Validation Databases for Simulation Models: Aboveground Biomass and Net Primary Productivity (NPP) Estimation Using Eastwide FIA Data

Jennifer C. Jenkins and Richard A. Birdsey

Abstract.—As interest grows in the role of forest growth in the carbon cycle, and as simulation models are applied to predict future forest productivity at large spatial scales, the need for reliable and field-based data for evaluation of model estimates is clear. We created estimates of potential forest biomass and annual aboveground production for the Chesapeake Bay watershed region from USDA Forest Service Forest Inventory and Analysis data. These estimates were developed primarily for model evaluation and represent the pilot phase of an effort to estimate potential and actual forest biomass and annual production for the entire nation.

As interest in the impacts of climate change and enhanced CO_2 on ecosystem processes has grown, process model predictions of vegetation growth rates and biomass accumulation are being developed at an accelerating rate. Even when they are based on the same input data sets, however, estimates made by different models can differ from one another by as much as 100 percent (VEMAP Members 1995, Jenkins *et al.* 1998). Still, scientists cannot be sure whether their models are giving accurate predictions, even for current conditions, because the availability of field-collected validation data has not kept pace with the need for model predictions. The objective of this study was to develop methods for estimating aboveground forest net primary productivity (ANPP) and aboveground biomass from USDA Forest Service Forest Inventory and Analysis (FIA) data using methods that would ensure compatibility with the model-based estimates. Assuming that the extensive network of field-measured FIA plots represents the best available estimate of current conditions, the potential ANPP and biomass predictions created from this work can be compared with process model predictions to evaluate the accuracy of the models.

The Chesapeake Bay, the nation's largest estuary, has experienced several anthropogenically induced stresses during the 19th and 20th centuries that have resulted in altered nutrient, sediment, and hydrologic regimes. Nitrogen (N) loss from forested systems has been cited as an important contributor to the nutrient loadings into the Bay. Since C and N cycles are inextricably linked in forested systems, assessing actual and potential C fixation rates in the Chesapeake Bay watershed is important for those attempting to understand the flow of N through the watershed's forests. Further, evaluating the accuracy of model predictions for this region will enable policymakers to rely with confidence on those predictions.

Research Forester and Program Manager, respectively, USDA Forest Service Northern Global Change Program, Radnor, PA, USA.

METHODS

Study Area

Estimates are presented for the seven-state mid-Atlantic (USA) region that surrounds the Chesapeake Bay watershed. For simplicity of analysis and to maximize sample size and geographical coverage, the states of Virginia, West Virginia, Maryland, Delaware, New Jersey, Pennsylvania, and New York were treated in their entirety.

Data Source

Data were obtained from the Eastwide Forest Inventory Data Base (Hansen *et al.* 1992) established and maintained by USDA Forest Service Forest Inventory and Analysis (FIA) units in the Northeastern, North Central, Southern, and Southeastern Research Stations. The plots in the seven-state region treated here represent a subset of the FIA plots in the region.

Choosing Plots for Analysis

Most forest ecosystem process models are designed to predict C, N, and/or water cycling rates in undisturbed, mature forests. To provide the most accurate model validation, we restricted the sample of FIA plots used for this study (cf. McNulty *et al.* (1994)) to those that most closely represented modeled conditions. In particular, all plots meeting the following conditions were included in the sample: (a) remeasured at least once; (b) classified as timberland or reserved timberland for the two most recent remeasurement periods; (c) classified as either poletimber or sawtimber in size at the time of the most recent measurement inventory; d) no evidence of damage by

insects, logging, disease, or fire between the two most recent inventories; and (e) "natural" in origin (i.e., not planted). Using these guidelines, we found 3,757 plots meeting all five criteria, out of 23,322 total plots in the seven-state region.

Because these estimates are based on a subset of the plots meant to represent the maximum biomass accumulation and ANPP conditions that are typically predicted by simulation models, we designate the predictions developed and presented here as "potential." There are weaknesses with this definition: in particular, we have not performed analyses to confirm that they do represent maximum achievable biomass accumulation and growth rates, and the use of stand size to represent closed-canopy mature conditions may be less appropriate than a variable such as basal area or stocking. However, the "potential" designation will serve to set these predictions apart from the "actual" conditions based on the full sample of inventory plots.

Aboveground Biomass

Individual FIA units develop and publish estimates of growing-stock volume and tree biomass (usually on a green-weight basis) to accompany the inventory statistics for each inventory period. The units also develop estimates of timber growth during the inventory cycle. However, those estimates typically use the entire inventory sample to obtain estimates of actual biomass and forest growth. Because of our emphasis on "potential" growth for simulation model validation, we developed separate estimates of aboveground biomass for the subsample of plots described above.

