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Biomass and carbon storage of the North American deciduous forest

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Abstract. Field measures of tree and shrub dimensions were used with established biomass equations in a stratified, two-stage cluster sampling design to estimate above-ground oven-dry woody biomass and carbon storage of the eastern deciduous forest of North America. Biomass averaged 8.1 ± 1.4 (95% C.I.) kg/m^2 and totaled 18.1 ± 3.1 (95% C.I.) gigatons. Carbon storage averaged 3.6 ± 0.6 (95% C.I.) kg/m^2 and totaled 8.1 ± 1.4 (95% C.I.) gigatons. These values are lower than previous estimates commonly used in the analysis of the global carbon budget which range from 17.1 to 23.1 kg/m^2 for biomass and 7.7 to 10.4 kg/m^2 for carbon storage. These new estimates for the deciduous forest, together with earlier work in the boreal forest begin to reveal a pattern of overestimation of global carbon storage by vegetation in analyses of the global carbon budget. We discuss reasons for the differences between the new and earlier estimates, as well as implications for our understanding of the global carbon cycle.

Introduction

The missing carbon problem, articulated in the late 1970s (Broecker et al. 1979), is still with us. At least 10% of the carbon added annually to the atmosphere by burning fossil fuel is unaccounted for, and the percentage may be much higher (Quay et al. 1992). There appear to be only two possible sinks for this missing carbon: biological uptake in the ocean and in forests. Recent papers argue that the missing carbon must be taken up by forests (Kauppi et al. 1992; Quay et al. 1992), but the matter remains unresolved after nearly two decades of discussion.

This issue cannot be resolved by direct measurement at the present time, because we do not have accurate global measurements of the rate of change in carbon storage by the forests of the Earth. This is not surprising; the task is difficult. Three methods are possible to determine this rate of change: (1) global monitoring of forest biomass, so that net changes are

observed directly over time; (2) global monitoring of leaf biomass in forests and a method to estimate net annual photosynthesis; and (3) an indirect method: examination of the annual oscillation in the carbon dioxide concentration in the atmosphere, such as the measurements at Mauna Loa (Boden et al. 1990). In the last case, an increase in the amplitude of the oscillations could represent an increase in photosynthetic capacity, suggesting an increase in forest biomass.

For each of these methods, available data appear inadequate to determine the rate of change in forest biomass. To correct part of this deficiency, we began a program in the 1980s to obtain field measurements to estimate biomass and carbon storage for large areas of the Earth's vegetation. The intention was to provide a baseline to establish the first statistically valid large-scale estimates of biomass and carbon storage in above-ground forest vegetation.

Our first studies indicated that estimates for the boreal forests of North America used in most of the literature on the global carbon cycle were two to four times too large (Botkin & Simpson 1990a). In this paper we report new results, derived from field measurements, for present biomass and carbon storage in the eastern deciduous forests of North America.

The eastern deciduous forest of the United States and the contiguous boreal forests of North America provide the largest area of continuous forest on the continent. As defined in this study, the eastern deciduous forest extends from the northern Great Lakes to the Gulf plains in the south and Coastal Plains in the east, and to the Mississippi River through the Ozark Mountains in the west. It is the most diverse and species-rich forest of North America and therefore is the most difficult to study. It was also the first forest cleared following European settlement, and it has been subject to some of the greatest human-induced alterations.

Methods

Sample design and selection

We used a stratified two-stage cluster design that was employed previously to estimate biomass and carbon storage of the North American boreal forest (Botkin & Simpson 1990a). For the deciduous forest of North America, sampling strata were defined by physiographic regions of Hunt (1967), except that some strata boundaries were modified to facilitate sampling and to allow the sampling area of the deciduous forest to be contiguous with the area we defined as boreal forest in our earlier work (Botkin & Simpson 1990a, 1990b; Simpson & Botkin 1992) (Fig. 1).

