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SPATIAL PATTERNS OF ABOVEGROUND PRODUCTION AND MORTALITY OF WOODY BIOMASS FOR EASTERN U.S. FORESTS

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Abstract. We developed maps of aboveground production and mortality of woody biomass for forests of the eastern United States based on data collected from an extensive network of permanent plots remeasured by the U.S. Forest Service Forest Inventory and Analysis units (FIA). Forest volume inventory data for growth and mortality were converted to units of aboveground biomass at the county level for hardwood and softwood forest types. Aboveground production of woody biomass (APWB) for hardwood forests ranged from 0.6 to 28 $Mg \cdot ha^{-1} \cdot yr^{-1}$ and averaged 5.2 $Mg \cdot ha^{-1} \cdot yr^{-1}$. For softwood forests, APWB ranged from 0.2 to 31 $Mg \cdot ha^{-1} \cdot yr^{-1}$ and averaged 4.9 $Mg \cdot ha^{-1} \cdot yr^{-1}$. Aboveground production of woody biomass was generally highest in southeastern and southern counties, mostly along an arc from southern Virginia to Louisiana and eastern Texas. Although this pattern is generally the result we would expect from the general climatic gradients of the region, it was confounded by the effects of different forest management intensities. No clear spatial pattern of mortality of woody biomass (MWB) existed, except for a distinct area of high mortality in South Carolina due to Hurricane Hugo in 1989. For hardwood forests, MWB ranged from 0 to 15 $Mg \cdot ha^{-1} \cdot yr^{-1}$ and averaged 1.1 $Mg \cdot ha^{-1} \cdot yr^{-1}$. The average MWB for softwood forests was 0.6 $Mg \cdot ha^{-1} \cdot yr^{-1}$ with a range of 0–10 $Mg \cdot ha^{-1} \cdot yr^{-1}$. The rate of MWB on an aboveground biomass basis averaged $<$1%/yr for both hardwood and softwood forests. A first-order carbon budget (the sum of the net change in carbon storage in all live trees, dead wood, and long-lived wood products) shows that eastern U.S. forests accumulated $\sim$174 Tg C/yr during the late 1980s and early 1990s. Although the root and soil pools are not included in this budget, it is likely that the forests are accumulating carbon in these components too, because the eastern forests are for the most part in various stages of regrowth and recovery from past human land uses and active forest management.

Key words: aboveground net primary production; biomass; biomass expansion factors; carbon budgets; forest inventories; hardwood forests; mortality; spruce–fir forests, United States.

Introduction

The global carbon cycle is recognized as one of the major biogeochemical cycles regulating the concentration of atmospheric CO_2, an important greenhouse gas (GHG) contributing to climate change (Schimel et al. 1995). Forests in turn play an important role in the global carbon cycle because they store large quantities of carbon in vegetation and soil, exchange large quantities of carbon with the atmosphere through photosynthesis and respiration, become sources of atmospheric carbon when they are disturbed by human or natural causes, become atmospheric carbon sinks during regrowth after disturbance, and can be managed to alter the magnitude and direction of their carbon fluxes (Brown et al. 1996). The Kyoto Protocol, which resulted from the 1997 meeting on climate change, established greenhouse gas (GHG) emission targets and commitment periods for industrialized countries (Annex 1 Parties of the UN Framework Convention on Climate Change); several forestry activities are being considered to offset carbon emissions in the commitment period to meet agreed targets. This Protocol clearly affirms the importance of increasing our understanding of forest carbon budgets and the factors that influence them, particularly at larger scales, to better determine the contribution of forests for meeting national GHG emissions targets.

The present and potential future role of forests in national carbon budgets is largely a result of past and present use and disturbance regimes of forest lands. In the eastern United States, there has been a long history of forest clearing, forest management, and disturbance. Virtually all of the forests in the eastern United States have been altered by humans to some degree at some time in the past (Perlin 1991, Whitney 1994). Today, many of these forests are recovering from past agricultural use and are actively managed. Thus, the resulting forest landscape is dominated by forests at dif-

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ferent stages of recovery (Brown et al. 1997) and with different carbon budgets.

Two key processes of forest carbon budgets are net primary production (NPP) and tree mortality. Both NPP and mortality change over time as stands develop. Net primary production, the difference between photosynthesis and plant respiration, is largely a function of growing conditions and age or stage of forest development. Net primary production of organic matter is allocated to aboveground accumulation of wood in standing live trees, the production of short-lived tissues such as leaves, fruits, and flowers, and the belowground accumulation and production of coarse and fine roots. Mortality depends on the rate and stage of stand development and frequency of disturbance (Peet and Christensen 1987, Harcombe et al. 1990). Trees die for a variety of complex and interacting reasons, including competition, suppression, old age, disease, disturbances like wind and fire, and other environmental stressors (Franklin et al. 1987, Lugo and Scatena 1996). Tree mortality is a key process in nutrient cycling and the dynamics of organic matter accumulation or loss (Waring and Schlesinger 1985).

Most estimates of NPP in forests are generally made for the aboveground components only; very few studies have included measurements of coarse and fine root production. Aboveground NPP (ANPP) estimates are often based on the summation of the net production of woody biomass (i.e., net increase in biomass of living trees) and the production of fine litter (Whittaker and Woodwell 1968). The net production of woody biomass is estimated from a combination of either tree remeasurements in permanent plots or from reconstruction of earlier diameters from tree cores and allometric regression equations. Reliable data on tree death or mortality must be obtained from remeasurements on permanent plots over many years because of their random nature and high year-to-year variability (Harmon et al. 1993). Tree death is then converted to mass estimates in a manner similar to that used for estimating live biomass increment.

Ecological studies in temperate forests have focused mostly on estimating ANPP based on measurements in relatively few and small ($<$1 ha) plots, usually located in mature forests (e.g., Whittaker 1966, DeAngelis et al. 1981), and not selected in a statistically valid manner from the population of interest. There are few published studies of tree mortality, expressed on a mass basis, for temperate forests (Franklin et al. 1987), and like NPP studies, these do not reflect forests at the larger scale. It has been shown for forest biomass studies that such approaches tend to give an unrealistic picture of the distribution of actual forest biomass over larger scales (McCune and Menges 1986, Brown and Lugo 1992, Brown et al. 1999). We propose that ecological studies of ANPP and mortality follow the same trend as for biomass, and that our understanding of their present patterns and magnitude in temperate forests may be distorted.

Data from ecological studies are not representative nor numerous enough to provide unbiased estimates of ANPP and mortality at scales suitable for questions related to global change. Instead, the ideal approach for estimating ANPP and mortality would be to use relevant data from a statistically designed, extensive system of permanent remeasurement plots. Such data are collected on a regular basis as part of national forest inventories of timberland areas and timber volumes by many countries, particularly industrialized ones. In the United States, forest inventory data are collected by the U.S. Forest Service, Forest Inventory and Analysis units (FIA). Among the data that the FIA reports are the timber volume of average net annual growth, annual mortality, and annual removals due to harvesting or other silvicultural operations over given time periods. We have developed methods to convert timber volume to total aboveground biomass (Schroeder et al. 1997) that can be used with these reported data to estimate aboveground production and mortality of woody biomass in live trees. Similar forest inventory data have been used successfully to produce spatially explicit estimates of biomass density (biomass per unit area) and pools (total standing crop) for forests of the eastern U.S. (Brown et al. 1999).

Geographically referenced analyses of ANPP and mortality are useful to (1) understand and predict the consequences of large-scale phenomena like global climate change, and (2) provide a data base for verification of regional and continental-scale ecosystem models (e.g., CENTURY, Parton et al. 1988; MAPSS, Neilson et al. 1992; BIOME, Prentice et al. 1992). However, characterizing important forest attributes at suitable spatial scales has proven to be difficult. The use of remote sensing techniques has been investigated for estimating forest biomass, but as yet this approach has met with little success for multiage, multispecies forests, and only with limited success for forests with few species and age classes (Wu and Strahler 1994, Hall et al. 1995). Detecting growth or changes in the size of the forest biomass pool with these techniques would be even more difficult.

The main goals of this study were to use the extensive FIA data base for the forests of the eastern United States to (1) determine the magnitude and patterns of aboveground production of woody biomass (APWB), which is a key component of ANPP, and mortality of woody biomass (MWB) for hardwood and softwood forests, and (2) produce geographically referenced estimates of APWB and MWB for hardwood and softwood forests at the county scale of resolution. We focus on the eastern U.S. forests because the data set for this part of the country is consistent and complete, and is readily available from the World Wide Web.