Estimates of aboveground forest biomass (dry-weight basis) were created for each plot by adding together the biomass contributions from each of the trees (both live and dead, expressed per unit area) on that plot. Regression equations were used to predict aboveground tree biomass on a dry-weight basis from diameter at breast height (dbh). The approach used by Wharton *et al.* (1997), in which biomass equations from different regions were used to predict biomass of individual species, was adopted for this study. Although most biomass equations are developed locally, independent studies (Jacobs and Monteith 1981, Barrett and Jastrembski 1990) have suggested that the differences among tree biomass in different parts of a region may not be large enough to prevent the use of regional regression equations. For both this study and the Wharton *et al.* (1997) study, equations from Maine (Young *et al.* 1980) were used for all evergreen species in addition to red maple, yellow birch, and quaking aspen; equations from West Virginia (Wiant *et al.* 1977) were used for Appalachian deciduous species such as hickory, yellow-poplar, black cherry, and oak species; and equations from New York (Monteith 1979) were used for sugar maple, American beech, and white ash (table 1). Species for which regression equations did not exist were matched with species for which equations were available by comparing wood densities, as described in Appendix B of Wharton *et al.* (1997). We assumed that the equations typically used for live trees were appropriate for dead trees as well.

Aboveground Net Primary Productivity (ANPP)

Net primary productivity (NPP) is defined as the net production of organic matter per unit area per year. While total NPP includes both aboveground and belowground components, aboveground NPP (ANPP) is more commonly (and more easily) measured. Annual ANPP was found as:

ANPP (kg ha^{-1} yr^{-1}) =
Wood production (kg ha^{-1} yr^{-1}) +
average annual litterfall (kg ha^{-1} yr^{-1}). (1)

Litterfall was not measured on these plots, so we used estimates developed by E. Matthews, W. Post, E.A. Holland and J. Sulzman (and cited in Brown and Schroeder (1998)) based on a review of the available literature for United States forests. Annual litterfall was estimated to be 3.2 Mg ha^{-1} yr^{-1} in spruce-fir forests, 4.0 Mg ha^{-1} yr^{-1} in pine forests, and 4.5 Mg ha^{-1} yr^{-1} in hardwood forests. We found annual wood production per tree as:

Wood production per tree (kg yr^{-1}) =
[aboveground biomass (kg) (t_1) –
aboveground biomass (kg) (t_0)]/[$t_1 - t_0$ (yr)]. (2)

Biomass estimates for current conditions (t_1) were found on a tree-by-tree basis using species-specific regression equations as described above. To find biomass and biomass increment on a per hectare basis from tree-level measurements, the tree-level estimates were multiplied by an expansion factor representing the number of trees per unit area represented by that individual stem. Biomass estimates for each stem at the previous inventory (t_0) were found as described below.

Dbh measurements existed for two consecutive measurement periods for 89,938 live stems (all greater than 12.7 cm dbh). Average yearly diameter increment for these stems (for the period roughly from 1980 to 1990, depending on the state) was 0.3351 cm yr^{-1}. There were 12,082 dead stems in the current inventory, and 65,131 more were ongrowth stems (i.e., they were measured in the current inventory, but were too small—less than 12.7 cm dbh—to have been measured in the previous inventory (Birdsey and Schreuder 1992)).

Table 1.—*Aboveground tree-weight regression coefficients for selected species. From Wharton* et al. *(1997)*

Equation forms:

$LnY = b_0 + b_1Ln(D)$ (1)

$Log_{10}Y = LOG_{10}b_0 + b_1LOG_{10}(D)$ (2)

$Y = b_0 + b_1(D) + b_2(D^2)$ (3)

Y = dry weight (pounds (eqs. 1 and 2) or kg (eq. 3))
D = dbh (inches (eqs. 1 and 2) or millimeters (eq. 3))

Species	Coefficients b_0	b_1	b_2	Equation number
Balsam fir	0.5958	2.4017		1
Eastern white pine	0.4080	2.4490		1
Red pine	0.7157	2.3865		1
Spruce spp.	0.8079	2.3316		1
Hemlock	0.6803	2.3617		1
N. white-cedar	1.1182	1.9269		1
Larch	0.8162	2.2453		1
Red maple	0.9392	2.3804		1
Sugar maple	5.2480	0.3661	0.0076	3
Yellow birch	1.1297	2.3376		1
Hickory	1.9338	2.6209		2
American beech	5.3373	-0.3257	0.0072	3
White ash	3.2031	-0.2337	0.0061	3
Yellow-poplar	1.5779	2.5153		2
Black cherry	2.5883	2.4253		2
Aspen	0.4689	2.6087		1
White oak	1.2892	2.7010		2
Scarlet oak	2.6574	2.4395		2
Chestnut oak	2.1202	2.5344		2
Northern red oak	1.6891	2.6598		2
Black oak	2.1457	2.5050		2

For dead and ongrowth stems, we assumed that all trees (regardless of size) grew at the average rate for the region, and that dead stems had died halfway through the previous inventory. The diameter of dead trees at t_0 was found as:

DBH (cm) at t_0 = DBH (cm) at t_1 – [(0.3351 cm yr^{-1})*(remeasurement period length (yr)/2)]. (3)

Ongrowth trees were grown back to their previous diameter using a similar equation:

DBH (cm) at t_0 = DBH (cm) at t_1 – [(0.3351 cm yr^{-1})*(remeasurement period length (yr)]. (4)

If the above equations resulted in a negative diameter, DBH (and thus biomass) at t_0 were set to zero.

