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BIOMASS AND NPP ESTIMATION FOR THE MID-ATLANTIC REGION (USA) USING PLOT-LEVEL FOREST INVENTORY DATA

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Abstract. As interest grows in quantification of global carbon cycles, process model predictions of forest biomass and net primary production (NPP) are being developed at an accelerating rate. Such models can provide useful predictions at large scales, but it has been difficult to evaluate their performance. Using the network of plots comprising the comprehensive and spatially extensive Forest Inventory and Analysis (FIA) data set collected and maintained by the USDA Forest Service, we applied methods typically used in field measurements to develop estimates of forest biomass and NPP for the mid-Atlantic region of the United States at a scale appropriate for comparison with model predictions. Plot-level and tree-level forest inventory data from a subset of plots were used together with species-specific biomass regression equations to calculate maximum current biomass and NPP values for the mid-Atlantic region. Estimates at the plot level were aggregated by forest type and to the $0.5^\circ \times 0.5^\circ$ scale for analysis and comparison with process model predictions.

Maximum current forest biomass averaged 248 and 200 $\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ in hardwood and softwood forest types, respectively; wood biomass increment averaged 559 and 460 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in hardwood and softwood forest types, respectively. Aggregated to the $0.5^\circ \times 0.5^\circ$ scale, forest biomass ranged from 101 to 326 Mg/ha , while wood biomass increment ranged from 254 to 1050 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$. Biomass and NPP estimates for closed-canopy forests from this study were consistent with values reported in the literature but were as much as 50% lower than values reported for old-growth stands. NPP predictions from three process models were fairly consistent with the FIA-based estimates, but model predictions of biomass were higher than estimates from FIA data for the region. By describing upper and lower bounds on reasonable biomass and NPP values for closed-canopy forests, these FIA-derived estimates provide a foundation for model comparison and continued model development.

Key words: biomass; forest C sequestration rates; Forest Inventory and Analysis (FIA); mid-Atlantic region (USA); net primary production (NPP); process model validation.

INTRODUCTION

Net primary production (NPP) is defined as the rate of accumulation of organic matter by vegetation, and is calculated as the difference between photosynthesis and autotrophic respiration. Because it accounts for the net carbon (C) fixed by vegetation per unit area per year, NPP represents the role of live vegetation in global C cycles. Forest biomass comprises close to 90% of all terrestrial vegetation biomass on earth (Olson et al. 1983, Dixon et al. 1994), and standing forest biomass represents the accumulated C stocks potentially available for harvest or decomposition. Forest biomass is thus another important component in the global C cycle.

Process model predictions

To predict forest biomass and NPP in assessments of global C cycling rates, process model predictions of forest growth rates and biomass accumulation are being

developed at an accelerating rate (e.g., Melillo et al. 1993, VEMAP Members 1995, Foley et al. 1996, Thompson et al. 1996, Burke et al. 1997, Ollinger et al. 1998, Xiao et al. 1998, Cramer et al. 1999, Schimel et al. 2000). Using gridded input data sets to represent forest type and environmental conditions, these models are frequently used to estimate the spatial and temporal variation in C fluxes between forests and the atmosphere. Even when they use the same input data sets, however, model predictions can differ by as much as 100% from one another (Bondeau et al. 1999, Jenkins et al. 1999, Kicklighter et al. 1999, Ruimy et al. 1999, Schloss et al. 1999).

While some variability among model estimates is to be expected, comparison of model estimates with independently measured validation data is required to determine the accuracy of modeled predictions (Scurlock et al. 1999). Measurements made at individual field plots can be used for this purpose, but difficulties with these comparisons are numerous. For example, (a) only a few widely scattered measurements exist for a given region, (b) many of the available data points cannot be used for validation because they were used for model parameterization, and (c) the fine scale var-

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iability of biomass and NPP is such that the small size of the field plots (often as small as 0.1 ha) compared with the large spatial resolution (often $0.5^\circ \times 0.5^\circ$, or ~ 50 km square at mid-latitudes) of model estimates limits the viability of these comparisons.

Many process models were originally developed and parameterized using data collected in relatively undisturbed, closed-canopy forests. As a result, validation data sets will be most comparable to model estimates if they, too, are based exclusively on data from undisturbed, closed-canopy forests. Exceptions, of course, are models parameterized to predict biomass and NPP directly from remotely sensed data (Prince and Goward 1995, Field et al. 1998), and process models that incorporate information on stand structure or land use history into their predictions (Pastor and Post 1986, Aber and Driscoll 1997, Aber et al. 1997, Friend et al. 1997).

United States forest C estimates from inventory data

The USDA Forest Service Forest Inventory and Analysis (FIA) protocols were originally designed to provide measurements of merchantable bole volume. Various methods have since been used to extend bole volume measurements to whole forest estimates of C stocks and fluxes (Birdsey 1992, Birdsey and Heath 1995, Turner et al. 1995, Brown and Schroeder 1999, Brown et al. 1999), though the published methods do have several things in common. In all methods used to date, bole volume in merchantable trees has been the starting point for biomass estimates; merchantable volume is multiplied by a forest-type or region-specific biomass expansion factor, which is meant to account for the additional biomass in nonmerchantable trees and non-bole components. In addition, previous FIA biomass and production estimates have been based on aggregated county-level volume, growth, harvest, and mortality data.

In this study, we developed and applied a new method for estimating forest biomass and NPP from plot-level FIA data. The method is similar to the approach typically used in field measurements of these parameters (Whittaker and Marks 1975). Tree diameters are used with allometric regression equations to estimate tree biomass, and biomass values from trees on each plot are added together to develop plot-level biomass estimates. Diameter growth information collected at remeasured plots is used to estimate wood biomass increment. Since we develop these estimates using individual tree data, we ensure that the biomass and biomass increment of all trees on a plot, no matter what their size or merchantability status, are included in our estimates. In addition, we develop estimates for individual plots rather than for aggregated units such as counties, which allows for analysis of (a) the plot-to-plot variability in biomass and NPP estimates, and (b) the characteristics of subsets of plots.

This paper describes the development of a database

containing estimates of forest biomass and NPP at the $0.5^\circ \times 0.5^\circ$ scale based on FIA data for the mid-Atlantic region of the United States. In addition, we compare our biomass and NPP estimates with published estimates from ecological field studies conducted in the region, and with NPP predictions from several ecosystem process models.

METHODS

Inventory structure

The FIA program has been conducting periodic surveys of the nation's forested land since 1928 (Birdsey and Schreuder 1992). While an annual sampling scheme is currently being implemented nationwide, recent inventories have typically been conducted every five to seven years in the southeastern states and every 10 to 15 yr in the northeastern states.

Inventory samples, performed sequentially for each state, follow a two-phase scheme known as double sampling for stratification (see Chojnacky [1998] for an example of this double sampling technique). In the first phase, a grid of sample points on air photos is interpreted, and the area covered by each vegetation class (as classified based on forest type, timber volume, and/or other characteristics deemed important for that state's inventory) is calculated. A random or systematic sample of the grid points is chosen for field measurement in the second phase. The number of sampled plots falling within each vegetation class is weighted according to the total amount of land falling within that class. The field plots are permanently marked for re-measurement in subsequent inventories to provide estimates of change.

A trained field crew visits each of the plots chosen for field sampling. If the plot has been classified as nonforest (i.e., any land currently developed for non-forest uses such as residences, improved roads, industry, and city parks), the crew verifies its location and confirms the air photo land classification. If the plot is classified as forest (i.e., any land currently supporting a stand of trees at least 1 acre [2.47 ha] in size with tree cover of at least 10%, whether those trees are suitable for timber harvest or not, and not developed for a different use), the crew establishes a forest sample plot using a specific plot design and sampling protocol. If the air photo interpretation process has resulted in misclassification of that plot, then the measurements taken by the field crew are used to reclassify it. The end result of the inventory sample for forested plots is a set of plot-level measurements such as geographic coordinates, basal area, and land use classification, and a set of tree-level measurements such as species, diameter at breast height (dbh), and status (i.e., live, dead, cut). If a plot is being revisited, the number of years since the last measurement is recorded and the previous dbh for each tree in the current inventory is recorded as a separate variable in the current sample.

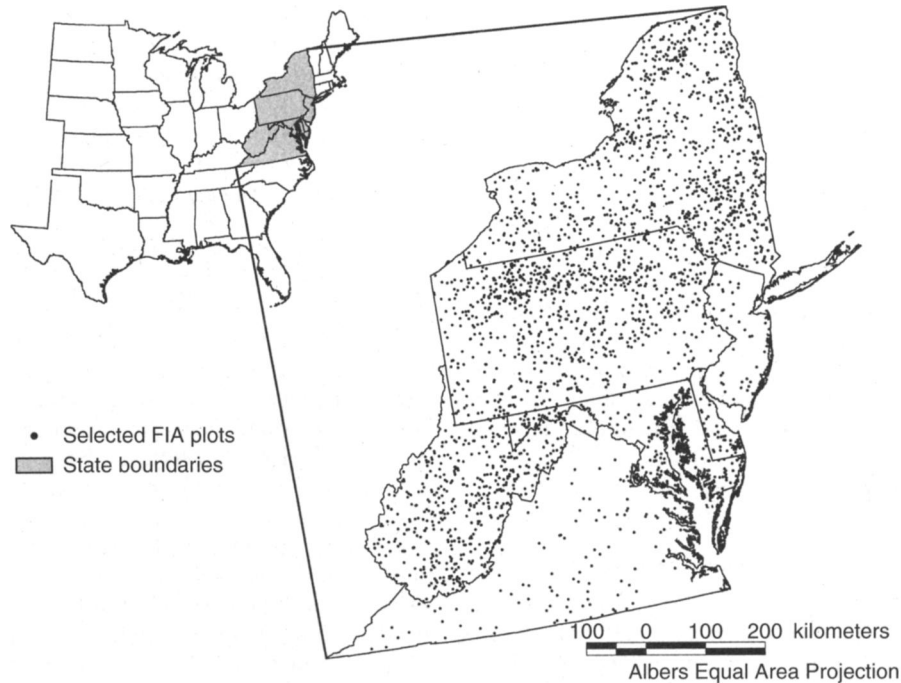


FIG. 1. Location of study region and FIA plots used for analysis.

FIA plots are designed to cover a 1-acre (2.47-ha) sample area. Various combinations of fixed- and variable-radius points are used to select trees for sampling within the area. In the past, the sample design has varied periodically through the years and from state to state. However, the FIA program has recently adopted a common plot design composed of four fixed-radius sample points 48 ft (14.6 m) in diameter with plot centers 120 ft (36.6 m) apart. Each of these fixed-radius points is overlain with two additional fixed-radius concentric sample points; one sapling 1"–5" (2.54–12.70 cm) dbh measurement point 13.6 ft (4.1 m) in diameter, and one seedling/shrub measurement point 7.4 ft (2.3 m) in diameter.

The inventory sample is designed to provide an unbiased representation of land area and forest characteristics. In addition, the inventory is required to meet sampling error standards for area, volume, and growth as specified in the Forest Service Handbook. At the state level, estimates are designed to be accurate to within 67% (± 1 SE). A 3% error for 1×10^6 acres (0.4×10^6 ha) of timberland is the maximum allowable sample error for total area, and a 5% error for 1×10^9 ft³ (28.3×10^6 m³) is the maximum allowable sample error for total volume and growth estimates of all species combined (Hansen et al. 1992, Woudenberg and Farrenkopf 1995). Larger area and volume estimates are associated with smaller error estimates, and vice versa.

Data source

County-, plot-, and tree-level forest inventory data for the eastern half of the United States are made avail-

able to the public via the Internet in the Eastwide Forest Inventory Data Base (Hansen et al. 1992).² Data for this study were obtained from this publicly available source.

