

Biometric and eddy-covariance based estimates of annual carbon storage in five eastern North American deciduous forests

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Abstract

Quantifying net carbon (C) storage by forests is a necessary step in the validation of carbon sequestration estimates and in assessing the possible role of these ecosystems in offsetting fossil fuel emissions. In eastern North America, five sites were established in deciduous forests to provide measurements of net ecosystem CO₂ exchange (NEE) using micro-meteorological methods, and measures of major carbon pools and fluxes, using a combination of forest mensurational, eco-physiological, and other biometric methods. The five study sites, part of the AmeriFlux network, ranged across 10° of latitude and 18° of longitude, but were all of similar age, canopy height, and stand basal area. Here we present a cross-site synthesis of annual carbon storage estimates, comparing meteorological and biometric approaches, and also comparing biometric estimates based on analyses of autotrophic carbon pools and heterotrophic carbon fluxes (net ecosystem production, NEP) versus those based on measurements of change in two major carbon pools (ΔC). Annual above-ground net primary production (ANPP) varied nearly two-fold among sites and was strongly correlated with average annual temperature and with annual soil nitrogen mineralization (N_{\min}). Estimates of NEP ranged from 0.7 Mg C per hectare per year in northern lower Michigan to 3.5 Mg C per hectare per year in central Indiana, and were also well correlated with N_{\min} . There was less variation among sites in estimates of ΔC (range, 1.8–3.2 Mg C per hectare per year). In general, ΔC more closely matched NEE than did NEP, but there was no systematic pattern among sites in over- versus under-estimation of the biometric compared to the meteorologically based measures. Root and soil carbon dynamics were significant sources of uncertainty in our biometric measures and represent a prerequisite area of study needed for accurate estimates of forest carbon storage.

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1. Introduction

Temperate deciduous forests are an important and much altered component of the Northern Hemisphere. Absent human disturbance, deciduous forests are the

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dominant vegetation type over most of temperate eastern North America. Much of the region was converted to agricultural land use, effectively removing more than 95% of the above-ground carbon from these systems. Tillage also resulted in carbon losses from soils (Lal et al., 1995; Compton and Boone, 2000). Much of these agricultural lands have since been abandoned, and a substantial portion of the eastern deciduous forest region contains trees less than a century old. However, these forests represent a substantial and growing carbon pool. Birdsey (1992) estimated from forest inventory data an average net accrual in the eastern deciduous forest region of from 1 to 2.4 Mg C per hectare per year, 45% of US forest carbon storage. Carbon is accruing in these forests not only in standing live wood, but also in other above- and below-ground carbon pools, including standing dead wood, forest floor litter, coarse woody debris, roots, and soil organic matter.

Because forests have substantially higher growth rates and hence carbon storage than most other native vegetation types, their importance in continental and global carbon cycling and storage is magnified. Temperate forests average from twice to 20 times higher productivities than desert, grassland, or shrubland vegetation (Whittaker and Likens, 1975) and store up to several orders of magnitude more carbon above-ground than do these other vegetation types. Consequently, much recent attention has focused on the status of temperate deciduous forests as sources or sinks in the global carbon cycle (Fan et al., 1998; Canadell et al., 2000). The net gain, or loss, of carbon from an ecosystem is defined as net ecosystem production (NEP, or P_{NE}) and results from the gain of carbon from autotrophic organisms (gross primary productivity, GPP, or P_{GP}) minus its loss from autotrophic (R_a) and heterotrophic (R_h) respiration:

$$P_{NE} = P_{GP} - R_a - R_h \quad (1)$$

The difference between GPP and R_a , or net primary production (NPP, or P_{NP}), has been of interest to ecologists for several decades (e.g. Reichle, 1970; Lieth and Whittaker, 1975; US National Committee for the International Biological Program, 1975). Forest NPP estimates have been based primarily upon measurements of stem, branch, woody root, and foliage mass gain using allometric relationships for

large trees (Baskerville, 1972) and harvest methods for other ecosystem components. That is

$$P_{NP} = P_{GP} - R_a = L + D + H \quad (2)$$

where for some unit of time (typically a year), L is the increment in live plant mass, D the increment in dead plant mass (detritus), and H is the increment lost to herbivory (Waring and Schlesinger, 1985). In principle, each variable includes above- and below-ground processes. For simplicity we define these and other plant- or soil-based approaches as ‘biometric’ measurements and note that all terms can be expressed on either a tissue dry mass or carbon mass basis.

Biometric NPP estimates commonly ignore volatile organic compounds which may be lost from ecosystems (Hanson and Hoffman, 1994; Isebrands et al., 1999) as well as the loss of dissolved organic carbon with water flow. Carbon transport by vertebrates (i.e. seed movements by birds and squirrels) is assumed to be random and losses from a particular area are balanced by gains from other locations. There are additional NPP components (e.g. nectar and pollen production) that commonly are not accounted for and are assumed to be small (but see Clark et al., 2001).

It follows that NEP can be expressed as the difference between NPP and R_h :

$$P_{NE} = (L + D + H) - R_h \quad (3)$$

or the summed increment of all autotrophic carbon pools less heterotrophic respiratory losses. Soil microbial respiration, usually measured as the difference between total soil respiration and root respiration (Hanson et al., 2000), is the main contributor to R_h .

If mass losses from H , volatile organic compounds, or other processes are small, and the annual increment in foliar and fine root mass is approximately zero, forest annual carbon storage can also be expressed as the annual increment in wood (W) plus soil (S) carbon pools:

$$\Delta C = W + S \quad (4)$$

since S is the difference between D and R_h . While NEP and ΔC are not independent, ΔC does not require measurement of below-ground D or R_h , variables which cannot be easily measured directly.

With improvements in micro-meteorological instrument technology, the eddy-covariance technique has been applied to the measurement of energy and

mass exchange over forest canopies, enhancing our understanding of soil–vegetation–atmosphere carbon exchanges (Wofsy et al., 1993; Baldocchi et al., 1996; Goulden et al., 1996, 1998; Baldocchi and Meyers, 1998). Net ecosystem CO₂ exchange (NEE), measured using eddy-covariance methods, integrates vegetation and soil CO₂ fluxes, and can provide a measure of net carbon exchange on a sub-hourly basis. However, eddy-covariance measurements become unreliable or unavailable during precipitation, icing, or very weak turbulence, as sometimes occurs at night (Lee, 1998; Baldocchi et al., 2000). A variety of modeling techniques (Schmid et al., 2000; and references in this volume) are used to make corrections for the estimation of annual NEE. Conceptually, NEE and NEP are equivalent in that both constitute the difference between GPP and total ecosystem respiration ($R_{\text{total}} = R_{\text{a}} + R_{\text{h}}$). Methodologically, however, they are independent, having unrelated measurement errors. As such, their comparison helps constrain estimates of forest carbon storage and may provide insight into the causes of within (Barford et al., 2001) and among site differences in annual carbon sequestration (Wofsy and Hollinger, 1998).

