

## 22. Estimating the Net Primary and Net Ecosystem Production of a Southeastern Upland *Quercus* Forest from an 8-Year Biometric Record

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### Introduction

Although 8 years of manipulated precipitation levels have not produced significant tree-growth responses in an upland *Quercus* forest in eastern Tennessee (Hanson et al. 2001), interannual differences in physiological processes (Chapters 3, 4, 6–8, and 10, this volume), storage carbohydrates (Chapter 5, this volume), tree and sapling growth rates (Chapter 15, this volume), root growth (Chapter 16, this volume), and foliar-litter production (Chapter 17, this volume) suggest that interannual differences in net primary production (NPP) and net ecosystem production (NEP) are likely. By accepted definition, NPP is the difference between carbon gain from autotrophic organisms (i.e., gross primary production, GPP) minus autotrophic respiration ( $R_{\text{auto}}$ ). NEP is the annual net change in ecosystem carbon storage defined as NPP minus heterotrophic respiration ( $R_{\text{hetero}}$ ). At the local scale, NEP may also be reduced from non-CO<sub>2</sub> losses of volatile organic compounds (VOCs) from vegetation (Guenther et al. 1996; Isebrands et al. 1999) and soils (Hanson and Hoffman 1994) and under ambient or flooded conditions from the gain or loss of CH<sub>4</sub> from soils, respectively (LeMer and Roger 2000). The following equations capture these processes:

$$\text{NPP} = \text{GPP} - R_{\text{auto}}, \quad (1)$$

$$\text{NEP} = \text{NPP} - R_{\text{hetero}} - \text{VOC} \pm \text{CH}_4. \quad (2)$$

Heterotrophic respiration includes all nonautotrophic production of  $\text{CO}_2$ , but vertebrate organisms are often ignored because their impact on carbon flux is small with respect to the magnitude of ecosystem carbon fluxes. Faunal-induced movement of carbon sources (e.g., seed transport by birds and squirrels) is assumed to be random, with losses to a particular area balancing gains from other locations. Loss of dissolved organic carbon into deep soils below the rooted soil profile is also commonly ignored, but specific quantitative estimates of this process are lacking.

Although the definitions behind Eqs. (1) and (2) are simple to conceptualize, direct measurements of NPP or NEP are not straightforward. Clark et al. (2001a) concluded that, although it is impossible to measure the annual NPP of an ecosystem directly, close approximations of NPP (i.e.,  $\text{NPP}^*$ ) could be attained from detailed measurements of the components of stand production, including the following: stem, branch, and stump growth; leaf, flower, and seed production; fine and coarse root production, estimates of leaf production lost to leaf herbivory; and other, minor components (e.g., pollen production). Curtis et al. (2002) proposed that NPP could be derived from incremental changes of live plant mass, detritus, and estimates of herbivory losses and termed such estimates of  $\text{NPP}^*$  as biometric measurements of NPP. They concluded that a biometric estimate of NEP ( $\text{NEP}^*$ ) could also be derived as follows:

$$\text{NEP}^* = \text{NPP}^* - R_{\text{hetero}}, \quad (3)$$

where  $R_{\text{hetero}}$  is obtained from integrated annual measurements of soil respiration minus the autotrophic root respiration (Hanson et al. 2000).

In this chapter, we apply biometric approaches (Curtis et al. 2002) to multiyear growth measurements of the Walker Branch Throughfall Displacement Experiment (TDE) (Hanson et al. 2001; Chapters 2, 15, and 17, this volume) for the determination of standing carbon stocks of an upland *Quercus* forest and for the interannual estimates of net primary production (Clark et al. 2001a) for 1993–2000. Additional estimates of  $\text{NEP}^*$  are calculated from the difference between  $\text{NPP}^*$  and interpolated data for ecosystem heterotrophic respiration. The magnitude and multiyear patterns of  $\text{NPP}^*$  for the upland *Quercus* forest of the TDE are compared to data published for other temperate deciduous forests. Similarly,  $\text{NEP}^*$  data for 1995–1999 are contrasted to the magnitude and the interannual pattern of independent eddy-covariance-based net ecosystem exchange data for Walker Branch Watershed (Wilson and Baldocchi 2001).

## Methods

### Site Description

The upland *Quercus* forest considered in this chapter is located on the Walker Branch watershed (35°58' N and 84°17' W) in the Ridge and Valley Province of East Tennessee (Johnson and Van Hook 1989). The local topography is repre-

sented by a series of repeating parallel ridges and valleys oriented from southwest to northeast and elevation ranges from 270 to 340 m. The soils are fairly acidic (pH 3.5–4.6), typic paleudults with a depth to bedrock of ~30 m. The long-term mean annual precipitation is 1358 mm and the mean temperature is 14.2°C. The site is dominated by *Quercus alba* L., *Q. prinus* L., and *Acer rubrum* L., and understory saplings are predominantly *A. rubrum* and *Cornus florida* L., with scattered individuals of less common species. Total stand basal-area averages 20–25 m<sup>2</sup> ha<sup>-1</sup>. Further details on the stand composition can be found in Hanson et al. (2001) and in Chapter 2 (this volume).

### Forest Carbon Stocks and Biometric NPP\*

Direct biometric estimates of standing carbon pools and annual NPP\* were determined from an 8-year (1993–2000) record of plant growth and litter production as a part of a multiyear TDE (Hanson et al. 2001; Joslin et al. 2000). The components of annual NPP\* that were considered for use in this analysis include the following items consistent with the recommendations of Clark et al. (2001a):

1. Allometric estimates of overstory branch, stem, and stump growth
2. Allometric estimates of sapling growth
3. Leaf production corrected for herbivory losses
4. Terminal branch litter production
5. Acorn production
6. Gross coarse and fine root production
7. The production of volatile organic compounds (VOCs)
8. Changes in nonstructural carbohydrate storage
9. Limited production of pollen and trichomes

Of these, only VOC, pollen, and trichome production are not included because they represent insignificant contributions to NEP\* in this upland *Quercus* forest. On the basis of the experimental data of Harley et al. (1997), VOC production in the form of isoprene emissions was calculated to contribute less than 15 g C m<sup>-2</sup> y<sup>-1</sup> to annual NPP; because it is volatile, it leaves the local forest stand, resulting in no net change in ecosystem carbon stocks. Pier and McDuffie (1997) and Sharkey et al. (1996) independently estimated that VOC emissions would be unlikely to exceed 20 g C m<sup>-2</sup> y<sup>-1</sup>. VOC losses in the form of monoterpene evaporation from soils represent less than 1 g C m<sup>-2</sup> y<sup>-1</sup> (Hanson and Hoffman 1994). Methane gains or losses from the well-drained upland soils at this site are inconsequential with respect to the ecosystem carbon budget (Bradford et al. 2001).