METHODS

The data base and general approach

Our analysis was based on forest inventory data that we downloaded directly from the FIA's World Wide Web site.[4] We acquired data for each county (~1950) in 28 eastern U.S. states (data for four northeastern states were not available on-line at the time we conducted our analysis) that consisted of estimates of area of timberland, growing-stock volume, average net annual growth and mortality of growing-stock volume, and average annual removal of growing-stock volume by harvest, all organized by forest type and stand size class (seedling/sapling, poletimber, and sawtimber stands).

Timberland is defined by the Forest Service as land producing or capable of producing in ''excess of 20 cubic feet per acre per year (or $\sim$1.4 $m^3 \cdot ha^{-1} \cdot yr^{-1}$) of industrial roundwood products.'' With respect to the eastern United States, timberland according to this definition accounts for 94% of all forest land (or 145 million ha out of a total of 154 million ha; Powell et al. 1993). Of the forest lands not included, about 3% are wilderness areas, parks, and other lands withdrawn from use for timber by statute or administrative regulation (mostly in the states of New York, Pennsylvania, and Minnesota) and 3% are forest lands of low primary production such as post oak and blackjack oak forests in Texas and Oklahoma (Powell et al. 1993). The Forest Service defines growing-stock volume as the net outside bark volume of growing-stock trees at least 12.5 cm in diameter to a point where the top diameter of the central stem is at least 10 cm, or to the point where the central stem breaks into limbs. Details of field data collection, subsequent manipulation, and the FIA data base itself are available at the World Wide Web site or by referring to Birdsey and Schreuder (1992) and Hansen et al. (1992).

Once the data were downloaded, our analysis consisted of (1) aggregating the data for all of the forest types into three broad forest categories (hardwoods, pines, and spruce–fir) by three stand-size classes (sawtimber, poletimber, and seedling/sapling), (2) developing biomass expansion factors (BEFs) to convert volume to biomass estimates, (3) applying the BEFs to estimate biomass of the average net annual change in growing stock and mortality, (4) estimating annual APWB, a component of ANPP, and MWB, (5) aggregating the pine and spruce–fir results to produce an estimate for all softwoods that was comparable to the estimate for all hardwoods, and (6) processing all of the county-level results within a geographic information system (GIS) for mapping.

Development of biomass expansion factors (BEF)

A key step in our approach is the development of BEFs (units of Mg/m^3), where BEFs are calculated as follows:

[4] URL: ⟨http://www.srsfia.usfs.msstate.edu/scripts/ew.htm⟩.

BEF = [total aboveground biomass of all living trees to a minimum diameter at breast height of 2.5 cm] ÷ [growing-stock volume].

The BEFs make it possible to convert an extensive forest volume inventory data base to biomass estimates. We aggregated the data base into three broad forest categories because it was not practical to attempt to formulate BEFs for every forest type in the eastern United States. In a previous study (Schroeder et al. 1997), we developed BEFs for hardwoods that were based on two forest types: oak–hickory and maple–beech–birch. Together these two forest types occupy approximately 70×10^6 ha and account for nearly half of all hardwood forests in the eastern United States. Because these forest types are so extensive, and because there was no significant difference between individual BEF functions for these two forest types, our earlier study concluded that a single pooled function was probably applicable to other hardwood forest types as well. Pine and spruce–fir forests are dissimilar enough, however, that we assumed, and subsequent analysis confirmed, that they should be analyzed separately.

Our previous study (Schroeder et al. 1997) presented a general approach to convert growing-stock volume to total aboveground biomass of all living trees (commercial and noncommercial species) for hardwood forests. Our approach accounted for noncommercial tree species, nonmerchantable commercial tree species (e.g., cull trees), noncommercial tree components (branches, twigs, and leaves), and all trees of diameter $\geq$2.5 and $<$12.5 cm, and reliably estimated aboveground biomass density of the tree component (AGBD, megagrams per hectare) directly from growing stock volume density (cubic meters per hectare). For hardwood forest types, Schroeder et al. (1997) found that BEF was a function of growing-stock volume (GSV):

$$\mathrm{BEF} = \exp\{1.912 - 0.344 \times \ln \mathrm{GSV}\} \qquad (1)$$

($r^2 = 0.85$, $n = 208$, 1 SE $= 0.109$). Biomass expansion factors decrease with increasing GSV, a pattern consistent with theoretical expectations. At high GSV, the slope approaches zero, beyond which point the BEF approaches a constant (Brown and Lugo 1992, Schroeder et al. 1997). We used Eq. 1 in the current study to convert volume estimates to aboveground biomass for the aggregated hardwood forest type. For growing-stock volume $>$200 m^3/ha, we used a constant BEF of 1.0.

We used the same methodology as Schroeder et al. (1997) to develop BEFs for pine and spruce–fir forest types for the eastern United States. The first step was to develop two allometric regression equations for estimating tree biomass as a function of diameter by pooling data from numerous pine and spruce–fir species. We assembled data from 11 published studies for eastern U.S. pine and spruce–fir forests. These data included diameter and aboveground oven-dry biomass

TABLE 1. Regression equations (untransformed) developed to estimate oven-dry tree biomass (kg) from tree diameter (cm).

Trees	Regression equation (Biomass =)	R^2	n	Diameter (cm) Minimum	Maximum	Mean
Pine†	$0.887 + \frac{10486\text{dbh}^{2.84}}{\text{dbh}^{2.84} + 376907}$	0.98	137	0.6	56.1	18.5
Spruce–fir‡	$0.357 + \frac{34185\text{dbh}^{2.47}}{\text{dbh}^{2.47} + 425676}$	0.98	83	2.9	71.6	18.4

† *Sources:* Baker 1962, Clark and Taras 1976, Howard 1973, Monk 1966, Nelson and Switzer 1975, Saucier and Boyd 1982, Vaidya 1961, Williams 1989.
‡ *Sources:* Sollins and Anderson 1971, Whittaker and Woodwell 1968, Woods et al. 1991.

for 137 trees and five pine species, and 83 trees and three spruce and fir species. Schroeder et al. (1997) evaluated a variety of regression models commonly used for biomass data on the basis of prediction errors, residual analysis, logical behavior of the models, r^2, and simplicity of the models. They found that for both hardwood and softwood species, log-transformed, nonlinear half-saturation functions performed best. Because the subsequent models conformed well to the above criteria, we used the same type of functions in this study (Table 1).

The two regression equations in Table 1 were applied to aggregated stock and stand table data (volume per hectare and number of trees per hectare, respectively, by 5 cm wide diameter classes) for loblolly/shortleaf pine and spruce–fir forest types that occur across much of the eastern United States. The aggregated stand tables were derived from the FIA forest inventory data by aggregating tree-level data to the scale of an inventory unit that comprises several counties within a state. Each inventory unit reported results for three aggregated stand-size classes: sawtimber, poletimber, and seedling/sapling. (See Schroeder et al. 1997 for a detailed description of the compilation of aggregated stand table data.) For the pine forest type, we assembled a total of 174 aggregated stock and stand tables, and for spruce–fir we assembled 49 aggregated stock and stand tables, both data sets representing a wide range of geographical distribution. The biomass regression equations were then used to estimate aboveground biomass of all living trees in each diameter class. Then volume and aboveground biomass were summed across all diameter classes, and the ratio of aboveground biomass to volume gave a BEF for each aggregated stock/stand table (Fig. 1). Because the stock/stand table data were aggregated from a number of plots over large areas, these BEFs represent regional factors derived from regional samples.

The relationship between BEF and GSV for spruce–fir showed the same type of pattern as observed for hardwood forest types (Schroeder et al. 1997). The BEFs ranged from a high of >2.0 Mg/m^3 for low growing-stock volumes (<40 m^3/ha) to a low of 1.0 Mg/m^3 for the highest growing-stock volume of 158 m^3/ha (Fig. 1). This relationship also conformed to theoretical expectations and we were able to fit the following function to it:

$$\text{BEF} = \exp\{1.771 - 0.339 \times \ln \text{GSV}\} \qquad (2)$$

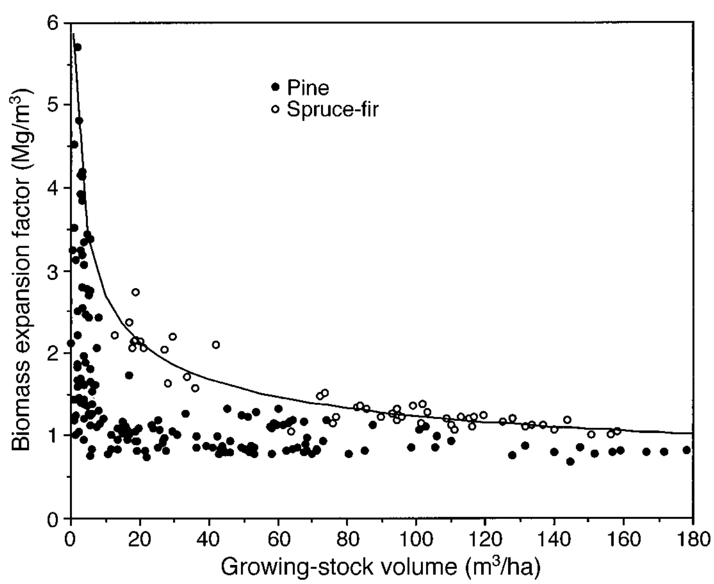

FIG. 1. Biomass expansion factor (BEF) as a function of growing-stock volume for loblolly/shortleaf pine and spruce–fir forest types. The BEF (Mg/m^3) is the ratio of aboveground biomass density (AGBD; megagrams per hectare) for all trees with a minimum diameter of 2.5 cm to growing-stock volume (cubic meters per hectare).