Study area

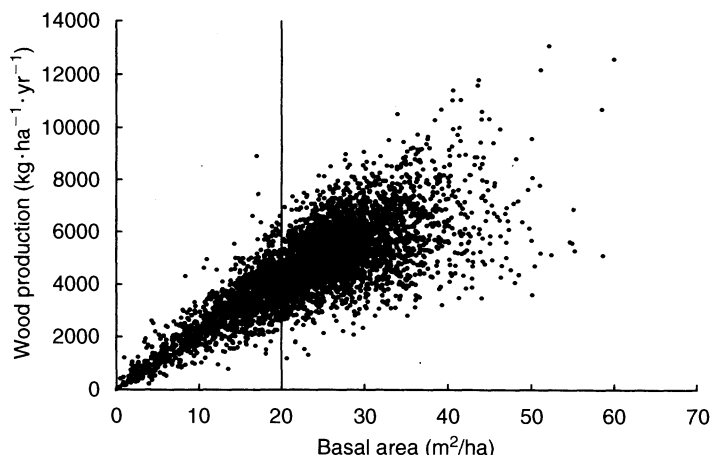
Estimates are presented here for the seven state (New York, Pennsylvania, New Jersey, Maryland, Delaware, West Virginia, Virginia) mid-Atlantic (USA) region surrounding the Chesapeake Bay watershed (Fig. 1), which extends roughly from 30° to 45° N latitude and from 73° to 83° W longitude. The plots included in this analysis are a subset of the FIA plots sampled in the region.

Choosing plots for analysis

A sample of FIA plots was selected to match closely the mature, closed-canopy conditions typically represented by most forest ecosystem process models. In particular, all plots meeting the following conditions were included in the sample; (a) measured at least twice (because of the shorter remeasurement period in southern states, plots in Virginia were included only if they had been measured three times), (b) classified as timberland (i.e., capable of producing crops [at least 20 ft³·acre⁻¹·yr⁻¹ (1.4 m³·ha⁻¹·yr⁻¹) of industrial wood] at the time of the two [or three in Virginia] most recent measurements, (c) no evidence of logging since the last measurement, (d) no evidence of damage by insects, disease, or fire since the last measurement, (e) not

² (<http://srsfia.usfs.msstate.edu/scripts/ew.htm>).

FIG. 2. Wood production vs. basal area for re-measured FIA plots meeting all but the basal-area criterion. Plots to the left of the vertical line at 20 m²/ha were not used in this analysis.



planted, and (f) closed-canopy forests, which were approximated as stands with total basal area (BA) ≥ 20 m²/ha. Preliminary analysis (Fig. 2) showed that estimated NPP is positively correlated with BA over the entire range of BA values in this sample, and 20 m²/ha was roughly the median BA value from the plots chosen based on the first five criteria.

Using these guidelines, 20 682 of the 23 322 plots in the region were excluded, leaving 2640 plots that met all six criteria (Fig. 1). Basal area values for this subset of sample plots ranged from 20.0 to 60.0 m²/ha, with a mean of 28.5 m²/ha. This sample includes $\sim 11.3\%$ of the available FIA plots in the region. This geographically distributed sample of 2640 FIA plots, however, is more representative of the region's closed-canopy forests than the very few sparsely distributed data points from ecological studies currently available for model validation in the region. Given the unbiased design of the FIA sample and the large number of sample points included in this analysis, this subset of plots provides an unbiased representation of the sample of interest; namely, closed-canopy forests in the mid-Atlantic states which have not been disturbed in the recent past. For the 2640 plots included in this analysis, plot characteristics are described in Fig. 3.

Biomass calculations

Estimates of forest biomass were made on a dry-mass basis for each plot by adding together the biomass contributions from each of the sample trees (both live and standing dead, expressed per unit area) on that plot. Aboveground biomass, above-stump biomass, and wood-only biomass values were estimated separately. Allometric regression equations relating tree mass to diameter at breast height (dbh) were used to estimate above-stump biomass values, and the remaining components were added or subtracted where appropriate.

Above-stump biomass.—The methods described by Wharton et al. (1997) and Wharton and Griffith (1998) were adapted for this study to find above-stump bio-

mass (note that the previous authors excluded the stump from their estimates of aboveground biomass).

Equations from Maine (Young et al. 1980) were used to estimate above-stump biomass for all evergreen species, red maple (*Acer rubrum* L.), yellow birch (*Betula lenta* L.), and quaking aspen (*Populus tremuloides* Michx.); equations from West Virginia (Wiart et al. 1977) were used for Appalachian deciduous species such as hickory (*Carya* spp.), yellow poplar (*Liriodendron tulipifera* L.), black cherry (*Prunus serotina* Ehrh.), and oak (*Quercus* spp.) species; and equations from New York (Monteith 1979) were used for sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), and white ash (*Fraxinus americana* L.) (see Appendix A). Species for which regression equations did not exist were matched with species for which equations were available (key species) by comparing wood densities, as described in Wharton and Griffith (1993, 1998) and Wharton et al. (1997) (see Appendix B). We assumed that the equations typically used for live trees were appropriate for standing dead trees as well. Above-stump biomass is defined here as

$$\text{ASB} = S + \text{Br} + \text{Tg} + \text{Fol} \quad (1)$$

(all units in kg), where ASB = above-stump tree biomass, *S* = stem biomass, Br = branch biomass (live and dead), Tg = twig biomass, and Fol = foliage biomass. Stump height was either 6" (15.24 cm) (Wiart et al. 1977, Young et al. 1980), or 12" (30.48 cm) (Monteith 1979).

The Young et al. (1980) and Monteith (1979) equations for above-stump biomass include foliage in their biomass estimates, but the Wiart et al. (1977) equations do not. To find foliage biomass for hickory, yellow poplar, black cherry, and oak species, we modified ratios originally developed from the Young et al. (1980) equations by Wharton and Griffith (1993, 1998) and Wharton et al. (1997). The ratios relate above-stump biomass to foliage biomass for evergreen and decid-

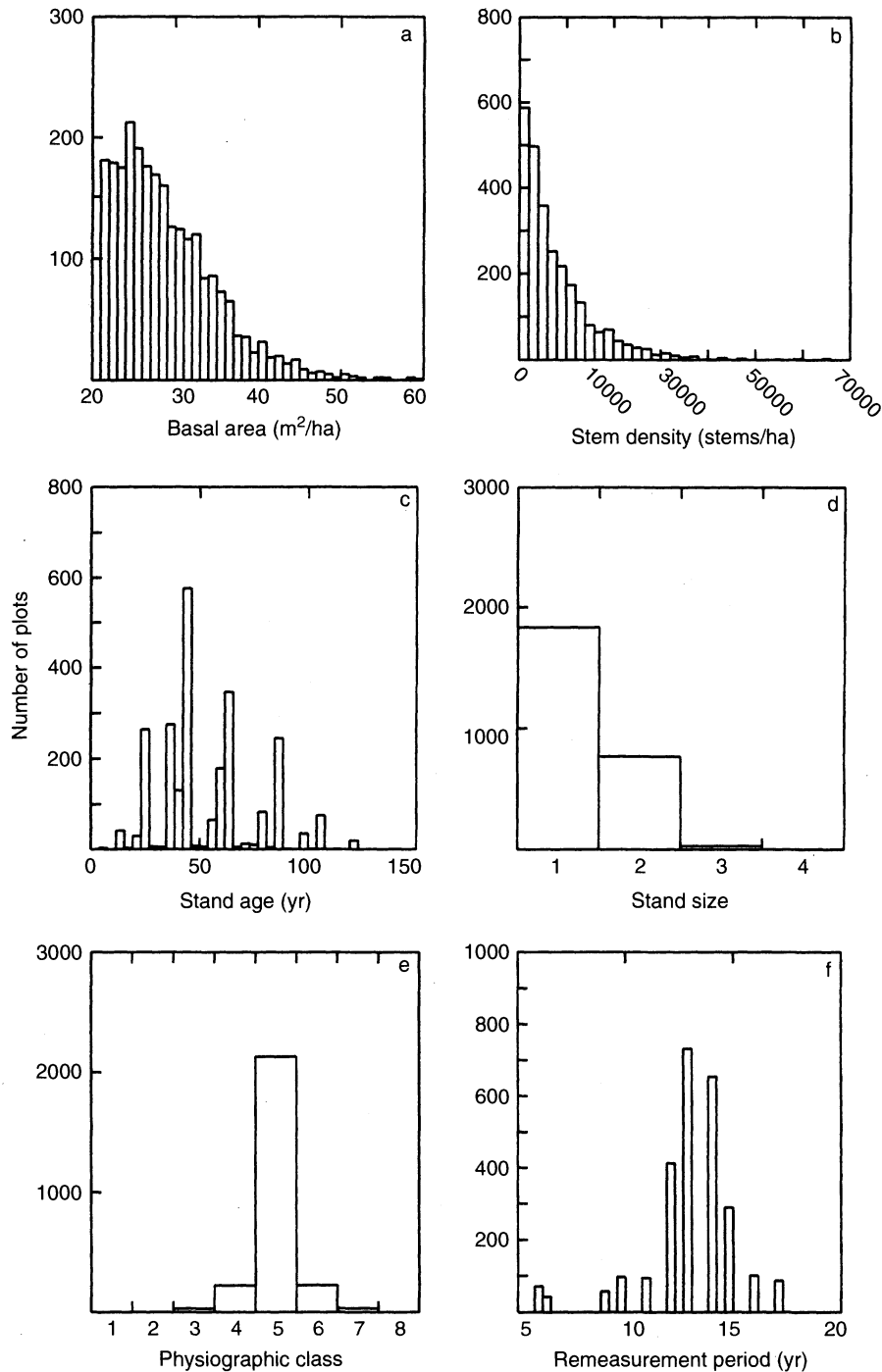


FIG. 3. Characteristics of sample plots, as described in the FIA Eastwide Data Base (Hansen et al. 1992) or calculated from tree-level data. (a) Basal area (m²/ha), calculated from tree-level data. (b) Stem density (stems/ha), calculated from tree-level data. (c) Stand age, taken from the FIA Eastwide Data Base for those plots for which age data exist. (d) Stand size: 1 = Sawtimber (stands with tree cover of at least 10%, where >50% of the stems are 5" dbh or larger, and the number of sawtimber size trees is equal to or greater than the number of poletimber size trees); 2 = Poletimber (same as "sawtimber," except that the number of sawtimber size trees is less than the number of poletimber size trees); 3 = Seedling/sapling (stands with tree cover of at least 10% where at least 50% of the stems are smaller than 5" dbh). (e) Physiographic class: 3 = Xeric (very dry soils where excessive drainage seriously limits both growth and species occurrence); 4 = Xeromesic (moderately dry soils where excessive drainage limits growth and species occurrence to some extent); 5 = Mesic (deep, well-drained soils where growth and species occurrence are limited only by climate); 6 = Hydromesic (moderately wet soils where insufficient drainage or infrequent flooding limits growth and species occurrence to some extent); 7 = Hydric (very wet sites where excess water seriously limits both growth and species occurrence). (f) Remeasurement period (number of years between remeasurements).

uous species based on tree size class (see Appendix C). On average, evergreen foliage comprises from 7.7% to 11.3% and deciduous foliage comprises from 1.2% to 3.5% of above-stump biomass.