Aboveground carbon stocks in wood were estimated at all sites with allometric equations relating diameter at breast height (dbh at 1.3 m) to bole, branch, and stump biomass. Allometric relationships for canopy trees (Harris et al. 1973) and saplings (Sollins and Anderson 1971) were developed from local tree harvests. Additional whole-tree harvests, conducted in 2001, confirmed that the allometric relationships of Harris et al. (1973) were not substantially different after 30 years

**Table 22.1.** Summary of regression coefficients for the relationship between mean tree or sapling component mass on tree diameter at breast height

Tree/sapling component (Y)	Constants		$R^2$	N	k
	a	b			
<b>Tree coefficients</b>					
Bole	-2.437	2.418	0.97	298	1.08
Branches	-3.188	2.226	0.91	298	1.26
Stump <sup>a</sup>	-2.392	1.845	0.77	18	1.06
<b>Sapling coefficients</b>					
Stem and branches	-3.166	2.866	0.94	122	na <sup>b</sup>

Note: The data for trees are reproduced with permission from Harris et al. (1973), and the coefficients for saplings were derived from sapling-dry-mass data published in Sollins and Anderson (1971). The regression takes the following form:

$$Y = e^{(a + \ln(X)b)} k,$$

where Y is the component mass (in kg), X is the dbh (in cm), and a, b, and k are constants.

<sup>a</sup> Harris et al. (1973) defined stump as the central root plus large support laterals to a radius of 60 cm.

<sup>b</sup> na = not applicable.

(data not shown). Coefficients for the allometric relationships for trees and saplings are provided in Table 22.1. Stem growth of trees > 0.1 m at dbh from 1993 to 2000 was evaluated with annual diameter measurements of all trees in the 1.92-ha experimental area (729 trees); however, stem-mass production for individual years was apportioned among years according to dendrometer-band observations collected on a subset of the trees (230 trees) (Hanson et al. 2001; Chapter 15, this volume). The annual increment of sapling-size vegetation (dbh < 0.1 m) was measured on randomly selected saplings along eight transects across the three plots. Herbaceous-layer plants (ferns and spring ephemerals) are not common on the southeast-facing slope that comprises the TDE study area and were not summarized as a separate carbon stock.

Fallen leaves and other materials (twigs, seeds, etc.) were collected from 147 baskets at fixed locations distributed across the TDE experimental area from 1992 through 2000, as described by Hanson et al. (Chapter 17, this volume). Once collected, the litter samples were dried and sorted to separate the foliage, terminal branch, and acorn components of annual NPP\*. Loss of leaf area 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 the TDE forest were reported as the mean of those measured in 1992, 1993, and 1994 (Shure et al. 1998; Chapter 18, this volume). They showed that annual reductions in foliar leaf area ranged from 6% to as much as 13% for *A. rubrum* and *Quercus* species, respectively.

Changes in the branch and bole sapwood total nonstructural carbohydrate pool (i.e., sugars and starch; TNC) were evaluated by Tschaplinski and Hanson (Chapter 5, this volume) during February of 1993, 1996, 1998, 1999, and 2000. These measures of carbon content were extrapolated to the stand level with the dbh-based relationships described by Wullschleger et al. (Chapter 21, this volume).

The amount of carbon stored belowground as wood (i.e., stumps and very large lateral roots) was derived from allometric equations relating dbh to woody-root

mass (Harris et al. 1973). The annual increment in woody-root carbon was estimated from the annual change in dbh. The fine (< 2 mm) and coarse (2–5 mm) root carbon pools were measured from soil cores collected on an 8 × 8-m grid across the TDE area (Chapter 16, this volume). Annual fine root production was estimated from direct observation of root turnover with minirhizotron cameras (Joslin et al. 2000), and the annual increment of woody roots was assumed to be 20% of the aboveground wood increment (Curtis et al. 2002).

Initial mineral–soil carbon pools were derived from soil-profile data (organic matter and bulk density) for the Fullerton cherty-silt loam soil on Walker Branch watershed (Peters et al. 1970), and the dynamics of change with time were inferred from a 21-year study on other Walker Branch permanent plots (Trettin et al. 1999). The forest-floor organic layers were sampled in 1992 and 1999 with replicate ( $n = 15\text{--}30$ ) 0.25-m<sup>2</sup> circular plots distributed across each treatment area of the TDE area (Johnson et al. 2002). Data from TDE site surveys of dead, coarse, woody litter in April 1992 (i.e., dead boles and branches) and organic soil horizons in January 1992 were used to establish the initial values for the respective forest carbon pools. Coarse-woody-debris carbon pools were quantified across the TDE area with the methods of Harmon and Sexton (1996).

Although the carbon content of the leaf, bark, wood, fine roots, and soil organic matter vary slightly from species to species and tissue to tissue (data not shown), we assume that all biomass is 47% carbon and calculate stand-level pools and annual fluxes of carbon as Mg C ha<sup>-1</sup> and g C m<sup>-2</sup> per ground area per year, respectively.