($r^2 = 0.88$, $n = 49$, 1 SE $= 0.095$). As for hardwood forests, the BEF approaches a constant at higher GSV. For GSV > 160 m^3/ha we used a constant BEF of 1.0.

For the pine forest type, BEFs ranged from 5.7 to 1.3 Mg/m^3 for stands with a GSV of <5 m^3/ha, then decreased rapidly to a range of <1.3–0.7 Mg/m^3 for stands with GSV > 5 to ~180 m^3/ha (Fig. 1). As no significant relationship was obtained, we used the following median BEFs for the indicated GSV categories:

$$\text{GSV} < 10 \text{ m}^3/\text{ha} \qquad \text{BEF} = 1.68 \text{ Mg/m}^3 \tag{3a}$$

($n = 72$, 1 SE $= 0.13$),

$$\text{GSV} = 10\text{–}100 \text{ m}^3/\text{ha} \qquad \text{BEF} = 0.95 \tag{3b}$$

($n = 86$, 1 SE $= 0.02$),

$$\text{GSV} > 100 \text{ m}^3/\text{ha} \qquad \text{BEF} = 0.81 \tag{3c}$$

($n = 16$, 1 SE $= 0.03$).

We used these BEF constants for all pine forest types. Because of the general similarity of pine forests in the eastern United States and their common structural characteristics and branching patterns, we assumed that they would have similar BEFs. The only other comparable analysis of pine data that we are aware of (Brown 1997) also found no relationship between GSV and BEF, which further demonstrates the similarity of pine forests.

Conversion of volumes to biomass

The data on average net annual growth and mortality in growing stock from the FIA web site were expressed as annual average wood volumes, in cubic per hectare per year, for the interval between two inventories, generally a period of 6–23 yr, and on average 12 yr for the eastern United States (Table 2). We used Eqs. 1–3 to calculate an average BEF for each forest category (hardwood, pine, or spruce–fir) by stand-size class for each county that was based on GSV density at the time of both the current and previous forest inventories. We calculated GSV density for the three forest categories by stand-size class (maximum of nine combinations) in every county at the time of the current inventory, by dividing GSV by the area of timberland. The GSV density at the time of the earlier inventory was not reported on the web site, so we had to derive this by simple calculations. We calculated GSV density at the time of the earlier inventory by multiplying the average net annual growth and mortality in growing stock by the number of years between the two inventories, and then adjusted the current GSV density accordingly. Although the relationship between BEF and GSV was nonlinear for hardwood and spruce–fir forests (Fig. 1), the difference between the GSV for the current and previous inventory for any forest category and stand-size class combination was sufficiently small that we believed it was reasonable to assume linearity for that segment of the relationship, and averaged the two BEFs. We applied the average BEFs to the net annual growth and mortality of GSV to convert them to estimates of biomass. All estimates of biomass for net annual growth and mortality of growing stock for the three stand-size classes were reaggregated, based on their area distribution, resulting in area-weighted averages for each forest category and county.

TABLE 2. Dates of current and previous inventory.

State	Previous inventory	Current inventory
Alabama	1981	1990
Arkansas	1988	1995
Delaware	1970	1986
Florida	1987	1995
Georgia	1982	1989
Illinois	1962	1985
Indiana	1966	1986
Iowa	1973	1990
Kentucky	1975	1988
Louisiana	1983	1991
Maine	1979	1995
Maryland	1975	1986
Michigan	1980	1993
Minnesota	1977	1990
Mississippi	1987	1994
Missouri	1971	1989
New Jersey	1971	1987
New York	1978	1993
North Carolina	1983	1990
Ohio	1977	1991
Oklahoma	1986	1993
Pennsylvania	1975	1989
South Carolina	1986	1993
Tennessee	1979	1989
Texas	1986	1992
Virginia	1984	1992
West Virginia	1973	1989
Wisconsin	1983	1996

Estimation of aboveground production and mortality of woody biomass

We used the biomass estimates of average net annual growth and mortality to calculate a major component of ANPP, i.e., the accumulation of live aboveground woody biomass over a given time interval or APWB. Strictly speaking, our estimate of the accumulation of live aboveground woody biomass based on the BEFs does include accumulation of biomass in leaves. However, this is such a small component of the aboveground production of biomass in closed-canopy forests ($<1\%$ of the total) that for practical purposes we refer to it as woody biomass. The FIA data base reports the average net annual growth in GSV for the time between two successive inventories, that is defined by the U.S. Forest Service as:

$$\begin{aligned}\text{Net annual growth in GSV}\\ &= \text{gross annual growth of GSV}\\ &\quad - \text{annual natural mortality of GSV.}\end{aligned} \tag{4}$$

The average gross annual growth of GSV, converted to units of mass, is the APWB or that component of ANPP that we need to estimate. The gross annual

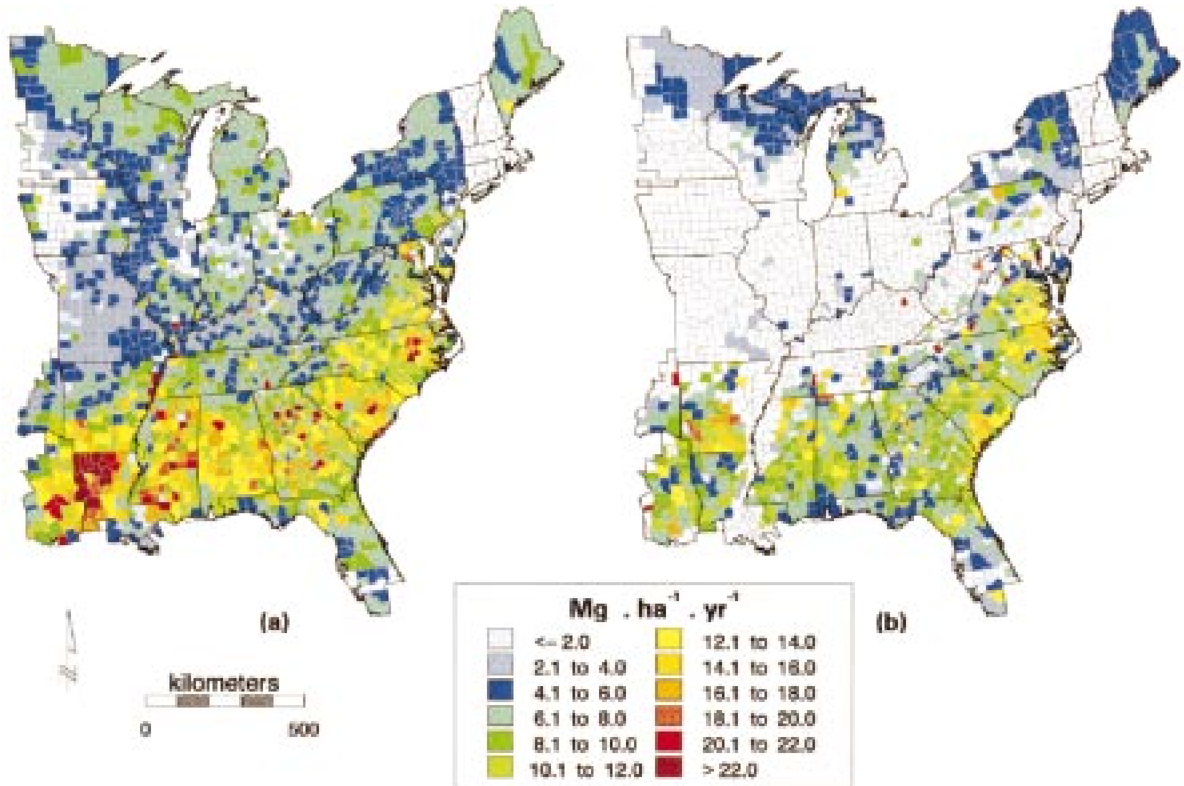

Fig. 2. Map of aboveground production of woody biomass for (a) hardwood and (b) softwood forests of the eastern United States. Counties with no color are those for which data are missing.

growth of GSV includes growth of surviving trees, ingrowth (volume of trees reaching 12.5 cm dbh during the period), growth on ingrowth, and growth on mortality and removals (Birdsey and Schreuder 1992). Annual growth of mortality and removals is modeled for that portion of the inventory interval for which they are estimated to have survived.

