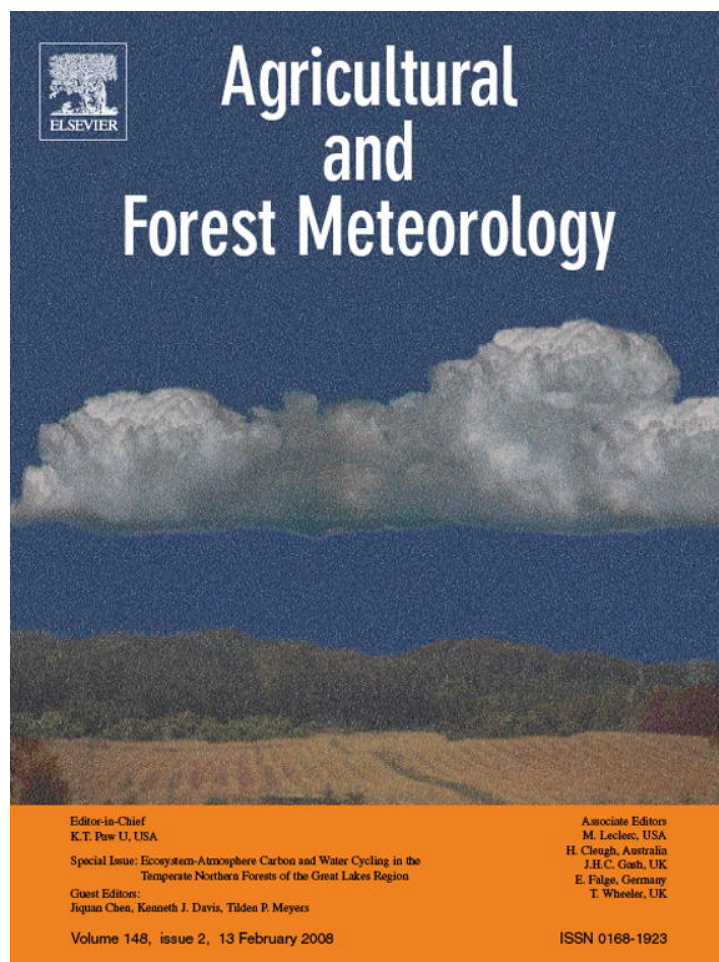


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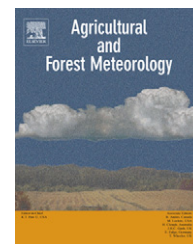


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## Multi-year convergence of biometric and meteorological estimates of forest carbon storage

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### ABSTRACT

We measured annual C storage, or net ecosystem production (NEP), from 1999 to 2003 in an aspen-dominated, mixed-deciduous forest in Michigan, USA. Measurements of the annual production of above- and below-ground live and dead mass, foliar herbivory, and soil respiration were used to develop biometric estimates of NEP (NEP<sub>B</sub>). Eddy-covariance measurements made above the canopy were used to construct meteorological estimates of NEP (NEP<sub>M</sub>). Over the 5-year study period, C stored annually in live mass (above- and below-ground wood) averaged 2.13 Mg C ha<sup>-1</sup> year<sup>-1</sup>, while annual detritus production (fine roots, leaf litter, woody debris) averaged 4.35 Mg C ha<sup>-1</sup> year<sup>-1</sup>. Fine root inputs were the largest component (41%) of annual net primary production.

The forest was a consistent C sink, with annual NEP ranging from 0.80 to 1.98 Mg C ha<sup>-1</sup> year<sup>-1</sup>, comparable in magnitude to other eastern North American forests. When annual NEP<sub>B</sub> and NEP<sub>M</sub> were compared in a given year, they differed from each other by 13–148%. However, when compared over 5 years, these independent estimates of C storage converged to within 1% of each other. Differences between same-year biometric and meteorological NEP estimates were explained in part by a lag between late-season net canopy photosynthesis and C allocated to tree growth the following spring. Weekly assessments of bole radial growth in 2001 and 2002 indicated that woody mass growth began prior to positive net canopy photosynthesis in the spring and that >25% of annual photosynthetic C assimilation occurred after growth had stopped in the autumn. Thus, while the temporal separation between photosynthesis and growth reduced agreement between annual NEP<sub>B</sub> and NEP<sub>M</sub> estimates, these metrics converged over several years. These results suggest that the allocation of recent photosynthate to storage carbohydrates, rather than to immediate growth, may obscure the relationship between shorter term, annual biometric and meteorological C storage estimates. Moreover, the 5-year convergence of biometric and meteorological NEP estimates serves as an important cross-validation, demonstrating that both approaches can yield accurate forest C storage assessments.

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## 1. Introduction

Northern deciduous forests occupy ~29 million ha in the United States alone (USDA, 2001) and are likely important contributors to the terrestrial North American carbon (C) sink (Ciais et al., 1995; Fan et al., 1998; Gurney et al., 2002). Although harvesting and agriculture over the past century depleted C stored in the deciduous forests of the upper Great Lakes region, estimates of annual C storage, or net ecosystem production (NEP), suggest that these ecosystems are now C sinks (Birdsey and Heath, 1995; Birdsey et al., 2000; Gough et al., 2007a). Afforestation has resulted in C storage at modest rates and recent C inventories indicate that northern U.S. forests, despite a short growing season, are often harvested less than other forests, making them an important terrestrial C sink (Birdsey et al., 2000).

While regional inventories can provide C storage estimates for large areas, ecosystem-level studies provide important process-level information on forest C dynamics as well as local validation of regional estimates. At the stand level, annual NEP can be estimated from a combination of biometric and ecophysiological measurements ( $NEP_B$ ; Barford et al., 2001; Curtis et al., 2002; Ehman et al., 2002; Law et al., 2003). Complete  $NEP_B$  estimates require measurements of above- and below-ground wood, leaf litter, woody debris, and fine root mass, mass losses to herbivory, and heterotrophic respiratory C losses ( $R_h$ ). Applied at a similar scale, meteorological methods have proven useful for measuring net ecosystem  $CO_2$  exchange (NEE) between forest and atmosphere at time intervals of less than 1 h (e.g., Wofsy et al., 1993; Goulden et al., 1996; Schmid et al., 2000). These methods provide an integrated measure of net ecosystem C uptake or loss that represents the sum of individual C fluxes occurring within an ecosystem, including multiple photosynthetic and respiratory sources. Cumulative annual NEE is the meteorological estimate of net ecosystem production ( $NEP_M$ ). Concurrent biometric and meteorological measurements thus allow for independent appraisals of ecosystem C storage (e.g., Canadell et al., 2000; Baldocchi, 2003). These comparisons are useful in gauging the accuracy of C storage estimates since multiple sources of uncertainty are associated with both approaches (Ehman et al., 2002; Schmid et al., 2003).

Previous biometric and meteorological annual C storage estimates indicate that northern deciduous forests sequester C from the atmosphere at variable rates, from 0.73 to 2.8 Mg C ha<sup>-1</sup> year<sup>-1</sup> across Canada and the United States (Lee et al., 1999; Barford et al., 2001; Curtis et al., 2002; Schmid et al., 2003). Spatial variability in C storage among deciduous forests has been related to site productivity (Curtis et al., 2002), stand age (Pregitzer and Euskirchen, 2004; Gough et al., 2007a) and prior disturbance (Gough et al., 2007a), while interannual variability in NEP has been attributed to climate-driven changes in photosynthesis and respiration. For example, interannual variability in canopy photosynthesis was positively related to air temperature and negatively associated with cloud cover in a central Massachusetts forest (Goulden et al., 1996). Air temperature affected the timing of leaf expansion and senescence, while cloud cover reduced canopy light interception. In contrast, respiratory C losses were correlated with temperature in two northern deciduous forests, including the current study site (Bolstad et al., 2004; Curtis et al., 2005).