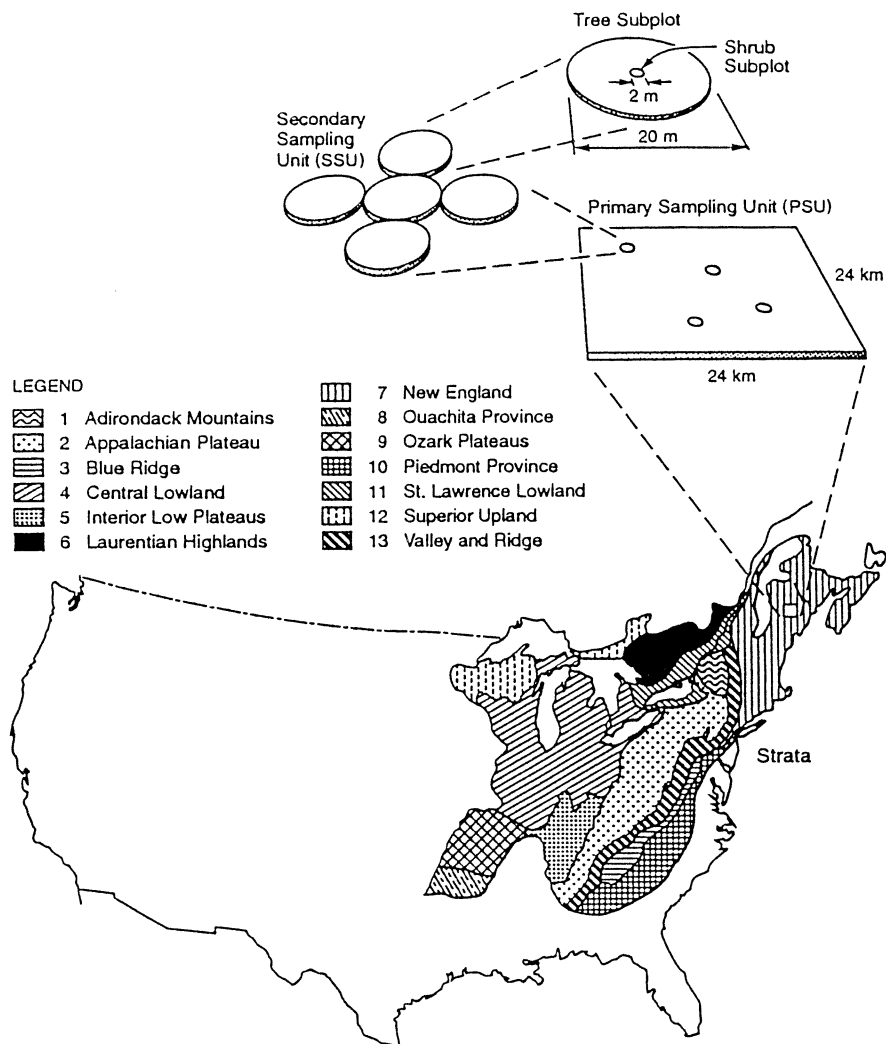


Fig. 1. Location of sampling strata used for estimating the biomass and carbon storage of the eastern deciduous forest of North America. Strata are based on physiographic regions of Hunt (1967). A diagram of the sample design is also presented showing the relationship between strata, primary sampling units and secondary sampling units.

These physiographic regions are defined according to non-vegetative criteria and may not correspond exactly with the area defined as deciduous forest in other studies.

Thirteen strata, based on physiographic regions, were used: Superior Upland; Laurentian Highlands; Piedmont Province; Blue Ridge Province;

Valley and Ridge Province; Appalachian Plateau; New England Province; Adirondack Province; St. Lawrence Lowland; Central Lowland; Interior Low Plateaus; Ozark Plateaus; and Ouachita Province (Fig. 1). The western boundary of the Central Lowland was defined by the Mississippi River. The northwest boundary of the Superior Upland was defined by the 20 °C July mean temperature isotherm, and its northeast boundary was defined by the 17.5 °C July mean temperature isotherm (World Meteorological Organization 1979). The northern boundaries of the Laurentian Highlands and New England Province were defined by the 17 °C July mean temperature isotherm.

A map of the strata was generated in a geographic information system (GIS), using the ERDAS (Earth Resources Data Analysis System) software. Once the original strata map was entered into the GIS, it was converted to an Albers equal area projection, and primary sampling units (PSUs), 24 × 24 km in size, were selected from the computer screen within each stratum using a table of randomly generated screen coordinates. Once selected, the longitude and latitude of the northwest corner of each PSU were recorded. The number of PSUs allocated to a stratum was proportional to its size (Table 1A), with at least two PSUs selected from each stratum to obtain an unbiased estimate of the variance. The total number of PSUs selected (47) was estimated as the minimum necessary based on previous data to give a sampling error of approximately 20 percent, subject to the constraint that every stratum must have at least 2 PSUs (Table 1A).