Although gross annual growth of GSV is measured by the U.S. Forest Service, it is not reported on their web site. We estimated average annual APWB by rearranging Eq. 4 as follows, after converting the volumes to biomass (all units in megagrams per hectare per year):

$$\text{APWB} = \text{net annual growth in woody biomass} + \text{annual mortality of woody biomass.} \quad (5)$$

Aboveground production of woody biomass was estimated for all counties and forest categories according to Eq. 5. No further manipulation of the data was required for mortality. We then aggregated all results for pine and spruce–fir forest types to produce overall estimates for softwood forest types.

Aboveground production and mortality of woody biomass were mapped at the county scale of resolution. The maps were produced and displayed using version 7.0 of ARC/INFO geographic information system software from Environmental Systems Research, Incorporated, Redlands, California, USA. The Albers conic equal-area projection was used with standard parallels of 9°30′ and 45°30′, the central meridian at −96° and the latitude of origin at 23°.

Error estimation

The FIA uses a statistically based sampling scheme designed to provide growing-stock volume estimates with a sampling error of 5% for 28.3×10^6 m^3, and forest area estimates with a sampling error of 3% for $0.4 \times$ ha (N. Cost, U.S. Forest Service, *personal communication*). Larger forest areas and volumes have smaller relative standard errors, and vice versa. For the southeastern United States, for example, analyses of measurement error, sampling error, and regression error indicated that the annual change in growing-stock volume over the 6–8 yr period between inventories had a 95% confidence interval of ±10% (D. L. Phillips, S. L. Brown, P. E. Schroeder, and R. A. Birdsey, *unpublished manuscript*); we expect that the annual change in biomass would have a somewhat higher confidence interval than this due to an increase in the regression error (Clark et al. 1986). The sampling error was the largest component of the total error in this example, accounting for 87% of the total. Analysis of the data at the county level, as done in this paper, would result in a larger confidence interval, mostly due to the increase in sampling error at this smaller scale. For example, the sampling errors for volume growth at the state level for Virginia and North Carolina (1.3 and 1.2%, respectively), increase by about an eight-fold factor or more at the county level (Brown 1993, Thompson and Johnson 1994). How the various sources of error compound into total error for production and mortality of woody biomass at the county level is not known, and clearly indicates an area of research deserving more attention.

RESULTS

Aboveground production of woody biomass (APWB)

Highest rates of APWB for hardwood forests (>6 $Mg \cdot ha^{-1} \cdot yr^{-1}$) generally occurred in the southeastern to southern U.S. counties, along an arc from southern Virginia to Louisiana and east Texas (Fig. 2a). High rates also occurred in the southern counties of Illinois and several counties of Ohio. Aboveground production of woody biomass was generally lowest (<3 $Mg \cdot ha^{-1} \cdot yr^{-1}$) for hardwood forests in the midwestern and north-central states of Iowa, Missouri, and southern Minnesota. And, intermediate APWB (3–6 $Mg \cdot ha^{-1} \cdot yr^{-1}$) were found for the northern tier of states stretching from Minnesota to Maine. This pattern is generally what we would expect resulting from transitions of more favorable to less favorable growing conditions along the south to north climatic gradient; however, the effects of different forest management intensities appear to confound this general climatic gradient.

Aboveground production of woody biomass for hardwood forests at the county level ranged from 0.6 to 28 $Mg \cdot ha^{-1} \cdot yr^{-1}$, with an area-weighted mean of 5.2 $Mg \cdot ha^{-1} \cdot yr^{-1}$. About 46% of all counties had an APWB of >4 to 6 $Mg \cdot ha^{-1} \cdot yr^{-1}$ (Fig. 3a). Only about 2.5% of the counties had biomass increments of >10 $Mg \cdot ha^{-1} \cdot yr^{-1}$, and these were located mostly in the southern part of the region.

The spatial distribution of APWB for softwood forests was generally similar to that for hardwoods, and once again tends to show the interaction between the effects of different management intensities and climatic gradients (Fig. 2b). The highest rates of APWB were for counties in the south and southeast (>7 $Mg \cdot ha^{-1} \cdot yr^{-1}$), again the result of favorable growing conditions in those regions, as well as forest management. Several counties in the northern states had forests with relatively high APWB. However, softwood forests were less extensive and their APWB was generally lower than for hardwoods. Softwood forests do not occur in most of the central section of the eastern U.S., from West Virginia to Missouri, Iowa, and southern Minnesota.

For softwood forests, the range of APWB was 0.2–31 $Mg \cdot ha^{-1} \cdot yr^{-1}$ and the area-weighted mean was 4.9 $Mg \cdot ha^{-1} \cdot yr^{-1}$. In general, the APWB for softwood forests tended to be lower than that for hardwoods, in that about 48% of the counties had APWB of >2 to 5 $Mg \cdot ha^{-1} \cdot yr^{-1}$ (Fig. 3b). Only 3% of the counties had APWB of >10 $Mg \cdot ha^{-1} \cdot yr^{-1}$, and these were scattered throughout much of the softwood forest region.

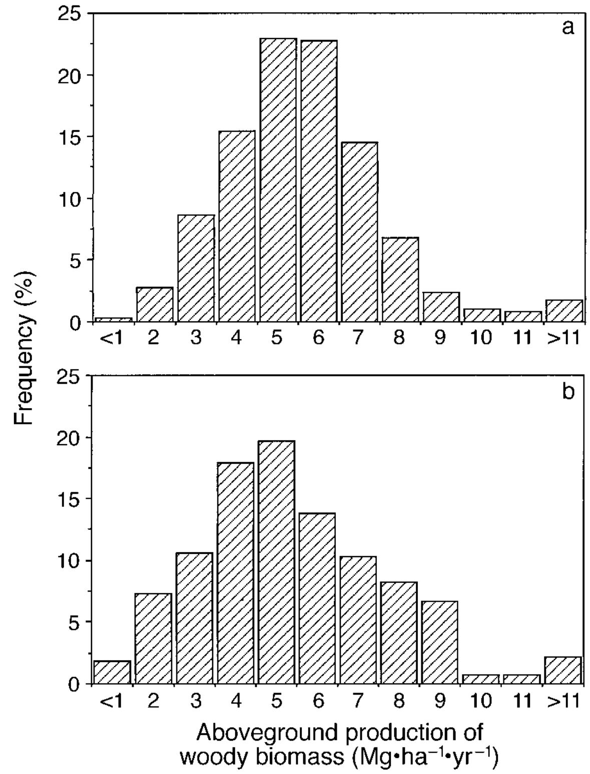

FIG. 3. Frequency distribution of aboveground production of woody biomass (APWB) for (a) hardwood and (b) softwood forests of the eastern United States. The values along the horizontal axes are the upper limits of the APWB class.

Total APWB, the product of the annual per hectare values and area for the entire eastern US, was 522 Tg/yr for hardwood forests and 176 Tg/yr for softwood forests. The combined total for all forests in the eastern U.S. was 699 Tg/yr.

Mortality of woody biomass (MWB)

Rates of MWB for eastern hardwood and softwood forests generally ranged between 0.0 to 3.3 $Mg \cdot ha^{-1} \cdot yr^{-1}$, and the rates were less for softwoods than for hardwoods (Fig. 4). No clear spatial pattern emerged across the region. The exception was a distinct area of high MWB (>10 $Mg \cdot ha^{-1} \cdot yr^{-1}$) for both hardwoods and softwoods in South Carolina that undoubtedly was caused by Hurricane Hugo in 1989.