In this paper we describe the estimation of annual carbon storage using biometric methods at five sites

within the eastern deciduous forest biome of North America and compare them with eddy-covariance based estimates of NEE from the same sites. These sites are part of the AmeriFlux carbon cycle research program (Wofsy and Hollinger, 1998). Our objective was to conduct a cross-site comparison of biometric estimates of annual carbon storage and to evaluate whether such a synthesis could provide an independent constraint on meteorologically based estimates of the same variable. We also hoped to gain insight into the major sources of uncertainty in our ecosystem carbon budgets.

2. Methods

At each of the five sites, efforts have been made to derive biometric estimates of annual carbon storage by measurement of major carbon pools and fluxes as presented in Table 1, and to measure annual NEE using eddy-covariance methods. Given their ecological similarities and their use of standard methods for quantifying many carbon cycle components, there was considerable overlap among sites in the details of their biometric and meteorological measurements. However, differences among sites in programmatic

Table 1

Components of NPP, ecosystem respiration, and soil carbon dynamics needed to derive a biometric estimate of annual NEP. Methods available for estimating each component and among which of the five study sites they are applied are shown (site abbreviations are as in Fig. 1)

Item	Method	Application
NPP components		
Stem increment	Allometry	All sites
Branch increment	Allometry	All sites
Leaf production	Litter baskets	All sites
Stump increment	Allometry	All sites
Flower and fruit production	Litter baskets	All sites
Fine root production	Coring, minnirhizotrons	WB, MMSF, HF
Coarse root production	Allometry	MMSF, HF, UMBS, WC
Herbivory losses	Leaf/litter assessments	WB, MMSF, UMBS
VOCs	Chambers/modeling	WB
Nonstructural carbohydrates	Tissue analysis/allometry	No sites
Pollen and trichomes	Micro-litter baskets	No sites
Respiration		
Total soil respiration	Chambers/modeling	All sites
Above-ground heterotrophs	Chamber experiments	No sites
Soil carbon		
Soil surface	Soil pits/cores, ¹⁴ C	WB, MMSF, HF, UMBS
Subsurface	¹⁴ C, resampling	WB, HF

objectives, expertise, measurement period, and intrinsic features of the ecosystems led to variation in sampling design and to the precision with which some carbon cycle components were measured. Here we present an overview of the important biogeographical features of each site and of the methods employed to quantify annual carbon storage.

2.1. Study sites

The five forest sites are distributed across 10° of latitude and 18° of longitude in eastern North

America (Fig. 1, Table 2). Mean annual temperatures vary more than three-fold, from a high of 13.8°C in eastern Tennessee, to a low of 4.8°C in central Wisconsin. Annual precipitation follows a similar pattern, with the most southern site receiving almost twice the rainfall as the most northern. Soils reflect differences in glacial history and parent material of these sites, from fine textured silty loams in the south to very sandy soils in the Great Lakes region.

The Walker Branch (WB) forest is in the ridge and valley province of eastern Tennessee. Local topography is represented by a series of repeating parallel

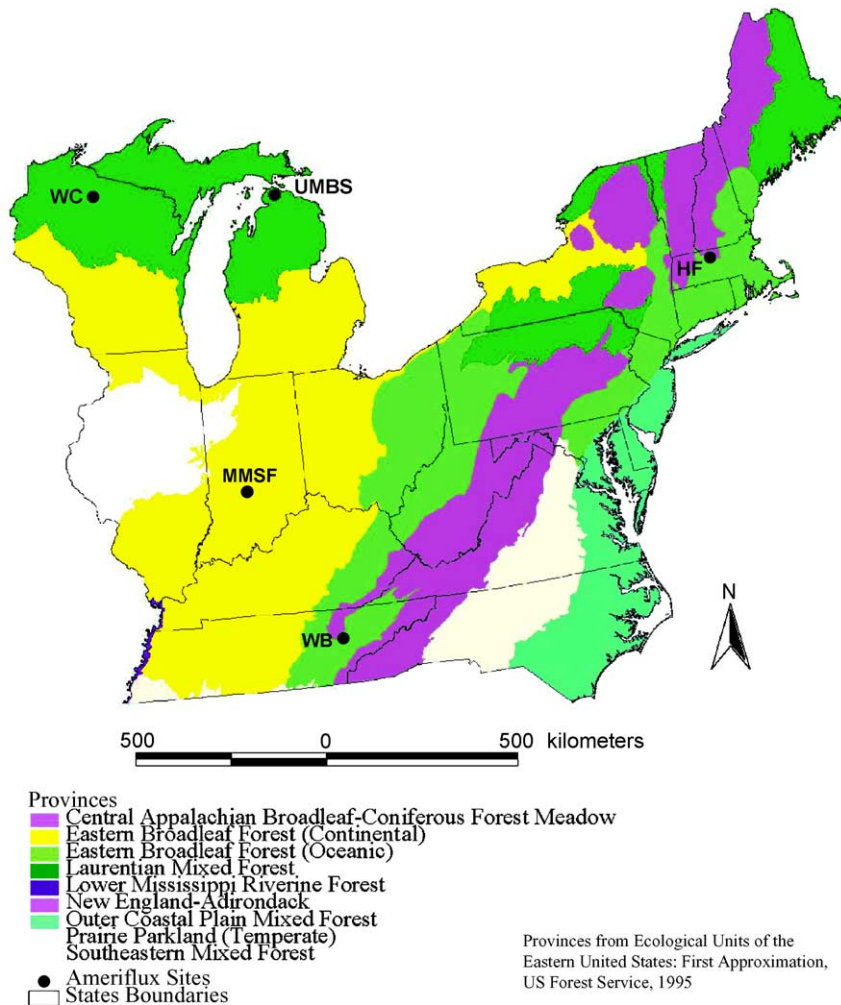


Fig. 1. Location within the eastern North American deciduous forest biome of the five study sites: Walker Branch (WB), in eastern Tennessee; Morgan Monroe State Forest (MMSF), in south-central Indiana; Harvard Forest (HF), in north-central Massachusetts; University of Michigan Biological Station (UMBS), in northern lower Michigan; and Willow Creek (WC), in north-central Wisconsin.