PSUs were then located and marked on United States Geological Survey topographic maps. Within each primary sampling unit (PSU), four secondary sampling units (SSUs) were selected and marked on the map using a table of randomly generated Universal Transverse Mercator (UTM) coordinates. Each SSU consisted of five 20 m diameter subplots with one subplot located in the center and four located tangentially in the cardinal directions. A 2 m diameter understory plot was established at the center of each subplot. If it occurred over a lake or river, an SSU was omitted and replaced by another chosen according to the same random sampling scheme. No other consideration, such as a clearing or exposed bedrock, eliminated an SSU, because our goal was to estimate the present mean biomass and carbon storage for entire strata.

Field methods

During the summers of 1989 and 1990, each SSU was located on the ground by pacing in an appropriate compass direction from a point clearly marked on topographic maps and clearly visible on aerial photographs. At

Table 1A. Area and sample size by strata for the temperate deciduous forest of eastern North America study area.

Stratum name	Area (Km ²)	% Area	Number of samples		
			PSUs ¹	SSUs ²	Subplots ³
1 Adirondack Mountains	36518	1.64	2	8	40
2 Appalachian Plateau	310349	13.92	5	20	100
3 Blue Ridge	65664	2.94	2	8	40
4 Central Lowland	528768	23.71	10	40	200
5 Interior Low Plateaus	111168	4.98	3	12	60
6 Laurentian Highlands	115315	5.17	3	12	60
7 New England	318643	14.29	5	20	100
8 Ouachita Province	48672	2.18	2	8	40
9 Ozark Plateaus	142906	6.41	3	12	60
10 Piedmont Province	179194	8.03	4	16	80
11 St. Lawrence Lowland	88819	3.98	2	8	40
12 Superior Upland	142906	6.41	3	12	60
13 Valley and Ridge	141350	6.34	3	12	60
Totals	2230272		47	188	940

¹ Primary sampling units — These are randomly selected 24 km × 24 km areas within each stratum.

² Secondary sampling units — there are 4 randomly selected SSUs in each PSU.

³ There are five 20 meter diameter subplots in each SSU. Subplots are arranged in a cross shape with one in the center and the others located tangent to it, one in each cardinal direction. It is not statistically valid to consider the subplots individually in this analysis because they are not independent.

each SSU, the following data were measured: for all trees ≥ 2 cm DBH (diameter at breast height — 1.37 m above the ground), total height, and species; for all tree seedlings and saplings > 2 cm DBH and shrubs in the understory plots, stem diameter at the base and at 15 cm above the ground. Data about site conditions were also collected at each plot, including: slope, aspect, topographic position, and type and degree of disturbance.

We did not consider the biomass of the litter, undecomposed organic matter, or below-ground biomass of the trees. These are important components of the total forest biomass, but analysis of these biomass components would at least triple the cost of the study and funds were not available to include these measurements. Given limited funding, we chose the logical place to begin the study of total forest biomass — analysis of the above-ground biomass of trees. Direct measurement of other important

aspects of the global carbon cycle, such as rates of forest photosynthesis and respiration, were also beyond the scope of this study.

Data analysis

Total above-ground oven-dry woody biomass was calculated for each secondary sampling unit using species-specific dimension-analysis equations developed by the U.S. Forest Service and Forestry Canada for most trees (Taras & Clark 1974; Taras & Clark 1977; Taras & Phillips 1978; Saucier & Boyd 1982; Evert 1985; Clark et al. 1986a; Clark & Schroeder 1986) and most shrubs (Stanek & State 1978; Ribe 1979; Smith & Brand 1983). When no equation was available for a species, an equation from a suitable analog species was used. The criteria for selecting appropriate analog species included genus or sub-genus, wood density, and form.

The methods allow calculation of totals, means, variances, and error bounds. However, estimates of variance and error bounds apply only to the spatial variation in our sample. Our primary concern was to make the first statistically valid estimate of forest biomass for the North American eastern deciduous forest. Rather than claim high precision or accuracy, our goal was to estimate biomass levels within an error bound of 20 percent of the mean.