For hardwood forests, MWB ranged from 0 to 15 $Mg \cdot ha^{-1} \cdot yr^{-1}$ with an area-weighted average of 1.1 $Mg \cdot ha^{-1} \cdot yr^{-1}$. The area-weighted average MWB for softwood forests was 0.7 $Mg \cdot ha^{-1} \cdot yr^{-1}$, with a range of 0–10 $Mg \cdot ha^{-1} \cdot yr^{-1}$. Almost 60% of the counties had hardwood forests with MWB between 0.3 and 1.2 $Mg \cdot ha^{-1} \cdot yr^{-1}$ (Fig. 5a), whereas 47% of counties had

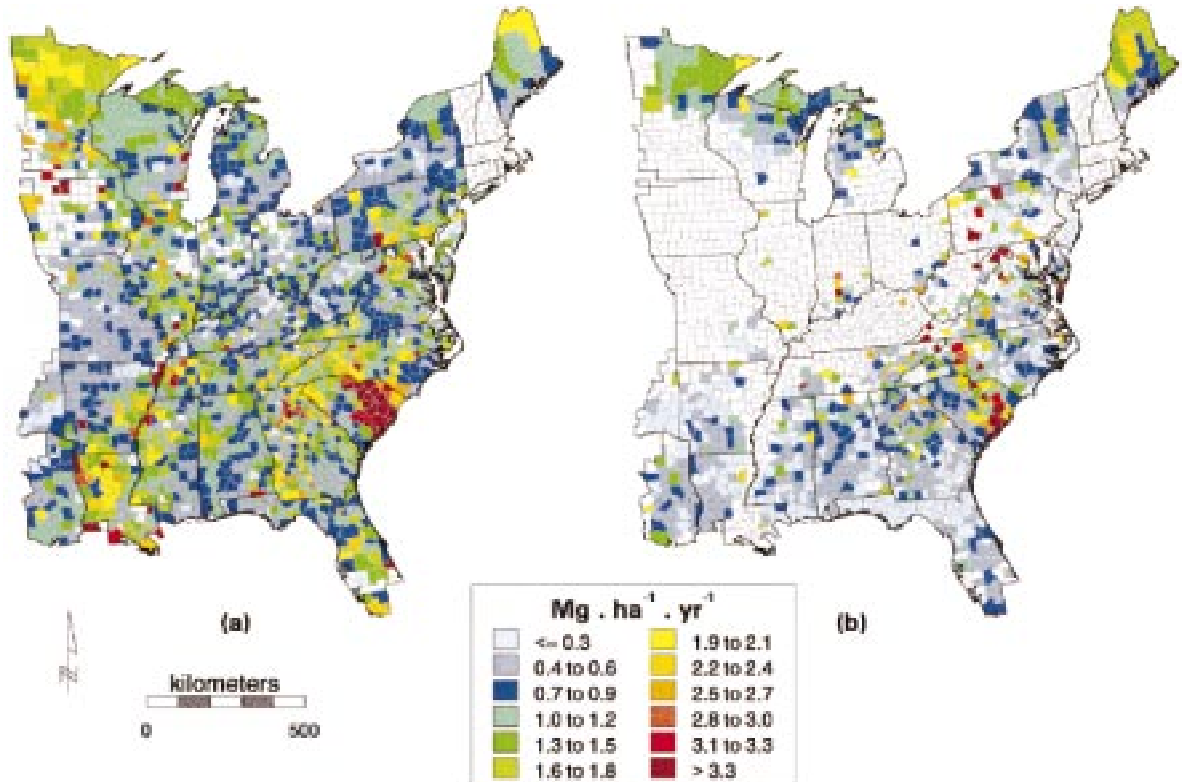

Fig. 4. Map of mortality of woody biomass for (a) hardwood and (b) softwood forests of the eastern United States. Counties with no color are those for which data are missing.

softwood forests with MWB <0.3 $Mg \cdot ha^{-1} \cdot yr^{-1}$ (Fig. 5b). Only 20% of counties had softwood MWB of >0.9 $Mg \cdot ha^{-1} \cdot yr^{-1}$, but nearly half of all counties had hardwood MWB of that magnitude.

Total MWB for the eastern U.S. was 138 Tg/yr, or about 20% of the total APWB. Hardwoods accounted for 81% of the total (112 Tg/yr) and softwoods for the remaining 19% (26 Tg/yr).

As a percentage of AGBD, MWB varied from 0 to 5%/yr for nearly the entire region, and averaged $<1\%$/yr for both hardwood and softwood forests. A total of 16 counties had MWB rates of >5 to 15%/yr. Most of these were in South Carolina (56%), but some were also scattered throughout the region.

Discussion

Aboveground production and mortality of woody biomass in relation to forest development

We have shown in earlier work that for mixed-age eastern hardwood forests, AGBD is a useful surrogate measure for stage of forest development (Brown et al. 1997). Forests in a regeneration stage had AGBD of <75 Mg/ha, those in an intermediate recovery stage of 80 to 150 Mg/ha, those in advanced recovery stage of 150 to 200+ Mg/ha, and those in the mature to old-growth stage of >250 Mg/ha. To investigate how APWB and MWB vary with stage of forest development, we plotted each of these two variables against corresponding county-level estimates of AGBD for the recent inventory (Brown et al. 1999). We first divided the data set into two zones: cool temperate forests in the north and warm temperate forests in the south (based on a life zone map of the United States; Lugo et al., *in press*).

Although no significant relationships were obtained between APWB and AGBD, several trends are evident (Fig. 6). First, the range in values of APWB for the cool temperate hardwood and softwood forests are similar to each other ($\sim$0.5–10 $Mg \cdot ha^{-1} \cdot yr^{-1}$, Fig. 6a and c). Aboveground production of woody biomass is generally positively related to AGBD for cool temperate hardwood and softwood forests (Fig. 6a and c), with some indication of a leveling with increasing AGBD beyond $\sim$200 Mg/ha. This pattern of APWB vs. stand development does not fit the classical view of declining NPP after canopy closure (Waring and Schlesinger 1985). Rather, the aboveground woody component of NPP for these cool temperate forests appears to be increasing or at least stable, even at an advanced stage of recovery. However, inclusion of belowground production may change the pattern. Finally, based on the biomass groupings above, very few of the northern counties appear to contain mature or old-growth forests. However, we cannot rule out the possibility that

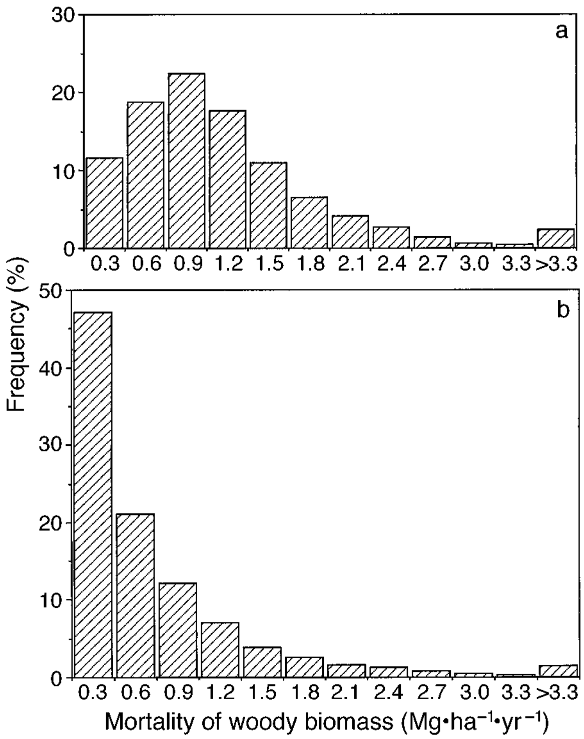

FIG. 5. Frequency distribution of mortality of woody biomass (MWB) for (a) hardwood and (b) softwood forests of the eastern United States. The values along the horizontal axes are the upper limits of the MWB class.

some old-growth forests exist in these northern counties; reporting of the results at the county level could mask the existence of some old-growth stands.

The range and variability in APWB for warm temperate hardwood and softwood forests is larger than for the northern cool temperate forests (Fig. 6b and d). And, like cool temperate forests, APWB is positively related to AGBD, with little evidence of a leveling of APWB, especially for softwood forests. The warm temperate forests are subject to fewer climatic limitations such as shorter growing season and cooler temperatures, and thus the effects of variability in soil types, moisture regimes, and management intensity are more evident. Most of the warm temperate hardwood forests seem to be in the intermediate stage of recovery, and to span the full range of APWB estimates (0.6–28 Mg/ha; Fig. 6b). The most variable pattern between APWB and AGBD is for warm temperate softwoods (Fig. 6d), which is most likely related to management intensity. For instance, many of the counties with forests of low AGBD (about 50 Mg/ha or less) had rates of APWB as high as those for more developed forests; over half of these forests had been harvested during the inventory period. Harvesting during the inventory interval would reduce AGBD as reported at the end of the interval, while at the same time provide conditions that enhance growth.