Aboveground biomass.—Aboveground biomass is defined here as:

$$AGB = ASB + St \quad (2)$$

(all units in kg), where AGB = aboveground tree biomass, ASB (see Eq. 1) = above-stump biomass, and St = stump biomass. To find stump biomass, tree diameters inside and outside the bark were estimated from dbh at a height halfway up the stump using species-specific equations as described by Raile (1982) (see Appendix D). From these diameters we computed total stump volume (outside bark) and stump wood volume (inside bark) assuming the stump was cylindrical. Stump bark volume was found by difference. Stump wood and bark volumes were multiplied by specific gravity (see Appendix D) and added together to find total stump biomass. For the 2640 plots included in this analysis, we calculated that, on average, the biomass in stumps 6" (15.24 cm) tall comprised 2.5% of aboveground biomass and accounted for 2.3% of aboveground wood production. To find the aboveground wood biomass estimates used for NPP calculations, foliage biomass was calculated using the ratio described above (see *Methods: Biomass calculations: Above-stump biomass*) where appropriate, and subtracted from the total (see also Appendix C)

Total wood biomass.—Total wood biomass for each tree (i.e., above- and belowground wood biomass) is defined here as

$$TW = ASW + StR \quad (3)$$

(all units in kg), where TW = total tree wood biomass, ASW = above-stump wood biomass (defined as S + Br + Tg), and StR = stump plus coarse root biomass (stump to 6-inch height). The Young et al. (1980) equations predicting total tree biomass (including coarse roots ≥ 1 -inch diameter, as defined previously in Young et al. 1964) were used directly for evergreen species as well as for red maple, yellow birch, and quaking aspen. For the other species, StR was found using ratios which were developed by Wharton and Griffith (1993, 1998) and Wharton et al. (1997) based on the Young et al. (1980) equations, and modified for this study. The ratios relate StR to TW for evergreen and deciduous species based on tree size class (see Appendix C for modifications). On average, StR accounts for between 20.3% and 20.4% of complete tree biomass for evergreen species, and between 18.4% and 21.1% of complete tree biomass for deciduous species. Where appropriate, foliage biomass was calculated using ratios based on above-stump biomass (see Appendix C), and subtracted from the total to find the biomass of woody tissue only.

Total biomass.—The total tree wood biomass (TW)

estimates (see Eq. 3) exclude both foliage and fine root biomass. Total forest biomass (including foliage and fine roots) was calculated on a per-unit-area basis and is defined here as

$$TBD = AGBD + BGBD \quad (4)$$

(all units in Mg/ha), where TBD = total biomass density, AGBD = aboveground biomass density (found as the sum of AGB for each plot), and BGBD = belowground biomass density. BGBD, including coarse plus fine roots, was found on a per-unit-area basis from AGBD using the equation developed by Cairns et al. (1997):

$$BGBD = \exp[-1.085 + 0.9256 \times \ln(AGBD)]. \quad (5)$$

Net primary production (NPP) calculations

Net primary production (NPP) is defined as the production of organic matter by vegetation per unit area per year. It is defined here as

$$NPP = TWP + L + R \quad (6)$$

(all units in $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$), where NPP = total NPP, TWP = total wood production (both above- and belowground), L = fine litterfall (this term includes foliar production), and R = fine root production. Fine litterfall and fine root production are not measured at FIA plots. Wood production (wood biomass increment) can be derived (using allometric equations) most directly from the data collected by FIA units and is thus the most reliable variable derived from this data set.

We found mean annual aboveground wood production for each tree as

$$AWP = [AGW(t_1) - AGW(t_0)]/[t_1 - t_0] \quad (7)$$

where AWP = aboveground wood production (kg/yr) and AGW = aboveground wood biomass (defined as ASW + St; kg), and where the difference between t_1 and t_0 in the denominator is expressed in years. Trees that died during the measurement interval were included in this calculation. Aboveground plus belowground wood production for each tree (again, including both live trees and those that died during the measurement interval) was found as

$$TWP = [TW(t_1) - TW(t_0)]/[t_1 - t_0] \quad (8)$$

where TWP = aboveground plus belowground wood production (kg/yr) and TW = total tree wood biomass (kg; see Eq. 3), and where the difference between t_1 and t_0 in the denominator is expressed in years. In both equations, t_1 refers to the most recent inventory, and t_0 refers to the inventory previous to t_1 . Aboveground and total tree-wood biomass estimates for current con-

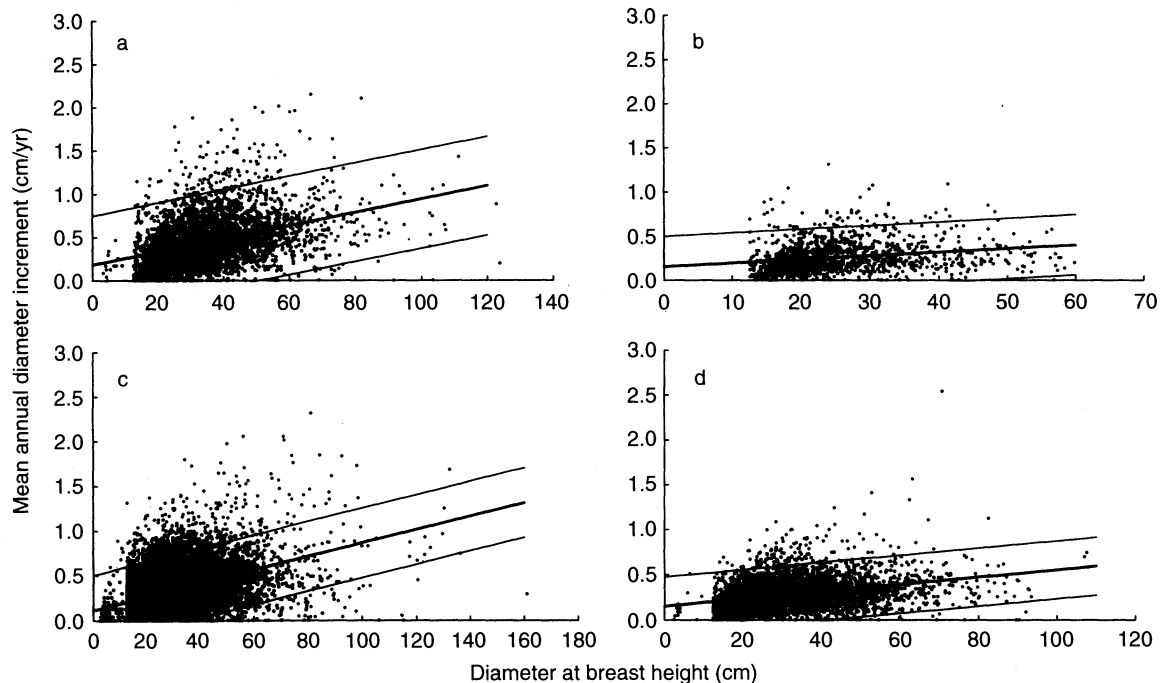


FIG. 4. Empirically derived algorithms relating the increment in diameter at breast height (dbh) to current dbh (t_1) by species group (see Appendix B for species group designations, and Appendix E for list of equation parameters) for four of the species groups analyzed. (a) Species group 4: red pine and Eastern white pine. (b) Species group 6: spruce and fir species. (c) Species group 17: red maple and silver maple. (d) Species group 18: American beech.

ditions (t_1) were found from current dbh on a tree-by-tree basis using species-specific regression equations.

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 sample tree. Dbh estimates for each tree at the previous inventory (t_0) were found as described in the following two paragraphs; biomass estimates were then found from dbh at t_0 using the methods as described for t_1 .

Dbh measurements existed for two consecutive measurement periods for 85 669 live stems. Based on the diameter measurements for these trees, we constructed a set of simple linear algorithms relating mean annual tree diameter increment to current tree diameter by general species group (see Appendices B, E). The positive slopes of the curves relating diameter increment to diameter (Fig. 4) are consistent with the silviculture literature. In closed-canopy stands, larger trees in dominant crown positions capture more stand-level resources such as light, water, and nutrients and thus attain diameter growth more quickly than smaller, suppressed trees (Trimble 1969, Smith 1986). As trees grow larger, of course, their respiratory load increases; if leaf area (and thus photosynthetic capacity) remains constant, diameter growth rates should eventually decline with increasing diameter. There was no evidence of this declining trend in the tree-level data. Further-

more, it is unlikely that the stands described here contain such large trees, as mean stand age was 53.6 ± 22.4 yr. These curves integrate over a large area and a variety of different site and stand conditions; the substantial variability about the regression lines is due most likely to within- and between-stand variability in site types and stand density.

These algorithms relating dbh increment to current dbh were used to find the mean annual dbh increment for trees lacking a dbh measurement at t_0 . Of 133 723 total stems larger than 1" (2.54-cm) dbh measured in this subset of sample plots in the current inventory, there were 43 784 live and 2337 dead ongrowth or nongrowth stems. These stems were large enough to be measured in the current inventory, but were either (a) too small to have been measured in the previous inventory (ongrowth), or (b) above the diameter limit for sampling in the previous inventory but not included in the previous sample due to plot design changes (nongrowth) (Birdsey and Schreuder 1992). While ongrowth and nongrowth stems totaled $\sim 35\%$ of the measured stems in the current inventory, they accounted for 70% of stems on a per-hectare basis.

Because we apply modeled or measured previous diameter and biomass values to all trees in the current sample, we do not quantify net biomass increments and losses between inventories at the aggregate county level, as is done by Brown and Schroeder (1999). Instead, we calculate biomass increment tree-by-tree on a per-

plot basis, making simple assumptions to estimate diameter growth for that portion of the sample where data are missing. Using this approach we constrain our estimates based on current conditions, and we are certain not to overlook the production contributed by any tree standing in the current sample. To quantify the uncertainty introduced by modeling diameter growth, we fitted curves to the upper and lower 95% prediction intervals for the diameter growth algorithms by species group (Fig. 4; also see Appendix E) and used these diameter growth algorithms, in addition to the algorithms representing mean diameter growth, to estimate NPP.

We assumed that dead stems had died halfway through the inventory period. The diameter of dead trees at t_0 (cm) was found as:

$$\begin{aligned} \text{dbh at } t_0 & \\ &= \text{dbh at } t_1 \\ &\quad - [(\text{average increment}) \\ &\quad \times (\text{remeasurement period length})/2] \end{aligned} \quad (9)$$

where the mean diameter increment (cm) was computed for each stem using the diameter growth equations and where the remeasurement period length was expressed in years. The diameter of ongrowth and nongrowth trees at t_0 was found using a similar equation:

$$\begin{aligned} \text{dbh at } t_0 & \\ &= \text{dbh at } t_1 \\ &\quad - [(\text{average increment}) \\ &\quad \times (\text{remeasurement period length})]. \end{aligned} \quad (10)$$

If these equations resulted in a negative number, dbh (and thus biomass) at t_0 was set to zero.

Litterfall and fine root production.—To compare our NPP estimates based on the FIA data set with estimates generated from models and found in the literature, we made simple assumptions about litterfall and fine root production to predict total NPP values. Aboveground NPP was computed as

$$\text{ANPP} = \text{AWNPP} + L \quad (11)$$

(all units in $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$), where ANPP = aboveground NPP, AWNPP = aboveground wood production, and L = annual fine litterfall (see Eq. 6). Coarse woody debris production was not accounted for. Total NPP was found using the common assumption that fine root production equals fine litterfall (Raich and Nadelhoffer 1989), such that

$$\text{NPP} = \text{AWNPP} + 2 \times L \quad (12)$$

(all units in $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$), where NPP (as defined in Eq. 6) = total NPP, and TAWNPP = aboveground and belowground (total tree) wood production on a per-unit-area basis.

We assumed constant litterfall values for general forest types. Such an assumption may overestimate litterfall for younger stands, but is not unreasonable for closed-canopy forests like the ones studied here, since leaf area index and litterfall tend to reach a maximum fairly quickly after disturbance (Marks 1974). We obtained fine litterfall data from the database compiled by M. Post, E. Matthews, E. Holland, J. Sulzman, and R. Stauffer (*personal communication*) for plots falling within the region studied here. These investigators have organized their litterfall data by vegetation types, as defined by Matthews (1983); we assigned each FIA plot to one of the Matthews vegetation classes using the forest type group classification assigned to that FIA plot. The fine litterfall data and forest type group assignments for the Matthews vegetation classes were as follows: temperate/subpolar evergreen needle-leaved forest ($3.78 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, $n = 11$, $\text{SD} = 2.20$) was assigned to white-red-jack pine, longleaf-slash pine, loblolly-shortleaf pine, and spruce-fir types; cold-deciduous forest with evergreens ($5.32 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, $n = 4$, $\text{SD} = 3.04$) was assigned to the oak-pine type; and cold-deciduous forest without evergreens ($4.04 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, $n = 33$, $\text{SD} = 1.50$) was assigned to the remaining hardwood types.