### Interannual Estimates of NEP\*

Annual estimates of NEP\* require a measurement of ecosystem heterotrophic respiration for subtraction from NPP\*. In practice, stand heterotrophic respiration is calculated as the sum of decomposition losses from soil and coarse, woody debris. Aboveground heterotrophic respiration is ignored in the current analysis because it has been estimated to be less than 1 g C m<sup>-2</sup> y<sup>-1</sup> (Reichle 1971; Edwards et al. 1980). Annual carbon losses from decomposition of the standing woody-debris pool were assumed to be ~10% per year based on observations that mass losses from bole sections of *Carya* and *Q. prinus* were 38 and 44%, respectively, over a 4-year period (Chapter 12, this volume). In a recent review of forest literature on soil respiration, Hanson et al. (2000) concluded that root respiration is often a dominant component of soil carbon cycles, typically accounting for 50% or more of the CO<sub>2</sub> leaving the forest floor. Direct point-in-time measurements of root contribution to soil respiration for the TDE site show substantial intra-annual variation, ranging from a high of 85% in the spring to a low of less than 20% in the fall (Trumbore et al., 2002). For the calculations in this chapter, we assumed that annual heterotrophic losses from soils were 50% of the annual soil-respiration totals from Hanson et al. (Chapter 10, this volume), consistent with the mean forest response reported by Hanson et al. (2000).

## Results and Discussion

### The Upland *Quercus* Forest and Its Carbon Pools

Prior to 1940, the experimental site was occupied by forest vegetation, but gaps were present because of past individual-tree logging associated with subsistence farming and grazing. Since 1940, natural successional processes have governed stand development, and the stand currently has a closed canopy with a mean annual leaf area index of  $\sim 6 \text{ m}^2 \text{ m}^{-2}$ . Individual tree ages in this stand range from 50 to 100+ years, but the majority of the overstory trees range in age from 70 to 100 years. Carbon pools for the TDE forest are summarized in Table 22.2. To a soil depth of 1 m, the forest stand contains  $171 \text{ Mg C ha}^{-1}$ . Of this total, 58% is found in the vegetation biomass (nearly 50% in branch, bole, and stump wood), with the balance being stored in organic wood and forest-floor litter ( $\sim 5\%$ ) and the mineral soil (37%). Because the potentially rooted soils at the TDE site are deep (up to 30 m), we also estimated the size of the soil carbon pool for a deep layer from 1 to 9 m, assuming a mean soil carbon concentration of 0.3%, a bulk density of  $1.2 \text{ g cm}^{-3}$ , and a coarse fraction content of 8%. Such a pool contains an additional  $88 \text{ Mg C ha}^{-1}$  and when included in the total stand carbon pool, it shifts the majority of stand carbon to the soils consistent with typical global patterns (Post et al. 1982, 1990; Dixon et al. 1994). Notwithstanding the function of deep soils as a large carbon reservoir, the turnover times of such carbon is very slow (Chapter 11, this volume) and changes in the deep-soil carbon pool are not considered to play a role in year-to-year estimates of NPP\*. The turnover times of the 0–1-m mineral-soil carbon pool is also long ( $> 80$  years; Chapter 11, this volume) and changes in the mineral soil carbon pool are not considered in the biometric estimates calculated below. In support of this assumption, Trettin et al. (1999) found little evidence for significant changes in the mineral-soil carbon pools of adjacent sites on Walker Branch from 1973 to 1993.

The total standing pool of carbon in the TDE forest is similar to that for six temperate forest stands of similar age found in the eastern United States (Table 22.2). Total stand carbon pools range from 90 to  $130 \text{ Mg C ha}^{-1}$ , and the above-ground totals range from 72 to  $106 \text{ Mg C ha}^{-1}$ . The *Quercus*-dominated and mixed-hardwood stands have 50% or more of their carbon stored in the living biomass, but the *Liriodendron* stands have the majority in the soil pool. The soil carbon of a *Populus* spp.-dominated northern hardwood stand (Curtis et al. 2002), not shown in Table 22.2, was also dominated by the soil carbon pool (i.e., only 39% of the carbon in living biomass). The carbon pools of these example stands are similar to recent estimates for the eastern United States derived from remote-sensing methods (Myneni et al. 2001).

### Estimates of NPP\*

Biometric estimates of NPP based on traditional methods ranged from 604 to  $840 \text{ g C m}^{-2} \text{ y}^{-1}$  from 1993 to 2000 for a mean annual NPP value of  $729 \text{ g C m}^{-2} \text{ y}^{-1}$  (Table 22.3). Percent contributions of leaf, wood, root, and acorn production

Table 22.2. Carbon pools in  $\text{Mg ha}^{-1}$  for the *Quercus* dominated TDE site in 1999 and similar temperate deciduous forests from other studies and time periods

Individual stands Components	<i>Quercus</i>	<i>Quercus/Carya</i>	<i>Q. prinus</i>	<i>Quercus/Tsuga</i>	<i>Liriodendron</i>	<i>Liriodendron</i>	Mixed species
	(this study)	(Edwards et al. 1989)	(Edwards et al. 1989)	(Curtis et al. 2002)	(Harris et al. 1975)	(Edwards et al. 1989)	(Curtis et al. 2002)
Location	Tennessee	Tennessee	Tennessee	Massachusetts	Tennessee	Tennessee	Indiana
Vegetation ( $\text{Mg C ha}^{-1}$ )							
Leaves	2.3	1.6	2.0	1.3	2.0	1.7	3.7
Branches	16.3	14.8	17.7	— <sup>a</sup>	—	16.8	—
Stems	59.9	56.0	67.6	105.0 <sup>b</sup>	78.1 <sup>b</sup>	63.7	98.2
Stumps	7.7	4.9	5.7	—	—	5.5	—
Coarse roots	9.4	na <sup>c</sup>	na	20.0	—	na	9.5
Fine roots	3.6	na	na	3.6	7.6	na	6.8
Total vegetation C	99.3	77.2 <sup>d</sup>	93.0 <sup>d</sup>	129.9	87.7	87.7 <sup>d</sup>	118.2
Soils ( $\text{Mg C ha}^{-1}$ )							
Coarse wood litter	4.1	na	na	na	na	na	na
Organic layers	4.3	15.0	15.5	—	2.4	8.5	—
Soil C (0–1 m)	~63.9	54.5	54.5	88.0	122.5	88.8	108.0
Total soil C	73.0	69.6	70.0	88.0	124.9	97.3	108.0
Total ( $\text{Mg C ha}^{-1}$ )	171.6	146.8	163.0	217.9	212.6	184.9	226.2
Stand age or range (y)	58–100	41–83	41–83	60	48	41–83	80
Stand C ( $\text{Mg C ha}^{-1}$ )	107.7	92.3	108.5	129.9	90.1	96.1	118.2
Rate ( $\text{g C m}^{-2} \text{y}^{-1}$ )	108–186	111–225	131–265	216	188	116–234	148

Note: Stand-age range and the rate of carbon accumulation for the biomass plus soil organic layer pools over that time period (i.e., recent carbon accumulation in  $\text{g C m}^{-2} \text{y}^{-1}$ ) are also calculated.