We also examined the relationship between MWB and AGBD and observed no trends (Fig. 7). As noted above (Fig. 4 and 5), MWB for softwoods was lower overall than for hardwoods. Softwood forests generally contained less biomass than hardwood forests (cf. Fig 7a and b), and were more intensely managed, so it is understandable that they would also exhibit lower levels of MWB.

Background mortality, that arising from the normal processes of stand dynamics and competition (Lugo and Scatena 1996), has been shown to be related to stand development (Franklin et al. 1987, Harcombe et al. 1990). Mortality expressed on the basis of number of stems dying has been shown to decrease with stand development (Franklin et al. 1987). However, mortality based on the amount of biomass dying has been shown to increase with stand age, particularly in the very late stage (Harcombe et al. 1990). At younger ages, when the number of trees dying is high, they are generally small, with little mass. As the forest ages, fewer trees die, but they are much larger and consequently contain more mass. We suspect that the lack of a relationship between background mortality and stand development, as measured by AGBD (Fig. 7), for eastern U.S. forests, is due to their relatively young stage of development and the lack of larger diameter trees (Brown et al. 1997).

Comparison with ecological studies

The APWB that we report is only one part of ANPP; estimates of the production of leaves, reproductive parts, and current year twigs, generally measured as fine litterfall, need to be added. From a summary of the literature on litterfall (E. Matthews, W. Post, E. A. Holland, and J. Sulzman, 1998, *personal communication*), we obtained the following rates for eastern U.S. forests: 4.5 ± 0.02 $Mg \cdot ha^{-1} \cdot yr^{-1}$ (mean ± 1 SE; n = 75) for hardwood forests, 4.0 ± 0.03 $Mg \cdot ha^{-1} \cdot yr^{-1}$ (n = 38) for pine forests, and 3.2 ± 0.05 $Mg \cdot ha^{-1} \cdot yr^{-1}$ (n = 12) for spruce–fir forests. We added these to the most common APWB classes (>3–7 and >2–6 $Mg \cdot ha^{-1} \cdot yr^{-1}$, for hardwood and softwood forests, respectively; Fig. 3) to arrive at the following range of estimates for ANPP: hardwoods, 7.5–11.5 $Mg \cdot ha^{-1} \cdot yr^{-1}$ with an area-weighted average of 9.7 $Mg \cdot ha^{-1} \cdot yr^{-1}$, and softwoods, 5.8–9.8 $Mg \cdot ha^{-1} \cdot yr^{-1}$ with an area-weighted average of 8.7 $Mg \cdot ha^{-1} \cdot yr^{-1}$. For many of the counties in the southern states (~13% of all eastern U.S. counties; cf. Fig. 3a), estimates of ANPP for hardwood forests range from 11.5 to 24.5 $Mg \cdot ha^{-1} \cdot yr^{-1}$.

Our estimates of ANPP are generally comparable, although the range is wider, to other published estimates based on ecological studies. For example, Whittaker (1966) and Whittaker et al. (1974) reported ANPP for nine hardwood forest types in the eastern U.S. (New Hampshire to Great Smoky Mountains, Tennessee); their estimates for the tree component ranged from 5.0 to 24.0 $Mg \cdot ha^{-1} \cdot yr^{-1}$, with an average of 10.2 $Mg \cdot ha^{-1} \cdot yr^{-1}$. Also for forests in the Great Smoky

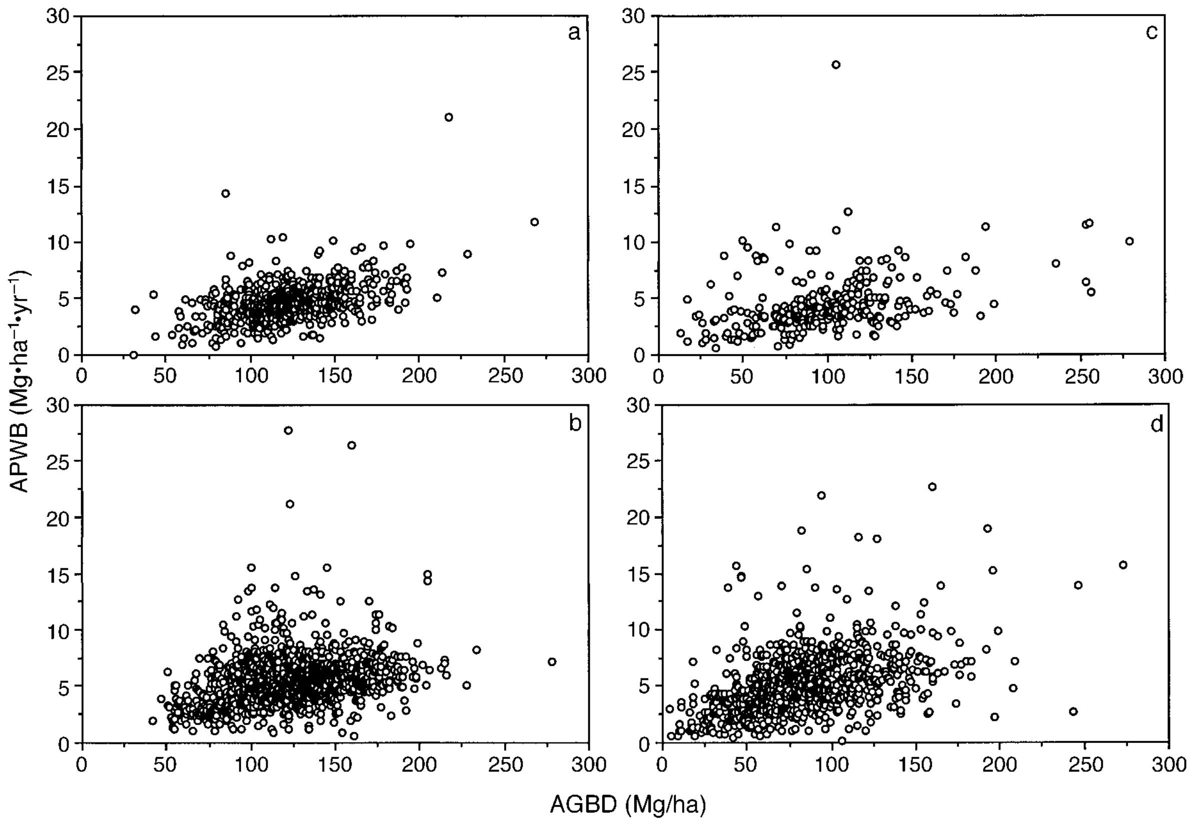

FIG. 6. Aboveground production of woody biomass (APWB) vs. aboveground biomass density (AGBD; county-level, area-weighted average for the most current inventory) for (a) cool temperate and (b) warm temperate hardwood and (c) cool temperate and (d) warm temperate softwood forests of the eastern United States.

Mountains, Busing et al. (1993) reported that ANPP averaged 12.2 $Mg \cdot ha^{-1} \cdot yr^{-1}$ for young (42–63-yr-old) hardwood stands, 8.3 $Mg \cdot ha^{-1} \cdot yr^{-1}$ for old-growth hardwood stands, and 8.8 $Mg \cdot ha^{-1} \cdot yr^{-1}$ for old-growth mixed hardwood–softwood stands. Whittaker (1966) reported ANPP estimates for pine and spruce–fir forests of 8.2–14.0 $Mg \cdot ha^{-1} \cdot yr^{-1}$ in the Great Smoky Mountains.

It is difficult to compare our MWB results with other studies in temperate forests because most other studies examined mortality in terms of numbers of stems, not biomass. For example, typical mortality rates on a tree density basis for temperate forests are 1–2%/yr (Weaver and Ashby 1971, Waring and Schlesinger 1985, Franklin et al. 1987, Parker 1989). These could be considered a background level of mortality, as opposed to catastrophic events like the hurricane that struck South Carolina, resulting in biomass-based mortality of 5–15%/yr. For mature, humid tropical forests, Carey et al. (1994) found that mortality rates based on biomass (0.1–3.9%/yr) were similar to the rates based on stems (0.5–3.3%/yr).