These estimates do not include measures of seedling and shrub production. Based on the work of Wharton *et al.* (1997) in New York, it is likely that this exclusion has biased our results downward by less than 3 percent.

Stand Characteristics

Plot basal area (m^2 ha^{-1}) (BA) was found by adding together the BA contributions from each of the live trees greater than 2.54 cm dbh on each plot. BA values ranged from 1.36 to 61.28 m^2 ha^{-1}, with a mean of 24.09 m^2 ha^{-1}. The sum of tree circumferences was used as a surrogate for sapwood area (cf. Smith (1986)) and was found by adding together the contribution of each live tree to a per hectare estimate of circumference outside bark (cm ha^{-1}). For all other stand characteristics (stocking, stand size, forest-type group, and stand age), the plot-level data from the Eastwide Data Base (Hansen *et al.* 1992) were used.

Ecoregions and Climate Data

The study region spans seven of the ecological Provinces delineated by the ECOMAP team of the USDA Forest Service (McNab and Avers 1994) and 79 of the smaller Sections described for the eastern United States by Keys *et al.* (1995). Province boundaries were obtained from the data published on CD-ROM by Keys *et al.* (1995). Plots were identified with individual Provinces by overlaying the plot locations with a map of Province boundaries (fig. 1). Because the approximate plot locations from the Eastwide Data Base are accurate to only within (roughly) 1 km, and because the Province boundaries are themselves fairly approximate, the error associated with this operation was considered small enough to ignore.

Temperature, precipitation, and elevation data were obtained by overlaying exact plot locations with maps representing average annual temperature (C), total annual precipitation (cm), and elevation above sea level (m). The climate maps were developed at 1-km resolution using modeling approaches as described by Pan *et al.* (1998), and the digital elevation model (DEM) was obtained from the United States Geological Survey at 1-km resolution. Across the study area, average annual temperature ranged from 4.21 to 15.38C, with an average of 9.28C. Total annual precipitation ranged from 77 to 173 cm yr^{-1} and averaged 110.56 cm yr^{-1}. Elevation ranged from 0 to 1,377 m above sea level, averaging 390 m for the region.

RESULTS

Aboveground Biomass

Results by Forest-Type Group, State, and Ecological Unit

Summarized by forest-type group, estimates of average aboveground biomass ranged from 107 Mg ha^{-1} in the loblolly-shortleaf pine forest-type group to 211.7 Mg ha^{-1} in the maple-beech-birch type group (table 2). Averaging results by state, the lowest average aboveground biomass (120.9 Mg ha^{-1}) was found in New Jersey and the highest (192.8 Mg ha^{-1}) was found in New York (table 3). When the results were summarized by ecological province, the lowest overall biomass in the region (133.0 Mg ha^{-1}) was found in the Southeastern Mixed Forest Province, while the highest (209.7 Mg ha^{-1}) was in the Adirondack-New England Mixed Forest-Coniferous Forest-Alpine Meadow Province (table 4). The range in biomass predictions was greatest when predictions were aggregated by forest-type group, and smallest when predictions were aggregated by state.

Multiplying the average potential aboveground biomass on timberland (Mg ha^{-1}) for each state by the total land area covered by timberland in that state, we estimate that the total potential aboveground biomass on timberland for the seven-state mid-Atlantic region is approximately 4.54 Pg (1 Pg = 10^{15} g). Taking 0.475 to represent the proportion of that biomass in carbon (Raich *et al.* 1991), the total potential C in aboveground standing biomass on timberland in the region is roughly 2.16 Pg. In contrast, Birdsey (1992) reported that a total of 1.57 Pg C can be found aboveground on timberland in this study region. The difference of roughly 30 percent between the two estimates might be seen as the difference between "actual" and "potential" aboveground C in standing biomass. Also based on data from Birdsey (1992), the C stored on timberland in this seven-state region makes up roughly 20 percent of the total aboveground C in all forested systems of the United States.

Trends in Aboveground Biomass

Not surprisingly, the best predictor of aboveground biomass at the plot level was basal area of live trees, as described by the equation:

$$\text{Log}_{10}\text{biomass (kg ha}^{-1}) = 14.07(\log_{10}(\text{basal area (m}^2\text{ha}^{-1}))) + 1.005 \quad (5)$$

(n = 3,757 plots; $R^2 = 0.593$, and p-values on coefficient and constant < 0.000).

In addition to basal area, aboveground biomass was also correlated with stocking, stand size classification (as sawtimber or poletimber), and forest-type group as described for each plot in the Eastwide Data Base. However, aboveground biomass as calculated here was not correlated with strongly climatic or physiographic characteristics such as temperature, precipitation, elevation, physiographic class, or site class (the latter two variables are described for each plot in the Eastwide Data Base as defined by Hansen *et al.* (1992)).