It is possible that our research might be sensitive to errors in the allometric equations used to predict tree biomass. We have investigated the sensitivity of the estimate to this possible source of error by substituting a simple equation developed from data for several species for species-specific equations. This was done twice, first using a general hardwood equation Clark et al. (1986a) developed by combining data of ten hardwood species in the Piedmont region, and second by using another general hardwood equation Clark et al. (1986b) developed by combining the data of seven species in the upland-south. In each of these sensitivity tests, a single allometric equation was used for all angiosperm stems. A discussion of additional error sources is presented in the Discussion section below.

Estimates of present storage

Biomass density for an SSU was calculated by dividing the sum of individual tree or shrub biomass by plot area for both the overstory and the understory. Mean oven-dry biomass density (kg/m^2), \bar{b} , for the eastern deciduous forest and its 95% error bound were calculated with a set of survey-sampling equations derived for the sample design (Yamane 1967).

Mean biomass =

$$\bar{b} = \frac{1}{N} \cdot \sum_{h=1}^L \left(\frac{N_h}{(n_h \times m_{hi})} \cdot \sum_{i=1}^{n_h} \sum_{j=1}^{m_{hi}} b_{hij} \right)$$

Error bound =

$$\hat{E} = \pm 1.96 \cdot \sqrt{(\hat{V}(\bar{b}))}$$

$$\hat{V}(\bar{b}) = \frac{1}{N^2} \cdot \sum_{h=1}^L N_h^2 \cdot \left[\left(\frac{N_h - n_h}{N_h} \cdot \frac{s_{1bi}^2}{n_h} \right) + \left(\frac{n_h}{N_h} \cdot \frac{s_{2ii}^2}{n_h m_{hi}} \right) \right]$$

$$s_{1bi}^2 = \frac{1}{n_h - 1} \cdot \sum_{i=1}^{n_h} \bar{b}_{hi}^2 - n_h \bar{b}_h^2$$

$$\sum_{i=1}^{n_h} \bar{b}_{hi}^2 = \left(\frac{1}{m_{hi}} \right)^2 \cdot \sum_{i=1}^{n_h} \left(\sum_{j=1}^{m_{hi}} b_{hij} \right)^2$$

$$\bar{b}_h^2 = \left(\frac{1}{n_h m_{hi}} \right)^2 \cdot \left(\sum_{i=1}^{n_h} \sum_{j=1}^{m_{hi}} b_{hij} \right)^2$$

$$s_{2ii}^2 = \frac{1}{n_h(m_{hi} - 1)} \cdot \left(\sum_{i=1}^{n_h} \sum_{j=1}^{m_{hi}} b_{hij}^2 - \left(\frac{1}{m_{hi}} \cdot \sum_{i=1}^{n_h} \left(\sum_{j=1}^{m_{hi}} b_{hij} \right)^2 \right) \right)$$

where L = number of strata; N = total number of PSUs; N_h = number of PSUs in stratum h ; n_h = number of PSUs sampled in stratum h ; m_{hi} = number of SSUs sampled in PSU i in stratum h ; b_{hij} = biomass density of SSU in kg/m²; s_{1bi}^2 = variance among PSUs; s_{2ii}^2 = variance within PSUs, among SSUs.

Total biomass of the eastern deciduous forest and its error bound were also calculated from equations derived for the sample design.

Total biomass =

$$\hat{B} = \sum_{h=1}^L \frac{N_h}{n_h} \cdot \sum_{i=1}^{n_h} \frac{M_{hi}}{m_{hi}} \cdot \sum_{j=1}^{m_{hi}} B_{hij}$$

Error bound =

$$\hat{E} = \pm 1.96 \cdot \sqrt{(\hat{V}(\hat{B}))}$$

$$\hat{V}(\hat{B}) = \sum_{h=1}^L \left[\left(N_h^2 \cdot \frac{N_h - n_h}{N_h} \cdot \frac{s_h^2}{n_h} \right) + \left(\frac{N_h}{n_h} \cdot \sum_{i=1}^{n_h} M_h^2 \cdot \frac{s_{hi}^2}{m_{hi}} \right) \right]$$

$$s_h^2 = \frac{1}{n_h - 1} \cdot \sum_{i=1}^{n_h} \left(M_{hi} \cdot \bar{B}_{hi} - \sum_{i=1}^{n_h} \frac{(M_{hi} \cdot \bar{B}_{hi})}{n_h} \right)^2$$