Implications for forest carbon budgets

From the above results it is tempting to construct a carbon budget for the aboveground components of eastern U.S. forests. Typically this has been calculated as the APWB minus MWB and removal of woody biomass by harvesting (e.g., Birdsey 1992). Performing such a calculation and converting our values to units of carbon (1 Mg biomass = 0.5 Mg C; Birdsey 1992) results in an estimated net accumulation of 72 Tg C/yr (APWB = 350 Tg C/yr, MWB = 69 Tg C/yr, and removal of woody biomass = 209 Tg C/yr). (The removal of woody biomass by harvesting, at the county scale, was estimated in the same manner as for APWB and MWB described in *Methods.*) Most of the net accumulation of carbon was in hardwood forests (73% of the total) because of the about three times larger extent of this forest category. The net accumulation of carbon in the eastern forests before harvesting was 281 Tg/yr, which is slightly larger than the 261 Tg/yr reported by Birdsey (1992) for approximately the same area (excludes the New England states but includes all of Texas).

There are however, problems with the simple budget approach, because it only tracks the net change in the carbon pool of living trees, and it implicitly assumes that the pool of dead wood and wood products does not increase during the interval period (i.e., all mortality and removals are decomposed or oxidized). Dead wood in temperate forests can in reality, take many decades to decompose, resulting in increases in the dead wood pool

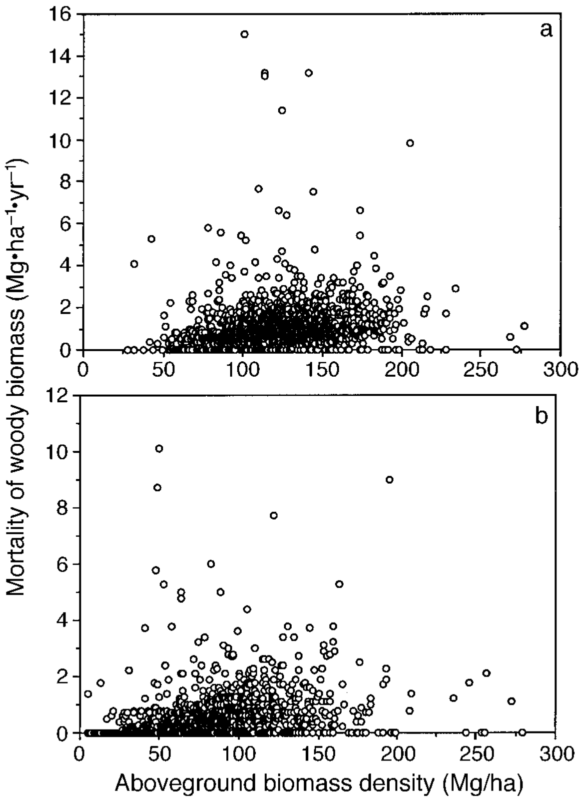

FIG. 7. Mortality of woody biomass (MWB) vs. aboveground biomass density (AGBD; county-level, area-weighted average for the most current inventory) for (a) hardwood and (b) softwood forests of the eastern United States.

over time (Harmon et al. 1986). During forest succession after disturbance, the dead wood pool at first decreases, and then increases until long after the aboveground vegetation matures. Mature vegetation will be composed of more trees of a larger diameter than at a younger stage. When these larger diameter trees die they will decompose more slowly because the larger the size of the woody debris, the slower it decomposes (Harmon et al. 1986). This could be a significant factor for the future of eastern hardwood forests as a carbon sink, because the forests are for the most part in younger stages of development (Brown et al. 1997).

Further, substantial quantities of slash and large debris that are often left in the forest after harvesting operations could also take a long time to decompose, depending upon their size, and other management activities such as site preparation. For the entire United States in 1990, Winjum et al. (1998) estimated that 33% of the pre harvested biomass was left as slash. Applying the 33% slash value to the biomass of removals from eastern U.S. forests (209 Tg C/yr) results in 70 Tg C/yr of slash, or about the same biomass as the natural mortality from these forests. Although clearly an important component of forest carbon budgets, it is amazing how poorly dead wood is treated in such budgets; current global carbon budgets essentially ignore it (Harmon et al. 1993).

After the wood is harvested, some goes into short-lived products, some into long-lived products, and some into waste. Long-lived wood products can be a carbon sink for the forest sector if the production of the products is greater than the emissions from the products already in use, often referred to as inherited emissions (Winjum et al. 1998). For the entire United States in 1990, Winjum et al. (1998) estimated that the increase in the long-lived wood product pool was 40 Tg C/yr.

From the results presented here, we constructed a first-order carbon budget, for aboveground components only, for eastern forests. The carbon budget is the sum of the change in the carbon pool of living trees, change in the carbon pool of dead wood, and change in the carbon pool of long-lived wood products. The change in the carbon pool of living trees is 72 Tg/yr. Of the total removals of wood by harvesting in the United States, 80% is from eastern forests (Birdsey 1992). We assume, therefore, that 80% of the change in the carbon pool in long-lived wood products, or 32 Tg C/yr, originates from eastern forests.

The change in the carbon pool of dead wood is the difference between the inputs of natural mortality and slash left behind after harvesting, and the outputs of decomposition of the dead wood pool. The inputs of natural mortality and slash are 69 Tg C/yr and 70 Tg C/yr respectively. The decomposition of dead wood is a function of the quantity of dead wood and its rate of decomposition. The amount of dead wood in eastern forests typically ranges from 10 to 20% of the aboveground biomass (Muller and Liu 1991, Turner et al. 1995). The total aboveground biomass carbon in eastern forests estimated from the FIA data base is 7690 Tg C (Brown et al. 1999). Thus, we estimate that the amount of dead wood in eastern forests is 769–1538 Tg C. Rates of decomposition of dead wood in eastern forests can range from 4 to 10%/yr or even higher, depending on how important fire is as a natural disturbance or in site preparation (Harmon et al. 1986, Turner et al. 1995). For our calculations here, we use an average rate of 6%/yr. Our estimate of the carbon flux from wood decomposition is 46–92 Tg C/yr, with a mid point of 69 Tg C/yr. Therefore, we estimate that the change in the carbon pool of dead wood is a gain of 70 Tg C/yr (range of 24 to 108 Tg C/yr). This increase in the dead wood pool is of similar magnitude to the increase in the live wood pool (i.e., in living trees). Although the calculation of the change in the dead wood pool is not as rigorous as the others budget components, the results suggest that dead wood is an important pool with respect to carbon storage and that it deserves more attention from the research and inventory community.

For our first-order carbon budget, we have a change in the carbon pool of living trees of 72 Tg C/yr. We have a change in the carbon pool of dead wood of 70 Tg C/yr. We have a change in the carbon pool of long-lived wood products of 32 Tg C/yr. Together, These add up to a total carbon pool change of 174 Tg C/yr. This net uptake of carbon by eastern forests represents about 13% of the carbon emissions from fossil fuel and cement manufacturing in the United States during the early 1990s (1.3 Pg C/yr; Marland et al. 1994). However, the net carbon uptake does not include changes in root and soil carbon pools. As the eastern forests are for the most part in various stages of regrowth and recovery from past and present human land uses such as agriculture and pasture, and forest management, it is likely that the forests are accumulating carbon in these missing components too.

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Literature Cited

Baker, J. B. 1962. Dry matter production in plantations of loblolly pine. Thesis. Duke University, School of Forestry, Durham, North Carolina, USA.

Birdsey, R. A. 1992. Carbon storage and accumulation in United States forest ecosystems. U.S. Forest Service General Technical Report **WO-59**.

Birdsey, R. A., and H. T. Schreuder. 1992. An overview of forest inventory and analysis estimation procedures in the eastern United States—with an emphasis on the components of change. U.S. Forest Service General Technical Report **RM-214**.

Brown, M. J. 1993. North Carolina's forests, 1990. U.S. Forest Service Resource Bulletin **SE-142**.

Brown, S. 1997. Estimating biomass and biomass change of tropical forests: a primer. FAO Forestry Paper 134, Food and Agriculture Organization, Rome, Italy.

Brown, S., and A. E. Lugo. 1992. Aboveground biomass estimates for tropical moist forests of the Brazilian Amazon. 1992. Interciencia **17**(1):8–18.

Brown, S., J. Sathaye, M. Cannell, and P. E. Kauppi. 1996. Management of forests for mitigation of greenhouse gas emissions. Pages 773–798 *in* R. T Watson, M. C. Zinyowera, and R. H. Moss, editors. Climate change 1995: impacts, adaptations and mitigation of climate change: scientific analyses. Contribution of Working Group II to the Second Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Brown, S., P. Schroeder, and R. Birdsey. 1997. Aboveground biomass distribution of US eastern hardwood forests and the use of large trees as an indicator of forest development. Forest Ecology and Management **96**:37–47.