Table 2

Climate, stand, and soil characteristics of five eastern North American forests: WB, MMSF, HF, UMBS, and WC (site abbreviations are as in Fig. 1)

Descriptor	WB	MMSF	HF	UMBS	WC
Location and climate					
Latitude	35°57'N	39°53'N	42°32'N	45°35'N	45°47'N
Longitude	84°17'W	86°25'W	72°10'W	84°42'W	90°5'W
Mean annual temperature (°C)	13.8	11.1	7.1	6.2	4.8
Annual precipitation (mm)	1352	1012	1066	750	776
Stand characteristics					
Stand age (year)	50–120	80	60	90	66
Canopy height (m)	25	27	26	20	24
LAI	6.2	4.9	4.0	3.7	4.2
Basal area (m ² per hectare)	25	26	32	24	25
Maximum dbh (cm)	86	86	67	62	48
Mean dbh (cm)	22	22	23	14	19
Soil characteristics					
Percent of sand, silt, clay ^a	34, 3, 63	34, 26, 40	–	90, 6, 1	–
Classification	Typic paleudult	Mesic typic dystrochrept	Typic dystrochrept	Entic haplorthod	Entic haplorthod
pH	3.5–4.6	~5.2	~3.8	4.8	5.1
Annual N_{\min} (kg per hectare per year) ^b	96	122	34	11	28

^a Soil A horizon.

^b Annual net nitrogen mineralization.

ridges and valleys oriented from southwest to northeast, and elevation ranges from 270 to 340 m. Soils are fairly acidic ultisols with depth to bedrock approximately 30 m. The forest canopy surrounding the eddy-covariance tower is dominated by white oak (*Quercus alba* L.), chestnut oak (*Quercus prinus* L.), red maple (*Acer rubrum* L.) and sugar maple (*Acer saccharum* Marshall.) with yellow poplar (*Liriodendron tulipifera* L.) also a canopy dominant on lower slope positions or mesic settings. Black tupelo (*Nyssa sylvatica* Marsh.) and sourwood (*Oxydendrum arboreum* L.) are the predominant mid-canopy species. Understory saplings are predominantly red maple and dogwood (*Cornus florida* L.) with scattered individuals of less common species. In some locations pine species contribute up to one-third of total stand basal area, but hardwoods are out-competing most pines at the current stage of stand development. Prior to 1940, closed forests were limited to ridge top locations with widespread subsistence farming and grazing taking place in the valleys and many side slope locations. Since 1940, natural successional processes have governed stand development. Periodic insect infestations,

wind, lightning, and occasional ice storms are the most common forms of disturbance.

Morgan Monroe State Forest (MMSF) is located in south-central Indiana, just south of the limit of the late Wisconsinian glaciation and is dominated by ridge/ravine topography. Soils are well drained inceptisols, formed in residuum from sandstone, siltstone, and shale. The region is covered primarily by late secondary successional broadleaf forests located within the maple-beech to oak-hickory transition zone of the eastern deciduous forest. Twenty-nine tree species occur in MMSF; dominant species (about 75% of total basal area) are sugar maple, yellow poplar, sassafras (*Sassafras albidum* Nutt.), white oak, and black oak (*Quercus velutina* Lam.). Common understory species include pawpaw (*Asimina triloba* L.), spicebush (*Lindera benzoin* L.), and sweet cicely (*Osmorhiza claytonii* Michx.), as well as seedlings and saplings of the dominant tree species. Most of Indiana was deforested by the early 1900s, but afforestation has occurred in much of central and southern Indiana after abandonment of marginally productive agricultural land. Timber harvests have not occurred in the source area of

the flux tower recently except in one small seed-tree area. Wind, lightning, and ice storms are the most common types of natural disturbances. Fires occur occasionally but are uncommon and never widespread.

Harvard Forest (HF) is in the central uplands of New England, an area of broad north–south oriented hills, with elevation ranging from 150 to 300 m. Soils are mostly inceptisols, developed from thin glacial till and are well drained, acidic sandy loams of relatively poor nutrient status, with poorly drained peat soils in a few low-lying areas. The vegetation assemblage is transitional hardwood, primarily red oak (*Quercus rubra* L.), black oak, and red maple, together with some hemlock (*Tsuga canadensis* L.) stands, white pine (*Pinus strobus* L.), and red pine (*Pinus resinosa* Aiton.) plantations. The relatively sparse understory contains saplings of the dominant trees plus woody shrubs such as blueberry (*Vaccinium* spp.), *Viburnum* spp., and witch hazel (*Hamamelis virginiana* L.). Most of the trees within the dominant fetch of the eddy-covariance tower were downed by a 1938 hurricane and salvaged. The canopy and understory are now relatively open and free of coarse woody debris.

The University of Michigan Biological Station (UMBS) lies on lake-border plains in northern lower Michigan, in the transition zone between the mixed hardwood and boreal forests. The study site lies on level to gently sloping high outwash plain derived from glacial drift, 1.3 km south and 3.5 km northwest of two large lakes, with the gradually ascending slope of an interlobate moraine lying approximately 1 km to the south. Soils are predominantly excessively drained spodosols. Bigtooth aspen (*Populus grandidentata* Michx.) and trembling aspen (*Populus tremuloides* Michx.) dominate within a 1 km radius of the eddy-covariance tower, but with significant representation by red oak, beech (*Fagus grandifolia* Ehrh.), sugar maple, white pine, and hemlock as well. The understory is dominated by bracken fern (*Pteridium aquilinum* L.) and saplings of red maple, red oak, beech, and white pine. The presettlement white pine, red pine, hemlock forest was cut around 1880, and the area disturbed repeatedly by fire until 1923.

The Willow Creek (WC) study site is in the Chequamegon National Forest in north–central Wisconsin. The area is flat with a slope less than 2%, and soils are fine sand to loamy fine sand spodosols. The surrounding region is a mix of upland forests

and wetlands, with aspen (*Populus* spp.) and northern hardwoods the most common upland types. The study site is occupied by an uneven-aged, closed-canopy forest dominated by sugar maple with significant American basswood (*Tilia americana* L.), green ash (*Fraxinus pennsylvanica* Marsh.), and red oak. The understory consists primarily of a mix of herbaceous species, including *P. aquilinum*, with scattered seedlings and saplings of the overstory species. The site has never been farmed, but has been logged at least twice. US Forest Service records indicate there was a second growth stand logged during the 1920s. Since then the stand has been periodically thinned, the last thinning occurring in the early 1970s.

