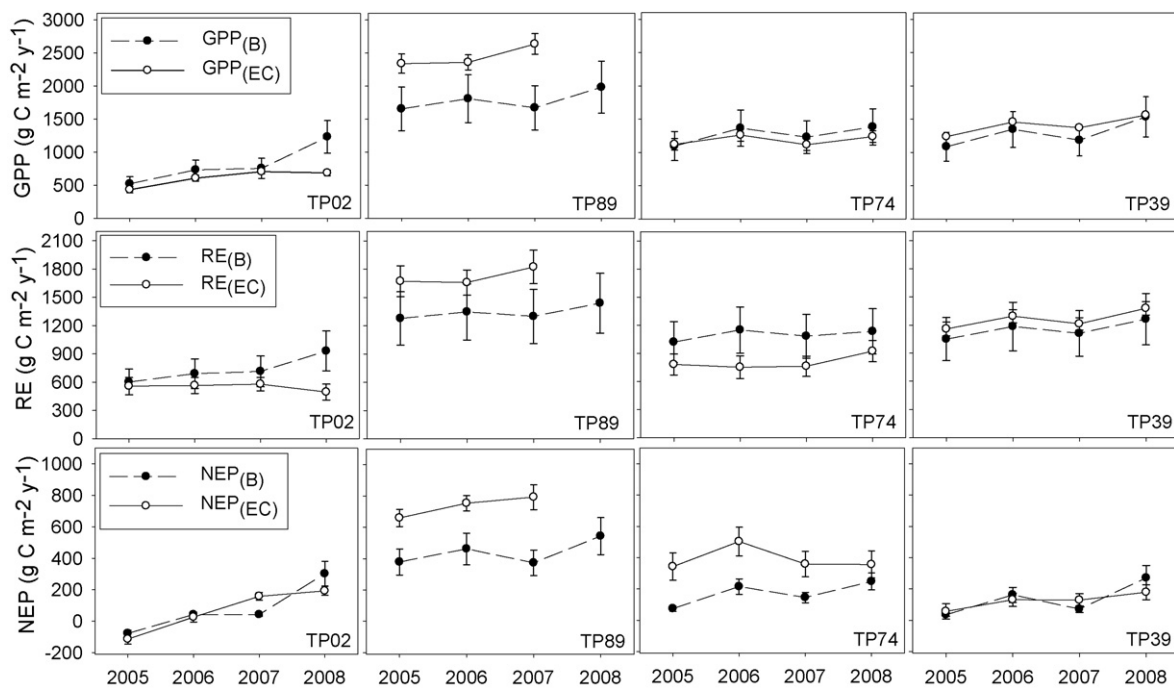
$NEP_{(B)}:NEP_{(EC)}$  ratios aggregated over periods of 1 to 4 years at the four age-sequence stands.

Period	TP02	TP89	TP74	TP39
1 year (2005)	0.68	0.57	0.22	0.62
2 years (2005–2006)	0.40	0.59	0.34	1.05
3 years (2005–2007)	0.09	0.55	0.36	0.85
4 years (2005–2008)	1.17	N.A.	0.43	1.09

Inter-annual patterns in  $RE_{(B)}$  suggested a reduction in RE of about  $50\text{ to }150\text{ g C m}^{-2} y^{-1}$  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  $50\text{ to }150\text{ g C m}^{-2} y^{-1}$  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.



**Fig. 3.** Inter-annual variability of GPP (upper row), RE (middle row), and NEP (bottom row) estimates from biometric (B) data (filled circles) and eddy-covariance (EC) data (open circle) at the four TP age-sequence sites TP02, TP89, TP74, and TP39 in 2005–2008. Error bars for EC and biometric estimates of GPP, RE, and NEP based on computations described in Section 2.6.