$$s_{2ii}^2 = \frac{1}{n_h(m_{hi} - 1)} \cdot \left(\sum_{i=1}^{n_h} \sum_{j=1}^{m_{hi}} b_{hij}^2 - \left(\frac{1}{m_{hi}} \cdot \sum_{i=1}^{n_h} \left(\sum_{j=1}^{m_{hi}} b_{hij} \right)^2 \right) \right)$$

$$s_{hi}^2 = \frac{1}{m_{hi} - 1} \cdot \sum_{j=1}^{m_{hi}} \left(B_{hij} - \frac{\sum_{j=1}^{m_{hi}} B_{hij}}{m_{hi}} \right)^2$$

where B_{hij} = total SSU biomass; M_{hi} = number of SSUs in PSU i in stratum h ; s_h^2 = variance among PSUs; s_{hi}^2 = variance within PSUs, among SSUs; other terms are the same as defined above.

The above equations weigh SSU mean and total biomass results by stratum and sample size. Between and within PSU variances are also weighted by stratum and sample size. This system of equations, along with the biomass equations cited earlier, was programmed in Microsoft C and the data were processed with a 386-PC microcomputer. All values were converted to carbon and applied to the forest area. Carbon content was taken to be 45% of the oven-dry biomass (Whittaker 1975).

Results

Direct field measurements yielded an estimate of 8.05 ± 1.38 (95% error bound) kg/m^2 for the density of aboveground woody biomass for the temperate deciduous forest of eastern North America. This is 52% to 65% lower than values used previously in efforts to balance the global carbon cycle (Table 1B; Table 2). Using the ten-species general hardwood equation from Clark et al. (1986a), the biomass density is estimated to be $9.89 \pm 1.76 \text{ kg/m}^2$. Using the seven-species general hardwood equation from Clark et al. (1986b), biomass density is estimated to be $9.19 \pm 1.59 \text{ kg/m}^2$ (Table 1B; Table 2). Both estimates are larger than that based on

Table 1B. Biomass estimates by strata for the temperate deciduous forest of eastern North America.

Stratum name	Full sample		Sample omitting recently logged or permanently cleared SSUs			
	Mean biomass density (kg/m ²)	Total biomass (gigatons)	Mean biomass density (kg/m ²)	Total biomass (gigatons)	Mean biomass density (kg/m ²)	Total biomass (gigatons)
1 Adirondack Mountains	8.46 ± 8.87	0.31 ± 0.32	8.46 ± 8.87	0.31 ± 0.32	8.46 ± 8.87	0.31 ± 0.32
2 Appalachian Plateau	17.24 ± 5.39	5.35 ± 1.66	18.15 ± 5.66	5.68 ± 1.70	18.15 ± 5.66	5.68 ± 1.70
3 Blue Ridge	14.27 ± 7.40	0.94 ± 0.48	16.31 ± 8.43	1.05 ± 0.2	16.31 ± 8.43	1.05 ± 0.2
4 Central Lowland	1.45 ± 1.40	0.77 ± 0.72	4.08 ± 3.04	2.12 ± 1.49	4.08 ± 3.04	2.12 ± 1.49
5 Interior Low Plateaus	6.86 ± 1.56	0.76 ± 0.16	9.15 ± 2.05	1.07 ± 0.31	9.15 ± 2.05	1.07 ± 0.31
6 Laurentian Highlands	6.80 ± 3.30	0.82 ± 0.44	6.80 ± 3.30	0.82 ± 0.44	6.80 ± 3.30	0.82 ± 0.44
7 New England	8.94 ± 3.47	2.84 ± 1.11	9.41 ± 3.65	2.94 ± 1.01	9.41 ± 3.65	2.94 ± 1.01
8 Ouachita Province	7.05 ± 6.18	0.34 ± 0.30	7.05 ± 6.18	0.34 ± 0.30	7.05 ± 6.18	0.34 ± 0.30
9 Ozark Plateaus	12.07 ± 7.85	1.72 ± 1.12	13.16 ± 8.55	1.79 ± 0.99	13.16 ± 8.55	1.79 ± 0.99
10 Piedmont Province	9.06 ± 3.88	1.62 ± 0.69	10.36 ± 4.43	1.97 ± 1.04	10.36 ± 4.43	1.97 ± 1.04
11 St. Lawrence Lowland	5.80 ± 7.25	0.51 ± 0.64	10.63 ± 4.03	1.00 ± 0.33	10.63 ± 4.03	1.00 ± 0.33
12 Superior Upland	6.46 ± 2.43	1.02 ± 0.31	7.05 ± 2.64	1.02 ± 0.31	7.05 ± 2.64	1.02 ± 0.31
13 Valley and Ridge	7.50 ± 10.16	1.06 ± 1.43	10.00 ± 13.54	1.14 ± 1.40	10.00 ± 13.54	1.14 ± 1.40
Totals	8.05 ± 1.38	18.07 ± 3.08	9.60 ± 1.66	21.73 ± 3.30	9.60 ± 1.66	21.73 ± 3.30

species-specific equations, but neither is significantly different from that estimate.