Few studies have conducted concurrent biometric and meteorological assessments of annual C storage, but those that have often report poor agreement between the two methods (Barford et al., 2001; Granier et al., 2000; Curtis et al., 2002; Ehman et al., 2002). In principle, differences between these estimates may occur when the meteorological footprint and ecological inventory plots do not adequately overlap (Schmid, 1994, 1997; Schmid and Lloyd, 1999). Agreement between methods also may be affected by sampling variability and gap-filling assumptions (Schmid et al., 2003; Ehman et al., 2002). Additionally, it is possible that biometric and meteorological approaches produce different results because these methods measure processes that are temporally offset. A lag between photosynthetic C uptake and growth may result when recently assimilated C is allocated to storage carbohydrates rather than applied to immediate growth. Barford et al. (2001) suggested that the presence of a lag between photosynthesis and growth might explain why biometric and meteorological C storage estimates were poorly aligned in a given year, but converged after 8 years in a Massachusetts forest. A temporal offset between these processes is supported by studies showing that photosynthesis responds instantaneously to current environmental conditions, while growth is often affected by environmental conditions occurring weeks to years earlier (Wofsy et al., 1993; Arneeth et al., 1998; Sampson et al., 2001; Chen et al., 2002; Hoch et al., 2003; Schmid et al., 2003; Loescher et al., 2003). Although a lag between photosynthesis and growth has never been demonstrated from concurrent biometric and meteorological measurements, understanding the temporal relationship between these processes could assist in explaining the consistently poor agreement between short-term, independent C storage estimates.

Here, we present annual C storage estimates over 5 years (1999–2003) for a north temperate deciduous forest located in northern lower Michigan, USA. Our study site is part of the AmeriFlux network of long-term C cycle research facilities (Baldocchi et al., 2001). Our primary objectives were to estimate annual NEP using both biometric and meteorological methods, to examine interannual variability in NEP, and to evaluate the effect of climate and phenology on annual NEP. We also examined the temporal relationship between canopy photosynthesis and growth, and evaluated the effect a lag between these processes could have on the convergence of annual biometric and meteorological C storage estimates.

## 2. Methods

### 2.1. Study site

Our study was conducted at the University of Michigan Biological Station (UMBS) in northern lower Michigan, USA (45°35.5'N, 84°43'W). The site is located in the transition zone between mixed hardwood and boreal forests. The study forest surrounds a meteorological tower on a level to gently sloping high outwash plain derived from glacial drift, 1.3 km south and 3.5 km west of two large lakes, with the gradually ascending slope of an interlobate moraine lying ~1 km to the south. Soils are excessively drained, sandy, mixed frigid

Entic Haplothods consisting of 92% sand, 7% silt and 1% clay. Mean annual temperature (1942–2003) is 5.5 °C and mean annual precipitation is 817 mm.

The forest within a 1 km radius of the meteorological tower is a secondary successional mixed northern hardwood forest. Over half of the standing live tree mass consists of bigtooth aspen (*Populus grandidentata* Michx.) and trembling aspen (*Populus tremuloides* Michx.). Other common overstory species include northern red oak (*Quercus rubra* L.), paper birch (*Betula papyrifera* Marsh.), American beech (*Fagus grandifolia* Ehrh.), sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.) and white pine (*Pinus strobus* L.). The understory is dominated by bracken fern (*Pteridium aquilinum* L.) and red maple, red oak, American beech and white pine seedlings and saplings. Canopy height is approximately 22 m. Old-growth white pine, red pine (*Pinus resinosa* Ait.) and eastern hemlock (*Tsuga canadensis* (L.) Carr.) were harvested in the late 19th century and subsequent cutting and patchy burns were a source of repeated disturbance in the area until the early 20th century. Tree age averages 85 years.

Biometric measurements were made in a 1.1 ha plot surrounding the meteorological tower and in 60, 0.08 ha plots located up to 1000 m from the tower. Transects were located 20° apart, from 225° to 15°, toward the prevailing northwest winds and the meteorological tower source footprint.

## 2.2. Environmental parameters and leaf phenology

Continuous measurements of various environmental parameters were made from 1999 through 2003. Air temperature ( $T_a$ ) and photosynthetic photon flux density (PPFD) were measured 21 m above the ground using ventilated temperature probes and PPFD sensors, respectively (model HPO-43, Rotronic Instrument Corp., Huntington, NY, USA; LI-190SZ, LICOR Inc., Lincoln, NE, USA). Soil temperature ( $T_s$ ) was measured at 7.5 cm depth in three locations near the base of the meteorological tower using type E thermocouples. Volumetric soil water content ( $\theta_s$ ) was recorded to a depth of 20 cm at one location in 1999 and at four locations in all other years using CS616 soil moisture probe (Campbell Scientific, Inc., Logan, UT, USA).

We monitored leaf phenology with a LAI-2000 Plant Canopy Analyzer (LI-COR Inc.). Readings were taken every 3 m along seven transects in the 1.1 ha plot for an average of 120 samples on each of ~12 sampling dates from May (leaf expansion) to November (leaf abscission).

## 2.3. Above- and below-ground woody mass

We measured aboveground woody mass ( $M_a$ ) using allometric equations relating bole diameter at 1.37 m height ( $D$ ) to  $M_a$  by

$$M_a = aD^b \quad (1)$$

where  $a$  and  $b$  are the species-specific coefficients developed from data collected at UMBS (Koerper, 1977; Cooper, 1981; Cooper, personal communication) or obtained from published reports from the Great Lakes states and eastern North America (Wiant et al., 1977; Ker, 1980; Young et al., 1980; Schmitt and Grigal, 1981; Crow and Erdmann, 1983; Hocker and Early, 1983;

Perala and Alban, 1994; Ter-Michaelian and Korzukhin, 1997). Annual  $D$  increment was measured on >700 trees with  $D \geq 10$  cm in the 1.1 and 0.08 ha plots (~20% of the population) using band dendrometers installed in summer, 1998 (Liming, 1957). During the 2001 and 2002 growing seasons,  $D$  was recorded every 1–2 weeks on 190 trees within the 1.1 ha plot.

We estimated below-ground woody mass ( $M_b$ ) using two independent methods. Coarse root mass was determined from soil samples and separately using an allometric equation relating  $M_b$  to  $M_a$  (Cairns et al., 1997). Ninety, 60 cm soil cores (1270 cm<sup>3</sup> core<sup>-1</sup>) were extracted from the 1.1 ha plot in 1998. Coarse roots (diameter > 2 mm) were separated from soil, dried, weighed, and burned in a muffle furnace to determine ash-free weight. We estimated standard errors of  $M_a$  and  $M_b$  from the inter-plot variance. Uncertainty associated with allometric equations was not estimated because coefficient standard errors typically were not published. A site-specific mean tissue-weighted fraction of C in bark, cork cambium, sapwood, and heartwood of the five dominant overstory species (0.49) was used to convert dry woody mass to C mass.

## 2.4. Leaf litter, fine, and coarse woody debris

We estimated annual leaf litter production ( $M_{ll}$ ) as the sum of understory and overstory litter mass. We measured overstory leaf litter mass, fine debris mass ( $M_{fd}$ ), and maximum overstory leaf area index ( $A_{lmax}$ ) with 26 litter traps (0.179 or 0.264 m<sup>2</sup>) randomly located within the 1.1 ha plot and from single litter traps placed in each of the 0.08 ha plots. Litter traps were emptied weekly during leaf abscission in the autumn and monthly otherwise. We estimated understory mass (primarily bracken fern) in 1999 and 2000 in the 1.1 ha plot. Thirty-five ferns were harvested, dried, weighed, and leaf area for each plant was approximated from frond length and width measurements. To estimate understory leaf mass, we developed a relationship relating bracken fern leaf area to mass. Understory leaf mass was estimated from leaf area measurements in 36, 1 m<sup>2</sup> subplots located within the 1.1 ha plot.

We measured net coarse woody debris production ( $M_{cd}$ ) in four, 0.08 ha subplots located within the 1.1 ha plot. Coarse woody debris (CWD) was defined as woody detritus  $\geq 0.1$  m in diameter. In 2000, CWD volume was estimated from individual diameter and length measurements, and a decay class was assigned according to Marra and Edmonds (1994). A second survey of CWD was conducted in 2003 and decay classes were reassessed. Decay class densities and volumes were used to calculate standing CWD mass ( $M_{scd}$ ). We determined the annual net production of  $M_{cd}$  through linear interpolation between survey dates.