To provide the widest possible upper and lower bounds on our estimates of ANPP in closed-canopy stands and to quantify the sensitivity of these estimates to modeled parameters, we calculated mean ANPP by forest type using three combinations of variables; (a) mean diameter growth algorithms combined with mean litterfall values, (b) the lower 95% prediction interval diameter growth algorithms combined with the lower standard deviation bound on litterfall (i.e., mean litterfall -1 SD), and (c) the upper 95% prediction interval diameter growth algorithms combined with the upper standard deviation bound on litterfall (i.e., mean litterfall $+1$ SD).

Because they are based on measurements made more than a decade apart, the NPP estimates presented here provide an integrated representation of conditions for that time period. These estimates do not include measures of seedling (<2.54 -cm dbh) and shrub production. Based on the work of Wharton et al. (1997) in New York and Wharton and Griffith (1998) in Maine, it is likely that this exclusion has biased our results downward by 3% to 5%.

Spatial analysis

The FIA sample is most reliable when statistics are computed and aggregated for large geographic units such as a county or state (e.g., see Frieswyk and DiGiovanni [1990] and Alerich and Drake [1995]). However, process models are typically parameterized to respond to spatial variability in land cover and environmental conditions, and thus their predictions are often presented as gridded maps, using grid cells of some uniform size. To present these model validation

TABLE 1. Total tree biomass, total wood-biomass increment, and minimum, mean, and maximum aboveground NPP by forest type for the mid-Atlantic region as found from selected FIA plots.

Forest type group description	FIA plots (no.)	Total tree biomass (Mg/ha)	Aboveground tree biomass (Mg/ha)
Oak-hickory	1132	244.2 (63.8) ^d	199.0 (52.8) ^d
Maple-beech-birch	964	253.9 (64.7) ^e	207.0 (53.5) ^e
White-red-jack pine	187	225.4 (66.7) ^{cd}	183.5 (55.0) ^{cd}
Oak-pine	106	199.8 (52.8) ^b	162.3 (43.6) ^b
Loblolly-shortleaf pine	94	156.9 (37.2) ^a	127.0 (30.5) ^a
Elm-ash-cottonwood	59	223.6 (67.2) ^{bcd}	182.0 (55.5) ^{bcd}
Spruce-fir	43	185.3 (48.9) ^{ab}	150.4 (40.3) ^{ab}
Aspen-birch	38	203.8 (59.8) ^{bc}	165.6 (49.3) ^{bc}
Oak-gum-cypress	16	291.1 (77.6) ^e	237.8 (64.2) ^e
Longleaf-slash pine	1	253.3	206.4

Notes: Values are presented as means (with 1 SD in parentheses). Values followed by the same superscript letter within a column are not significantly different from one another (ANOVA with the Tukey pairwise mean comparison test; $P < 0.05$).

† Found using mean $-$ 1 SD litterfall values and equations fit to the lower 95% prediction interval of diameter increment for trees lacking a dbh measurement at t_0 .

‡ Found using mean litterfall values and equations predicting the mean diameter increment for trees lacking a dbh measurement at t_0 .

§ Found using mean $+$ 1 SD litterfall values and equations fit to the upper 95% prediction interval of diameter increment for trees lacking a dbh measurement at t_0 .

data at a scale appropriate for comparison with process model predictions, we aggregated the plot-based estimates of biomass and NPP to the $0.5^\circ \times 0.5^\circ$ grid scale.

A weighted average for each grid cell was computed from the per-unit-area biomass and NPP estimates developed for each plot, based on the area expansion factor describing the number of acres represented by that plot. This was accomplished for each $0.5^\circ \times 0.5^\circ$ grid cell using plots whose centers fell within that cell. The number of plots falling within a grid cell varied from one to 46; the accuracy of the biomass and NPP estimates at the individual grid cell level is likely to vary with the number of plots represented. To quantify the variability in these spatially explicit biomass and NPP estimates, we computed the within-grid-cell variance for each of the $0.5^\circ \times 0.5^\circ$ grid cells containing biomass and NPP estimates.

To perform a true analysis of within-grid-cell variance based on these weighted biomass and NPP values would require recomputation of the plot-level area expansion factors at the 0.5° scale from the data used to select plots in the first phase of sampling (Chojnacky 1998). Instead of this time consuming analysis, we chose a simpler approach. For this study, the coefficient of variation (CV) on the weighted averages of biomass and NPP for each grid cell was computed using the weighted CV algorithm in SAS 6.12 (SAS Institute, Cary, North Carolina, USA), which multiplies each record by its corresponding weight variable to derive an appropriate overall CV value (DiIorio 1991). Plot-level weights were computed by dividing the area expansion factor for each plot by the minimum expansion factor assigned to those plots falling within each $0.5^\circ \times 0.5^\circ$ grid cell. The minimum weight on each plot was thus 1.00 and the maximum weight was 5.75, with median and mean of 1.18 and 1.43, respectively.

Additional data sets

Model predictions.—Estimates of total NPP and total biomass developed at the $0.5^\circ \times 0.5^\circ$ scale by the biogeochemistry models included in the second phase of the VEMAP activity (Schimel et al. 2000) were compared against the FIA-based NPP and biomass estimates. For each $0.5^\circ \times 0.5^\circ$ grid cell, model results developed for the years from 1980 to 1993 were averaged. This subset of 14 yr was chosen for comparison because it corresponds most closely with the FIA measurement period used for this study. The $0.5^\circ \times 0.5^\circ$ grid cell estimates developed from FIA data were overlain with the vegetation data set from the VEMAP project to stratify the FIA-based $0.5^\circ \times 0.5^\circ$ estimates by forest type for comparison with the model estimates. Biomass and NPP estimates from this study were converted to units of carbon (C) for comparison with model estimates using 0.475 as the proportion C in biomass (Raich et al. 1991).

RESULTS

Forest biomass by forest type

Aggregated by forest type, maximum current biomass values ranged from 157 Mg/ha in loblolly-shortleaf pine forests to 291 Mg/ha in oak-gum-cypress forests. In this region, oak-gum-cypress includes swamp chestnut oak-cherrybark oak, sweetgum-Nuttall oak-willow oak, sugarberry-American elm-green ash, and sweetbay-swamp tupelo-red maple types (Table 1). Total biomass for closed-canopy stands averaged 248 and 200 Mg/ha in hardwood and softwood forest types, respectively. Mean aboveground biomass values ranged from 127 Mg/ha in loblolly-shortleaf pine forests to 238 Mg/ha in the oak-gum-cypress type,

TABLE 1. Extended.

Wood-biomass increment ($\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$)	Aboveground NPP ($\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$)		
	Minimum†	Mean‡	Maximum§
568.8 (135.7) ^d	607.6 (123.4) ^d	868.3 (111.1) ^d	1108.0 (163.4) ^b
544.3 (128.7) ^c	590.2 (110.3) ^c	847.8 (104.7) ^c	1085.6 (143.5) ^b
480.8 (113.7) ^b	515.2 (104.1) ^b	805.0 (104.2) ^b	1073.9 (153.3) ^b
488.5 (120.4) ^b	515.3 (113.0) ^b	803.8 (99.8) ^b	1073.9 (171.7) ^b
448.7 (173.2) ^{ab}	504.4 (175.9) ^{ab}	777.6 (145.6) ^{ab}	1056.0 (209.8) ^{ab}
588.2 (168.7) ^d	637.2 (155.7) ^d	886.9 (140.3) ^d	1114.2 (165.7) ^b
389.0 (108.7) ^a	441.2 (89.8) ^a	719.6 (87.2) ^a	968.0 (151.8) ^a
563.0 (124.5) ^{cd}	569.7 (115.4) ^b	868.9 (103.0) ^d	1129.2 (141.2) ^b
659.3 (189.1) ^d	556.6 (155.7) ^b	942.4 (154.6) ^d	1322.7 (229.3) ^c
545.3	510.5	851.6	1161.6

and averaged 163 and 200 Mg/ha in softwood and hardwood forest types, respectively.

Forest biomass at the $0.5^\circ \times 0.5^\circ$ scale

Maximum current aboveground biomass at the $0.5^\circ \times 0.5^\circ$ scale ranged more widely, from 81 to 266 Mg/ha (Fig. 5a) with a mean of 187 Mg/ha. Total biomass values also ranged widely, from 101 to 326 Mg/ha (Fig. 5b) with a mean of 230 Mg/ha. The lowest biomass values occurred in southern New Jersey and central Virginia, while a pocket of the highest values were found in the mountains of eastern West Virginia. Nine grid cells at the perimeter of the region included only one plot; coefficients of variation were computed for the remaining 200 $0.5^\circ \times 0.5^\circ$ grid cells. Within-grid-cell weighted CV's ranged from 2% to 67% for aboveground biomass and total biomass (Fig. 5), with no clear spatial pattern aside from selected high values in areas characterized by dense human settlement or represented by relatively few FIA data points.

Forest NPP

Wood production by forest type.—Closed-canopy aboveground plus belowground wood production ranged from 389 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in spruce–fir forests to 659 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in oak–gum–cypress forests (Table 1). Wood production averaged 559 and 460 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in hardwood and softwood forests, respectively.

Aboveground NPP by forest type.—Mean ANPP (computed using mean values for litterfall and tree diameter growth) ranged from 720 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in spruce–fir forests to 942 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in oak–gum–cypress forests (Table 1). Mean ANPP values averaged 860 and 786 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ overall in hardwood and softwood forest types, respectively.

Ongrowth and nongrowth trees (i.e., trees for which dbh at t_0 was modeled using algorithms relating dbh at t_1 to mean annual diameter increment) contributed 26% of aboveground wood production (expressed on a per-hectare basis). The combined impact of uncertainty in litterfall values and diameter growth estimates on ANPP estimates was substantial. The minimum ANPP

estimates amounted to between 42% and 57% of the maximum ANPP estimates for all forest types (Table 1), though differences between the mean and minimum or maximum estimates averaged $\sim 30\%$ of the mean. These minimum and maximum mean values for ANPP provide upper and lower bounds on reasonable ANPP values for closed-canopy forests in the mid-Atlantic region. However, due to the large number of FIA sample plots used to develop these estimates, we have accurately represented both mean diameter growth increment and mean wood production for the closed-canopy forest sample of interest despite substantial tree-to-tree variation in diameter growth and plot-to-plot variation in biomass increment. We cannot make similar statements about litterfall data, as very few measurements of litterfall exist for this or any other region. Instead, we suggest that the bounds provided by two standard deviations about the mean, especially for this case where the sample size is small, are reasonable upper and lower limits for litterfall in these closed-canopy stands.

We further emphasize that while this exercise is useful for examining the sensitivity of these predictions to modeled parameters and for providing reasonable upper and lower limits on model estimates of forest productivity, applying the upper or lower prediction intervals for tree diameter growth (Fig. 4) to all trees lacking a dbh measurement at t_0 would be unrealistic when applied to regional-scale estimates. The upper limits on diameter growth predictions, for example, would be accurate at the regional scale only if 95% of the stems lacking a dbh measurement at t_0 were indeed growing at their species-specific maximum for the region. On the other hand, selected plots are indeed experiencing the maximum regional productivity; for these plots, the maximum ANPP estimate presented does apply. For the remaining portions of this analysis focusing on regional-scale trends in NPP, we will present mean NPP estimates.