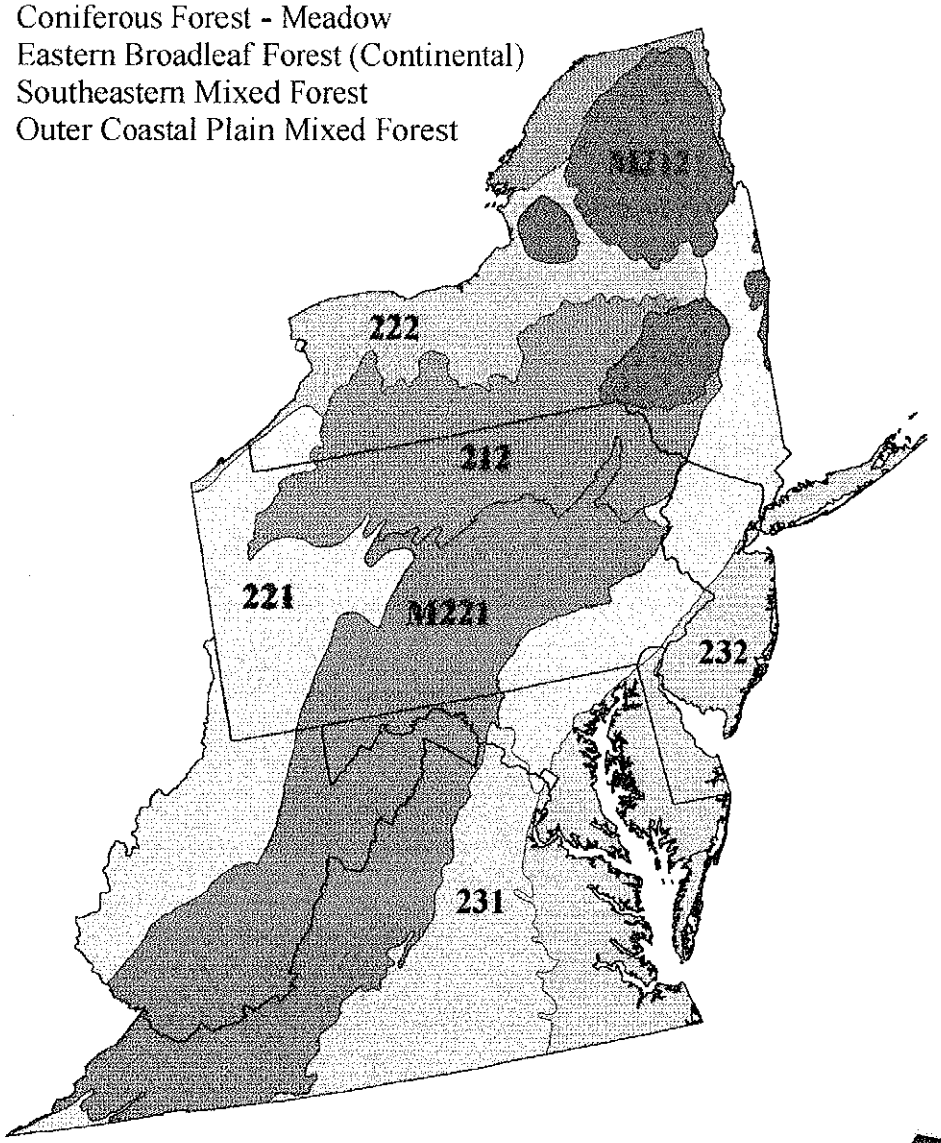
Wood Production and Aboveground Net Primary Productivity

Results by Forest-type Group, State, and Ecological Unit

Averaged by forest-type group, the lowest annual wood production (4,346.4 kg ha^{-1} yr^{-1}) occurred in the loblolly-shortleaf pine forest type (table 2). The range in annual wood production estimates (1,000 kg ha^{-1} yr^{-1}) between the least and most productive forest types was much narrower than the corresponding range in average aboveground biomass estimates (104.7 Mg ha^{-1}, or 104,700 kg ha^{-1}). The highest average annual wood production (5,227 kg ha^{-1} yr^{-1}) occurred in the aspen-birch type group. Because forest-type group was used to find annual litter production, these trends were identical for ANPP and for wood production.