<sup>a</sup> Data are included in another category.

<sup>b</sup> Includes branches, boles, and sometimes stumps.

<sup>c</sup> na = not available

<sup>d</sup> Does not include carbon in the coarse or fine root pools.

Table 22.3. Components of forest NPP and NEP for the upland *Quercus* forest of the TDE from 1993 to 2000

Components	1993	1994	1995	1996	1997	1998	1999	2000	Annual mean $\pm$ CI (g C m <sup>-2</sup> y <sup>-1</sup> )
<b>NPP</b>									
Leaf production	233.1	236.4	238.3	245.8	243.5	229.4	233.6	257.6	240 $\pm$ 7
Herbivory <sup>a</sup>	18.6	25.1	21.4	~22.1	21.9	20.6	21.0	23.2	22 $\pm$ 2
Wood production <sup>b</sup>	168.1	266.3	191.3	293.9	215.5	211	240.2	209.5	224 $\pm$ 32
Saplings	7.1	7.1	7.1	7.1	14.6	7.5	7.1	5.3	8 $\pm$ 2
Terminal branches	40.4	55.5	112.8	43.7	55.9	40.4	95.9	32.4	60 $\pm$ 23
Acorn production	0.5	0.5	28.3	4.4	15.1	0.5	40.7	1.0	11 $\pm$ 11
Coarse roots (> 5 mm)	8.1	11.1	22.6	8.7	11.2	8.1	19.2	6.5	12 $\pm$ 5
Small roots (< 5 mm) <sup>c</sup>	128.3	160.7	119.9	207.7	135.8	120.3	182.4	167.3	153 $\pm$ 51
Total NPP	604	763	742	833	713	637.8	840.0	702.8	729 $\pm$ 69
<b>Heterotrophic respiration<sup>d</sup></b>									
Soils	416	476	422	459	457	470	469	476	456 $\pm$ 18
Dead wood	99	93	86	87	91	89	79	69	87 $\pm$ 7
Total HR	515	569	508	546	548	559	548	545	542 $\pm$ 16
NEP (total NPP - HR)	89	194	234	287	165	79	292	158	187 $\pm$ 67

Note: The 95% confidence interval (CI) representing interannual variation does not include the error associated with measurement approaches or spatial heterogeneity. Soil and litter-layer carbon pools are assumed to be constant for this analysis (Tretin et al. 1999).

<sup>a</sup> Loss of leaf area and associated mass was measured in 1993, 1994, and 1995 by Shure et al. (1998). Values for 1996-2000 are estimates based on the mean of the first 3 years.

<sup>b</sup> Annual wood increment includes growth of branches, boles, and coarse structural roots.

<sup>c</sup> Fine root production was estimated from the direct observation of root turnover using minirhizotron cameras (Joslin et al. 2000).

<sup>d</sup> Heterotrophic respiration was assumed to be 50% of total soil respiration (Hanson et al. 2000) on the basis of the interpolated annual estimates from Hanson et al. (Chapter 10, this volume).



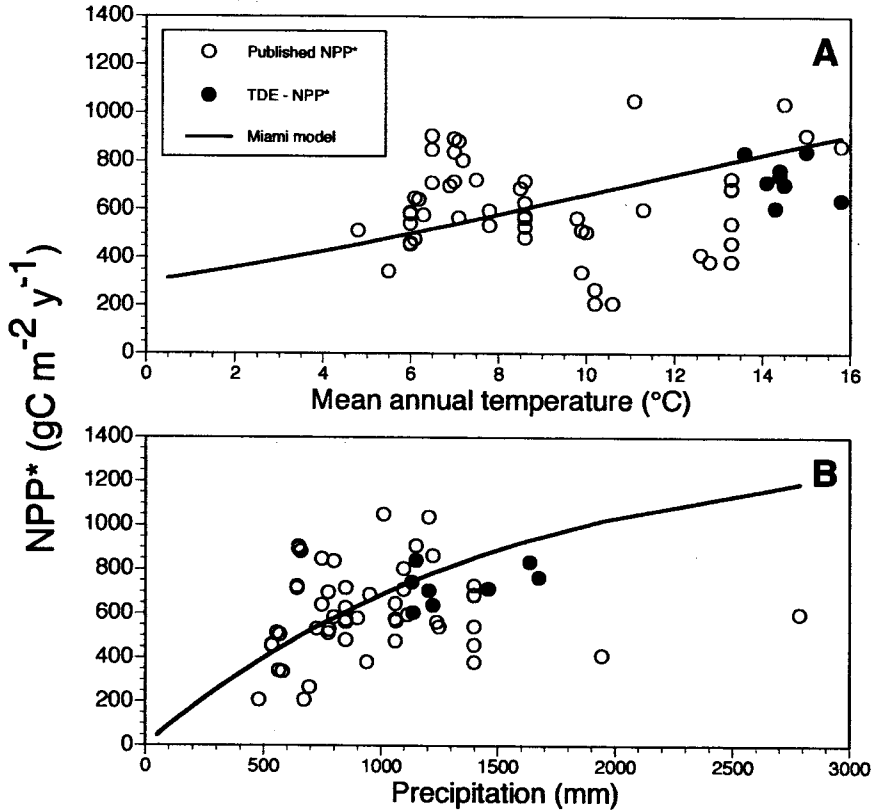
to mean annual NPP\* were 36%, 40%, 23%, and 1%, respectively. In peak mast years (e.g., 1999), acorn production can contribute as much as 5% of NPP\*. The two lowest values of NPP were associated with drought years in 1993 and 1998 having water stress integrals (WSIs) of  $-81$  and  $-175$  MPa, respectively (Chapter 2, this volume). Whereas 1995 was also a significant drought year (WSI =  $-133$  MPa), it was also a year with high late-season mast production ( $28.3 \text{ g C m}^{-2} \text{ y}^{-1}$ ), which may have offset losses to wood production limiting the correlation to midseason drought. Early onset of spring leafout in 1996 (Chapter 17, this volume) may explain the high wood production for that year (Table 22.3).