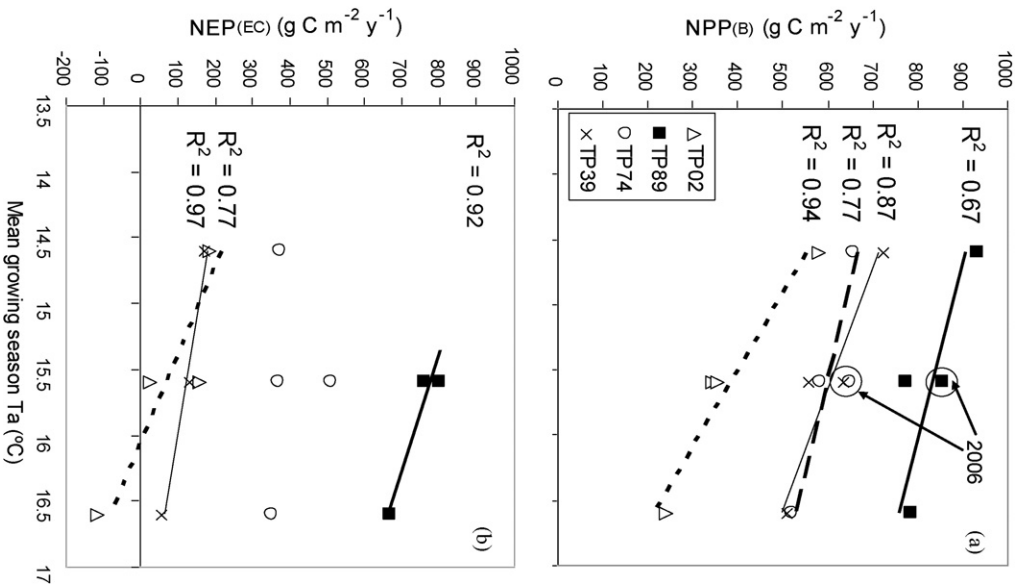
**Table 5**

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.

Ratio	TP02					TP89					TP74					TP39				
	2005	2006	2007	2008	Mean	2005	2006	2007	2008	Mean	2005	2006	2007	2008	Mean	2005	2006	2007	2008	Mean
<i>Biometric</i>																				
$NPP_{(B)}:GPP_{(EC)}^a$	0.55	0.56	0.50	0.84	0.61	0.33	0.36	0.30	N.A.	0.33	0.46	0.51	0.52	0.53	0.50	0.41	0.43	0.41	0.46	0.43
$NEP_{(B)}:GPP_{(B)}$	-0.15	0.06	0.06	0.24	0.05	0.23	0.26	0.22	0.27	0.25***	0.07	0.16	0.12	0.18	0.13**	0.03	0.12	0.06	0.18	0.10*
$NEP_{(B)}:RE_{(B)}$	-0.13	0.06	0.06	0.32	0.08	0.30	0.34	0.29	0.38	0.33***	0.07	0.19	0.13	0.22	0.15**	0.03	0.14	0.06	0.21	0.11*
$RH:NPP_{(B)}$	1.31	0.86	0.86	0.47	0.87	0.48	0.43	0.49	0.39	0.45*	0.78	0.60	0.68	0.55	0.65**	0.83	0.66	0.78	0.55	0.70***
<i>EC</i>																				
$NPP_{(EC)}:GPP_{(EC)}$	0.47	0.54	0.67	0.68	0.59	0.45	0.48	0.46	N.A.	0.46	0.70	0.74	0.71	0.62	0.69	0.43	0.41	0.45	0.40	0.42
$NEP_{(EC)}:GPP_{(EC)}$	-0.26	0.04	0.22	0.28	0.07	0.28	0.32	0.30	N.A.	0.30	0.31	0.40	0.32	0.29	0.33	0.05	0.09	0.09	0.11	0.09
$NEP_{(EC)}:RE_{(EC)}$	-0.20	0.05	0.28	0.38	0.13	0.40	0.45	0.44	N.A.	0.43	0.44	0.67	0.48	0.38	0.49	0.05	0.10	0.11	0.13	0.10
$RH:NPP_{(EC)}$	1.54	0.90	0.65	0.58	0.92	0.36	0.32	0.32	N.A.	0.33*	0.51	0.42	0.49	0.47	0.47**	0.80	0.70	0.70	0.63	0.71***
$RA:RH$	0.9	1.3	1.3	2.4	1.5	2.2	2.5	2.1	2.7	2.4***	1.3	1.7	1.5	1.8	1.6**	1.2	1.5	1.3	1.8	1.4*
$TBCF:GPP_{(EC)}$	0.74	0.59	0.47	0.61	0.60	0.22	0.21	0.18	N.A.	0.20	0.42	0.38	0.39	0.35	0.39	0.32	0.32	0.30	0.24	0.29
$ANPP:BNPP$	4.5	4.4	4.8	4.1	4.4	3.7	3.9	3.3	3.6	3.6	1.6	2.0	2.0	2.1	1.9	3.8	2.5	2.8	3.6	3.2