2.2. Biometric measurements

2.2.1. Above-ground net primary productivity

Above-ground carbon stored in wood was estimated at all sites by allometric equations relating diameter at breast height (dbh) to bole, branch, and stump biomass. Annual wood increment was estimated by measuring change in dbh using band dendrometers. At WB, wood increment was determined as the average across a 7-year record of tree and sapling stem growth (1993–1999) conducted as a part of a multi-year throughfall displacement experiment (TDE: [Joslin et al., 2000](#); [Hanson et al., 2001](#)). The TDE experimental site lies on the edge of the eddy-covariance tower footprint, but species composition, stand age, and biomass distributions are comparable. Allometric relationships for canopy trees ([Harris et al., 1973](#)) and saplings ([Sollins and Anderson, 1971](#)) were developed from local tree harvests. At MMSF, wood increment measurements were averaged across two years (1998–1999) from plots located randomly within three topographic categories <1 km from the eddy-covariance tower. Species-specific allometric equations ([Ter-Mikaelian and Korzukhin, 1997](#)) or those for general hardwoods ([Harris et al., 1973](#)) were employed. At HF and UMBS, measurements were reported for a single year (1999) from plots arrayed on transects in the dominant fetch of the eddy-covariance tower. Allometric equations were developed from on site harvests (UMBS: [Cooper, 1981](#)) or from general allometries for northeastern trees (UMBS: [Young et al., 1980](#); [Perala and Alban, 1994](#); HF: [Tritton and Hornbeck, 1982](#)). At WC, measurements were made

in plots northwest, northeast, southwest, and southeast of the eddy-covariance tower. In addition to band dendrometer data, diameter growth from 1989 to 1999 at WC was measured from increment cores. Annual wood increment was estimated as the average of these 10 years growth using general allometric equations for northeastern trees (Ter-Mikaelian and Korzukhin, 1997). Limited harvests were conducted at some sites (WB, UMBS) to confirm older site-specific or general allometric relationships but in many cases published equations were used without further validation from current harvest data.

Annual production of fine litter (leaves, flowers, fruits, etc.) was estimated at all sites using baskets placed on the forest floor which were emptied periodically and their contents dried and weighed. Measurement periods were the same as for annual wood increment. Understory and herbaceous contributions to ANPP were estimated by allometric equations for woody vegetation (all sites) and biomass harvest of herbaceous vegetation at MMSF, HF, UMBS, and WC. Loss of leaf carbon to herbivores was estimated by collecting leaves prior to abscission and comparing their remaining area to that of undamaged leaves of the same size. Herbivore losses for WB were reported as the mean of that measured in 1992, 1993, and 1994 (Shure et al., 1998), for MMSF as that measured in 1998 and 1999, and for UMBS as that measured in 2000. Herbivore losses have not been estimated at HF and WC.

2.2.2. *Below-ground net primary productivity*

The amount of carbon stored below-ground as wood (i.e. stumps and very large lateral roots) was derived from allometric equations relating dbh to woody root mass. For most tree species only general relationships are available, in which below-ground wood mass is set at a fixed fraction of above-ground wood mass (generally ~20%, e.g. Perala and Alban, 1994). This simple scaling of below- to above-ground wood mass was employed at HF while more species-specific relationships were used at MMSF, WB (Harris et al., 1973), and UMBS. Estimates made at WC did not include the below-ground portion of the stump mass. Annual increment in woody root carbon was estimated from annual change in dbh (MMSF, HF, UMBS) or scaled as 20% of the above-ground wood increment (WB, WC). Fine root production was estimated at

WB from direct observation of root turnover using minirhizotron cameras (Joslin et al., 2000), and at HF from estimates of fine root mass, annual production, and decomposition rate (McClaugherty et al., 1982; Gaudinski et al., 2000). At these sites fine roots were considered those with diameter <2.0 mm. At MMSF, UMBS, and WC fine root production was estimated after the method of Aber et al. (1985) in which annual soil N mineralization (N_{\min}) was related empirically to the fine root pool fraction cycling annually. The fine root carbon pool was measured from soil cores at MMSF, UMBS, WB, and WC, and defined at these sites as roots with diameter <0.5 mm.

2.2.3. *Soil respiration*

Soil respiration measurements at WB were conducted *in situ* at periodic intervals from 1992 to 1998 using a static chamber infra-red gas analysis system (LiCor 6200 and 6000-09 soil chamber, LiCor Inc., Lincoln Nebraska). Annual estimates were derived from the relationship between soil respiration, soil temperature and soil water potential following the modeling approach of Hanson et al. (1993). At MMSF, total soil CO₂ fluxes were measured using two static chamber infra-red gas analysis methods: bi-weekly measurements to assess spatial variation (LiCor LI-6200 and 6000-09 soil chamber), and continuous measurements in one location to assess temporal variation (LiCor LI-6262 and eight automated chambers). Soil respiration at HF was measured using chambers and by monitoring CO₂ gas profiles on a separate set of plots within the study area (Davidson et al., 1998). At UMBS and WC, total soil respiration was measured periodically within the flux footprint using static chambers (LiCor LI-6400 soil CO₂ flux chamber) with linear interpolation between measurement points to yield annual flux estimates. In all cases, R_h was calculated as 50% of total soil respiration (R_s) (Hanson et al., 2000). Coarse woody debris was quantified within subplots at each site using the methods of Harmon and Sexton (1996), but respiration from this pool was estimated only at MMSF, using a relationship developed by Todd et al. (1976).

2.2.4. *Soil carbon and nitrogen dynamics*

At MMSF, the soil carbon pool and its change over time was quantified from multiple forest floor litter samples and soil excavated to 1 m within multiple

Table 3

Eddy-covariance and below-canopy carbon storage measurement locations, period of measurement, and the equipment used at each of the five study sites (site abbreviations are as in Fig. 1)

	Site				
	WB	MMSF	HF	UMBS	WC
Eddy-covariance measurement heights (height above canopy) (m)	37 (10)	34 (7), 46 (19)	30 (4)	34 (14), 46 (26)	30 (6)
Sonic anemometer	ATI "K" probe	CSAT-3	ATI "K" probe	CSAT-3	CSAT-3
CO ₂ analyzer	Open path	LI-6262	LI-6262	LI-6262	LI-6262
Number of below-canopy storage measurement heights	4	8	8	8	7
Period of NEE measurement	1995-present	1997-present	1990-present	1998-present	1998-present

subplots. Soil carbon dynamics at HF were estimated from soil carbon and ¹⁴C inventories (Gaudinski et al., 2000), at WB from a 21-year study of soil carbon pools (Trettin et al., 1999), and at UMBS from an analysis of surface O and upper A horizons across a successional chronosequence (Schaeztl, 1994). At WC annual soil carbon change was assumed to be near zero based on stand age and successional status. Annual net N_{\min} was estimated at MMSF, HF, and UMBS from *in situ* anaerobic incubations in the upper 10 cm using the buried bag technique (Robertson et al., 1999). At MMSF and UMBS, analyses were made on a monthly basis during the 1999 growing season and over 3–6 months during the winter, while at HF values are the average obtained in control plots of a soil warming experiment from 1991 to 1997 (J. Mellilo, unpublished data). Estimates of N_{\min} at WB were based on aerobic laboratory incubations as outlined by Garten et al. (1994). At WC, N_{\min} was set as the average of two northern Wisconsin conifer stands growing on similar soils reported by Reich et al. (1997).