Field measurements give a total present biomass of 18.07 ± 3.08 gigatons (Table 1B; Table 2). Average present carbon density is estimated to be 3.6 ± 0.6 kg/m², and an average present total carbon of 8.1 ± 1.4 gigatons.

Overstory trees contain more than 99% of the biomass and carbon (Table 2). The highest biomass densities occur in the Appalachian Plateau, Blue Ridge, and Ozark Plateaus strata (Table 1A); the lowest biomass is in the largest stratum, the Central Lowland (Table 1A) (Fig. 1).

Discussion

The reader should recognize that the survey sampling methodology used in this study samples a total of 188 plots, but these sum to a total of 29.53 ha, a tiny percentage of the 223 million ha in the North American

Table 2. Estimates of above-ground biomass and carbon in the temperate deciduous forest of eastern North America from this study and commonly used estimates from other sources.

Source ^d	Biomass ^e (kg/m ²)	Carbon ^f (kg/m ²)	Total Biomass (gigatons) ^g	Total Carbon (gigatons) ^d
<i>This study^h</i>				
<i>Current</i>				
Overstory	8.0 ± 1.4	3.6 ± 0.6		
Understory	0.1 ± 0.0	0.0 ± 0.0		
Total	8.1 ± 1.4	3.6 ± 0.6	18.1 ± 3.1	8.1 ± 1.4
Total ⁱ	9.8 ± 1.8	4.4 ± 0.8	22.2 ± 3.9	10.0 ± 1.8
Total ^j	9.2 ± 1.6	4.1 ± 0.7	20.6 ± 3.5	9.3 ± 1.6
<i>Previous studies</i>				
(1)	21.6	9.7	48	22
(2)	23.1	10.4	52	23
(3)	17.1	7.7	38	17
(4)	17.1	7.7	38	17
(5) ^k	23.1	10.4	52	23
(5) ^l	17.1	7.7	38	17

^d 1 — Ajtay et al. 1979; 2 — Whittaker and Likens 1973; 3 — Olson et al. 1978; 4 — Olson et al. 1983; 5 — Houghton et al. 1983.

^e Values in this column are for total above-ground biomass. Previous studies give total (above and below ground) biomass, which is corrected by us assuming that 23% of the total biomass is in below ground roots. (Most reference give this percentage; Leith and Marks (1975) give 17%; we have chosen to use the larger value to give a more conservative comparison.)

^f Carbon is assumed to be 45% of total biomass following Whittaker (1975).

^g Assuming our estimate of the areal extent of our study area — 2,230,272 Km².

^h Above-ground woody plants only.

ⁱ Using the general hardwoods biomass equation from Clark et al. (1986a) on all angiosperms.

^j Using the general hardwoods biomass equation from Clark et al. (1986b) on all angiosperms.

^k Undisturbed forest.

^l Secondary forest.

deciduous forest. However, this methodology has been thoroughly tested in agricultural studies, which show that a small sample of a large area is sufficient to provide an estimate within 20 percent of the mean of the sample variables (Yamane 1967). This is characteristic of many statistical methods used to sample large populations. This sample was the maximum that could be obtained with available funding. Even though the error of

our estimate is within 20 percent of the mean biomass value, we hope that funds will be available eventually to sample a larger area.

Field measurements yield estimates of present biomass and carbon storage that are dramatically smaller than earlier estimates. The question arises: what accounts for these differences? Earlier large-scale estimates were based on expert opinion or extrapolations from unrelated studies. Such methods create unexpected and hidden biases. None of the previous estimates was based on a statistically valid sampling scheme. Furthermore, earlier estimates were extrapolated from a few plots, usually of old-age forest believed to be near maximum biomass. These estimates assumed that the entire area was homogeneous, at the same successional state, and at maximum biomass, assumptions that few ecologists accept today.