The calculated estimates of NPP\* for this study are in the middle range of values expected for temperate deciduous forests (Leith 1975a; DeAngelis et al. 1981, 1997; Edwards et al. 1989; Vogt 1991; Mellilo et al. 1993; Esser et al. 1997; Esser 1998; Amthor et al. 1998) and reach only the low end of the range for NPP\* of old-growth tropical forests (i.e.,  $200\text{--}2000 \text{ g C m}^{-2} \text{ y}^{-1}$ ) (Clark et al. (2001b). Edwards et al. (1980) reported an average temperate forest NPP value of  $561 \text{ g C m}^{-2} \text{ y}^{-1}$ , but showed specific values for a *Quercus-Pinus* forest in New York (Woodwell and Botkin 1970) of  $280 \text{ g C m}^{-2} \text{ y}^{-1}$ , and a *Quercus* forest in Britain of  $354 \text{ g C m}^{-2} \text{ y}^{-1}$ . Figure 22.1 shows the range of published NPP\* data for temperate deciduous forests, with the TDE estimates falling in the upper half. Within the range of climate conditions that support the growth of temperate deciduous forests (e.g.,  $4\text{--}16^\circ\text{C}$  mean annual temperature and  $400\text{--}2000$  mm in annual precipitation), the correlation of NPP\* with temperature or precipitation is not strong, but it is consistent with the interbiome relationships of the Miami model proposed by Lieth (1975b). Knapp and Smith (2001) found a positive correlation between aboveground NPP and annual precipitation for a range of ecosystems ranging from NPP values around  $200 \text{ g C m}^{-2} \text{ y}^{-1}$  at  $300\text{--}400$  mm of precipitation to NPP values greater than  $600 \text{ g C m}^{-2} \text{ y}^{-1}$  for annual precipitation levels exceeding  $1100$  mm. The mean annual aboveground NPP\* for the TDE forest of  $729 \text{ g C m}^{-2} \text{ y}^{-1}$  consistent with the Miami model (Fig. 22.1) and the relationships reported by Knapp and Smith (2001).

#### Estimates of NEP\*

Estimates of NEP\* were derived from interpolated data for  $R_{\text{hetero}}$ , which ranged from  $515$  to  $569 \text{ g C m}^{-2} \text{ y}^{-1}$  and showed little year-to-year variation even though temperatures gradually increased from 1993 to 2000. NEP\* ranged from a low of  $79 \text{ g C m}^{-2} \text{ y}^{-1}$  in 1998 to a high of  $292 \text{ g C m}^{-2} \text{ y}^{-1}$  in 1999 for an overall 8-year mean NEP\* of  $187 \text{ g C m}^{-2} \text{ y}^{-1}$ . The range of NEP\* estimates from 1993 to 2000 demonstrates the variable interannual nature of NEP. Birdsey (1992) used forest-inventory data to estimate the range of net accumulation of carbon by forests of the eastern United States and found a range from  $100$  to  $240 \text{ g C m}^{-2} \text{ y}^{-1}$ , which is in good agreement with the NEP\* values reported here.

Johnson et al. (1987) concluded that no significant change in soil carbon accumulation (including litter layers) had occurred in *Quercus-Carya* and *Q. prinus* stands on Walker Branch watershed from 1972 through 1982, and more recent