\*/\*\*/\*\*\* 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.

<sup>a</sup> Because of the assumption  $GPP_{(B)} = 2.13 \times NPP_{(B)}$ ,  $GPP_{(EC)}$  was used to estimate the biometric plant C use efficiency ratio.



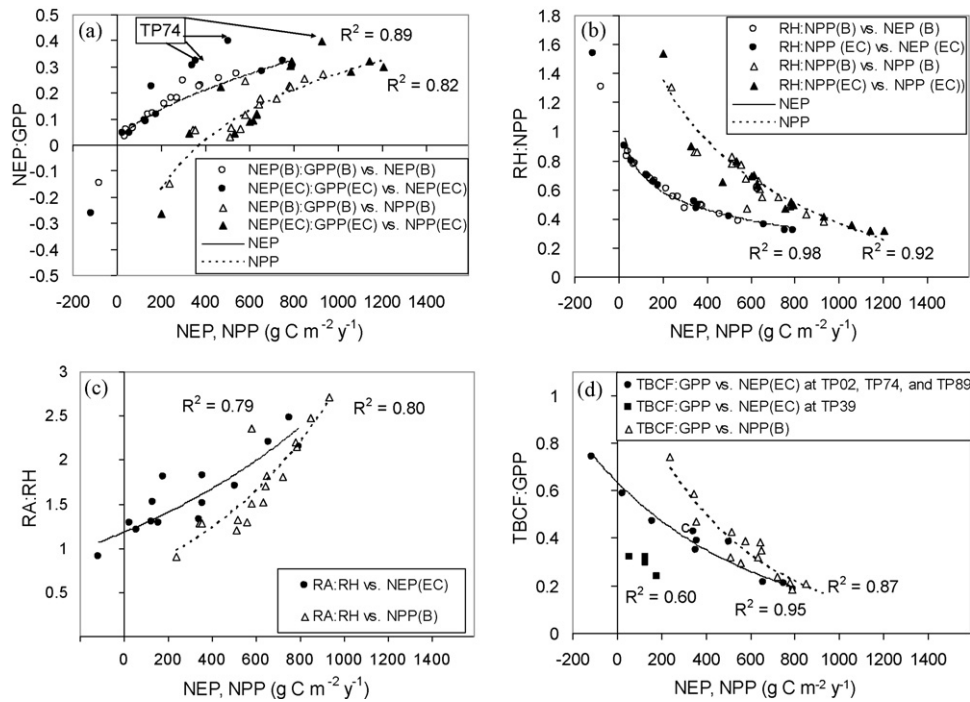
**Fig. 4.** Relationship between mean growing season air temperature ( $T_a$ ) with (a) annual net primary productivity (NPP) and (b) annual net ecosystem productivity (NEP) across the forest age-sequence.

### 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-sequence for both the biometric and EC (by excluding TP74) methods (Fig. 5a). A similar positive correlation was observed between  $NEP:RE$  and forest productivity (data not shown).