In reality, large forested areas tend to be heterogeneous, composed of a mosaic of stands at different stages in ecological succession (Hall et al. 1991) and storing different amounts of biomass. The temperate deciduous forest of eastern North America is additionally heterogeneous because of land use changes over the last 400 years, because of intrinsic edaphic variation, and due to natural forest dynamics. Extrapolations from studies that are conducted primarily in mature forests are biased upwards, leading to overestimates of biomass and carbon storage in woody vegetation.

The distribution of biomass among the sample strata is a function of land-use change and the original distribution of biomass in the region. The high biomass densities of the Appalachian Plateau, Blue Ridge, and Ozark Plateaus strata are not surprising, because these areas have always been dominated by forests and have undergone less alteration by human activities than other strata. The Appalachian Plateau and Blue Ridge Province include areas where the eastern deciduous forest has a high species diversity (Currie & Paquin 1987) and where areas are believed to have reached the highest development and biomass densities (Braun 1950; Greller 1988). Historically, this region was cleared for farming and grazing, but, typically, the land was soon abandoned. Because of the hilly and mountainous terrain that dominates these regions, there has been no reestablishment of farming and much of the land has reverted to forest (Smith & Linnartz 1980). The same circumstances are true for the Ozark Plateaus, a region now dominated by forest.

The lowest biomass density occurs in the largest stratum, the Central Lowlands. This is an area dominated by level terrain that has been farmed continuously since it was cleared in the last century. Three-fourths of the SSUs measured in this stratum occurred in agricultural fields and therefore had no woody biomass. It should be noted also that, before European settlement, a large portion of the western half of this stratum was domi-

nated by prairie (Braun 1950). Thus, significant portions may not have supported forests at the time of the first European settlement.

Along with our earlier work in the boreal forest (Botkin & Simpson 1990a), this study reveals a history of overestimation of the present mean values of biomass and carbon storage. These overestimates have been used in analyses and formal models of the global carbon cycle and appealed to in attempts to understand and balance the global carbon budget. Such previous studies suggest that total carbon stored in these two North American biomes is between 31 and 63 gigatons, based on the combined area of our boreal and eastern deciduous forest studies (7,356,699 km²) and earlier carbon storage densities (Table 2; Botkin & Simpson 1990a). Using our estimates of carbon density and the combined area of the two biomes, we find that the carbon presently stored in the combined area is 17.8 gigatons, about one half to one third the estimate based on commonly accepted earlier values of carbon density.

Estimates of the global vegetation carbon reservoir range between 420 and 830 gigatons (Post et al. 1990). Houghton et al. (1983) used carbon density values derived by Whittaker & Likens (1973) for each biome to compute a value of 744 gigatons for the carbon storage of the global vegetation carbon reservoir (Table 1). We recalculated this estimate using the area of major biomes from Houghton et al. (1983), carbon density values for the closed tropical forest reported by Brown et al. (1989), carbon density values for the boreal forest reported by Botkin & Simpson (1990a), and carbon density values for the temperate deciduous forest reported here. For purposes of this calculation, we reduced carbon densities for the tropical seasonal forest and the temperate evergreen forest of Houghton et al. (1983) by 62%, which is the difference between the value of the tropical forest carbon density reported by Whittaker & Likens (1973) and that reported by Brown et al. (1989). The result is 328 gigatons for the global vegetation carbon reservoir, which is much lower than any previous estimate (Table 3).

Sources of error

There are two primary sources of error associated with the kind of estimate reported here: sampling error and measurement error. The 17.1% error bound estimated in this study is only for sampling error associated with the selection of plots to be measured. The sampling error associated with the biomass regression equations has not been estimated. Cunia (1986) experimented with estimates of forest biomass for fixed forested areas. He found that, if the sampling error associated with the biomass regression equations was ignored, the error bound was underestimated by about 20

Table 3. Estimation of the global vegetation carbon pool using the latest estimates of total carbon density for forests.