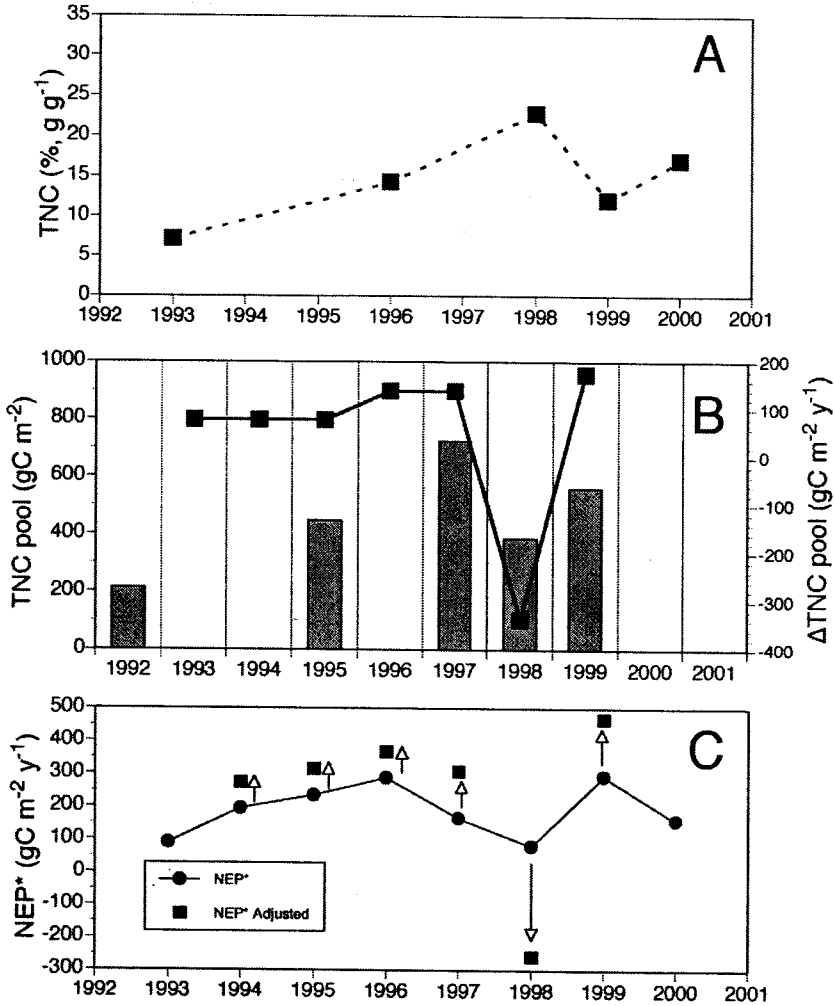


**Figure 22.1.** Relationship between NPP\* and mean annual air temperature (A) or precipitation (B) for data from this study (filled symbols) and data from the published literature (open symbols). Published estimates of NPP\* are from DeAngelis et al. (1981, 1997), Edwards et al. (1989), Valentini et al. (1996), Esser et al. (1997), Esser (1998), and Norby et al. (2002). The lines in each graph are the relationships between NPP and mean annual temperature or precipitation, as proposed by Lieth (1975b).

analyses of 1992 soil samples lead to the same conclusion (Trettin et al. 1999). Therefore, we conclude that any net annual carbon accumulation in these upland *Quercus* stands represents an addition to the live biomass pool made up mostly of large woody branches, roots, and tree boles.

#### Potential Confounding of NPP\* and NEP\* from Variable Nonstructural Carbohydrate Storage

Measured changes in dormant-season TNC stocks were substantial from 1993 to 2000 (Fig. 22.2A). The dormant-season TNC levels ranged from a low of ~7% in February of 1993 to a high of ~23% in February of 1998. Following the severe summer drought of 1998, TNC values fell to around 12%. Such large interannual changes of the size of the TNC pool reflect a significant change in tissue mass



**Figure 22.2.** (A) Multiyear patterns of dormant-season TNC measured in February of the respective years; (B) estimated stocks of TNC and estimated annual rates of change in the TNC stocks; (C) influence of changing stocks of TNC estimated in graph B on the biometric estimates of net ecosystem production (NEP\*).

that is not reflected in the application of fixed allometric relationships to the calculation of NPP\* and NEP\*. Furthermore, because TNC changes are bidirectional, the bias introduced might be positive in one annual cycle and negative in the next. To determine the potential magnitude of changing TNC concentrations (Fig. 22.2A) on stand carbon pools, we multiplied the known TNC concentrations by sapwood mass per unit ground area (derived from estimates of sapwood area [Chapter 21, this volume] converted to mass) and divided the change in pool size between measurement intervals by the appropriate increment of time (i.e., 1–3

years) (Fig. 22.2B) to yield the annual change in TNC pools ( $\Delta\text{TNC}$ ). The net change in the TNC carbon pool ranged from  $-338$  to  $174 \text{ g C m}^{-2} \text{ y}^{-1}$ , which is similar in magnitude to annual increments of foliar or wood production (Fig. 22.2B). Changes of this magnitude are substantial and would produce dramatic changes in  $\text{NEP}^*$  (Fig. 22.2C). However, when year-to-year changes in TNC stocks are averaged over time, the net change in TNC stocks tends to cancel out, and the long-term impacts of changes on the TNC pool would likely be small. Temporally resolved data for TNC levels of multiple tissue types will be required to fully evaluate the impact of changing TNC pools on biometric estimates of  $\text{NEP}^*$ .

### Estimates of Error Associated with $\text{NPP}^*$ and $\text{NEP}^*$

Complete estimates of error for the individual components of  $\text{NPP}^*$  and  $\text{NEP}^*$  would include stochastic variation associated with measurement approaches, spatial heterogeneity, and temporal heterogeneity. The application of consistent measurement approaches to identical plots from 1993 to 2000 allowed for the calculation of confidence intervals for year-to-year differences in  $\text{NPP}^*$  and  $\text{NEP}^*$  (Table 22.3). However, developing an accurate estimate of cumulative error for the biometric estimates of  $\text{NPP}^*$  and  $\text{NEP}^*$  and their components is not possible because the estimated and/or empirical error terms for all components are not equivalent.

Calculated relative-error estimates of measured variation (i.e., a 95% confidence interval) are as follows. The spatial and measurement error associated with leaf production or leaf standing stocks is  $\pm 4\%$ . The error associated with the cumulative estimate of aboveground biomass is  $\pm 20\%$ . The error associated with the estimate of standing coarse- and fine-root carbon stocks are  $\pm 54\%$  and  $\pm 16\%$ , respectively. The error associated with the measurement of organic-layer carbon is  $\pm 13\%$ . Estimates of error associated with the spatial variation of carbon stocks and annual carbon increments for upland *Quercus* forests could, and should, be done by the independent evaluation of multiple forest stands.