Both methods indicated that mean soil C gain or loss as indicated by the ratio of  $RH:NPP$  was somewhat in balance (ratio close to 1.0) at the seedling site TP02, but increased with stand age from



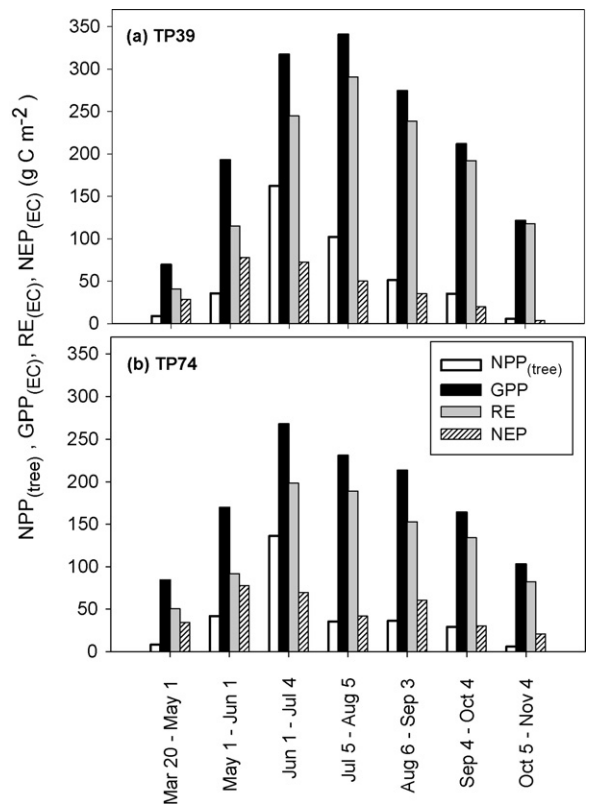
**Fig. 5.** Relationship of annual net primary productivity (NPP) and net ecosystem productivity (NEP) with (a) NEP:GPP, (b) RH:NPP, (c) RA:RH, and (d) TBCF:GPP based on biometric (B) and eddy-covariance (EC) data across the forest age-sequence. Solid and dotted lines show logarithmic (NEP:GPP, RH:NPP) and exponential (TBCF:GPP, RA:RH) fits between ratios and NEP (NEP > 0) and NPP, respectively.

~0.33 to ~0.71 among the three older stands resulting in a decreasing soil C sequestration potential throughout the stand maturing phase (Table 5). At the two oldest sites, lower RH:NPP ratios were observed during the warm and dry years 2005 and 2007. This pattern may have been related to inter-annual variations in forest productivity as both biometric and EC-based estimates of RH:NPP showed the same distinct negative relationship with forest productivity (for both NPP and NEP) across the age-sequence (Fig. 5b).

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).

3.6. Seasonal variation in C allocation

Monthly GPP<sub>(EC)</sub> and RE<sub>(EC)</sub> 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<sub>(EC)</sub> was likely related to greater contribution from broadleaf understorey 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<sub>tree</sub>)



**Fig. 6.** Monthly totals of tree biomass production (NPP<sub>tree</sub>); including aboveground and coarse root biomass production, GPP<sub>(EC)</sub>, RE<sub>(EC)</sub>, and NEP<sub>(EC)</sub> at (a) TP39 and (b) TP74 during the growing season of 2008.

peaked in June and maximum monthly  $NEP_{(EC)}$  occurred in May when soil temperature and therefore  $RE_{(EC)}$  was still low.

At both sites,  $NPP_{tree}$  was about 50% of  $GPP_{(EC)}$  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  $NPP_{tree}$  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  $NPP_{tree}$  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 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  $tC\ ha^{-1}$  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  $tC\ ha^{-1}$  (assuming no change in mineral soil C pool). The mean C sequestration over 70 years based on these three estimates resulted in  $175 \pm 48\ tC\ ha^{-1}$ , suggesting a mean annual sequestration rate of  $2.5\ tC\ ha^{-1}\ y^{-1}$ .