Wood production at $0.5^\circ \times 0.5^\circ$ scale.—The range of total tree wood production values at the $0.5^\circ \times 0.5^\circ$ scale was wider, from 254 to 1050 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ with a

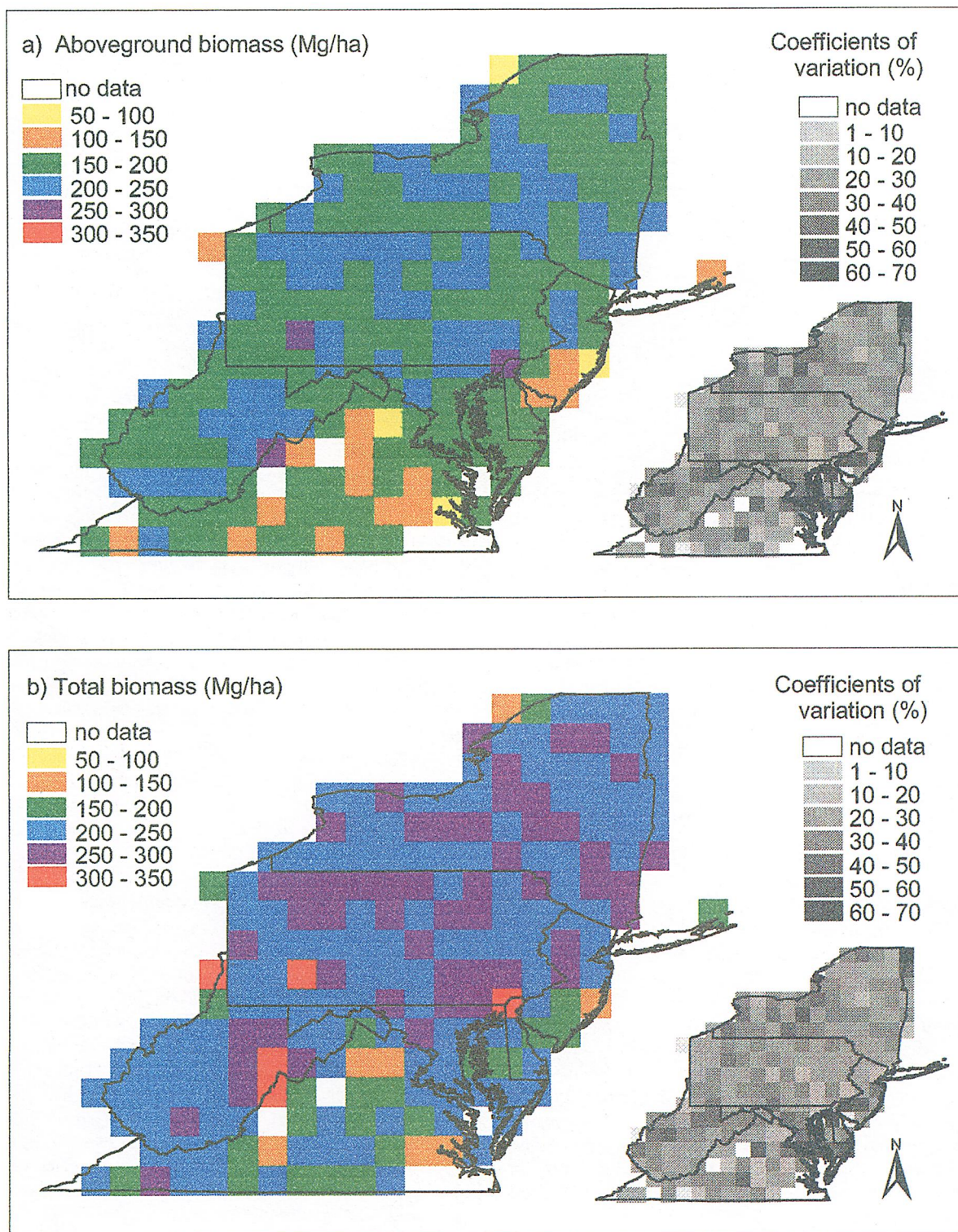


FIG. 5. Biomass estimates at the 0.5° scale, together with associated coefficients of variation, derived from FIA data: (a) aboveground and (b) total.

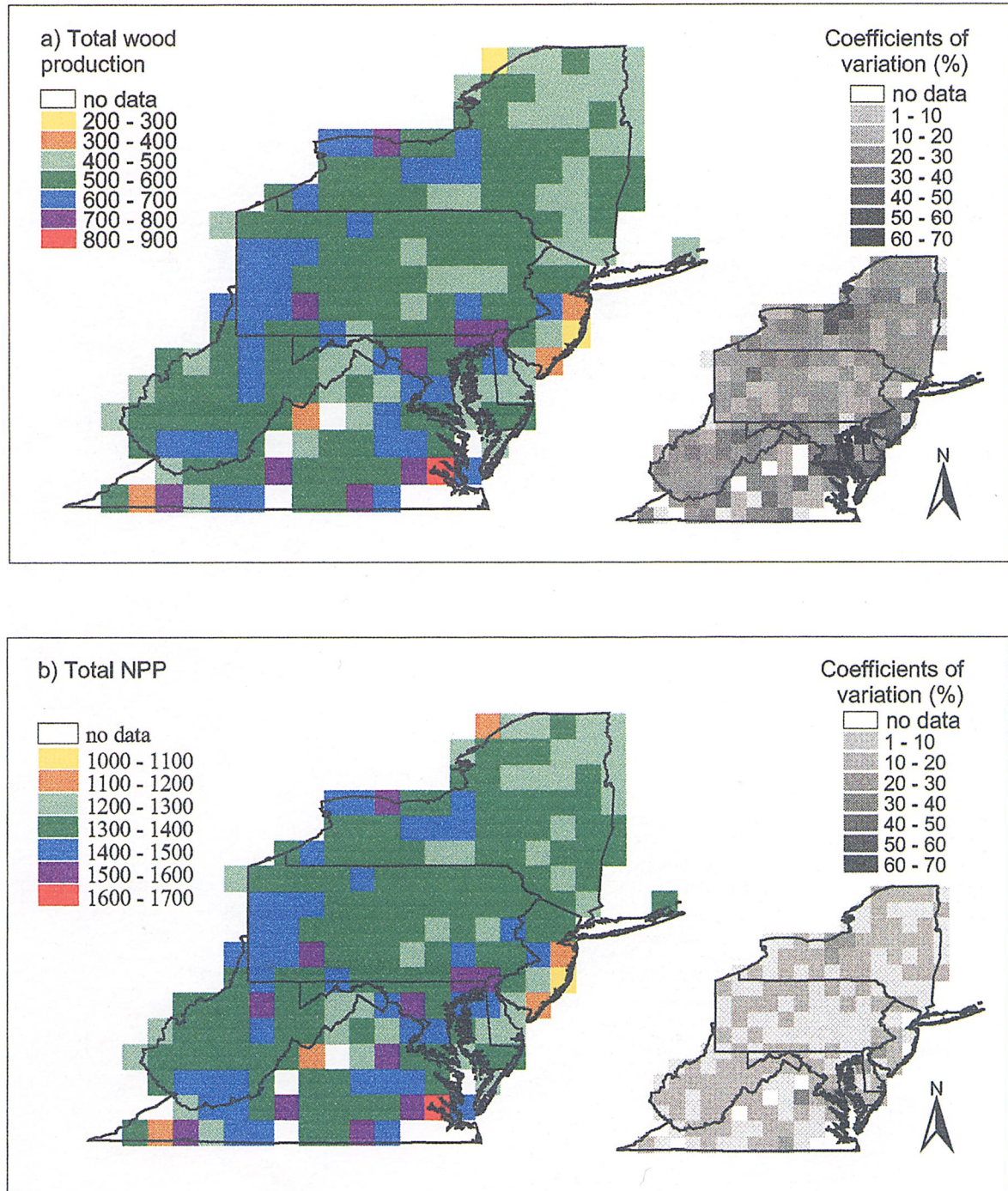


FIG. 6. (a) Total wood production ($\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) and (b) total NPP estimates ($\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) at the 0.5° scale, together with associated coefficients of variation, derived from FIA data.

mean of $550 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ (Fig. 6a). The lowest wood production values occurred in the northern parts of New York and in southeastern New Jersey, while higher production values were more likely toward western Pennsylvania, western New York, and parts of Virginia (Fig. 6a).

Total production at the $0.5^\circ \times 0.5^\circ$ scale.—Total

NPP values at the $0.5^\circ \times 0.5^\circ$ scale ranged from 1062 to $1858 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, with spatial patterns similar to those for wood production (Fig. 6b). Within-grid-cell cv's ranged from 0.1% to 70.6% for wood production, and from 0.03% to 32.7% for total NPP (Fig. 6). No clear spatial pattern in within-grid-cell variability was present, aside from selected high values in areas charac-

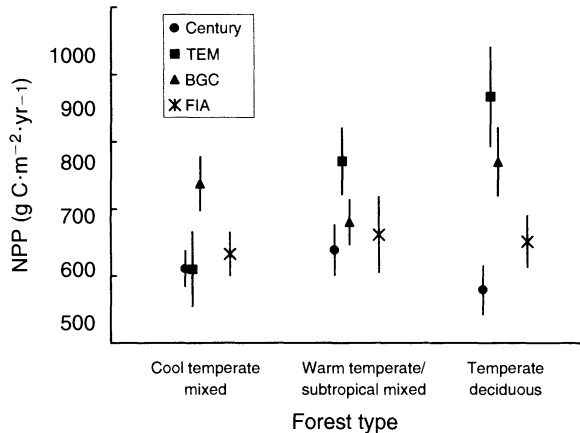


FIG. 7. Comparisons by VEMAP vegetation type between FIA-based total NPP estimates and estimates from biogeochemistry models included in the VEMAP2 comparison. FIA = FIA-based estimates from this study; BGC = Biome-BGC; TEM = Terrestrial Ecosystem Model. Each symbol represents $0.5^\circ \times 0.5^\circ$ estimates averaged by VEMAP vegetation type.

terized by dense human settlement or represented by relatively few FIA data points.

Comparisons with model estimates

NPP estimates from Century (Parton et al. 1987, 1988, 1993) averaged 7% lower than the FIA estimates, while Biome-BGC (Hunt and Running 1992, Running and Hunt 1993) and TEM (Raich et al. 1991, McGuire et al. 1992, 1995, 1997) estimates averaged 14% and 17% higher, respectively (Fig. 7). Total biomass carbon (C) estimates from Century, Biome-BGC, and TEM averaged 1%, 392%, and 63% higher than the FIA-based estimates, respectively (Fig. 8).

Comparisons with published data

Aboveground biomass values for hardwoods reported in the ecological literature ranged from 31.9 to 431 Mg/ha for stands from 10 to 340 yr old (Table 2). Clearly, substantial variability in biomass can be expected, based most likely on physiographic conditions, land use and management history, stand age, species composition, and climate. Still, the mean aboveground biomass value developed from inventory plots from this study for hardwood forests (200 Mg/ha) is well within this range, and is similar to the mean values expected based on the published data for mature hardwood stands (from ~160 to 280 Mg/ha) (Table 2). The two published ANPP values for hardwoods in the region were measured for stands in wet sites and varied less widely, from 615 to 1537 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$. However, the range in ANPP values (from minimum to maximum) for hardwood forest types in this study (from 557 to 1323 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) (Table 1) is included almost entirely between the two published values. The range in mean ANPP values for hardwoods (from 848 to 942

$\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) was smaller, but was also included within the two published values.

Aboveground biomass values from the literature for pine stands (both planted and naturally regenerating) ranged from 46.2 to 233.1 Mg/ha for stands 17 to 80 yr old (Table 2). The mean aboveground biomass value in pine stands from this study was ~170 Mg/ha, again well within the range for mature forest stands (from ~50 to 200 Mg/ha) expected from the published data (Table 2). The published ANPP values for pine stands varied less widely, from 670 to 1470 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$. And as with the hardwood stands, the range of minimum and maximum ANPP values for pine forest types in this study (from 504 to 1162 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) (Table 1) was included almost entirely within the published range of ANPP values for pine stands. Finally, the range of mean ANPP values for pine stands (from 778 to 852 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) was also well within the range of the published estimates.