KEY:

212	Laurentian Mixed Forest
M212	Adirondack - New England Mixed Forest Coniferous Forest - Alpine Meadow
221	Eastern Broadleaf Forest (Oceanic)
M221	Central Appalachian Broadleaf Forest - Coniferous Forest - Meadow
222	Eastern Broadleaf Forest (Continental)
231	Southeastern Mixed Forest
232	Outer Coastal Plain Mixed Forest



Albers Equal Area Projection

50 0 50 100 150 Kilometers

USDA Forest Service
Northern Global Change Program

Figure 1.—*Ecological Province boundaries for the mid-Atlantic (USA) region, as defined in digital data of Keys* et al. *(1995).*

Table 2.—*Summary of aboveground biomass, wood production, and aboveground NPP estimates by forest type group. All values are presented as mean (S.D.). Values within a column followed by different letters are significantly different, as determined by ANOVA ($p < 0.05$).*

Forest-type group description	Plots	Aboveground biomass	Wood production	ANPP
	Number	*Mg ha^{-1}*	*kg ha^{-1} yr^{-1}*	*kg ha^{-1} yr^{-1}*
Oak-Hickory	1,649	176.4 (63.6)^{d}	4815.8 (1513.8)^{bcd}	9315.8 (1513.8)^{c}
Maple-Beech-Birch	1,233	211.7 (87.6)^{e}	5042.3 (1450.3)^{d}	9542.3 (1450.3)^{d}
White-Red-Jack Pine	243	162.7 (69.3)^{bcd}	5037.6 (1565.6)^{cd}	9037.6 (1565.6)^{c}
Loblolly-Shortleaf Pine	183	107.0 (40.0)^{a}	4346.4 (2036.3)^{a}	8346.4 (2036.3)^{ab}
Oak-Pine	176	137.9 (53.0)^{bc}	4604.6 (1609.7)^{abc}	9104.6 (1609.7)^{c}
Elm-Ash-Cottonwood	121	141.4 (69.7)^{bc}	4395.5 (2027.5)^{ab}	8895.5 (2027.5)^{bc}
Aspen-Birch	67	137.4 (70.7)^{abc}	5227.0 (1844.4)^{d}	9727.0 (1844.4)^{d}
Spruce-Fir	51	131.9 (48.6)^{ab}	4761.4 (1548.5)^{abcd}	7961.4 (1548.5)^{a}
Oak-Gum-Cypress	33	169.0 (89.7)^{bcd}	4972.0 (2324.9)^{bcd}	9472.0 (2324.9)^{cd}
Longleaf-Slash Pine	1	200.0	4762.6	8762.6

Table 3.—*Summary of aboveground biomass, wood production, and aboveground NPP estimates by state. All values are presented as mean (S.D.). Values within a column followed by different letters are significantly different, as determined by ANOVA ($p < 0.05$).*

State	Plots	Aboveground biomass	Total C in timberland	Wood production	ANPP	Annual total C storage in timberland
	Number	*Mg ha^{-1}*	*Tg C = 10^{12} g C*	*kg ha^{-1} yr^{-1}*	*kg ha^{-1} yr^{-1}*	*Tg C yr^{-1} = 10^{12} g C yr^{-1}*
New York	1,258	192.8 (86.4)^{c}	587.72	4914.2 (1528.1)^{bc}	9302.8 (1548.7)^{cd}	14.98
Pennsylvania	1,086	188.3 (73.2)^{c}	609.26	5091.5 (1426.7)^{c}	9558.0 (1443.3)^{d}	16.47
West Virginia	704	180.0 (68.7)^{c}	415.54	4791.3 (1523.5)^{b}	9264.7 (1537.7)^{bcd}	11.06
Virginia	364	133.3 (52.6)^{a}	409.63	4654.5 (1944.9)^{b}	9017.2 (1919.5)^{b}	14.30
Maryland	211	159.5 (60.7)^{b}	79.03	4715.3 (1573.1)^{b}	9139.5 (1607.6)^{bc}	2.34
New Jersey	93	120.9 (72.3)^{a}	43.92	3324.6 (1710.9)^{a}	7668.7 (1818.7)^{a}	1.21
Delaware	41	168.2 (52.7)^{bc}	12.27	4860.6 (1464.6)^{bc}	9263.1 (1500.6)^{bcd}	0.35

Table 4.—*Summary of aboveground biomass, wood production, and aboveground NPP estimates by ecoregion (province). All values are presented as mean (S.D.). Values within a column followed by different letters are significantly different, as determined by ANOVA ($p < 0.05$).*

Province ID (USDA classification)	Province description	Plots[1]	Aboveground biomass	Wood production	ANPP
		Number	*Mg ha^{-1}*	*kg ha^{-1} yr^{-1}*	*kg ha^{-1} yr^{-1}*
M221	Central Appalachian Broadleaf Forest - Coniferous Forest - Meadow	1017	173.5 (67.8)^{b}	4706.7 (1576.3)^{ab}	9169.6 (1596.9)^{ab}
212	Laurentian Mixed Forest	867	198.8 (79.5)^{d}	4983.2 (1402.7)^{c}	9422.6 (1416.7)^{c}
221	Eastern Broadleaf Forest (Oceanic)	744	175.8 (69.7)^{bc}	4900.0 (1504.8)^{bc}	9360.5 (1511.1)^{bc}
M212	Adirondack - New England Mixed Forest Coniferous Forest - Alpine Meadow	436	209.7 (90.3)^{d}	4926.2 (1321.3)^{bc}	9257.2 (1379.0)^{abc}
232	Outer Coastal Plain Mixed Forest	294	136.0 (60.5)^{a}	4556.7 (1896.2)^{a}	8908.7 (1941.3)^{a}
222	Eastern Broadleaf Forest (Continental)	226	175.8 (91.4)^{bc}	5163.4 (1977.1)^{c}	9590.4 (1987.1)^{c}
231	Southeastern Mixed Forest	160	133.0 (52.0)^{a}	5096.0 (1936.5)^{c}	9442.9 (1925.6)^{c}

[1]Due to the inexact nature of the boundaries, some of the FIA plots fell within areas classified as "water" on the ecoregion map; those plots were omitted from this analysis.