Brown, S., P. Schroeder, and J. Kern. 1999. Spatial distribution of biomass in forests of the eastern USA. Forest Ecology and Management, *in press*.

Busing, R. T., E. E. C. Clebesch, and P. S. White. 1993. Biomass and production of southern Appalachian cove forests re-examined. Canadian Journal of Forest Research **23**: 760–765.

Carey, E. V., S. Brown, A. J. R. Gillespie, and A. E. Lugo. 1994. Tree mortality in mature lowland tropical moist and tropical lower montane moist forests of Venezuela. Biotropica **26**(3):255–265.

Clark, A., D. R. Phillips, and D. J. Frederick. 1986. Weight, volume, and physical properties of major hardwood species in the Piedmont. U.S. Forest Service Research Paper **SE-255**.

Clark A., III, and M. A. Taras. 1976. Biomass of shortleaf pine in a natural sawtimber stand in northern Mississippi. U.S. Forest Service Research Paper **SE-146**.

DeAngelis, D. L., R. H. Gardener, and H. H. Shugart, Jr. 1981. Productivity of forest ecosystems studied during IBP: the woodlands data set. Pages 567–672 *in* D. E. Reichle, editor. Dynamic properties of forest ecosystems. Cambridge University Press, New York, New York, USA.

Franklin, J. F., H. H. Shugart, and M. E. Harmon. 1987. Tree death as an ecological process. BioScience **37**:550–556.

Hall, F. G., Y. E. Shimabukuro, and K. F. Huemmrich. 1995. Remote sensing of forest biophysical structure using mixture decomposition and geometric reflectance modes. Ecological Applications **5**:993–1013.

Hansen, M. H., T. Frieswyk, J. F. Glover, and J. F. Kelly. 1992. The eastwide forest inventory database: users manual. U.S. Forest Service General Technical Report **NC-151**.

Harcombe, P. A., M. E. Harmon, and S. E. Greene. 1990. Changes in biomass and production over 53 years in a coastal *Picea sitchensis–Tsuga heterophylla* forest approaching maturity. Canadian Journal of Forest Research **20**:1602–1610.

Harmon, M. E., S. Brown, and S. T. Gower. 1993. Consequences of tree mortality to the global carbon cycle. Pages 167–177 *in* T. S. Vinson and T. P. Kolchugina, editors. Carbon cycling in boreal forest and sub-arctic ecosystems: biospheric responses and feedbacks to global climate change. EPA/600/R-93/084, U.S. Environmental Protection Agency, Corvallis, Oregon, USA.

Harmon, M. E., J. F. Franklin, F. G. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack Jr., and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research **15**:133–302.

Howard, E. T. 1973. Physical and chemical properties of slash pine tree parts. Wood Science **5**(4):312–317.

Lugo, A. E., S. L. Brown, R. Dodson, T. S. Smith, and H. H. Shugart. *In press.* The Holdridge life zones of the conterminous United States in relation to ecosystem mapping. Journal of Biogeography.

Lugo, A. E., and F. N. Scatena. 1996. Background and catastrophic tree mortality in tropical moist, wet, and rain forests. Biotropica **28**(4a):585–599.

Marland, G., R. J. Andres, and T. A. Boden. 1994. Global, regional, and national CO_2 emissions. Pages 505–584 *in* T. A. Boden, D. P. Kaiser, R. J. Sepanski, and F. W. Stoss, editors. Trends '93: a compendium of data on global change. ORNL/CDIAC-65. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA.

McCune, B., and E. S. Menges. 1986. Quality of historical data on mid-western old-growth forests. American Midland Naturalist **116**:163–172.

Monk, C. D. 1966. Root-shoot dry weights in loblolly pine. Botanical Gazette **127**:246–248.

Muller, R. N., and Y. Liu. 1991. Coarse wood debris in an old-growth deciduous forest on the Cumberland plateau, southeastern Kentucky. Canadian Journal of Forest Research **21**:1567–1572.

Neilson, R. P., G. A. King, and G. Koerper. 1992. Towards a rule-based biome model. Landscape Ecology **7**:27–43.

Nelson, L. E., and G. L. Switzer. 1975. Estimating weights of loblolly pine trees and their components in natural stands and plantations in central Mississippi. Technical Bulletin 73, Mississippi Agricultural and Forestry Experiment Station, Mississippi State University Mississippi, USA.

Parker, G. R. 1989. Old-growth forests of the central hardwood region. Natural Areas Journal **9**(1):5–11.

Parton, W. J., J. W. B. Stewart, and C. V. Cole. 1988. Dynamics of C, N, P and S in grassland soils: a model. Biogeochemistry **5**:109–131.

Peet, R. K., and N. L. Christensen. 1987. Competition and tree death. BioScience **37**:586–595.

Perlin, J. 1991. A forest journey: the role of wood in the development of civilization. Harvard University Press, Cambridge, Massachusetts, USA.

Powell, D. S., J. L. Faulkner, D. R. Darr, A. Zhu, and D. W. MacCleery. 1993. Forest resources of the United States, 1992. U.S. Forest Service General Technical Report **RM-234**. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Prentice, I. C., W. Cramer, S. P. Harrison, R. Leemans, R. A. Monserud, and A. M. Solomon. 1992. A global biome model based on plant physiology and dominance, soil properties and climate. Journal of Biogeography **19**:117–134.

Saucier, J. R., and J. A. Boyd. 1982. Aboveground biomass of Virginia pine in north Georgia. U.S. Forest Service Research Paper **SE-232**.

Schimel, D., I. G. Enting, M. Heimann, T. M. L. Wigley, D. Rayneud, D. Alves, and U. Seigenthaler. 1995. CO_2 and the carbon cycle. Pages 35–71 *in* J. T. Houghton, L. G. Meira Filho, J. Bruce, H. Lee, B. A. Callander, E. Haites, N. Harris, and K. Maskell, editors. Climate change 1994: radiative forcing of climate change and an evaluation of the IPCC IS92 emission scenarios. Cambridge University Press, Cambridge, UK.

Schroeder, P. E., S. Brown, J. Mo, R. Birdsey, and C. Cieszewski. 1997. Biomass estimation for temperate broadleaf forests of the United States using inventory data. Forest Science **43**(3):424–434.

Sollins, P., and R. M. Anderson. 1971. Dry-weight and other data for trees and woody shrubs of the southeastern United States. Oak Ridge National Laboratory, Environmental Science Division, Publication Number 407, Oak Ridge, Tennessee, USA.

Thompson, M. T., and T. G. Johnson. 1994. Virginia's forests, 1992. U.S. Forest Service Resource Bulletin **SE-151**.

Turner, D. P., G. Koerper, M. E. Harmon, and J. J. Lee. 1995. A carbon budget for forests of the conterminous United States. Ecological Applications **5**:421–436.

Vaidya, M. S. L. 1961. Dry matter production and nutrient accumulation in plantations of shortleaf pine. Dissertation. Duke University, School of Forestry, Durham, North Carolina, USA.

Waring, R. H., and W. H. Schlesinger. 1985. Forest ecosystems: concepts and management. Academic Press, New York, New York, USA.

Weaver, G. T., and W. C. Ashby. 1971. Composition and structure of an old-growth forest remnant in southwestern Illinois. American Midland Naturalist **86**(1):46–56.

Whitney, G. G. 1994. From coastal wilderness to fruited plain. Cambridge University Press, Cambridge, UK.

Whittaker, R. H. 1966. Forest dimensions and production in the Great Smoky Mountains. Ecology **47**(1):103–121.

Whittaker, R. H., F. H. Bormann, G. E. Likens, and T. G. Siccama. 1974. The Hubbard Brook ecosystem study: forest biomass and production. Ecological Monographs **44**: 233–254.

Whittaker, R. H., and G. M. Woodwell. 1968. Dimension and production relations of trees and shrubs in the Brookhaven Forest, New York. Journal of Ecology **56**:1–25.

Williams, R. A. 1989. Use of randomized branch and importance sampling to estimate loblolly pine biomass. Southern Journal of Applied Forestry **13**(4):181–184.

Winjum, J. K., S. Brown, and B. Schlamadinger. 1998. Forest harvests and wood products: sources and sinks of atmospheric carbon dioxide. Forest Science **44**:272–284.

Woods, K. D., A. H. Fieveson, and D. B. Botkin. 1991. Statistical error analysis for biomass density and leaf area index estimation. Canadian Journal of Forest Research **21**: 974–989.

Wu, Y., and A. H. Strahler. 1994. Remote estimation of crown size, stand density, and biomass on the Oregon transect. Ecological Applications **4**:299–312.