A site-specific C fraction of  $M_{ll}$  (0.49) was used to convert dry mass to C mass. We also assumed a C fraction of 0.49 for  $M_{fd}$  and  $M_{cd}$ . We estimated standard errors of  $M_{ll}$ ,  $M_{fd}$ , and  $M_{cd}$  from the inter-plot variance.

## 2.5. Fine root mass and turnover

We sampled standing fine root mass ( $M_{sfr}$ ) in 2000 and 2003 in the 1.1 and 0.08 ha plots. Roots were sampled to a depth of 80 cm using soil cores (1700 cm<sup>3</sup> sample<sup>-1</sup>,  $n = 30$ ). Fine roots

(diameter  $\leq 2$  mm) were separated from soil using a 2 mm mesh sieve. Soil was sieved multiple times to maximize root recovery. Roots were washed, dried, weighed, and burned in a muffle furnace to determine ash-free mass.

We estimated annual fine root turnover ( $\kappa_{fr}$ ) using three different approaches. Clark et al. (2001) suggested the use of multiple methods to estimate  $\kappa_{fr}$  because of uncertainties associated with each approach. First, we used minirhizotron-based cohort analyses to estimate mortality rates for up to 14 months in six root cohorts (total number of roots > 9700). Root images were collected in May–August, and October 2002 and in May–July 2003 from 54 clear minirhizotron tubes (Hendrick and Pregitzer, 1993; Johnson et al., 2001) distributed across the 1.1 ha and in eight, 0.08 ha plots. Images were recorded to a depth of  $\sim 1$  m using a portable digital camera with a horizontal visual field of 18 mm (model # BTC-2, Bartz Technology Corp., Santa Barbara, CA, USA) and analyzed using Roottracker V2.0 software (Duke University, Durham, NC, USA). A root cohort was defined as the group of new roots appearing between image collection dates. A root was considered dead when it no longer appeared in an image. Individual cohort mortality vs. time (i.e., a cohort life curve) was analyzed using SAS statistical software (SAS V8, SAS Institute, Cary, NC, USA). Daily mortality rate for each cohort was calculated as

$$\kappa_{fr} = \frac{(n_t - n_{t+1})/n_t}{d_{t+1} - d_t} \quad (2)$$

where  $\kappa_{fr}$  is the fine root mortality rate ( $d^{-1}$ ),  $n$  the number of roots in a cohort at time  $t$ , and  $d$  is the cohort age at time  $t$ . We then developed a linear model relating  $\kappa_{fr}$  to mean  $T_s$  during the corresponding period of mortality ( $r^2 = 0.47$ ;  $P = 0.0009$ ; Tierney et al., 2003). Annual  $\kappa_{fr}$  was estimated from this model through simple linear scaling by multiplying the slope and intercept by the number of days per year. Annual  $\kappa_{fr}$  was estimated from mean annual  $T_s$  as

$$\kappa_{fr} = 0.0113 + 0.035T_s \quad (3)$$

In the second method, we estimated  $\kappa_{fr}$  from an empirical relationship relating available soil N to annual  $\kappa_{fr}$  (Aber et al., 1985):

$$\kappa_{fr} = 0.789 - 0.0191N_{avail} + 0.000211N_{avail}^2 \quad (4)$$

where  $N_{avail}$  is the sum of mineralized and nitrified soil N, and atmospheric N deposition. We measured N mineralization and nitrification using the buried bag technique (Hart et al., 1994) from June 1999 to May 2000 in a total of 70 locations within the 1.1 ha and 0.08 ha plots. Atmospheric N deposition (wet + dry) was estimated from Baumgardner et al. (2002).

Lastly, we estimated  $\kappa_{fr}$  using the mass balance approach of Raich and Nadelhoffer (1989) where

$$\kappa_{fr} = \frac{R_h - (M_{ll} + M_{fd})}{M_{sfr}} \quad (5)$$

This model assumes heterotrophic respiration,  $R_h$ , is equivalent to detritus (fine root, leaf litter, and woody debris) inputs.

Annual production of fine root litter ( $M_{fr}$ ) was estimated as the product of the standing crop of fine root mass ( $M_{sfr}$ ) and  $\kappa_{fr}$  averaged across the three methods. The site-specific C fraction of  $M_{sfr}$  (0.47) was used to convert dry mass to C mass. We estimated standard errors of  $M_{fr}$  from inter-plot and inter-method variances.

## 2.6. Soil carbon

We sampled soil C mass ( $M_s$ ) in 1998 and 2003 in the 1.1 ha plot and in eight, 0.08 ha plots. Soil was excavated to a depth of 20 cm using soil cores ( $425 \text{ cm}^3 \text{ sample}^{-1}$ ,  $n = 40$ ). Mineral soil was sieved through a 2 mm mesh screen to remove roots, dried, and ground with a mortar and pestle. Soil C concentration was assessed with an elemental analyzer (Perkin-Elmer 2400, Perkin-Elmer Inc., Wellesley, MA, USA).

## 2.7. Herbivory

We estimated annual foliar C losses to herbivory ( $H$ ) in 2000 and 2001 by measuring damage to green leaves, collection of insect frass below the canopy, and through caterpillar feeding trials relating leaf mass loss to frass production. The proportion of leaf area lost to herbivory was determined using a LAI-3100 leaf area meter (LI-COR Inc.) following the collection of green leaves from 4 dominant canopy species ( $n = 180$ ). Insect frass was collected every 2–3 days during leaf-on from 20,  $0.18 \text{ m}^2$  traps on the forest floor and caterpillar feeding trials were conducted using fresh bigtooth aspen and northern red oak leaves ( $n = 10$ ). Herbivory was calculated from ecosystem frass production estimates and a relationship relating leaf mass losses to frass production. Annual  $H$  was greatest in 2001 during a mild outbreak of forest tent caterpillars (*Malacosoma disstria* Hubner), averaging 7% of  $M_{ll}$ . Annual  $H$  was 4% of  $M_{ll}$  in 2000 and this value was applied to all other years. We estimated the standard error of  $H$  from the inter-method variance.

## 2.8. Heterotrophic soil respiration

We measured soil respiration ( $R_s$ ) in the 1.1 ha plot and in 30, 0.08 ha plots using a LI-COR LI-6400 equipped with a LI-6400-09 soil  $\text{CO}_2$  flux chamber (LI-COR Inc.). Measurements and analyses are described in detail by Curtis et al. (2005). Briefly, we modeled  $R_s$  as a function of  $T_s$  using a two-parameter exponential function with an additive log-linear or linear  $\theta_s$  function. Models were developed separately for the early growing season (days 130–200), late growing season (days 201–279), and winter (days 280–129) of each year. Continuous hourly  $R_s$  was estimated from  $T_s$  and  $\theta_s$  data and was summed over the year to determine annual  $R_s$ .

We partitioned  $R_s$  into heterotrophic ( $R_h$ ) and autotrophic ( $R_a$ ) components using the component integration method (Hanson et al., 2000). The O-horizon and the top 20 cm of mineral soil were excavated from eight, 0.08 ha plots in July 2004 and the mineral soil was sieved through a 2 mm mesh screen to remove roots. Soil samples (200 g) were adjusted to 15%  $\theta_s$ , placed in 500 mL jars and incubated at room temperature for 1–2 weeks. We measured the respiratory response of O-horizon and mineral soil to temperature

between 2 and 30 °C (Winkler et al., 1996). A subsample of this soil was analyzed for C content. We then compared mineral soil and O-horizon respiration normalized for C content with total  $R_s$  to estimate the contribution of  $R_h$  to soil C efflux. The standard error of  $R_h$  was calculated from the inter-sample variance and the variance of  $R_s$ .