For spruce and fir stands, published biomass values ranged from 32.5 to 196.9 Mg/ha for stands from 10 to 60 yr old (Table 2). The value of 150 Mg/ha for mature spruce–fir stands in this study (Table 1) corresponds to the highest portion of the published range. The mean ANPP value from this study of 720 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ is almost identical to the published value of 710 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$.

DISCUSSION

Sources of uncertainty

Errors in any analysis using FIA data are potentially associated with sampling, measurement, and regression (Cunia 1987). The FIA sampling designs ensure an unbiased representation of the landscape, thus minimizing sampling error. We assume that in selecting plots, we have retained the unbiased nature of the FIA

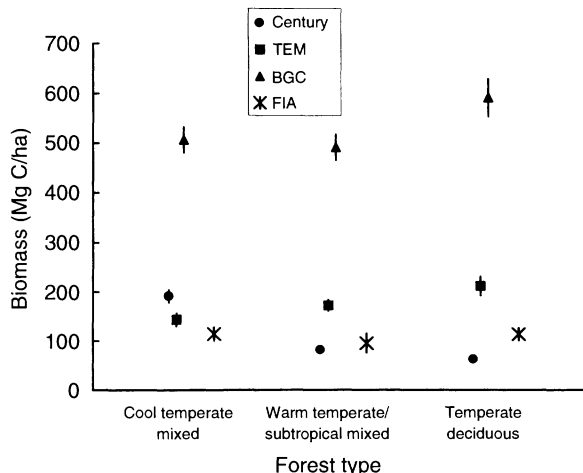


FIG. 8. Comparisons by VEMAP vegetation type between FIA-based total biomass estimates and estimates from biogeochemistry models included in the VEMAP2 comparison. Abbreviations are as in Fig. 7.

sample. In other words, the plots used for this analysis are an unbiased sample of the existing population of mid-Atlantic closed-canopy forests that have not been disturbed in the recent past. Measurement error is unavoidable in any field sampling effort, but is minimized in FIA sampling by training field crews annually and by sending experienced crews periodically to check their work. Regression error was potentially introduced by applying biomass regressions to regions in which they were not developed. Since felling trees and making biomass measurements on each stem would be impossible at the regional scale, however, for large-scale biomass analyses the allometric regression approach is the best method currently available.

An additional source of uncertainty in this analysis relates to modeling diameter growth for ongrowth and nongrowth trees. The curves specific to species groups that are used to develop estimates of dbh (t_0) for ongrowth and nongrowth trees, however, are based on measured data from hundreds to thousands of trees in the study area for which two dbh measurements were recorded. Variability about these regressions is apparent, but the very large number of sample points ensures that these algorithms accurately represent the average relationship between diameter and diameter increment for each species group in the region.

A final source of uncertainty specific to this analysis relates to the spatial extrapolation from plots to $0.5^\circ \times 0.5^\circ$ cells. The coefficients of variation on biomass and NPP estimates within $0.5^\circ \times 0.5^\circ$ grid cells range from 0.03% to 70.6%. High uncertainty is associated with grid cells represented by very few plots, and vice versa. The scarcity of FIA plots in certain grid cells (and the resulting uncertainty of biomass and NPP estimates in those grid cells) is an inevitable artifact of the selection procedure used to limit this analysis to FIA plots meeting certain criteria for comparison with process model estimates.

Comparisons with published measurements

Whittaker and Marks (1975) describe a linear relationship between aboveground biomass and ANPP for a series of climax or near-climax stands in a variety of forest types. Rearranging the dependent and independent axes from their original equation to predict ANPP from current biomass, duplicating the $\pm 100 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ they drew to approximate bounds on the relationship, and calculating a similar regression (with 95% confidence intervals) based on our data, the shape of the biomass—ANPP relationship using FIA-based data from this study is similar to that drawn based on their analysis of classic ecological studies (Fig. 9). Whittaker and Marks (1975) do not claim that their stands have reached steady state (i.e., that biomass value where annual biomass increment matches biomass loss).

All else being equal, younger stands should have lower biomass and higher ANPP values than older for-

ests. The higher ANPP values at low biomass for our study relative to the Whittaker and Marks (1975) study suggest that some of the forests included in our analysis may indeed be younger (and therefore may have higher NPP and lower biomass) than the stands used in the previous study. The stands studied here are quite young ($54 \pm 22 \text{ yr}$) compared to the advanced age at which forest stands reportedly show signs of NPP decline (Gower et al. 1996, Ryan et al. 1997). It is also possible that (a) the constant litterfall estimates used for this study overestimate litter production in the lowest biomass stands, or (b) the relationship between diameter increment and diameter growth for smaller trees is non-linear, such that small trees increase in diameter more slowly than a simple linear extrapolation from large trees might suggest. We cannot make statistical comparisons between the two curves because the original authors did not report regression statistics. Despite the difference in ANPP at low values of biomass, however, the similarity of the ANPP vs. biomass relationship from the two studies suggests that our NPP estimates are similar to previously published field data for stands described as “climax or near climax,” and that the ANPP vs. biomass relationship developed using FIA data is similar to what one would expect based on the ecological literature.

O’Neill and DeAngelis (1981) published a review of forest wood production values for the forests studied as part of the International Biological Programme (IBP). These researchers grouped wood production values by latitude. They calculated that forest wood production between 30° and 40° N latitude averaged $450 \pm 90 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, and that forest wood production between 40° and 50° N latitude averaged $500 \pm 90 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$. With the exception of the $659 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ value for oak–gum–cypress forests, wood production values developed from this study fall within the $\pm 1 \text{ SD}$ range ($360\text{--}590 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) expected based on that global data set for the mid-Atlantic latitudes. This positive result is especially important because it suggests that wood production, the production variable most directly calculated from FIA data, is accurately estimated using our methods.

The stands used for this analysis can be classified as closed-canopy forests, but they have clearly not reached steady state. Old-growth eastern hardwood forests in the midwest United States and New Hampshire have aboveground biomass values ranging from 220 to 330 Mg/ha (Brown et al. 1997, Goodale and Aber 2001). The hardwood forests in the FIA sample used for this analysis have aboveground biomass values 6–51% lower than this, due primarily to the impacts of human settlement and forest management. If allowed to grow undisturbed until steady state is reached, these forests would achieve biomass values up to 50% higher than those presented in this analysis. Thus, the estimates presented here do not represent “potential” conditions, but they do provide estimates of the biomass

TABLE 2. Aboveground tree biomass and aboveground NPP data from ecological studies conducted in the mid-Atlantic (USA) study region.

General forest type	Species composition	Location	Latitude	Longitude
Hardwood	<i>Liriodendron tulipifera</i>	Annapolis, Maryland	38°53'	76°33'
	<i>Acer saccharum</i>	Allegheny Uplands, New York	42°30'	76°
	Mixed	Great Dismal Swamp, Virginia
	<i>Acer-Nyssa</i>	Great Dismal Swamp, Virginia
	<i>Quercus</i> spp.	Shaver Hollow, Virginia	38°37'	78°21'
Mixed hardwood/pine	<i>Quercus-Pinus</i> mixed	Long Island, New York
	<i>Quercus-Pinus</i> mixed	Pine Barrens, New Jersey	40°	74°30'
Pine	<i>Pinus virginiana</i>	Blacksburg, Virginia	37°15'	80°25'
	<i>Pinus rigida</i>	Shawangunk Mountains, New York	41°25'	74°40'
	<i>Pinus rigida</i>	Long Island, New York	40°45'	73°
	<i>Pinus resinosa</i>	Warrensburg, New York	43°28'	73°47'
	<i>Pinus resinosa</i>	Warrensburg, New York	43°28'	73°47'
	<i>Pinus resinosa</i>	central Pennsylvania	~41°	~78°
	<i>Picea abies</i>	central Pennsylvania	~41°	~78°
Spruce-Fir	<i>Abies balsamea</i>	Whiteface Mountain, New York	44°22'	73°54'
	<i>Picea abies</i>	central Pennsylvania	~41°	~78°
Other	<i>Taxodium distichum</i>	Great Dismal Swamp, Virginia
	<i>Chamaecyparis thyoides</i>	Great Dismal Swamp, Virginia

† Tree biomass (includes foliage).

‡ Tree stratum (excludes shrubs and herbs).

§ Sources:

¹ Brown and Parker (1994) (includes stems ≥ 2 cm dbh);

² Bickelhaupt et al. (1973);

³ Day (1982, 1984), Gomez and Day (1982), and Megonigal and Day (1988) (cited in Vogt [1991]; converted from C units assuming 0.475 C in biomass);

⁴ Harrison and Shugart (1990) (plot data not reported; includes stems with dbh > 2.54 cm);

⁵ Whittaker and Woodwell (1969);

⁶ Olsvig-Whittaker (1980) (cited in Cannell [1982]);

⁷ Madgwick (1968) (cited in Cannell [1982] and Gower et al. [1994]);

⁸ Olsvig-Whittaker (1980) (cited in Cannell [1982] and Gower et al. [1994]);

⁹ Leaf et al. (1975) and Wittwer et al. (1975) (cited in Cannell [1982]);

¹⁰ Madgwick (1962) and Madgwick et al. (1970) (cited in Gower et al. [1994]; ANPP measured at one plot only; basal area mean of five stands);

¹¹ Singer and Hutnik (1966) (cited in Cannell [1982]; stem density = 1076–2990 individuals/ha);

¹² Sprugel (1984) (basal area not reported separately by plot; biomass and NPP data are from “average” stands of different ages).

and NPP values one might realistically expect in mature, closed-canopy forests in the region. Our estimates are useful bounds for model predictions, especially when model results are presented as representing the conditions that currently exist on the landscape.

Comparisons with model estimates

Averaged together, the NPP estimates from the three VEMAP2 biogeochemistry models were similar to the NPP estimates developed from FIA data for this study. However, agreement between individual model predictions and FIA-based NPP estimates was not as good, especially for the temperate deciduous forest. Possible reasons for this discrepancy between model predictions and FIA-based estimates are numerous. These reasons include the following; (a) the models may be calibrated to more or less productive forests than currently exist in this region, (b) the vegetation cover data set used for model estimates may not be representative of the current forest, or (c) actual forest production, even for the most productive stands in the region, is below what the models predict due to disturbance or management history.

FIA-based biomass estimates were lower, on aver-

age, than modeled biomass estimates. Agreement between individual model predictions and FIA-based biomass estimates was not as close. In particular, Biome-BGC biomass predictions were nearly 400% higher than the FIA-based estimates. The mean total biomass value (541 Mg C/ha) predicted by Biome-BGC for this region was also substantially higher than any of the measured biomass values for old-growth stands in the eastern United States (total old-growth biomass would range from 131 to 196 Mg C/ha, assuming root biomass is 25% of aboveground biomass). Again, explanations for the discrepancy between FIA-based and modeled estimates are numerous; including that (a) the models may be calibrated to older forests with more biomass than currently exist in this region, or (b) the exclusion of land use processes such as forest regrowth from the model simulations has resulted in artificially high modeled biomass values.

For both NPP and biomass, discrepancies between model simulations and FIA-based estimates may arise from the input parameters used for the VEMAP2 simulations (e.g., mortality rates and disturbance histories), rather than from errors in model simulations of fundamental processes such as photosynthesis or C

TABLE 2. Extended.