Biome	Area ^a (10 ⁶ ha)	Houghton et al. (1983)		This study	
		Carbon density (ton/ha)	Total carbon (gigatons)	Carbon density (ton/ha)	Total carbon (gigatons)
Tropical moist forest	1352	200	270	76 ^b	103
Tropical seasonal forest	653	160	104	61 ^c	40
Temperate evergreen forest	546	160	87	61 ^c	33
Temperate deciduous forest	612	135	83	47 ^d	29
Boreal forest	1179	90	106	25 ^e	29
Trop. woodland and shrubland	945	27	26	27 ^f	26
Temp. woodland and shrubland	753	27	20	27 ^f	20
Tropical grassland	425	18	26	18 ^f	26
Temperate grassland	2051	7	14	7 ^f	14
Tundra and alpine meadow	706	3	2	3 ^f	2
Desert scrub	2152	3	6	3 ^f	6
Total	11374		744		328

^a From Houghton et al. (1983).

^b Calculated from Brown et al. (1989).

^c Value from Houghton et al. (1983) reduced by 62%.

^d Total carbon density calculated by multiplying above-ground estimate from this study by 1.3 because total biomass is converted to above-ground biomass by reducing by 23%.

^e Total carbon density calculated by multiplying above-ground estimate from Botkin and Simpson (1990a) by 1.3.

^f Value after Houghton et al. (1983).

percent. If the same were true for our study, our error bound would increase from 17.1 percent of the mean to 21.4 percent of the mean, which is still near our goal of a 20 percent error bound. Measurement errors cannot be estimated statistically, but can be discussed (Cunia 1986). There are several possible sources of measurement errors in a study such as ours. Species could have been misidentified, data miswritten, and measurements improperly conducted or biased in some way.

Improper species identification would result in the assignment of the wrong biomass equation to the tree. Our analysis using non species-specific equations suggests that the estimate is not affected significantly by improper assignment of equations.

It is assumed that random measurement and recording errors may cancel out, but it is possible that our data have unknown systematic errors that would not. In a study of measurements of hardwood forests of Europe, it was found that the variation in height and diameter measure-

ments was highest in the smallest trees, which contribute only a small amount to the overall biomass of the stand (Auclair 1986). In addition, the error in measurement of height increased with the height of a tree, especially for the tallest trees whose tops were hard to see clearly. The bias introduced, however, was that height was systematically overestimated for these trees, which would lead to an overestimation of biomass. Thus, if such an error exists in our data, our estimates are too high.

One purpose of our biomass studies was to develop a method to obtain accurate estimates of biomass over very large areas that is simple, fast, and inexpensive, based on the method of survey sampling. This method is commonly used to obtain information about populations that would otherwise be physically impossible or too costly to obtain. We applied and modified the method for forests by beginning with a relatively simple forest, the North American boreal forest. While our estimate was based on a very sparse sample, the results were consistent with those of Bonner (1985) in a study that used thousands of sample plots located throughout Canada (Botkin & Simpson 1990a). Although the estimate by Bonner (1985) represents a valuable advance over previous analyses, because it included thousands of plots, these plots were part of many unrelated studies lacking a single statistical sampling design, and do not provide a statistically valid estimate of error. Our methods give similar results, but provide an estimate of sampling error and can be gathered by 20 people, each working a total of 6 months in the field. This method makes it feasible to obtain useable global measures of biomass at a reasonable cost in a short period of time.

The differences between ours and previous estimates have important implications for the global carbon budget. First, the amount of carbon released to the atmosphere is typically calculated by multiplying some estimate of forest biomass density by the area cleared (e.g. Houghton et al. 1987; Melillo et al. 1988). If our estimate of biomass density is substituted in those analyses, then the estimate of the present flux of carbon from forests to the atmosphere will be cut at least in half.

The potential of massive reforestation as a means to sequester carbon dioxide from the atmosphere is frequently discussed as a means to reduce the buildup of this greenhouse gas and slow the rate of global warming (Rosenfeld & Botkin 1990). International negotiations between nations that produce large amounts of carbon dioxide through burning of fossil fuels and nations with the potential to plant large areas of forest are one indication of the interest in this process. Determining the amount of carbon stored and the rate at which forests release and sequester carbon is important for understanding the potentials of such uses of forests.

Accurate estimates of carbon storage are also necessary to determine

the fate of 'missing carbon' — carbon added to the atmosphere by burning fossil fuels, but not accounted for by presently understood processes (Broecker et al. 1979). The most recent effort to account for the missing carbon is based on many forest inventories using different methods with no estimates of error (Kauppi et al. 1992).

The methods used in our study are comparatively fast and efficient. We hope that the methods we have applied in North America will be used elsewhere, and that eventually a program of global monitoring of carbon storage, using such methods, can be put in place.

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