### 2.9. Meteorological measurements

We used meteorological observations from a tower to evaluate net ecosystem CO<sub>2</sub> exchange (NEE) between forest and atmosphere. Meteorological tower instrumentation and specifications are described by Schmid et al. (2003). A 46 m tower equipped with eddy-covariance systems at 34 and 46 m provided continuous measurements of: (1) 3D turbulent velocity fluctuations and eddy-covariance fluxes of momentum (sonic anemometers; CSAT-3, Campbell Scientific Inc.); (2) net radiation (net radiometer; Q\*7.1, REBS Inc., Seattle, WA, USA) and; (3) water vapor and CO<sub>2</sub> (infrared gas analyzer; LI-6262; LI-COR Inc.). Below-canopy CO<sub>2</sub> storage was determined from eight vertically separated locations on a nearby tower and used in combination with environmental data to calculate half-hourly NEE. Nocturnal NEE was deemed acceptable for flux calculations and for gap-filling data when friction velocity ( $u^*$ ) was  $>0.35 \text{ m s}^{-1}$ . These criteria were met 44% of the time. Results described in the current study originated from data collected at 46 m. A detailed description of the data analyses, including processing of the raw eddy-covariance data, flux selection criteria, and gap-filling methods is provided by Schmid et al. (2003).

### 2.10. Net primary production and net ecosystem production

We estimated net primary production (NPP) and net ecosystem production (NEP) using both biometric and meteorological data. Biometric net primary production ( $NPP_B$ ) was estimated as

$$NPP_B = \Delta L + D + H \quad (6)$$

where  $\Delta L$  is the annual live mass increment ( $=\Delta M_a + \Delta M_b$ ), and  $D$  the is annual dead mass (or detritus) production ( $=M_{ll} + M_{fd} + M_{cd} + M_{fr}$ ; Waring and Schlesinger, 1985). Net ecosystem production estimated from biometric data ( $NEP_B$ ) was

(e.g., Curtis et al., 2002; Ehman et al., 2002):

$$NEP_B = \Delta L + D + H - R_h \quad (7)$$

The standard errors of  $NPP_B$  and  $NEP_B$  were estimated as the quadratic sum of component errors.

Meteorological net primary production ( $NPP_M$ ) was calculated as the sum of  $NEP_M$  and chamber-based  $R_h$  (Griffis et al., 2004):

$$NPP_M = NEP_M + R_h \quad (8)$$

Meteorological net ecosystem production ( $NEP_M$ ) was estimated as the cumulative sum of half-hourly NEE over 1 year (e.g., Schmid et al., 2003):

$$NEP_M = \sum_{t=1}^n NEE \quad (9)$$

where  $t$  is the time and  $n$  is the number of half-hourly observations throughout the year.

## 3. Results

### 3.1. Environmental conditions

Climatic variables of importance to NEP are summarized in Table 1. Mean annual  $T_a$  ranged from 6.5–8.1 °C. Mean annual  $T_s$  averaged between 7.5 and 8.8 °C and was consistently higher than  $T_a$ , largely because soil freezing during the winter was uncommon. Cold winter temperatures in 2003 resulted in the lowest annual  $T_a$  and  $T_s$  for the study period. Mean growing season PPFd ranged from 359 to 417  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Mean annual  $\theta_s$  varied from 13.5% to 16.3%, with mean growing season  $\theta_s$  slightly lower. Total annual precipitation ( $\Phi_a$ ) was variable, averaging 824 mm and ranging from 570 mm in 2000 to 973 mm in 2001.

### 3.2. Net primary production and heterotrophic respiration

Biometric net primary production ( $NPP_B$ ) averaged 6.54 Mg C  $\text{ha}^{-1} \text{year}^{-1}$  over 5 years, ranging from 6.07 to 7.01 Mg C  $\text{ha}^{-1} \text{year}^{-1}$  (Table 2). Annual fine root turnover averaged 0.45  $\text{year}^{-1}$  (Table 3), resulting in fine root litter production

**Table 1 – Climatic and phenological drivers of primary production at UMBS, 1999–2003**

Year	$T_a$		$T_s$		PPFD		$\theta_s$		$\Phi_a$	$A_{lmax}$
	A	GS	A	GS	A	GS	A	GS		
1999	7.9	17.2	8.8	15.7	284	417	13.6	11.6	774	3.3
2000	6.9	16.0	8.3	14.7	272	395	13.5	10.4	570	3.6
2001	8.1	16.9	8.6	15.4	250	366	14.9	11.9	973	3.2
2002	7.1	17.5	8.1	15.6	231	363	16.2	13.1	929	4.0
2003	6.5	16.6	7.5	14.6	245	359	14.7	12.5	874	3.6

Mean annual (A) and growing season (GS, days 130–279) air temperature at 21 m ( $T_a$ , °C), soil temperature at 7.5 cm ( $T_s$ , °C), photosynthetic photon flux density at 21 m (PPFD,  $\mu\text{mol m}^{-2} \text{s}^{-2}$ ), soil moisture to 20 cm ( $\theta_s$ , %), and annual precipitation ( $\Phi_a$ , mm). Maximum leaf area index ( $A_{lmax}$ ) was assessed from material recovered in litter traps.

**Table 2 – Forest carbon (C) fluxes and pools at UMBS**

Year	$\Delta L$		D			H	NPP <sub>B</sub>	R <sub>h</sub>	NEP <sub>B</sub>
	$\Delta M_a$	$\Delta M_b$	M <sub>ll</sub>	M <sub>fd+cd</sub>	M <sub>fr</sub>				
<b>Fluxes</b>									
1999	1.51 (0.18)	0.35 (0.04)	1.42 (0.12)	0.20 (0.59)	3.00 (0.58)	0.06 (0.01)	6.54 (0.86)	-5.58 (0.95)	0.96 (1.28)
2000	1.82 (0.08)	0.42 (0.02)	1.60 (0.13)	0.16 (0.58)	2.67 (0.41)	0.06 (0.01)	6.73 (0.73)	-4.94 (0.86)	1.79 (1.13)
2001	2.09 (0.07)	0.48 (0.02)	1.44 (0.12)	0.15 (0.58)	2.75 (0.44)	0.10 (0.01)	7.01 (0.74)	-5.03 (0.85)	1.98 (1.13)
2002	1.46 (0.05)	0.33 (0.01)	1.52 (0.15)	0.16 (0.58)	2.54 (0.40)	0.06 (0.01)	6.07 (0.72)	-4.73 (0.80)	1.34 (1.08)
2003	1.75 (0.11)	0.40 (0.03)	1.48 (0.14)	0.18 (0.58)	2.49 (0.45)	0.06 (0.01)	6.36 (0.76)	-4.80 (0.82)	1.56 (1.12)
Total	8.63 (0.49)	1.98 (0.12)	7.46 (0.66)	0.85 (2.91)	13.45 (2.28)	0.34 (0.05)	32.71 (3.80)	-25.08 (4.28)	7.63 (5.73)
Mean	1.73 (0.10)	0.40 (0.02)	1.49 (0.13)	0.17 (0.58)	2.69 (0.46)	0.07 (0.01)	6.54 (0.76)	-5.02 (0.86)	1.53 (1.15)
%NPP <sub>B</sub>	26.4	6.1	22.8	2.6	41.1	1.0			
	M <sub>a</sub>	M <sub>b</sub>	M <sub>ll</sub>	M <sub>fd + scd</sub>	M <sub>sfr</sub>	M <sub>s</sub>	S <sub>E</sub>		
<b>Pools</b>									
2003	71.7 (3.0)	17.7 (0.7)	1.5 (0.1)	3.2 (0.3)	5.86 (0.9)	80.4 (12.4)	180.5 (12.8)		
%S <sub>E</sub>	39.8	9.8	0.9	1.8	3.2	44.5			