2.3. Micro-meteorological methods

All sites used similar approaches to measuring meteorological variables above and within the canopy (Table 3). Mixing ratios of CO₂ and H₂O were measured with either closed or open path infra-red gas analyzers, and wind and temperature using three-dimensional sonic anemometers. The height at which eddy-covariance measurements were made varied among sites, from <5 to >20 m above the canopy. Vertical CO₂ profiles below the canopy were measured at all sites, as was net radiation, photosynthetically

active radiation and soil heat flux. The details of data processing and gap-filling also varied somewhat among sites and were described by Wilson and Baldocchi (2001) for WB, Schmid et al. (2000) for MMSF and UMBS, Goulden et al. (1996) for HF, and Berger et al. (2001) for WC. Annual net NEE reported here is the mean value from 1995 to 1999 at WB, from 1998 to 1999 at MMSF, and for 1999 at HF, UMBS, and WC.

3. Results

Annual soil net N_{\min} varied more than 10-fold among sites but with two distinct groups evident: two southern sites on fine textured soils with high N_{\min} , and three northern sites on sandy soils with much lower N_{\min} (Table 2). Climatic and edaphic differences notwithstanding, the five sites are quite similar in stand age and structure. All are late secondary successional forests of comparable height and stand basal area, having regrown following widespread disturbance in the late 19th or early 20th century. Leaf area index and maximum tree dbh did vary among sites, however, with the largest trees and densest canopies occurring on the more productive, southern sites.

Above-ground carbon stored in wood was greatest at HF and least at UMBS, reflecting variation among sites in stand basal area (Tables 2 and 4) since bole and branch biomass estimates were derived from individual tree dbh measurements. Annual wood increment and leaf litter fall, which represent the annual carbon fluxes into wood and fine litter, respectively, more closely reflected differences in climate and site fertil-

Table 4

Pools (Mg C per hectare) and fluxes (Mg C per hectare per year) of the major components of NPP and net ecosystem carbon storage for five eastern North American deciduous forests. Annual net carbon storage was calculated both as NEP and as the change in carbon pool size (ΔC). Net ecosystem exchange was derived from eddy-covariance data (site abbreviations are as in Fig. 1)

C budget component	Site									
	WB		MMSF		HF		UMBS		WC	
	Pool	Flux	Pool	Flux	Pool	Flux	Pool	Flux	Pool	Flux
(a) Wood	91.1	2.20	83.5	2.92	99.0	1.30	62.6	1.85	73.5	1.55
(b) Leaves	2.3	2.26	3.7	2.13	na ^a	1.30	na	1.33	1.4	1.35
(c) Understory/herbivory	3.9	0.93	14.7	0.24	6.0	0.60	na	0.20	3.7	0.10
(d) Woody roots	9.4	0.44	9.5	0.28	20.0	0.25	9.9	0.26	2.7	0.31
(e) Fine roots	3.6	1.44	6.8	4.92	3.6	2.20	6.1	2.75	4.0	1.80
(f) NPP (a + b + c + d + e)	–	7.27	–	10.49	–	5.65	–	6.39	–	5.11
(g) Total soil respiration	–	9.50	–	12.07	–	8.00	–	11.32	–	8.10
(h) Heterotrophic respiration (0.5* g)	–	4.75	–	6.04	–	4.00	–	5.66	–	4.05
(i) Woody debris/other respiration	–	na	–	0.92	–	na	–	na	–	na
(j) Soil carbon	78.9	0.0	108.0	0.0	88.0	0.20	na	0.01	216.0	0.0 ^b
NEP (f – h – i)		2.52		3.54		1.65		0.73		1.06
ΔC (a + d + j)		2.64		3.20		1.75		2.12		1.86
NEE		5.77		2.36		2.00		1.67		2.20

^a Data not available.

^b Inferred from successional stage.

ity, with WB and MMSF on average producing more than 60% more carbon annually in these above-ground tissues than did the three northern sites. The size of the understory carbon pool varied considerably among sites, with no obvious relation to site fertility or other carbon pools. Annual carbon fluxes into this component combined with carbon losses to herbivores were

always less than 1 Mg C per hectare, but nonetheless constituted more than 15% of ANPP at WB and HF.

The sum of wood, leaf, and understory plus herbivory carbon fluxes, or ANPP, was positively related to mean annual temperature and to N_{min} across our five sites (Fig. 2), with the two southern sites clustering at one end of these relationships and the three northern

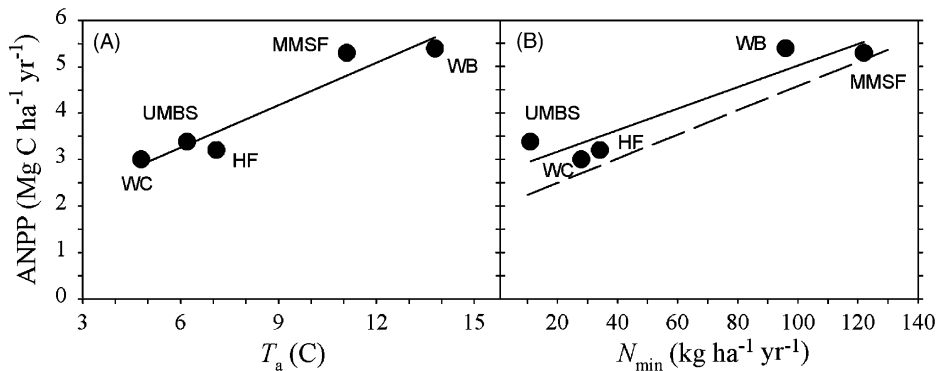


Fig. 2. Above-ground net primary productivity (ANPP, or P_{ANP}) for five North American deciduous forests compared to their mean annual temperature (T_a) (A) and their annual net nitrogen mineralization rate (N_{min}) (B). Solid lines are linear regressions across the five sites ($P_{ANP} = 1.4 + 0.304T_a$, $r^2 = 0.92$; $P_{ANP} = 2.7 + 0.023N_{min}$, $r^2 = 0.88$), while the dashed line is the relationship between N_{min} and ANPP for 50 forest stands in the north-central US reported by Reich et al. (1997) assuming a 49% carbon content in woody biomass ($P_{ANP} = 2.0 + 0.026N_{min}$) (site abbreviations are as in Fig. 1).

sites at the other. The range of N_{\min} in our sites was similar to that reported by Reich et al. (1997) for 50 forest plots in Wisconsin and Minnesota including both deciduous and coniferous stands (Fig. 2B). Three of our sites fell very close to the regression line calculated by Reich et al. (1997), while UMBS and WB were both more productive than would be predicted from their relationship. However, neither the slope nor the intercept of the linear relationship calculated for our five sites was significantly different from that of the Reich et al. (1997) data set (analysis of covariance).