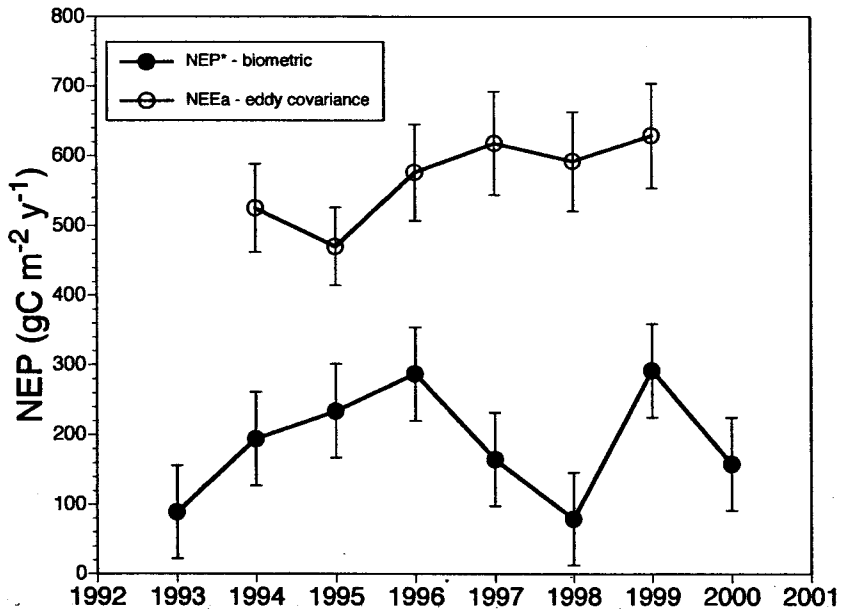
Interannual variability in  $\text{NEP}^*$  for Walker Branch is in the range of  $\pm 36\%$ . Although we can have confidence in the biometric estimates of  $\text{NPP}^*$  because they are largely based on directly measured carbon pools, the ability to estimate  $\text{NEP}^*$  is limited by our inability to differentiate autotrophic versus heterotrophic sources of soil respiration (Hanson et al. 2000); therefore, the true variability around  $\text{NEP}^*$  is probably higher than the  $\pm 36\%$ .

### $\text{NEP}^*$ Versus Eddy-Covariance Estimates

While the TDE study has been operating, continuous eddy-covariance observations of landscape-scale  $\text{CO}_2$  and water-vapor flux (Baldocchi et al. 1996) were collected from 1995 to 1999 over a nearly identical vegetation footprint 1 km to the southwest of the TDE study area (Wilson and Baldocchi 2001). Curtis et al. (2002) suggest that biometric  $\text{NEP}^*$  data should be directly comparable to eddy-covariance-based net-ecosystem-exchange data when integrated over an annual

time step ( $NEE_a$ ). Furthermore, the two estimates of NEP should be highly correlated over time and should produce the same mean NEP estimates when accounting for the errors of both approaches. Unfortunately, neither condition appears to hold for the  $NEP^*$  and  $NEE_a$  comparison at Walker Branch (Fig. 22.3). Although the measurement footprint for the eddy-covariance tower and the TDE site do not overlap, the species composition, leaf area index, soils, and weather for the respective stands are very similar, and site-to-site differences are not expected to confound the comparison of each approaches' estimate of NEP.

The Walker Branch  $NEE_a$  estimates from Wilson and Baldocchi (2001) are  $230\text{--}450\text{ g C m}^{-2}\text{ y}^{-1}$  higher than the  $NEP^*$  estimates developed in this chapter (Table 22.3). Law et al. (2002) conclude that  $NEE_a$  data have a total error of  $\sim \pm 12\%$  and the  $NEP^*$  data have a minimum error of  $\pm 37\%$ . Combining these two assumptions, we should anticipate  $NEP^*$  to agree within at least  $100\text{ g C m}^{-2}\text{ y}^{-1}$ . Because this was not the case for the  $NEP^*$  and  $NEE_a$  comparison for Walker Branch, we cannot conclude that the  $NEE_a$  estimates have been validated by the  $NEP^*$  values. Furthermore, the interannual pattern of accumulation between the  $NEP^*$  and  $NEE_a$  was not significantly correlated ( $R = 0.059$ ;  $P = 0.91$ ), suggesting that the assumptions driving the interannual differences in NEP



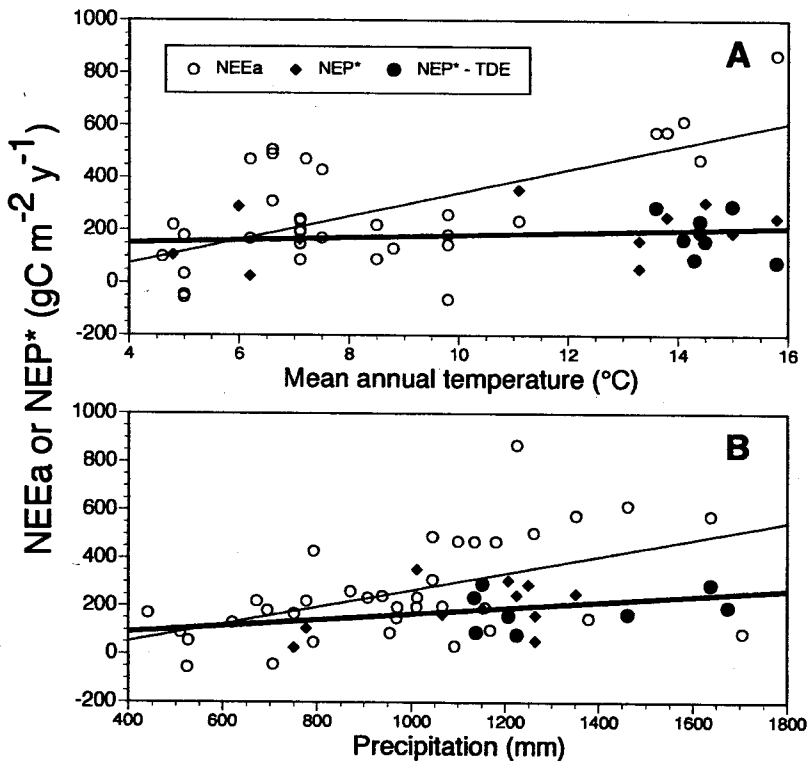
**Figure 22.3.** Net ecosystem production ( $NEP^*$ ) estimates from biometric approaches (Table 22.3) for 1993 to 2000 and analogous estimates based on eddy-covariance data ( $NEE_a$ ) [Greco and Baldocchi (1996); Valentini et al. (1996); Wilson and Baldocchi (2001)] for the period from 1994 to 1999. Error bars for  $NEE_a$  are only approximate and follow the range suggested by Law et al. (2002). Error bars for  $NEP^*$  represent a confidence interval associated with interannual variation (Table 22.3) and are only a minimum estimate of the total variation around the calculated value.

as derived by both approaches do not agree. Lack of correlation between inter-annual patterns of  $NEP^*$  and  $NEE_a$  might be partly explained by hidden changes in nonstructural storage carbohydrates and the transport of dissolved organic carbon to deep soil storage (as discussed previously).