State boundaries provide convenient and understandable geographic units for analysis. Summarizing results by state, we found that New Jersey had dramatically lower wood production (3,324.6 kg ha^{-1} yr^{-1}) than any of the other states, perhaps because of its predominantly sandy soils. Virginia had the next lowest annual wood production, at 4,654.5 kg ha^{-1} yr^{-1} (table 2). Pennsylvania's timberland produced the highest average woody biomass increment, at 5,091.5 kg ha^{-1} yr^{-1}. The range in aboveground wood production was 1,767 kg ha^{-1} yr^{-1}. The corresponding range in ANPP was similar, at 1,889 kg ha^{-1} yr^{-1}.

When results were aggregated by ecological province, timberland plots falling within the Continental Eastern Broadleaf and Southeastern Mixed Forest Provinces had average annual wood production higher than that reported for any of the states or forest types (5,163.4 kg ha^{-1} yr^{-1} and 5,096.0 kg ha^{-1} yr^{-1}, respectively) (table 3). The lowest wood production (4,556.7 kg ha^{-1} yr^{-1}) was found for those plots falling within the Outer Coastal Plain Mixed Forest. Trends were similar for ANPP, with the Continental Eastern Broadleaf Forest having the highest ANPP (9,590.4 kg ha^{-1} yr^{-1}) and the Outer Coastal Plain Mixed Forest having the lowest ANPP (8,908.7 kg ha^{-1} yr^{-1}).

Multiplying the average potential wood production on timberland (kg ha^{-1} yr^{-1}) in each state by the amount of timberland in that state, we estimate that maximum aboveground biomass accumulation by forests on timberland in the mid-Atlantic region is about 127.82 Tg OM yr^{-1} (1 Tg = 10^{12} g). Again taking 0.475 as the proportion of carbon in biomass, mid-Atlantic forests may potentially sequester 60.71 Tg C yr^{-1} in aboveground biomass. It is important to note, again, that these figures do not represent the full sample of the inventory plots, and that they also do not include the C potentially being added to (or lost from) belowground biomass and soil organic matter.

Trends in Aboveground Wood Production and ANPP

The best individual predictor of aboveground wood production was plot-level basal area, as described by the equation:

$$\text{Log}_{10}\text{wood production (kg ha}^{-1}\text{ yr}^{-1}) = 1.345(\log_{10}(\text{basal area (m}^2\text{ ha}^{-1}))) + 0.7957 \quad (6)$$

(n = 3,757 plots; $R^2 = 0.336$, and p-values on coefficient and constant < 0.000).

Adding stem density to the predictive equation explained ~10 percent more of the variation in wood production:

$$\text{Log}_{10}\text{wood production (kg ha}^{-1}\text{ yr}^{-1}) = 1.343(\log_{10}(\text{basal area (m}^2\text{ ha}^{-1}))) + 0.131(\log_{10}(\text{stem density (stems ha}^{-1}))) + 0.6719 \quad (7)$$

(n = 3,757 plots; $R^2 = 0.435$, and p-values on coefficients and constant < 0.000).

Despite the assumed relationship between sapwood area, the sum of tree circumferences, and wood production, the sum of circumferences was a poorer predictor of wood production than was basal area:

$$\text{Log}_{10}\text{wood production (kg ha}^{-1}\text{ yr}^{-1}) = 0.111(\log_{10}(\text{sum of circumferences (cm ha}^{-1}))) + 0.5 \quad (8)$$

(n = 3757 plots; $R^2 = 0.289$, and p-values on coefficient and constant < 0.000).

Finally, aboveground biomass was a better predictor of wood production than the sum of tree circumferences, but a poorer predictor than basal area:

$$\text{Log}_{10}\text{wood production (kg ha}^{-1}\text{ yr}^{-1}) = 0.0178(\log_{10}(\text{aboveground biomass (kg ha}^{-1}))) + 0.7986 \quad (9)$$

(n = 3,757 plots; $R^2 = 0.310$, and p-values on coefficient and constant < 0.000).

These variables were also the strongest predictors of ANPP, but the predictive relationships were not as strong: basal area, stem density, and aboveground biomass explained between 2 and 5 percent less of the variation in ANPP than in wood production.