Plots (no.)	Stand age (yrs.)	Basal Area (m ² /ha)	Aboveground biomass (Mg/ha)†	ANPP (g·m ⁻² ·yr ⁻¹)‡	Source§
24	10–340	19.0–50.5 (\bar{x} = 36.6)	57–431 (\bar{x} = 281.5)	...	1
1	40–45	22.8	31.9	...	2
1	78	...	204.8	1537	3
1	52	...	206.0	614.7	3
220	164.3	...	4
5	...	15.6	64.03	796	5
2	10–24	4.1; 6.2	3.54; 4.30	...	6
1	17	25.3	75.3	1470	7
2	20–24	14.9; 13.8	11.37; 8.72	...	6
2	60–80	15.7; 18.8	61.2; 87.9	740; 870	8
1	35–40	...	77.2	...	9
7	29–32	24.6–30.4 (\bar{x} = 26.8)	46.2–77.3 (\bar{x} = 59.9)	670	10
3	42	...	186.7–233.1 (\bar{x} = 204.3)	...	11
3	42	...	158.5–196.9 (\bar{x} = 178.1)	...	11
29	10–60	5–60	32.5–123.0 (\bar{x} = 84.6)	710–965 (\bar{x} = 746)	12
1	86	...	363.4	892.6	3
1	57	...	230.9	962.0	3

gain. For the simulations presented here, the VEMAP2 models did assume a no-human-impact scenario. As a result, one would expect FIA-based biomass estimates, even for the set of mature closed-canopy forests described here, to be somewhat lower than the model estimates.

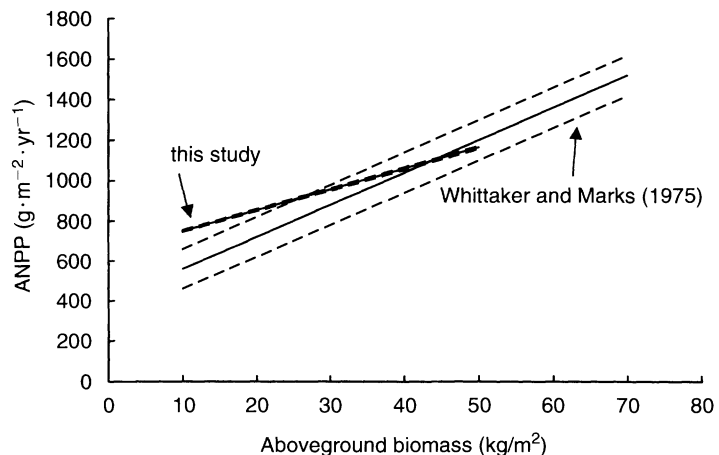
Calculating carbon budgets

If we assume that forests represent the potential vegetation in this region and we ignore the impacts of human settlement on land use patterns, we can calculate the total forest biomass and live biomass increment that would be achievable if all forests were allowed to reach the mature, closed-canopy status of the plots in this analysis (we will call this value “potential,” with the understanding that it does not refer to steady-state forests in this example). We used our area-weighted estimates of biomass and NPP at the 0.5° × 0.5° grid cell level to calculate potential biomass and wood biomass increment for the seven mid-Atlantic states. Converting to units of carbon using 0.475 as the proportion C in

biomass (Raich et al. 1991), potential C storage in forest biomass in this region is 4.98 Pg C (1 Pg = 10¹⁵ g) (4.06 in aboveground biomass), and potential wood biomass increment (above- and belowground) is 119.2 Tg C/yr (1 Tg = 10¹² g).

Based on the full sample of inventory plots for this region, Birdsey (1992) reported that total biomass C storage in tree biomass on forested land in 1990 was 1.63 Pg C, or 32.7% of this potential value. If we reduce the total potential biomass and biomass increment estimates from this study to account for only the 61.4% of land area (~27.8 × 10⁶ ha) in this seven state region that is forested (Powell et al. 1994), then the potential total C storage in wood biomass and annual wood biomass increment from this study on forested land are 3.06 Pg C and 73.2 Tg C/yr, respectively. This potential biomass increment value corresponds to 2.6 Mg C·ha⁻¹·yr⁻¹; we emphasize that while this value is consistent with the highest values reported in the ecological literature, it exceeds what one would expect based on the entire inventory sample and should thus be con-

FIG. 9. Aboveground NPP vs. aboveground biomass curve, redrawn from Whittaker and Marks (1975) and overlain with a similar curve developed from FIA data as part of this study. The Whittaker and Marks equation is given as: ANPP (g·m⁻²·yr⁻¹) = 400 + 16 × aboveground biomass (kg/m²). Confidence intervals reflect ±100 g·m⁻²·yr⁻¹ limits suggested by original authors. The FIA-based equation is given as: ANPP (g·m⁻²·yr⁻¹) = 645.85 + 10.40 × aboveground biomass (kg/m²); n = 2640, R² = 0.254, and P values <0.005 on coefficient and constant. The upper 95% confidence interval based on FIA data is: ANPP g·m⁻²·yr⁻¹ = 649.02 + 10.50 × aboveground biomass (kg/m²). The lower 95% confidence interval is: ANPP (g·m⁻²·yr⁻¹) = 642.67 + 10.30 × aboveground biomass (kg/m²).



sidered an overestimate of actual gross C sequestration rates.

The 1.63 Pg C estimate presented by Birdsey (1992) totals 53.3% of this forest-only potential biomass value; the remaining 46.7% represents the difference between “actual” and “potential” C storage in forests in this region. “Actual” forest C storage refers to forests that have not yet achieved closed-canopy status (i.e., that have basal area values lower than 20 m²/ha), that have experienced harvesting or damage in the recent past, and that exist on sites not capable of producing at least 1.4 m³·ha⁻¹·yr⁻¹ (20 ft³·acre⁻¹·yr⁻¹) of industrial wood. Of course, if the “potential” forest biomass condition referred to old-growth status, when total biomass would be as much as 50% higher than the biomass values presented here, the difference between “actual” and “potential” C storage would be even greater.

The difference in magnitude between these two sets of estimates underlines an important point, which is also discussed by Olson et al. (1983) and Botkin et al. (1993). Total C storage or biomass increment estimates based on a non-random sample of field plots, especially a sample based on studies made by ecological researchers who established the plots using criteria other than regional representativeness, will overestimate the actual values at larger scales. The same is true of ecological models. To represent accurately the spatial variation in patterns of NPP across the continent and the globe, the models must take into account the effects of human settlement and land management patterns.

The FIA data set, because it is based on random plot selection and takes into account every portion of the landscape, forested or not, in its two-phase sample design, is uniquely suited to provide accurate large-scale estimates of current forest C storage and sequestration rates. Efforts are currently underway to create estimates of both potential and actual NPP using methods similar to those described here for the continental United States. Results from that analysis will enable us to validate process models and to estimate gross C sequestration rates by forest vegetation on a much larger scale.

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LITERATURE CITED

- Aber, J. D., and C. T. Driscoll. 1997. Effects of land use, climate variation and N deposition on N cycling and C storage in northern hardwood forests. *Global Biogeochemical Cycles* **11**:639–648.
- Aber, J. D., S. V. Ollinger, and C. T. Driscoll. 1997. Modeling nitrogen saturation in forest ecosystems in response to land use and atmospheric deposition. *Ecological Modelling* **101**: 61–78.
- Alerich, C. L., and D. A. Drake. 1995. Forest statistics for New York: 1980 and 1993. Resource Bulletin NE-132. USDA Forest Service Northeastern Forest Experiment Station, Radnor, Pennsylvania, USA.
- Bickelhaupt, D., A. Leaf, and N. Richards. 1973. Effect of branching habit on above-ground dry weight estimates of *Acer saccharum* stands. Pages 219–230 in H. Young, editor. IUFRO biomass studies: Nancy, France and Vancouver, British Columbia, Canada. University of Maine, College of Life Sciences and Agriculture, Orono, Maine, USA.
- Birdsey, R. A. 1992. Carbon storage and accumulation in United States forest ecosystems. General Technical Report WO-59. USDA Forest Service, Washington, D.C., USA.
- Birdsey, R. A., and L. S. Heath. 1995. Carbon changes in U.S. forests. Pages 56–70 in L. A. Joyce, editor. Productivity of America's forests and climate change. General Technical Report RM-GTR-271. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.
- 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. General Technical Report RM-214. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.
- Bondeau, A., D. Kicklighter, A. Kaduk, and Participants Potsdam NPP Model Intercomparison. 1999. Comparing global models of terrestrial net primary productivity (NPP): importance of vegetation structure on seasonal NPP estimates. *Global Change Biology* **5**:35–45.
- Botkin, D., L. Simpson, and R. Nisbet. 1993. Biomass and carbon storage of the North American deciduous forest. *Biogeochemistry* **20**:1–17.
- Brown, M., and G. Parker. 1994. Canopy light transmittance in a chronosequence of mixed-species deciduous forests. *Canadian Journal of Forest Research* **24**:1694–1703.
- Brown, S. L., and P. E. Schroeder. 1999. Spatial patterns of aboveground production and mortality of woody biomass for eastern U.S. forests. *Ecological Applications* **9**:968–980.
- Brown, S., P. Schroeder, and R. Birdsey. 1997. Aboveground biomass distribution of U.S. eastern hardwood forests and the use of large trees as an indicator of forest development. *Forest Ecology and Management* **96**:37–47.
- Brown, S. L., P. Schroeder, and J. S. Kern. 1999. Spatial distribution of biomass in forests of the Eastern USA. *Forest Ecology and Management* **123**:81–90.
- Burke, I. C., W. K. Lauenroth, and W. J. Parton. 1997. Regional and temporal variation in net primary production and nitrogen mineralization in grasslands. *Ecology* **78**: 1330–1340.
- Cairns, M. A., S. Brown, E. H. Helmer, and G. A. Baumgardner. 1997. Root biomass allocation in the world's upland forests. *Oecologia* **111**:1–11.
- Cannell, M. 1982. World forest biomass and primary production data. Academic Press, London, UK.
- Chojnacky, D. C. 1998. Double sampling for stratification: a forest inventory application in the Interior West. Research