Annual net primary production (NPP<sub>B</sub>) and annual net ecosystem production (NEP<sub>B</sub>) were calculated from biometric measurements of C pools, 1999–2003. Live mass increment ( $\Delta L$ ) is the sum of above- ( $\Delta M_a$ ) and below-ground ( $\Delta M_b$ ) wood mass increment. Detritus mass production (D) is the sum of leaf (M<sub>ll</sub>), fine and coarse woody debris (M<sub>fd+cd</sub>), and fine root litter production (M<sub>fr</sub>). Foliar losses to herbivory (H) and soil heterotrophic respiration (R<sub>h</sub>) are also presented. Annual NPP<sub>B</sub> was estimated as the sum of  $\Delta L$ , D, and H; NEP<sub>B</sub> was calculated as the sum of  $\Delta L$ , D, H and R<sub>h</sub>. Total ecosystem C storage (S<sub>E</sub>) for 2003 is the sum of above- (M<sub>a</sub>) and below-ground wood mass (M<sub>b</sub>), leaf litter mass (M<sub>ll</sub>), fine debris and standing coarse woody debris mass (M<sub>fd+scd</sub>), standing fine root mass (M<sub>sfr</sub>), and soil carbon mass (M<sub>s</sub>). Standard errors are in parentheses. All flux units are in Mg C ha<sup>-1</sup> year<sup>-1</sup>, except 5-year totals, and pools are Mg C ha<sup>-1</sup>.

rates of 2.69 Mg C ha<sup>-1</sup> year<sup>-1</sup>. Fine root litter inputs were the largest contributor to NPP<sub>B</sub>, representing over 41% of net primary production. Aboveground woody mass increment was the second largest contributor to growth, accounting for 26.4% of the total NPP<sub>B</sub> or 1.73 Mg C ha<sup>-1</sup> year<sup>-1</sup>. Production by this pool varied annually by >0.6 Mg C ha<sup>-1</sup> year<sup>-1</sup>. Annual leaf litter inputs were less variable, comprising 22.8% of NPP<sub>B</sub> and contributing 1.49 Mg C ha<sup>-1</sup> year<sup>-1</sup> to production. Below-ground woody mass, woody debris mass, and mass losses to herbivory collectively accounted for <10% of NPP<sub>B</sub>. Carbon stored in below-ground woody mass averaged 0.40 Mg C ha<sup>-1</sup> year<sup>-1</sup>, representing 6.1% of NPP<sub>B</sub>. Coarse and fine debris mass combined made up 2.6% of NPP<sub>B</sub>, contributing 0.17 Mg C ha<sup>-1</sup> year<sup>-1</sup>. Coarse debris represented only 10% of the total woody debris inputs (data not shown). Herbivory losses were the most minor component of NPP<sub>B</sub>, averaging 0.07 Mg C ha<sup>-1</sup> year<sup>-1</sup> and constituting only 1% of the total C

budget. Even during a mild insect outbreak in 2001, foliar C consumed by herbivores was only 1.4% of total NPP<sub>B</sub>.

Detritus production was double that of live tissues (Table 2). Over the 5-year period, live mass production averaged 2.13 Mg C ha<sup>-1</sup> year<sup>-1</sup>, while dead mass production was 4.35 Mg C ha<sup>-1</sup> year<sup>-1</sup>. Total C stored in longer-lived woody pools over the 5-year period was 10.61 Mg C ha<sup>-1</sup> while inputs to the more ephemeral detritus pools were 21.74 Mg C ha<sup>-1</sup>. Carbon losses from soil heterotrophic respiration (R<sub>h</sub>) were a substantial fraction of NPP<sub>B</sub>. Carbon loss from R<sub>h</sub> varied annually from 4.73 to 5.58 Mg C ha<sup>-1</sup> year<sup>-1</sup>, and the 25.07 Mg C ha<sup>-1</sup> lost over the 5-year increment is 15% greater than the estimated detritus inputs to the soil.

### 3.3. Net ecosystem production

Biometric net ecosystem production (NEP<sub>B</sub>), or net forest C storage, reflected the balance between C gain from growth (NPP<sub>B</sub>) and C losses from R<sub>h</sub>. Annual NEP<sub>B</sub> averaged 1.53 Mg C ha<sup>-1</sup> year<sup>-1</sup>, but varied by >100%, from a low of 0.96 Mg C ha<sup>-1</sup> year<sup>-1</sup> in 1999 to a high of 1.98 Mg C ha<sup>-1</sup> year<sup>-1</sup> in 2001 (Table 2). Estimated meteorological net primary production (NEP<sub>M</sub>) varied between a low of 0.80 Mg C ha<sup>-1</sup> year<sup>-1</sup> in 2001 and a high of 1.77 Mg C ha<sup>-1</sup> year<sup>-1</sup> in 2003, averaging 1.51 Mg C ha<sup>-1</sup> year<sup>-1</sup> (Fig. 1). Despite having similar ranges, NEP<sub>B</sub> and NEP<sub>M</sub> in any given year were poorly correlated (Fig. 2). The difference between annual NEP<sub>B</sub> and NEP<sub>M</sub> within a given year varied between 13% (2000) and 148% (2001).

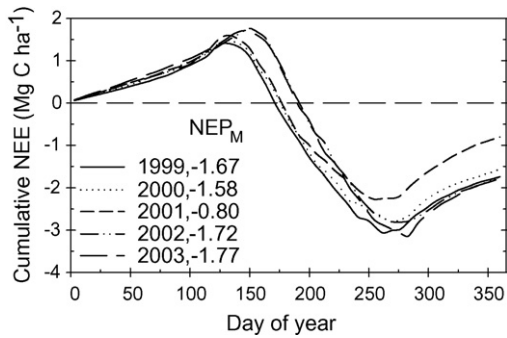
### 3.4. Climatic and phenological impacts on annual production

Forest C gains (NPP) and losses (R<sub>h</sub>) both were positively correlated with environmental factors typically associated

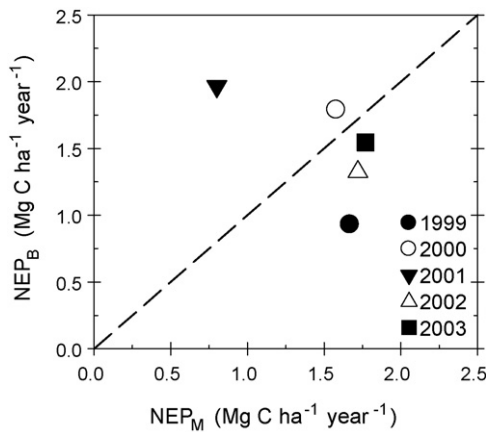
**Table 3 – Annual fine root turnover ( $k_{fr}$ , year<sup>-1</sup>) at UMBS over 5 years**

Year	Method			$\bar{x}$
	A	B	C	
1999	0.32	0.49	0.65	0.49
2000	0.30	0.49	0.52	0.44
2001	0.31	0.49	0.56	0.45
2002	0.29	0.49	0.50	0.43
2003	0.27	0.49	0.51	0.42

Fine root turnover was estimated using three different methods: (A) fine root mortality in response to soil temperature (Tierney et al., 2003); (B) soil available nitrogen model (Aber et al., 1985); (C) mass balance approach (Raich and Nadelhoffer, 1989). The mean of the three methods ( $\bar{x}$ ) was used to calculate fine root C inputs.

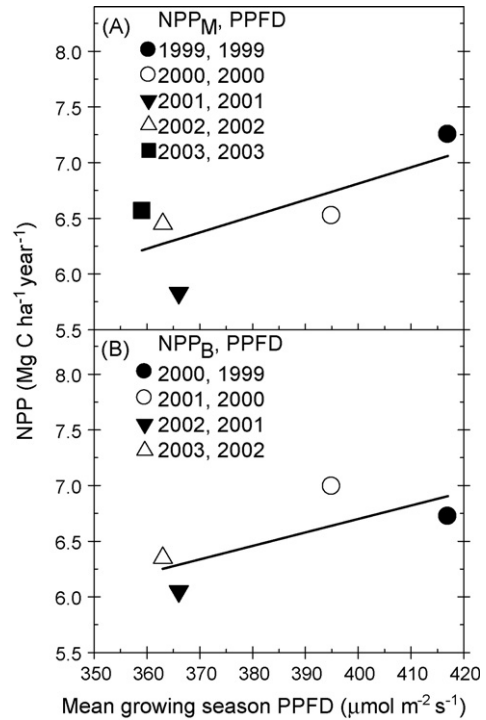


**Fig. 1** – Cumulative net ecosystem C exchange (NEE) by the UMBS forest, 1999–2003. Negative fluxes represent carbon uptake while positive fluxes indicate carbon loss. Net ecosystem production, the annual sum of NEE, is also presented ( $NEP_M = \text{Mg C ha}^{-1} \text{ year}^{-1}$ ).