Woody root carbon pools are difficult to measure directly and our estimates were made using a number of approaches, from a simple proportion of the above-ground wood carbon pool to species-specific allometric equations accounting for stump wood and recoverable large roots. Consequently, estimates of this pool ranged from a high of 20 Mg C per hectare at HF to less than 3 Mg C per hectare at WC (Table 4). Woody root carbon fluxes, based on allometric scaling against change in dbh (MMSF, HF, UMBS) or as a fixed proportion of annual above-ground wood increment (WB, WC), were relatively small and quite uniform across sites. Quantifying the size of the fine root pool and the annual carbon fluxes through it presented similar challenges and our estimates again came from a variety of methods, including direct observation of root turnover and modeling based on leaf litter N fluxes. In contrast to the pattern seen in leaf carbon flux, annual fine root carbon flux did not separate distinctly according to site fertility (Table 4). The most fertile site (MMSF) had almost twice the fine root carbon flux as any other site, yet WB, the next most fertile site, had the lowest estimated flux. The sum of annual above- and below-ground carbon fluxes represents annual net primary productivity (NPP), which varied more than two-fold from our least (WC) to our most (MMSF) productive site. The three northern sites were all quite similar in NPP, while WB was intermediate between that group and MMSF.

Total soil respiration was by far the single greatest carbon flux measured, exceeding NPP at all sites (Table 4). Two of the northern sites (WC and HF) had similar soil carbon fluxes, but the third site (UMBS) was intermediate between WB and MMSF. Soil heterotrophic respiration (R_h) was estimated in each case as 50% of R_s . Respiratory losses from coarse woody

debris were only estimated at MMSF. Total soil carbon pool was estimated at all sites except UMBS and varied over five-fold, with WC having the largest pool. Annual net change in the soil carbon pool was only directly measured at WB, MMSF and HF, and was very small in all three cases. At UMBS and WC work in similar forest stands suggested little or no change in soil carbon over a 1-year period.

Combining the annual increment in all measured autotrophic carbon pools with heterotrophic respiratory carbon fluxes to calculate NEP yielded estimates of ecosystem net carbon storage ranging from 0.7 Mg C per hectare per year at UMBS to 3.5 Mg C per hectare per year at MMSF (Table 4). Net ecosystem production showed a strong positive relationship to site N_{\min} (Fig. 3A), with a slope similar to that found for ANPP versus N_{\min} (Fig. 2). Summing the annual increments in wood and soil carbon pools (ΔC) produced similar estimates of ecosystem carbon storage for WB and HF, a small reduction in estimated

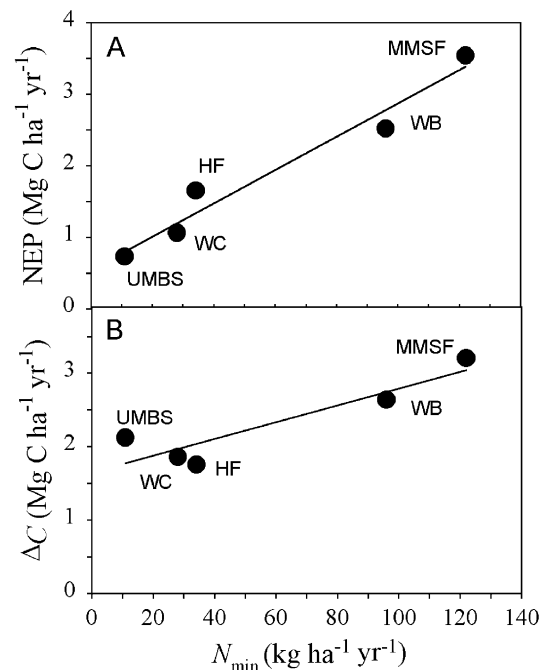


Fig. 3. (A) Net ecosystem production (NEP or P_{NE}) and (B) annual increment in carbon stocks (ΔC) for five North American deciduous forests compared to their annual net nitrogen mineralization rate (N_{\min}). Solid lines are linear regressions across the sites ($P_{NE} = 0.54 + 0.023N_{\min}$, $r^2 = 0.96$, $\Delta C = 1.65 + 0.011N_{\min}$, $r^2 = 0.83$) (site abbreviations are as in Fig. 1).

carbon storage for MMSF, and sizable increases for UMBS and WC (Table 4). Variation in carbon storage among sites was consequently less, ranging from 1.7 Mg C per hectare per year at HF to 3.2 Mg C per hectare per year at MMSF. ΔC was also positively related to N_{\min} (Fig. 3B), but this relationship was weaker than was found for NEP and with a shallower slope, due primarily to the increased estimates of annual carbon storage at UMBS and WC.

Net ecosystem exchange estimated by eddy-covariance methods ranged from 1.7 Mg C per hectare per year at UMBS to 5.8 Mg C per hectare per year at WB (Table 4). There was no clear relationship between NEE and N_{\min} ($r^2 = 0.17$, NS), and four of the five sites were separated by less than 1 Mg C per hectare per year. Comparing NEP to NEE, WC, UMBS and WB showed >50% lower NEP relative to NEE, and MMSF 50% higher NEP than NEE (Fig. 4A). The two estimates agreed well at HF (i.e. only 17% lower). Comparing ΔC and NEE, WC, UMBS, and HF all

showed fairly good agreement among the two measures, while MMSF showed 36% greater and WB 54% lower estimates of annual carbon storage from ΔC than from NEE (Fig. 4B).

4. Discussion

Above-ground net primary productivity at these five AmeriFlux sites fell within the range expected for eastern North American deciduous forests. We found in the more productive, southern sites annual carbon accumulation of ~ 5 Mg C per hectare per year, comparable to that reported for similar aged stands in New Hampshire (Whittaker et al., 1974), Wisconsin (Pastor and Bockheim, 1981), and Kentucky (Liu and Muller, 1993). Our northern sites, growing on poorer soils and experiencing colder temperatures, had very similar ANPP (~ 3 Mg C per hectare per year) as mesic hardwood stands of Wisconsin and Minnesota (Reich et al., 1997) and an upper-elevation gray beech forest in Tennessee (Whittaker et al., 1974).