Concern over the lack of agreement between the  $NEP^*$  and  $NEE_a$  data for the Walker Branch site must be put in perspective. First,  $NEP$  is likely to be a highly variable quantity, simply because it is a small difference between two large and diametrically opposed fluxes. The reader should not conclude from this single-site example that better comparisons between  $NEP^*$  and  $NEE$  are not possible. When five temperate deciduous hardwood sites, including Walker Branch, were combined in a similar comparison (Curtis et al. 2002), reasonable agreement between biometric  $NEP^*$  and eddy-covariance  $NEE_a$  was found for several sites. Barford et al. (2001) found mean annual  $NEP^*$  data for a *Quercus/Tsuga* site in Massachusetts to be only  $40 \text{ g C m}^{-2} \text{ y}^{-1}$  lower than the mean  $NEE_a$  data for a 9-year period. Ehman et al. (2002) found  $NEP^*$  to overestimate  $NEE_a$  by 34 and  $90 \text{ g C m}^{-2} \text{ y}^{-1}$  for 1998 and 1999, respectively. It would appear that the difficult site and environmental conditions (i.e., sloping terrain and low night turbulence) on Walker Branch represent a severe limitation to the direct integration of short-term  $NEE$  data to annual totals (Baldocchi et al. 2000; Curtis et al. 2002), and it is therefore not easy to reconcile  $NEE_a$  derived from the integrating approaches of Wilson and Baldocchi (2001) with the  $NEP^*$  data presented in this chapter.

Although both the  $NEP^*$  and  $NEE_a$  approaches are subject to error, two lines of reasoning lead us to believe that the  $NEP^*$  data represent the more accurate estimate of  $NEP$  for the upland *Quercus* forests at Walker Branch, Tennessee. First, a simple evaluation of the standing pool of carbon at Walker Branch divided by the age of the stand (Table 22.2) suggests that mean annual carbon accumulation would be unlikely to exceed  $200 \text{ g C m}^{-2} \text{ y}^{-1}$ . In fact, similar checks for other temperate deciduous forests throughout the eastern United States also support a mean annual carbon accumulation over the life of the forest of no more than  $300 \text{ g C m}^{-2} \text{ y}^{-1}$  (Table 22.2). Second, it is not clear where the additional carbon (i.e.,  $230\text{--}450 \text{ g C m}^{-2} \text{ y}^{-1}$ ) would be accumulating in the Walker Branch forest. Gaudinski and Trumbore (Chapter 11, this volume) showed that changing soil carbon was not a likely storage pool, and Chapter 16 (this volume) concluded that no change in belowground root mass was observed during the 8 years of their observations on the TDE. Dissolved-organic-carbon losses from the leaching of water below the rooting zone (Jardine et al. 1990) represents an unquantified pathway for carbon transport that might help resolve differences in  $NEP$  and  $NEE$  within sites. New research is underway to evaluate the magnitude of deep-soil carbon storage via the translocation of dissolved organic carbon using background-level  $^{14}\text{C}$  tracers (Trumbore et al. 2002), but carbon-storage levels of sufficient size to account for the differences between  $NEP^*$  and  $NEE_a$  for the Walker Branch site are not expected. Finally, errors associated with the allometric estimation of the annual aboveground biomass increment might contribute an additional  $50\text{--}70 \text{ g C m}^{-2} \text{ y}^{-1}$ , as discussed previously, but would not bridge the gap between the  $NEP^*$  and  $NEE_a$  estimates.

A comparison of published  $NEP^*$  and  $NEE_a$  data for temperate deciduous hardwood forests (Valentini et al. 2000; Law et al. 2002; Norby et al. 2002) and data from this study (Fig. 22.4) also demonstrates that biometrically based  $NEP^*$  data tend to be lower than some but not all  $NEE_a$  data, especially at high mean annual temperatures and precipitation levels. However, neither method yields a strong relationship between  $NEP$  values for temperate deciduous forests and temperature or precipitation. Janssens et al. (2001) used EUROFLUX network  $NEE_a$  data collected across a range of both deciduous and coniferous forest stands to conclude that productivity, not temperature, was the primary driver for explaining site-to-site differences in  $NEE_a$ . Although it is convenient and satisfying to identify simple relationships between environmental variables and  $NEP$ , long-term goals should focus on the development of mechanistic explanations for observed  $NEP$ . Models designed to explain the magnitude and interannual variation of  $NEP$  will undoubtedly require mechanisms that respond to a full range of environmental conditions, including radiation inputs, temperature, soil-water and nutrient availability, growing-season duration, and herbivory.



**Figure 22.4.** Relationship between  $NEP^*$  or  $NEE_a$  and mean annual air temperature (A) or precipitation (B) for data from this study (filled symbols) and data from the published literature [open symbols are from Valentini et al. (2000); Law et al. (2002); and Norby et al. (2002)].

## Conclusions

The standing pools of carbon in the 58- to 100-year upland *Quercus* forest of Walker Branch Watershed show the majority to be tied up in the living biomass. Because little change in belowground root density and soil-carbon content has been observed in recent years (Trettin et al. 1999; Chapter 16, this volume), we anticipate that annual NEP for this stand represents accumulation of carbon in coarse woody material. Estimates of NPP\* and NEP\* from biometric methods yielded mean annual values of 729 and 187 g C m<sup>-2</sup> y<sup>-1</sup>, respectively. Interannual differences in NPP\* and NEP\* were ±10 or 36%, and the extremely low estimates were attributed to changes in forest water status. Interannual changes in the TNC carbon stocks were shown to represent a potentially large hidden change in carbon storage that is often overlooked in the calculation of NPP\* and NEP\*. Finally, for the TDE and Walker Branch study areas, interpolated eddy-covariance measurements of NEE<sub>a</sub> appear to systematically overestimate NEP and must be interpreted with caution.

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