**Fig. 2** – Biometric net ecosystem production ( $NEP_B$ ) compared to meteorological net primary production ( $NEP_M$ ) for the UMBS forest, 1999–2003. Dashed line illustrates the 1:1 relationship.

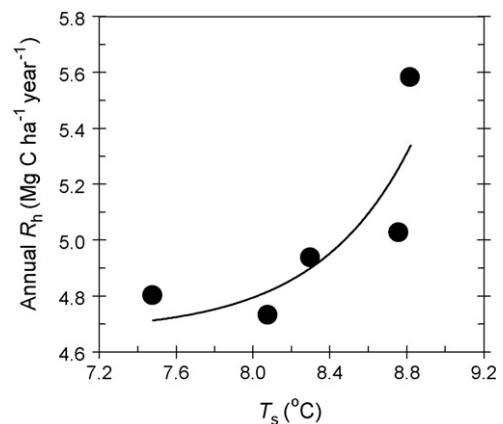
with photosynthesis, respiration, and growth (Figs. 3 and 4). However, while annual  $NPP_M$  and  $R_h$  were correlated with present-year environmental conditions, current-year climate was much better related to following-year  $NPP_B$ . Mean growing season PPFD was correlated with current-year  $NPP_M$ , but with following-year  $NPP_B$  ( $r^2 = 0.53$ ,  $n = 5$ ;  $0.57$ ,  $n = 4$ , respectively; Fig. 3). These relationships suggest that annual NPP varied by  $\sim 0.14 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  in response to a  $10 \mu\text{mol m}^{-2} \text{ s}^{-1}$  change in mean growing season PPFD. Annual C losses from  $R_h$  were positively related to changes in mean annual  $T_s$ , differing by  $0.85 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  over a  $1.3 \text{ }^\circ\text{C}$  range ( $r^2 = 0.71$ ,  $n = 5$ ; Fig. 4). Across years,  $NEP_B$  and  $NEP_M$  showed no significant relationship with  $T_a$ ,  $T_s$ , PPFD,  $\theta_s$ , or  $\phi_a$  in the current or following year ( $r^2 < 0.25$ ). However, because NEP is the balance between NPP and  $R_h$ , annual PPFD and  $T_s$  directly affect annual C storage by constraining the rates of C uptake and loss. Maximum leaf area index ( $A_{lmax}$ ) was positively correlated with annual  $NEP_M$  ( $r^2 = 0.40$ ,  $n = 5$ ), but not with  $NPP_M$ ,  $NEP_B$  or  $NPP_B$ .



**Fig. 3** – The effect of mean growing season photon flux density (PPFD) on meteorological net primary production ( $NPP_M$ ; A) and biometric net primary production ( $NPP_B$ ; B). Annual  $NPP_M$  is plotted against PPFD from that year, while annual  $NPP_B$  is plotted against PPFD from the previous year ( $NPP_M$ :  $r^2 = 0.53$ ,  $y = 0.97 + 0.015x$ ; and  $NPP_B$ :  $r^2 = 0.57$ ,  $y = 1.86 + 0.012x$ ).

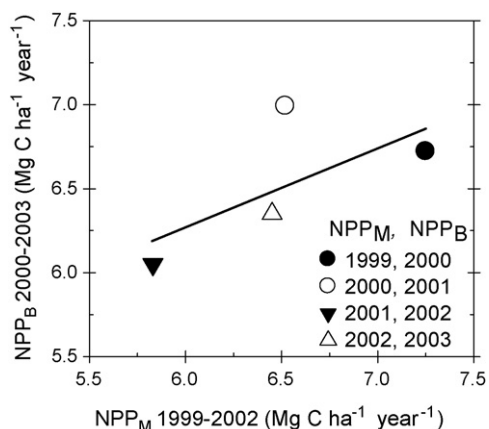
### 3.5. Annual canopy photosynthesis and growth

Although  $NPP_B$  and  $NPP_M$  in the same year were poorly correlated, this relationship improved markedly when annual  $NPP_B$  was compared with prior-year  $NPP_M$  ( $r^2 = 0.45$ ,  $n = 4$ ; Fig. 5). One explanation for this apparent offset in the two measures is that wood and foliage growth lags behind canopy



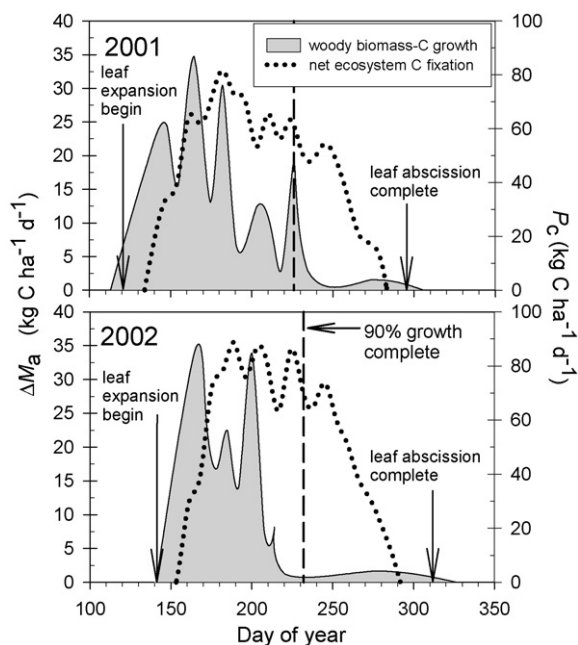
**Fig. 4** – The relationship between annual heterotrophic soil respiration ( $R_h$ ) and mean annual soil temperature ( $T_s$ ) at UMBS, 1999–2003 ( $r^2 = 0.71$ ;  $y = 4.79 + 4.15E - 78 e^{20.18T_s}$ ).



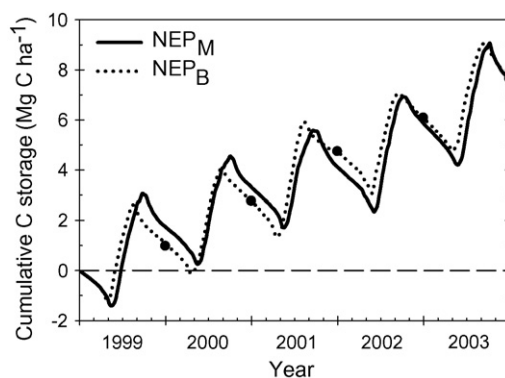


**Fig. 5 – Biometric net primary production (NPP<sub>B</sub>) compared to meteorological net primary production in the previous year (NPP<sub>M</sub>) for the UMBS forest ( $r^2 = 0.45$ ;  $y = 3.45 + 0.47x$ ). Each annual NPP<sub>B</sub> estimate is offset 1-year from the corresponding NPP<sub>M</sub> estimate.**

photosynthesis. That is, not all assimilated C was allocated to growth in any given year. Our biometric and meteorological data support this suggestion. In 2001 and 2002, aboveground growth began prior to positive canopy photosynthesis (Fig. 6). Post-growth canopy photosynthesis was 1.86 and 2.37 Mg C ha<sup>-1</sup> in 2001 and 2002, respectively, accounting for >25% of annual NPP<sub>M</sub>. These results suggest that C assimilated late in



**Fig. 6 – Aboveground woody mass production ( $\Delta M_a$ ) and net canopy photosynthesis ( $P_c$ ) during the 2001 and 2002 growing seasons.  $P_c = NPP_B = NPP_M + R_h$  on a daily timestep. Vertical dashed line indicates the date on which 90% of the total cumulative  $\Delta M_a$  was achieved (2001 = day 226; 2002 = day 232). Leaf expansion began nearly 20 days earlier in 2001 than in 2002 when mean annual air temperatures were  $\sim 1^\circ\text{C}$  warmer.**



**Fig. 7 – Cumulative C storage based on meteorological and biometric measurements. Meteorological C storage (NEP<sub>M</sub>) was based on continuous eddy-covariance measurements. Continuous biometric C storage (NEP<sub>B</sub>) was estimated from measured annual C storage (closed circles) and  $\sim$ weekly growth measurements during the 2001, 2002 growing seasons. NEP<sub>B</sub> and NEP<sub>M</sub> differed by 74, 18, 17, 5 and 1% after 1, 2, 3, 4 and 5 years, respectively.**

the growing season was allocated to early season growth the following year. While our results support a lag between canopy photosynthesis and wood growth, uncertainty in these fluxes makes estimates of the timing and magnitude of this offset imprecise. For example, we used indirect approaches to estimate heterotrophic soil respiration, a flux required to calculate canopy photosynthesis and NPP<sub>M</sub>, and wood growth, which may not fully account for seasonal changes in these C fluxes.