Although our sites differed in many ways, including local climate, soil characteristics, species composition, land use history, and measurement period, variation among sites in ANPP followed a pattern observed by many others in which soil N availability and growing season length are important determinants of productivity (Pastor et al., 1984; Nadelhoffer et al., 1985; Zak et al., 1989). Indeed, the relationship we observed between ANPP and N_{\min} was the same as that found by Reich et al. (1997) across 50 deciduous and coniferous stands. Inaccuracies in allometric equations are a potential source of error in our estimates, because the equations are highly nonlinear and small errors in the measurements of large trees could have a large impact on our estimates of annual growth. However, these comparisons and relationships to environmental variables provide assurance that these AmeriFlux sites are typical of others in the eastern deciduous forest in their above-ground growth characteristics.

Below-ground growth estimates are more difficult to evaluate as far less attention has been paid by forest ecologists to this component of NPP. Root wood increment estimates, based on allometric equations derived from limited numbers of whole tree harvests, suggest that this growth component is generally a fairly small (<20%) fraction of above-ground

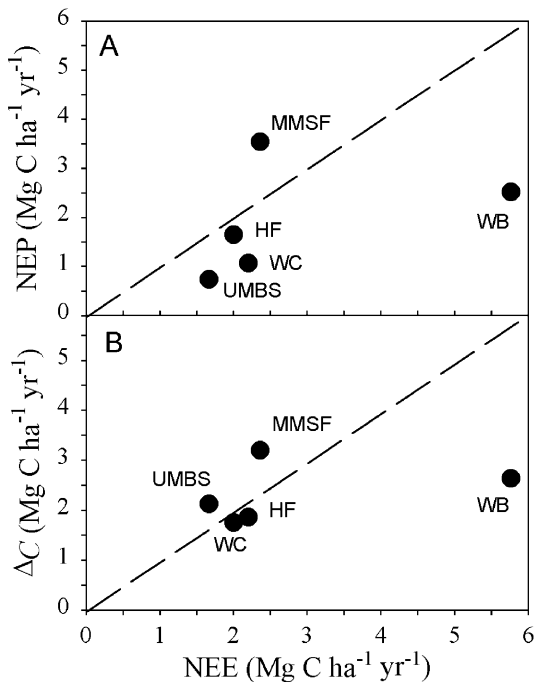


Fig. 4. (A) Net ecosystem production (NEP), and (B) annual increment in carbon stocks (ΔC) for five North American deciduous forests compared to their net ecosystem exchange of carbon (NEE) calculated from eddy-covariance data. Dashed lines represent the 1:1 relationship (site abbreviations are as in Fig. 1).

wood increment (Perala and Alban, 1994). A larger, and probably much more variable, component of below-ground productivity is the fine root carbon pool and its turnover. However, below-ground detritus production is not well estimated using allometrics, and is difficult to measure directly. Burton et al. (2000), using direct observation of fine roots with minirhizotron cameras, found higher root standing crop and higher root turnover in low compared to higher fertility northern hardwood forests, a pattern at variance with that reported by Aber et al. (1985) from a review of predominantly soil coring studies. In oak dominated systems Gaudinski et al. (2000) applied ^{14}C isotopic signature methods and found considerably longer fine root lifespans (i.e. >2 years) than had previously been reported from coring or minirhizotron based studies. Clearly, more work is needed to resolve site-to-site differences in fine root carbon pools and fluxes.

Previous biometric estimates of NPP for temperate deciduous forests which consider both above- and below-ground production provide a useful comparative context for our results. Summarizing the international biosphere program (IBP) efforts of the 1960s and 1970s, Edwards et al. (1980) reported a range in NPP from 5.4 Mg C per hectare per year for an oak-pine forest in New York to 19.2 Mg C per hectare per year for an oak forest in Britain. A complete summary of the IBP woodlands data set is described by Deangelis et al. (1980) and can be found as a part of the web based NPP summary compiled by R.J. Olson and others (http://www-eosdis.ornl.gov/npp/npp_home.html). More recently Jenkins et al. (2000) predicted northern forest NPP using the mechanistic models PnET-II and TEM 4.0. These two models, which differ fundamentally in their construction, showed remarkable agreement in their prediction of NPP under contemporary conditions, with an average of 6.6 Mg C per hectare per year for hardwood and hardwood/pine forests. Our biometric estimate of average NPP across the five AmeriFlux sites was 7.0 Mg C per hectare per year.

Our primary interest in R_s was as a means to estimate R_h , that fraction of R_s contributed by soil heterotrophs. Lacking convincing data suggesting otherwise, we applied the average value of R_h/R_s (0.50) obtained by Hanson et al. (2000) from a review of 37 forest studies. Such a simple partitioning coefficient is unlikely to be correct for all five sites and it also

masks seasonal variation in the relative contribution of R_a and R_h to R_s . Therefore, given the magnitude of soil CO_2 efflux, this simplistic partitioning of R_s is a major source of uncertainty in our NEP estimates. Decomposition of coarse woody debris also releases CO_2 to the atmosphere, but where this flux has been measured (Ehman et al., 2002), it was only $\sim 7\%$ of R_s .

Soil C, excluding surface litter, is generally considered to be relatively stable in late-successional forests such as ours (WB: Trettin et al., 1999). Change in the mineral soil carbon pool size was estimated using ^{14}C (Gaudinski et al., 2000) at WB and HF and by mass balance at MMSF and this was indeed found to be the case. Surface litter, however, may be quite dynamic: at HF, the mean age (turnover time) of O horizon carbon was 4 years. Although soil carbon pools at WC and UMBS were inferred as in steady state based on successional status or on previous work from soil chronosequences, it is unlikely in the absence of major disturbance that this carbon pool would be very dynamic over the 1- or 2-year time period of our studies. Thus, while more work needs to be done at most of our sites to better characterize this carbon pool, particularly the surface layers, this is probably not a major source of error in our overall carbon budget estimates. That S measured directly rarely equaled the difference between measured D and R_h reflects the substantial uncertainties involved in the latter estimates and the differing time scales over which these measurements generally were made.