Other stand-level variables, such as stand size, forest-type group, and stand age were not strongly related to aboveground wood production or ANPP. Physical variables such as physiographic class, site class, precipitation, temperature, and elevation were not related at all to annual production, suggesting that inherent stand characteristics (and not these climatic or physiographic variables) may be the best predictors of annual forest growth rates in this region.

DISCUSSION

Current and Future C Assimilation

The patterns and magnitudes of woody biomass increments presented here are consistent with those presented by Brown and Schroeder (1998), who used data from the

Eastwide FIA Data Base to map biomass increments at the county level for the eastern United States. Based on the current analysis, aboveground C sequestration by live timberland in the region is currently potentially responsible for mitigating about 5 percent of the estimated annual emissions from fossil fuel and cement production in the United States (1.3 Pg yr^{-1}) (Marland *et al.* 1994). The magnitude of C accumulation in "dead" material (soil and forest floor) has historically been at least as great as that in aboveground live biomass (Birdsey and Heath 1995). Based on an analysis of FIA data collected over the past few decades, Birdsey and Heath (1995) concluded that United States forests (mostly in the eastern half of the nation) have actually been responsible for mitigating about 25 percent of annual the nation's C emissions.

In the very long term (200-300+ years), however, it is unlikely that eastern forests will continue to accumulate organic matter and C in their tissues, because substantial evidence suggests that NPP declines significantly with stand age (Gower *et al.* 1996, Ryan *et al.* 1997, Ryan and Yoder 1997). The average age for the plots analyzed here was 48.8 (+/- 23.4) years; decades are likely to pass before the growth rates for these forests reach a minimum.

What Determines Wood Production and Biomass Accumulation?

Physiographic characteristics such as drainage class, site index, and elevation were poor predictors of annual wood production. Similarly, climatic variables such as temperature and precipitation were not related to wood production or total aboveground biomass. Instead, measures of forest structure—basal area, stem density, stocking, forest composition, and the sum of tree circumferences—were the best predictors of annual production and total aboveground biomass. Yet the plots chosen for analysis in this study should most closely reflect differences in physiographic, edaphic, and climatic characteristics, because this sample was restricted to plots that had experienced no damage or harvesting since the last inventory and that should have represented closed-canopy forests.

Several explanations for this phenomenon are possible: (a) the physiographic and/or climatic characteristics as reported in the Eastwide Data Base and in the data layers used here may not adequately represent the physical characteristics found at forested plots; (b) the FIA sample plots are not well-distributed with respect to the range of climatic and physiographic conditions (i.e., there were too few plots at the extremes of climate or physiography); (c) some other physical variable, such as soil texture, soil water holding capacity, slope, or aspect, may better explain variation in biomass accumulation and wood production; or (d) the effects of management activities or the legacy of previous land use may overwhelm the impacts of physiographic and climatic characteristics on aboveground biomass and annual wood production. These alternative explanations represent hypotheses to be tested in future research.

It is important to note, however, that ecosystem process models have typically ignored the influences of management and land-use history on NPP (but see Aber and Driscoll (1997) and Aber *et al.* (1997)), instead using vegetation-type-specific algorithms driven by climate and physiography. Some modeling groups have even used "potential vegetation" to create NPP predictions (VEMAP Members 1995); our results suggest that the impacts of management and land-use history are critical to accurate predictions of both potential and actual growth rates in U.S. forests.

Next Steps

As we begin to consider the United States as a whole, considering seedling and shrub production (perhaps by using some of the FIA data not included in the Eastwide Data Base) will add completeness to these estimates. In addition, estimating belowground production will enable us to create more accurate predictions of overall C storage by forest systems. The utility of site-specific regression equations when applied to entire regions has been questioned; we will need to address this uncertainty as well. To determine the extent to which these estimates are representative of well-studied forests in the mid-Atlantic, we will compare these biomass and ANPP estimates to those developed and/or published by other researchers for study sites in the region. And, of course, we will compare these estimates to process model predictions to evaluate model accuracy. Finally, to quantify actual C stocks and fluxes for the region and the nation, we will need to expand our sample to include the entire set of FIA plots.

ACKNOWLEDGMENTS

We are especially grateful to Carol Alerich and Tom Frieswyk for their patience and assistance with the FIA database, to Yude Pan for sharing her climate and elevation data, and to Rachel Riemann for her help with geographic overlays. Scott Thomasma was instrumental in helping to debug the computer programs used to develop these estimates. Finally, we thank Linda Heath, John Aber, Marie-Louise Smith, and J. Morgan Grove for helpful discussions.

This paper was reviewed before publication by Will McWilliams, Forest Inventory and Analysis Unit, and James Steinman, Forest Health Monitoring Program, USDA Forest Service Northeastern Research Station, Radnor, PA, USA.

LITERATURE CITED

Aber, J.D.; Driscoll, C.T. 1997. Effects of land use, climate variation and N deposition on N cycling and C storage in northern hardwood forests. Global Biogeochemical Cycles. 11(4): 639-648.