### 3.6. Convergence of carbon storage estimates

The agreement between biometric and meteorological C storage estimates improved substantially when compared over multiple years (Fig. 7). We calculated cumulative NEP<sub>M</sub> from continuous meteorological measurements, and approximated continuous cumulative NEP<sub>B</sub> from measured annual NEP<sub>B</sub> and weekly growth and canopy photosynthesis observations during 2001 and 2002. This assessment suggests that cumulative NEP<sub>B</sub> trended upward prior to NEP<sub>M</sub> in the late spring due to a 2–3 weeks offset between growth and canopy photosynthesis. The multi-year convergence of C storage estimates resulted from converging growth (NPP<sub>B</sub>) and net canopy photosynthesis (NPP<sub>M</sub>) estimates, which differed by <1% over 5 years (32.6 Mg C ha<sup>-1</sup> versus 32.7 Mg C ha<sup>-1</sup>; Table 2, Fig. 1). Biometric and meteorological C storage estimates differed by 74% after the first year, but by <1% over 5 years (7.63 Mg C ha<sup>-1</sup> versus 7.54 Mg C ha<sup>-1</sup>, respectively; Fig. 7).

## 4. Discussion

### 4.1. Net primary production and ecosystem carbon storage

Mean annual NPP in the UMBS forest (6.54 Mg C ha<sup>-1</sup> year<sup>-1</sup>) was very similar to that of other aspen-dominated forests,

such as a 74-year-old aspen forest in Saskatchewan ( $6.75 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ ) and an uneven-aged aspen-dominated stand in Wisconsin ( $5.11 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ ; Curtis et al., 2002; Griggs et al., 2004). We found that fine root litter production was the largest component of NPP (41%) and detritus production was twice that of the live mass increment. The relative contribution of C pools to annual NPP was similar to that found in a north-central Wisconsin forest, where fine root litter production comprised 35% of NPP and detritus made up nearly two-thirds of annual C production (Curtis et al., 2002). Our annual fine root litter production of  $2.69 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  was much higher than that reported for a 60-year-old aspen stand in Canada ( $0.43 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ ; Steele et al., 1997) and an uneven-aged forest in Wisconsin ( $1.8 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ ; Curtis et al., 2002). However, our estimated aboveground NPP of  $3.39 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  is within the range of  $2.16$ – $3.52 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  reported for other aspen forests (Gower et al., 1997; Hansen et al., 2000; Curtis et al., 2002; Burrows et al., 2003).

The UMBS forest was a consistent C sink from 1999 to 2003, with annual C storage ranging from  $0.80$  to  $1.98 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  depending on the year and estimation method. This range is comparable to other northern deciduous forests, such as the mixed hardwood forests of central Massachusetts (Barford et al., 2001) and north-central Wisconsin (Curtis et al., 2002), and aspen and maple-dominated forests of southern Ontario (Lee et al., 1999). Our average C storage rate of  $1.52 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  compares reasonably well with the Birdsey and Heath (1995) inventory-based estimate of  $2.3 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  for forests in the northeastern U.S., and the Pregitzer and Euskirchen (2004) biometric-based estimate of  $1.9 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  for temperate forests of similar age. However, our average annual C storage estimate is only half that reported for a single year in an aspen-dominated stand in Saskatchewan (Griggs et al., 2004).

Our results suggest that relatively minor shifts in annual light and temperature conditions can have substantial impacts on annual C storage by affecting the rate of forest C uptake and loss. Because NEP is the small difference between growth or net photosynthetic C uptake (NPP) and C losses from heterotrophic respiration ( $R_h$ ), a minor shift in annual C gains or losses could severely alter the net carbon balance. For example, a  $10 \mu\text{mol m}^{-2} \text{ s}^{-1}$  change in mean growing season PPFD was correlated with a change of  $\sim 0.14 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  in NPP. Previous work at our site has shown that instantaneous gross canopy photosynthesis and PPFD were well correlated (Schmid et al., 2003), suggesting that PPFD is a good predictor of both instantaneous and annual C assimilation rates at UMBS. These data support other studies linking the light environment to both instantaneous and annual C storage in northern deciduous forests (Goulden et al., 1996; Lee et al., 1999; Rocha et al., 2004). In contrast to canopy C gains, soil C losses were positively correlated with relatively small changes in annual  $T_s$ . Annual  $R_h$  varied by  $0.85 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  across a mean annual  $T_s$  span of  $1.3^\circ\text{C}$ . Soil temperature is the primary driver of  $R_s$  from diurnal to annual scales (Hanson et al., 1993; Law et al., 1999; Smith et al., 2003; Curtis et al., 2005; Euskirchen et al., 2006). This sensitivity of NPP and  $R_h$  to subtle changes in PPFD and  $T_s$  suggests that even minor changes in future climate may alter C storage at UMBS.

#### 4.2. Convergence of biometric and meteorological carbon storage estimates

Short-term biometric and meteorological C storage estimates often exhibit rather poor agreement. Meteorological C storage estimates were 12% lower to 129% higher than biometric based estimates across five deciduous forests in the eastern U.S. (Curtis et al., 2002; Ehman et al., 2002). Granier et al. (2000) estimated nearly 100% greater annual C storage by a European beech forest from biometric observations compared with meteorological data. However, improved agreement between methods was observed when 8 years of data were compared at Harvard Forest (Barford et al., 2001). Our two estimates of forest C storage,  $\text{NEP}_B$  and  $\text{NEP}_M$ , differed by 13% to 148% when compared on an annual basis. Cumulative  $\text{NEP}_B$  and  $\text{NEP}_M$  differed by 74% after the first year, but by 18, 17, 5, and 1% over 2, 3, 4 and 5-year increments, respectively. The convergence of  $\text{NEP}_B$  and  $\text{NEP}_M$  over 5 years suggests that several years of measurements may be required to make robust estimates of C storage (Barford et al., 2001; Baldocchi, 2003).

Our results additionally suggest that annual biometric and meteorological C storage estimates are poorly correlated because of temporal offsets between photosynthesis and growth. Such offsets occur when photosynthate is allocated to storage carbohydrates rather than growth (Arneeth et al., 1998; Barford et al., 2001; Sampson et al., 2001; Hoch et al., 2003). For example, stored labile C was critical to loblolly pine (*Pinus taeda* L.) growth during the early growing season, and starch accumulation by sugar maple in late summer was vital for early spring growth (Sampson et al., 2001; Wong et al., 2003). Seasonal variability in tree ring  $^{13}\text{C}/^{12}\text{C}$  also strongly suggests a reliance of early season growth on storage carbohydrates (Helle and Schleser, 2004).