### 3.8. Uncertainty in C flux estimates

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

## 4. Discussion

### 4.1. NPP component fluxes and associated uncertainties

Our estimates of  $ANPP$  ( $309\text{--}654\ gC\ m^{-2}\ y^{-1}$ ) and  $BNPP$  ( $71\text{--}205\ gC\ m^{-2}\ y^{-1}$ ) were well within and at the lower end, respectively, compared to the range ( $ANPP = 56\text{--}1490\ gC\ m^{-2}\ y^{-1}$ ;  $BNPP = 150\text{--}566\ gC\ m^{-2}\ y^{-1}$ ) 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 ( $379\text{--}1135\ gC\ m^{-2}\ y^{-1}$ ) were within the range of  $150\text{--}400\ gC\ m^{-2}\ y^{-1}$  for recently initiated stands (Law et al., 2003; Schwalm et al., 2007) and  $400\text{--}2400\ gC\ m^{-2}\ y^{-1}$  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  $NPP_{FR}$  estimates became critical at TP74 where  $NPP_{FR}$  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 ( $549\text{--}1717\ gC\ m^{-2}\ y^{-1}$ ) and GPP ( $610\text{--}2445\ gC\ m^{-2}\ y^{-1}$ ) at our sites was comparable to other temperate conifer forests ( $\sim 700$  to  $1600$  and  $700$  to  $2100\ gC\ m^{-2}\ y^{-1}$  for RE and GPP, respectively) (Law et al., 2002), although both  $RE_{(EC)}$  and  $GPP_{(EC)}$  were exceptionally high at TP89. Similarly, NEP at our sites ( $-114$  to  $793\ gC\ m^{-2}\ y^{-1}$ ) spanned the entire range ( $-105$  to  $707\ gC\ m^{-2}\ y^{-1}$ ) 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 TP89 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,  $RE_{(EC)}$  of  $<800\ gC\ m^{-2}\ y^{-1}$  may be an underestimation considering that  $RE_{(B)}$  at the three older sites and  $RE_{(EC)}$  at TP89 and TP39 were consistently above  $1000\ gC\ m^{-2}\ y^{-1}$ . At TP89, we suspect that lower  $GPP_{(B)}$  and  $RE_{(B)}$  compared to  $GPP_{(EC)}$  and  $RE_{(EC)}$  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 ( $\sim 1\ m$  per year) therefore underestimating tree NPP and  $RA_C$ .

Previous comparison studies have primarily focused on forest NEP 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 NEP estimates. In the specific case of our TP74 site, the poor agreement between  $NEP_{(B)}$  and  $NEP_{(EC)}$  resulted primarily from a good agreement in GPP estimates while  $RE_{(B)}$  exceeded  $RE_{(EC)}$ . In contrast, reasonable agreement between  $NEP_{(B)}$  and  $NEP_{(EC)}$  may be achieved if both  $GPP_{(EC)}$  and  $RE_{(EC)}$  differ from  $GPP_{(B)}$  and  $RE_{(B)}$  in similar magnitude and essentially outbalanced each other, thereby producing similar NEP estimates. Thus, biometric and EC methods may fail in producing similar estimates of the independent component fluxes (GPP and RE) but coincidentally 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 NEP 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 Arneeth et al. (1998) reported a conservative relationship between  $NEP_{(EC)}$  and woody tissue NPP. This relationship could therefore provide an efficient way to determine approximate annual NEP estimates on regional scales from existing forest

**Table 6**

Uncertainty ( $\sigma$ ) of biometric NPP components in  $\text{g C m}^{-2} \text{y}^{-1}$  and in % of total NPP as a mean of four 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; SV = within-stand spatial variability.

Source of uncertainty	Symbol	TP02		TP89		TP74		TP39	
		$\text{g C m}^{-2} \text{y}^{-1}$	% of NPP	$\text{g C m}^{-2} \text{y}^{-1}$	% of NPP	$\text{g C m}^{-2} \text{y}^{-1}$	% of NPP	$\text{g C m}^{-2} \text{y}^{-1}$	% of NPP
Tree biomass production <sup>a</sup>	$\sigma_{\text{LB}}$	69 (29)	20 (5)	104 (22)	12 (2)	73 (12)	11 (2)	152 (56)	24 (8)
SV of detritus production	$\sigma_{\text{DB}}$	N.A.	N.A.	21 (4)	3 (1)	38 (33)	6 (6)	14 (17)	3 (3)
SV of understorey/ground vegetation production <sup>d</sup>	$\sigma_{\text{UG}}$	40 (7)	11 (2)	1 (N.A.)	<1	17 (N.A.)	3 (N.A.)	13 (N.A.)	2 (N.A.)
SV of litter production	$\sigma_{\text{L}}$	N.A.	N.A.	51 (10)	6 (1)	40 (2)	6 (3)	60 (11)	10 (2)
Fine root production	$\sigma_{\text{FR}}$	1 (<1)	<1	26 (7)	3 (1)	82 (4)	14 (7)	57 (8)	10 (3)
		CV (%)		CV (%)		CV (%)		CV (%)	
NPP <sup>b</sup>	$\sigma_{\text{NPP}}$	23 (1)		14 (1)		21 (2)		28 (6)	
RH	$\sigma_{\text{RH}}$	16		15		13		14	
NEP <sup>c</sup>	$\sigma_{\text{NEP}}$	28		21		24		32	