Aber, J.D.; Ollinger, S.V.; Driscoll, C.T. 1997. Modeling nitrogen saturation in forest ecosystems in response to land use and atmospheric deposition. Ecological Modelling. 101: 61-78.

Barrett, J.; Jastrembski, J. 1990. Regional greenweight biomass equations for the Northeast. Northern Journal of Applied Forestry. 7: 187-189.

Birdsey, R.A. 1992. Carbon storage and accumulation in United States forest ecosystems. Gen. Tech. Rep. WO-59. Washington, DC: U.S. Department of Agriculture, Forest Service.

Birdsey, R.A.; Heath, L.S. 1995. Carbon changes in U.S. forests. In: Productivity of America's forests and climate change. Gen. Tech. Rep. RM-271. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Birdsey, R.A.; Schreuder, H.T. 1992. An overview of forest inventory and analysis estimation procedures in the Eastern United States—with an emphasis on the components of change. Gen. Tech. Rep. RM-214. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station..

Brown, S.L.; Schroeder, P.E. 1998. Spatial patterns of biomass increment and mortality based on inventory data for eastern U.S. forests. Ecological Applications in review.

Gower, S.T.; McMurtrie, R.E.; Murty, D. 1996. Aboveground net primary production decline with stand age: Potential causes. Trends in Ecology and Evolution. 11(9): 378-382.

Hansen, M.H.; Frieswyk, T.; Glover, J.F.; Kelly, J.F. 1992. The eastwide forest inventory data base: users manual. Gen. Tech. Rep. NC-151. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station.

Jacobs, M.W.; Monteith, D.B. 1981. Feasibility of developing regional weight tables. Journal of Forestry. October: 676-677.

Jenkins, J.C.; Kicklighter, D.W.; Ollinger, S.V.; Aber, J.D.; Melillo, J.M. 1998. Sources of variability in NPP predictions at the regional scale: a comparison using PnET-II and TEM 4.0 in northeastern U.S. forests. Ecosystems in review.

Keys, J.J.; Carpenter, C.; Hooks, S.; Koenig, F.; McNab, W.; Russell, W.; Smith, M.-L. 1995. Ecological units of the eastern United States—first approximation (map, booklet of map unit tables, and CD-ROM with GIS coverages). Atlanta, GA: U.S. Department of Agriculture, Forest Service.

Marland, G.; Andres, R.; Boden, T. 1994. Trends '93: a compendium of data on global change. Oak Ridge, TN: Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory. ORNL/CDIAC-65.

McNab, W.; Avers, P. 1994. Ecological subregions of the United States: section descriptions. Admin. Publ. WO-WSA-5. Washington, DC: U.S. Department of Agriculture, Forest Service.

McNulty, S.G.; Vose, J.M.; Swank, W.T.; Aber, J.D.; Federer, C.A. 1994. Regional-scale forest ecosystem modeling: database development, model predictions and validation using a Geographic Information System. Climate Research. 4: 223-231.

Monteith, D. 1979. Whole tree weight tables for New York. AFRI Res. Rep. 40. Syracuse, NY: State University of New York College of Environmental Science and Forestry, Applied Forestry Research Institute.

Pan, Y.; Grove, J.; Hom, J.; Holt, H.; Jenkins, J.; Aber, J. 1998. Regional estimation and validation of forest production and water yield for Chesapeake Bay basin with PnET-II model and field data. Ecological Society of America Annual Meeting Abstracts. 83: 104.

Raich, J.W.; Rastetter, E.B.; Melillo, J.M.; Kicklighter, D.W.; Steudler, P.A.; Peterson, B.J. 1991. Potential net primary productivity in South America: application of a global model. Ecological Applications. 1: 399-429.

Ryan, M.G.; Yoder, B.J. 1997. Hydraulic limits to tree height and tree growth. BioScience. 47(4): 235-242.

Ryan, M.G.; Binkley, D.; Fownes, J.H. 1997. Age-related decline in forest productivity: pattern and process. Advances in Ecological Research. 27: 214-262.

Smith, D. 1986. The practice of silviculture. New York, NY: John Wiley & Sons.

VEMAP Members. 1995. Vegetation/ecosystem modeling and analysis project: comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO2 doubling. Global Biogeochemical Cycles. 9(4): 407-437.

Wharton, E.H.; Alerich, A.L.; Drake, D.A. 1997. Estimating total forest biomass in New York, 1993. Resour. Bull. NE-139. Radnor, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station.

Wiant, H.V.J.; Sheetz, C.; Colaninno, A.; DeMoss, J.; Castaneda, F. 1977. Tables and procedures for estimating weights of some Appalachian hardwoods. Bull. 659T. Morgantown, WV: West Virginia University, Agricultural and Forestry Experiment Station, College of Agriculture and Forestry.

Young, H.E.; Ribe, J.H.; Wainwright, K. 1980. Weight tables for tree and shrub species in Maine. Misc. Rep. 230. Orono, ME: University of Maine Life Sciences and Agriculture Experiment Station.