Our data provide two lines of evidence in support of a lag between photosynthesis and growth. First, the initiation of growth preceded positive net canopy  $\text{CO}_2$  uptake by  $\sim 2$ – $3$  weeks in the spring and  $>25\%$  of annual C assimilation occurred after growth had effectively ceased in the autumn. These results suggest that C assimilated late in the growing season was allocated to early-season growth the following year and supports earlier proposals that C allocation to storage carbohydrates rather than growth obscures agreement between annual  $\text{NEP}_B$  and  $\text{NEP}_M$  (Barford et al., 2001; Curtis et al., 2002; Ryan, 2002). Second, annual  $\text{NPP}_B$  (i.e., growth) was moderately correlated with prior-year  $\text{NPP}_M$  (i.e., photosynthesis) and prior-year PPFD, suggesting that PPFD had an immediate effect on canopy photosynthesis, but a delayed effect on growth. This is consistent with our understanding of environmental constraints on canopy-level C uptake. Rapid fluctuations in NEE due to changes in the light environment are well documented (Wofsy et al., 1993; Chen et al., 2002; Schmid et al., 2003; Loescher et al., 2003). While an annual lag between growing season PPFD and growth has not previously been reported to our knowledge, multi-year lags between environmental stimuli such as drought and growth have been reported from tree ring studies (Orwig and Abrams, 1997; Pederson, 1998). Although tree-level studies support a lag between photosynthesis and growth, the timing of this offset was quantified with limited precision because estimates of canopy photosynthesis and wood growth are highly uncertain.

Also, we note that the temporal lag between canopy photosynthesis and forest growth was inferred from a single pool, aboveground wood, because we did not measure the growth of other pools at the same high temporal resolution. However, monthly measurements of fine root growth and more frequent analyses of leaf area index do not indicate that changes in wood growth were offset by growth of other plant tissues.

Our data also suggest that interannual variation in the timing of photosynthesis and growth was related to temperature-driven changes in canopy phenology. Cooler temperatures in 2002 than in 2001 resulted in a considerably later leaf expansion date (by 20 days), which corresponded with delayed initiation of both photosynthesis and growth. Despite a later leaf expansion date in 2002, leaf abscission occurred later in the season and a higher  $A_{\text{Imax}}$  prolonged and augmented canopy photosynthesis, resulting in greater  $\text{NPP}_M$  in 2002. Air temperature is an important regulator of leaf phenology and associated live mass production and C storage in other forests as well (Goulden et al., 1996; Baldocchi and Meyers, 1998; Baldocchi et al., 2001; Rotzer et al., 2004).

#### 4.3. Uncertainty analysis

Biometric C storage estimates are not free of error, in part because of the spatial variability associated with C mass and also because many C fluxes are not directly measured, but are derived from allometric relationships (Clark et al., 2001). Uncertainty analyses provide an important constraint on C storage estimates and are useful in modeling efforts and comparative analyses (Clark et al., 2001). While the statistical confidence in our estimates was variable (CV = 5–341%), levels of uncertainty were comparable to those reported for other forests (Clark et al., 2001; Ehman et al., 2002). On average, confidence in the woody mass increment ( $\Delta L$ ; CV = 6%) was higher than for other pools. Annual  $\Delta L$  for aspen, the dominant forest component, was estimated from allometric equations developed onsite. We also found very good agreement between  $M_b$  estimated from root sampling and that estimated from allometry (~1% difference). However, not all of the allometric models used to estimate  $\Delta L$  were developed at UMBS, potentially resulting in biased estimates (King et al., 1999; Clark et al., 2001). The magnitude of this potential bias is unknown, but Clark et al. (2001) suggested that using off-site allometric equations could alter NPP by as much as 20%. Also, these allometric relationships do not take into account seasonal changes in wood C concentration that may occur. Uncertainty associated with leaf litter production ( $M_{\text{ll}}$ ; CV = 9%) and herbivory ( $H$ ; CV = 14%) was fairly low as well, reflecting the low variability among plots in the case of leaf litter and among methodologies in the case of herbivory. The highest rates of uncertainty were in woody debris production ( $M_{\text{fd}} + M_{\text{cd}}$ ; CV = 341%), principally resulting from high variability among coarse debris sampling plots. We may have not adequately quantified annual variability in CWD production because our surveys were conducted 3 years apart. However, an independent assessment indicates that CWD production is  $<0.1 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  at our site, suggesting that our estimates are reasonable (Gough et al., 2007b). Coarse woody debris pools can be difficult to measure precisely due to the

heterogeneous distribution of forest floor detritus (Clark et al., 2001; Ehman et al., 2002).

Methodological constraints universally limit the certainty of below-ground C storage estimates (Clark et al., 2001). Our fine root litter production uncertainty was modest ( $M_{\text{fr}}$ ; CV = 17%), resulting primarily from variability in the outcome of the three approaches used to estimate annual fine root turnover,  $\kappa_{\text{fr}}$ . The three methods produced estimates varying from 0.27 to  $0.65 \text{ year}^{-1}$ . These values generally fall within the range reported for other northern deciduous forests (Hendrick and Pregitzer, 1993; Gaudinski et al., 2001; Tierney and Fahey, 2002).  $\kappa_{\text{fr}}$  estimates for a deciduous forest in New Hampshire varied from 0.30 to  $0.86 \text{ year}^{-1}$  depending on methodology (Tierney and Fahey, 2001, 2002). Our average minirhizotron-based  $\kappa_{\text{fr}}$  estimate of  $0.30 \text{ year}^{-1}$  is the same as that reported by Tierney and Fahey (2002). However, minirhizotron-based analyses may underestimate  $\kappa_{\text{fr}}$  since root death can be difficult to determine from images (Johnson et al., 2001; Tierney and Fahey, 2002). While we assumed N availability did not vary annually in our calculations of  $\kappa_{\text{fr}}$ , our N mineralization rates were similar to those reported for an adjacent forest a year prior to our measurements (White et al., 2004). Our mass balance-based estimates of  $\kappa_{\text{fr}}$ , which assume detritus inputs are equal to soil C losses, were higher than those from minirhizotron or available N approaches. However, mean  $\kappa_{\text{fr}}$  (across methods) suggested that soil C losses were greater than detritus inputs. If soil C losses exceeded inputs, we should have observed a decrease in soil C over time. Although we did not detect a change in mineral soil C in the top 20 cm, a loss or gain of C below 20 cm nonetheless is possible. Small changes in soil C are difficult to detect due to both sampling and instrument limitations. For example, an annual change of 1% C in the top 1 m of the mineral soil would result in a  $\sim 1 \text{ Mg C ha}^{-1}$  change in our annual C storage estimates.

Partitioning  $R_s$  into  $R_h$  and autotrophic soil respiration ( $R_a$ ) components is a critical step in biometric estimates of NEP because C storage is the difference between  $\text{NPP}_B$  and  $R_h$ . Uncertainty in our  $R_h$  estimates was modest (CV = 17%) and primarily originated from uncertainty in the empirical relationship used to partition  $R_s$  into  $R_h$  and  $R_a$ . We estimated that heterotrophic contributions to  $R_s$  were  $\sim 50\%$  using the component integration method. This estimate agrees with the summary value reported by Hanson et al. (2000) and is equal to the assumed heterotrophic contribution to  $R_s$  used in other estimates of forest C storage (Tate et al., 2000; Curtis et al., 2002; Ehman et al., 2002). This simple partitioning does not take into account seasonal variability in  $R_h$  due to changes in C substrate inputs and environmental conditions (Randerson et al., 1996; Lee et al., 2003; Gu et al., 2004). Clearly, improved techniques that allow for less invasive monitoring of below-ground C pools will lead to enhanced confidence in C storage estimates.

## 5. Conclusions

The aspen-dominated forests at UMBS are moderately productive and a consistent sink for atmospheric C ( $\text{NPP} \cong 6.5 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ ,  $\text{NEP} \cong 1.5 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ ). However, interannual variability in NEP was  $>100\%$ . Mean growing season PPFD and mean annual  $T_s$  were positively related to

annual NPP and  $R_h$ , respectively, demonstrating that relatively small changes in annual climate can affect rates of annual C storage by altering ecosystem processes that collectively regulate NEP. Canopy leaf phenology and seasonal patterns of photosynthesis were also sensitive to variation in annual  $T_a$ . Observed incongruities between biometric and meteorological estimates of annual C storage resulted, in part, from a temporal offset between canopy photosynthesis and growth. However, these independent C storage estimates converged to within <1% of each other after 5 years of observation. This suggests that differences between annual biometric and meteorological C storage estimates occur, in part, because recently assimilated C is temporarily allocated to storage rather than applied to current growth. Importantly, the long-term convergence of biometric and meteorological C storage estimates provides an essential cross-validation of these independently derived estimates.

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