$$^a \sigma_{\text{LB}} = \sqrt{\sigma_{\text{D}}^2 + \sigma_{\text{EQ}}^2 + \sigma_{\text{DBH}}^2 + \sigma_{\text{H}}^2 + \sigma_{\text{SD}}^2}$$

$$^b \sigma_{\text{NPP}} = \sqrt{\sigma_{\text{LB}}^2 + \sigma_{\text{DB}}^2 + \sigma_{\text{UG}}^2 + \sigma_{\text{L}}^2 + \sigma_{\text{FR}}^2}$$

$$^c \sigma_{\text{NEP}} = \sqrt{\sigma_{\text{NPP}}^2 + \sigma_{\text{RH}}^2}$$

<sup>d</sup> 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  $\text{RA}_{\text{C}}$  and  $\text{GPP}_{(\text{B})}$  may explain why inter-annual patterns in  $\text{RE}_{(\text{B})}$  followed patterns in  $\text{GPP}_{(\text{B})}$ . In contrast,  $\text{RE}_{(\text{EC})}$  estimates were rather constant among years, likely because soil temperature showed little inter-annual variation. Inter-annual variation in  $\text{NEP}_{(\text{B})}$  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 from photosynthetic uptake being stored within the stem during autumn and used for stem growth during spring of the following year cause discrepancies between  $\text{NEP}_{(\text{B})}$  and  $\text{NEP}_{(\text{EC})}$  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  $\pm 50 \text{ g}$  between GPP and tree NPP in October could possibly explain annual differences in  $\text{NEP}_{(\text{B})}$  and  $\text{NEP}_{(\text{EC})}$  at our mature site.

At the two middle-age stands however, our study suggests a somewhat constant offset between  $\text{NEP}_{(\text{B})}$  and  $\text{NEP}_{(\text{EC})}$  rather than convergence over four years. Similarly, Ehman et al. (2002), Keith et al. (2009) and Black et al. (2005) reported annual  $\text{NEP}_{(\text{B})}$  to exceed  $\text{NEP}_{(\text{EC})}$  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  $\text{NPP}_{\text{FR}}$ ) 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  $\text{NEP}_{(\text{B})}$  and  $\text{NEP}_{(\text{EC})}$ .

#### 4.5. Ecosystem C use efficiency and C allocation

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

The range of  $\text{CUE}_{(\text{E})}$  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  $\text{CUE}_{(\text{E})}$  and  $\text{NEP}:\text{RE}$ , as well as the increase of  $\text{RH}:\text{NPP}$  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-sequence stands. In contrast, Schwalm et al. (2007) found a continuous increase of  $\text{CUE}_{(\text{E})}$  and  $\text{NEP}:\text{RE}$ , and a decrease of  $\text{RH}:\text{NPP}$  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  $\text{CUE}_{(\text{E})}$  and higher  $\text{RH}:\text{NPP}$  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 ( $175 \text{ t C ha}^{-1}$ ) is considerably larger compared to  $21 \text{ t C ha}^{-1}$  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  $106 \text{ t C ha}^{-1}$  sequestered in maturing (31–70 years old) temperate forests, while Hooker and Compton (2003) suggested  $\sim 150 \text{ t C ha}^{-1}$  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 were 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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