Our biometric estimates of NEP varied from 0.7 Mg C per hectare per year at UMBS to 3.5 Mg C per hectare per year at MMSF, with an overall average of 1.9 Mg C per hectare per year. These values are quite comparable to earlier IBP estimates made using similar techniques which ranged from 0 Mg C per hectare per year for a beech forest in Denmark, to 3.5 Mg C per hectare per year for a British oak forest (Edwards et al., 1980). Differences among our sites were less when carbon storage was estimated from ΔC (low of 1.8 and a high of 3.2 Mg C per hectare per year), and the average was slightly higher (2.2 Mg C per hectare per year). These two estimates of annual carbon storage were most different for WC and UMBS, in both cases storage based on ΔC being larger than that based on NEP. This appeared to be driven by a relatively large estimated R_h relative to above- and below-ground litter inputs at these two

sites, which reduced NEP but was not considered in ΔC calculations. Neither WC nor UMBS have at present direct estimates of fine root production, making it difficult to evaluate which estimate of carbon storage is more accurate. In general, since ΔC involves fewer measurements than does NEP, we might expect greater confidence in measures of annual carbon storage based on ΔC . One trade-off is in a lack of information on mechanisms of carbon exchange that might prove important to interpreting spatial or temporal variation in carbon storage. Most comparable estimates of annual carbon storage in northern US forests have been based on analysis of changes in carbon pools over time. For example, Johnson and Strimbeck (1995) found an average gain of 0.9 Mg C per hectare per year across 33 years in 23 sugar maple stands in Vermont, while intensively managed, rapidly growing hardwood stands in the Great Lakes region gained as much as 9 Mg C per hectare annually (Strong, 1997). Based on a broad regional analysis of forest stocks, harvests, and carbon storage in soil and forest products, Birdsey and Heath (1995) estimated an average carbon sequestration rate of 2.3 Mg C per hectare per year across the northern US forests, very similar to the average ΔC across our five sites.

We found a significant linear relationship between NEP and N_{\min} , similar in slope but with a different intercept, as was found for the ANPP: N_{\min} relationship. There was also a relationship between ΔC and N_{\min} , although not as strong. The specifics of the functional relationship reported here, however, should be viewed with caution, since not all components of the NEP estimates at all sites are independent of N_{\min} . For example, the annual fine root turnover fraction at UMBS was estimated based on the model of Aber et al. (1985), which uses N_{\min} as an input variable. Nonetheless, the relative ranking of carbon storage estimates based on soil N availability is consistent with our understanding of environmental controls over carbon cycling in forest ecosystems and again provides an important comparative context for evaluating the accuracy of these estimates.

Our eddy-covariance based estimates of annual carbon storage (NEE) fall well within the range reported for temperate forests. Baldocchi et al. (2001) summarized results from 10 temperate deciduous broadleaf sites in North America, Europe, and Japan, and reported NEE values between 0.7 and 7.4 Mg C per

hectare per year. The results from these sites fell into a general pattern of dependence of NEE on growing season length.

No systematic difference between NEP and NEE estimates was found across all five sites. NEP estimates for WB, UMBS and WC were lower than annual NEE, NEP, HF was similar to its NEE, and NEP for MMSF was higher than its NEE. Lacking a systematic difference between NEP and NEE across sites, it was not clear why biometric data would underestimate NEE at some sites, but overestimate NEE at others. One obvious difference among sites is the time over which biometric and meteorological data were collected. Data from these two approaches that have been averaged over multiple years, such as was true for WB (7 years) and MMSF (2 years) might be expected to correspond more closely than comparisons based on single year observations (HF, UMBS, WC). This is because of the differing temporal dynamics of the carbon cycle processes measured by biometric compared to meteorological methods (Barford et al., 2001). For example, soil respiratory carbon losses may lag significantly behind carbon inputs to soil organic matter, particularly in colder and/or drier sites. Similarly, stress affecting GPP in 1 year may only be expressed as altered wood increment the following year (Orwig and Abrams, 1997; Pedersen, 1998; but see Hanson et al., 2001).

The largest deviation between NEP or ΔC and NEE occurred at WB. Errors in both the biometric and the eddy-covariance methods likely contributed to this difference. Because of commonly occurring low wind velocities, stagnant night conditions, and possible cold air drainage of CO₂ out of the measurement footprint at WB, NEE measurements by eddy-covariance are difficult and the derivation of definitive annual sums requires a combination of integration and modeling (Wilson and Baldocchi, 2001), as is the case at all five sites. Potential errors in biometric estimates of woody carbon increment at WB are also possible, because measurable growth does not accumulate throughout the growing season (Hanson and Weltzin, 2000; Hanson et al., 2001). During late season periods (August–October) when above-ground growth has ceased and below-ground growth is very slow, substantial carbon gain continues and is apparently distributed to stored carbohydrate reserves. Biometric estimates of NEP for WB would be increased and come closer to estimated NEE if

nonstructural carbohydrate pools accumulating late in the growing season were accounted for. Dissolved organic carbon losses from leaching of water below the rooting zone (Jardine et al., 1990) represent another unquantified pathway of carbon transport that might help resolve differences in NEP and NEE within sites.

Potential problems contributing to differences between NEE and NEP at MMSF and HF are similar to those at WB. Gaps in the eddy-covariance data-stream occur due to precipitation events, icing in winter, lightning damage, and other equipment failure. Such gaps are typically filled by parametric models that relate soil temperatures to ecosystem respiration, and radiation to GPP (see Goulden et al., 1996; Schmid et al., 2000). The spatial scale to which these parameterizations refer is different from that of the eddy-fluxes, and different again from that of the measurements contributing to the NEP estimates. In the ubiquitous inhomogeneity of natural forest ecosystems this mismatch of scales can lead to systematic errors, whose magnitude or even sign is unknown.

Annual carbon storage estimated as NEP was also less than NEE at UMBS and WC. Given the low N_{\min} at these sites, it is unlikely that NPP was significantly greater than estimated. At UMBS, R_s , and hence R_h , was considerably higher than expected based on above-ground litter inputs (Davidson et al., 2002), suggesting either chamber effects that might inflate R_s (Davidson and Savage, 2002), an annual or longer time lag between surface litter decomposition and litter inputs, or significantly different partitioning between soil autotrophic and heterotrophic respiration from the estimated 1:1 relationship. The NEE estimate at WC of 2.2 Mg C per hectare per year is more closely approximated by ΔC , again suggesting that the bulk of our uncertainty lies in below-ground processes.

In summary, the goals of the AmeriFlux network are to address concerns regarding the present and future global carbon cycle by measuring net carbon exchange at the whole-ecosystem scale over long time periods and by elucidating the factors causing fluctuations on seasonal, annual and decadal time scales. Both biometric and meteorological estimates of carbon storage are critical elements to achieving these goals. We found that biometric estimates of NPP across these forests conformed to expectations based on site-specific differences in soils and climate and compared well with other empirical and modeling estimates of temperate

deciduous forest productivity. Annual carbon storage differed by as much as 2.8 Mg C per hectare per year between the most and least productive sites, with the greatest uncertainty in NEP being in the magnitude of below-ground detritus production and soil heterotrophic respiration. There were no systematic, cross-site differences between biometric and meteorologically based estimates of annual carbon storage, but agreement was generally better when fewer below-ground processes were explicitly incorporated into the biometric estimates. Where discrepancies among estimates were large, our synthesis provided a valuable comparative context from which to explore errors and uncertainties in either approach.

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