- Paper RMRS-RP-7. USDA Forest Service Rocky Mountain Research Station, Ogden, Utah, USA.
- Cramer, W., D. Kicklighter, A. Bondeau, B. I. Moore, G. Churkina, B. Nemry, A. Ruimy, A. Schloss, and Participants Potsdam NPP Model Intercomparison. 1999. Comparing global models of terrestrial net primary productivity (NPP): overview and key results. *Global Change Biology* **5**:1–15.
- Cunia, T. 1987. Error of forest inventory estimates: its main components. Pages 1–14 in E. Wharton and T. Cunia, editors. Estimating tree biomass regressions and their error: proceedings of the workshop on tree biomass regression functions and their contribution to the error of forest inventory estimates. General Technical Report NE-117, USDA Forest Service Northeastern Forest Experiment Station, Syracuse, New York, USA.
- Day, F. J. 1982. Litter decomposition rates in the seasonally flooded Great Dismal Swamp. *Ecology* **63**:670–678.
- Day, F. J. 1984. Biomass and litter accumulation in the Great Dismal Swamp. Pages 386–392 in K. Ewel and H. Odum, editors. *Cypress Swamps*. University of Florida Press, Gainesville, Florida, USA.
- DiIorio, F. C. 1991. SAS applications programming: a gentle introduction. Duxbury Press, Pacific Grove, California, USA.
- Dixon, R. K., S. A. Brown, R. A. Houghton, A. M. Solomon, M. C. Trexler, and J. Wisniewski. 1994. Carbon pools and flux of global forest ecosystems. *Science* **263**:185–190.
- Field, C., M. Berenfeld, J. Randerson, and P. Falkowski. 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. *Science* **281**:237–240.
- Foley, J., I. Prentice, N. Ramankutty, S. Levis, D. Pollard, S. Sitch, and A. Haxeltine. 1996. An integrated biosphere model of land surface processes, terrestrial carbon balance and vegetation dynamics. *Global Biogeochemical Cycles* **10**:603–628.
- Friend, A. D., A. K. Stevens, R. G. Knox, and M. G. R. Cannell. 1997. A process-based, terrestrial biosphere model of ecosystem dynamics (Hybrid 3.0). *Ecological Modelling* **95**:249–287.
- Frieswyk, T. S., and D. M. DiGiovanni. 1990. Biomass statistics for Maryland—1986. Resource Bulletin NE-113. USDA Forest Service Northeastern Forest Experiment Station, Radnor, Pennsylvania, USA.
- Gomez, M., and F. J. Day. 1982. Litter nutrient content and production in the Great Dismal Swamp. *American Journal of Botany* **69**:1314–1321.
- Goodale, C., and J. Aber. 2001. The long-term effects of land-use history on nitrogen cycling in northern hardwood forests. *Ecological Applications* **11**:253–267.
- Gower, S., H. Gholz, K. Makane, and V. Baldwin. 1994. Production and carbon allocation patterns of pine forests. *Ecological Bulletins (Copenhagen)* **43**:115–135.
- Gower, S. T., R. E. McMurtrie, and D. Murty. 1996. Above-ground net primary production decline with stand age: potential causes. *Trends in Ecology and Evolution* **11**:378–382.
- Hansen, M. H., T. Frieswyk, J. F. Glover, and J. F. Kelly. 1992. The Eastwide Forest Inventory Data Base: users manual. General Technical Report NC-151. USDA Forest Service North Central Experiment Station, St. Paul, Minnesota, USA.
- Harrison, E., and H. Shugart. 1990. Evaluating performance of an Appalachian oak forest dynamics model. *Vegetatio* **86**:1–13.
- Hunt, E. R. J., and S. W. Running. 1992. Simulated dry matter yields for aspen and spruce stands in the North American boreal forest. *Canadian Journal of Remote Sensing* **18**:126–133.
- Jenkins, J. C., D. W. Kicklighter, S. V. Ollinger, J. D. Aber, and J. M. Melillo. 1999. 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* **2**:555–570.
- Kicklighter, D. W., A. Bondeau, A. L. Schloss, J. Kaduk, A. D. McGuire, and Participants Potsdam NPP Model Intercomparison. 1999. Comparing global models of terrestrial net primary productivity (NPP): global pattern and differentiation by major biomes. *Global Change Biology* **5**:16–24.
- Leaf, A., R. Leonard, R. Wittwer, and D. Bickelhaupt. 1975. Four-year growth responses of plantation red pine to potash fertilization and irrigation in New York. *Forest Science* **21**:88–96.
- Madgwick, H. 1962. Studies in the growth and nutrition of *Pinus resinosa* Ait. Dissertation. State University College of Forestry, Syracuse University, Syracuse, New York, USA.
- Madgwick, H. 1968. Seasonal changes in biomass and annual production of an old field *Pinus virginiana* stand. *Ecology* **49**:149–152.
- Madgwick, H., E. White, G. Xydias, and A. Leaf. 1970. Biomass of *Pinus resinosa* in relation to potassium nutrition. *Forest Science* **16**:154–159.
- Marks, P. C. 1974. The role of pin cherry (*Prunus pennsylvanica* L.) in the maintenance of stability in northern hardwood ecosystems. *Ecological Monographs* **44**:73–88.
- Matthews, E. 1983. Global vegetation and land use: new high-resolution databases for climate studies. *Journal of Climate and Applied Meteorology* **22**:474–487.
- McGuire, A. D., J. M. Melillo, and L. A. Joyce. 1995. The role of nitrogen in the response of forest net primary production to elevated carbon dioxide. *Annual Review of Ecology and Systematics* **26**:473–503.
- McGuire, A. D., J. M. Melillo, L. A. Joyce, D. W. Kicklighter, A. L. Grace, B. Moore III, and C. J. Vörösmarty. 1992. Interactions between carbon and nitrogen dynamics in estimating net primary productivity for potential vegetation in North America. *Global Biogeochemical Cycles* **6**:101–124.
- McGuire, A. D., J. M. Melillo, D. W. Kicklighter, Y. Pan, X. Xiao, J. Helfrich, B. Moore III, C. J. Vörösmarty, and A. L. Schloss. 1997. Equilibrium responses of global net primary production and carbon storage to doubled atmospheric carbon dioxide: sensitivity to changes in vegetation nitrogen concentration. *Global Biogeochemical Cycles* **11**:173–189.
- Megonigal, J. P., and F. P. Day, Jr. 1988. Organic matter dynamics in four seasonally flooded forest communities of the Dismal Swamp. *American Journal of Botany* **75**:1334–1343.
- Melillo, J. M., A. D. McGuire, D. W. Kicklighter, B. Moore III, C. J. Vörösmarty, and A. L. Schloss. 1993. Global climate change and terrestrial net primary production. *Nature* **363**:234–239.
- Monteith, D. 1979. Whole tree weight tables for New York. AFRI Research Report No. 40. State University of New York College of Environmental Science and Forestry, Applied Forestry Research Institute, Syracuse, New York, USA.
- Ollinger, S. V., J. D. Aber, and C. A. Federer. 1998. Estimating regional forest productivity and water yield using an ecosystem model linked to a GIS. *Landscape Ecology* **13**:323–334.
- Olson, J., J. Watts, and L. Allison. 1983. Carbon in live vegetation of major world ecosystems. Publication No. 1997, ORNL-5862. Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA.
- Olsvig-Whittaker, L. 1980. A comparative study of northeastern Pine Barrens vegetation. Dissertation. Cornell University, Ithaca, New York, USA.
- O'Neill, R., and D. DeAngelis. 1981. Comparative productivity and biomass relations of forest ecosystems. Pages

- 411–450 in D. Reichle, editor. Dynamic properties of forest ecosystems. Cambridge University Press, Cambridge, UK.
- Parton, W. J., D. S. Schimel, C. V. Cole, and D. S. Ojima. 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. *Soil Science Society of America Journal* **51**:1173–1179.
- Parton, W. J., J. M. O. Scurlock, D. S. Ojima, T. G. Gilmanov, R. J. Scholes, D. S. Schimel, T. Kirchner, J.-C. Menaut, T. Seastedt, E. Garcia Moya, A. Kamnalrut, and J. I. Kinyamario. 1993. Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide. *Global Biogeochemical Cycles* **7**:785–809.
- 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.
- Pastor, J., and W. M. Post. 1986. Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles. *Biogeochemistry* **2**:3–27.
- Powell, D., J. Faulkner, D. Darr, Z. Zhu, and D. MacCleery. 1994. Forest resources of the United States, 1992. General Technical Report RM-234 (revised). USDA Forest Service Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.
- Prince, S. D., and S. N. Goward. 1995. Global net primary production: a remote sensing approach. *Journal of Biogeography* **22**:815–835.
- Raich, J. W., and K. J. Nadelhoffer. 1989. Belowground carbon allocation in forest ecosystems: global trends. *Ecology* **70**:1346–1354.
- Raich, J. W., E. B. Rastetter, J. M. Melillo, D. W. Kicklighter, P. A. Steudler, and B. J. Peterson. 1991. Potential net primary productivity in South America: application of a global model. *Ecological Applications* **1**:399–429.
- Raile, G. 1982. Estimating stump volume. Research Paper NC-224. USDA Forest Service North Central Forest Experiment Station, St. Paul, Minnesota, USA.
- Ruimy, A., L. Kergoat, A. Bondeau, and Participants Potsdam NPP Model Intercomparison. 1999. Comparing global models of terrestrial net primary productivity (NPP): analysis of differences in light absorption and light-use efficiency. *Global Change Biology* **5**:56–64.
- Running, S. W., and E. R. J. Hunt. 1993. Generalization of a forest ecosystem process model for other biomes, BIOME-BGC, and an application for global-scale models. Pages 141–158 in J. R. Ehleringer and C. Field, editors. Scaling processes between leaf and landscape levels. Academic Press, Orlando, Florida, USA.
- Ryan, M. G., D. Binkley, and J. H. Fownes. 1997. Age-related decline in forest productivity: pattern and process. *Advances in Ecological Research* **27**:214–262.
- Schimel, D., J. Melillo, H. Tian, A. McGuire, D. Kicklighter, T. Kittel, N. Rosenbloom, S. Running, P. Thornton, D. Ojima, W. Parton, R. Kelly, M. Sykes, R. Neilson, and B. Rizzo. 2000. Contribution of increasing CO₂ and climate to carbon storage by ecosystems in the United States. *Science* **287**:2004–2006.
- Schloss, A. L., D. Kicklighter, J. Kaduk, U. Wittenberg, and Participants Potsdam NPP Model Intercomparison. 1999. Comparing global models of terrestrial net primary productivity (NPP): comparison of annual NPP to climate and the normalized difference vegetation index. *Global Change Biology* **5**:25–34.
- Scurlock, J., W. Cramer, R. Olson, W. Parton, and S. Prince. 1999. Terrestrial NPP: toward a consistent data set for global model evaluation. *Ecological Applications* **9**:913–919.
- Singer, F., and R. Hutnik. 1966. Accumulation of organic matter in red pine and Norway spruce plantations of different spacings. Pennsylvania State University Research Briefs **1**:22–28.
- Smith, D. 1986. The practice of silviculture. John Wiley & Sons, New York, New York, USA.
- Sprugel, D. G. 1984. Density, biomass, productivity, and nutrient cycling changes during stand development in wave-regenerated balsam fir forests. *Ecological Monographs* **54**:164–186.
- Thompson, M. V., J. T. Randerson, C. M. Malmstrom, and C. B. Field. 1996. Change in net primary production and heterotrophic respiration: how much is necessary to sustain the terrestrial carbon sink? *Global Biogeochemical Cycles* **10**:711–726.
- Trimble, G., Jr. 1969. Diameter growth of individual hardwood trees—the effect of certain tree and environmental factors on the growth of several species. Research Paper NE-145. USDA Forest Service Northeastern Forest Experiment Station, Upper Darby, Pennsylvania, USA.
- Turner, D. P., G. J. Koerber, M. E. Harmon, and J. J. Lee. 1995. A carbon budget for forests of the conterminous United States. *Ecological Applications* **5**:421–436.
- 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**:407–437.
- Vogt, K. 1991. Carbon budgets of temperate forest ecosystems. *Tree Physiology* **9**:69–86.
- Wharton, E. H., A. L. Alerich, and D. A. Drake. 1997. Estimating total forest biomass in New York, 1993. Resource Bulletin NE-139. USDA Forest Service, Northeastern Forest Experiment Station, Radnor, Pennsylvania, USA.
- Wharton, E. H., and D. M. Griffith. 1993. Methods to estimate total forest biomass for extensive forest inventories: applications in the northeastern U.S. Research Paper NE-681. USDA Forest Service Northeastern Forest Experiment Station, Radnor, Pennsylvania, USA.
- Wharton, E. H., and D. M. Griffith. 1998. Estimating total forest biomass in Maine, 1995. Resource Bulletin NE-142. USDA Forest Service Northeastern Forest Research Station, Radnor, Pennsylvania, USA.
- Whittaker, R. H., and P. L. Marks. 1975. Methods of assessing terrestrial productivity. Pages 55–118 in H. Lieth and R. H. Whittaker, editors. Primary productivity of the Biosphere. Springer-Verlag, New York, New York, USA.
- Whittaker, R., and G. Woodwell. 1969. Structure, production, and diversity of the oak-pine forest at Brookhaven, New York. *Journal of Ecology* **57**:155–174.
- Wiant, H. V. J., C. Sheetz, A. Colaninno, J. DeMoss, and F. Castaneda. 1977. Tables and procedures for estimating weights of some Appalachian hardwoods. Bulletin 659T. West Virginia University, Agricultural and Forestry Experiment Station, College of Agriculture and Forestry, Morgantown, West Virginia, USA.
- Wittwer, R., A. Leaf, and D. Bickelhaupt. 1975. Biomass and chemical composition of fertilized and/or irrigated *Pinus resinosa* Ait. plantations. *Plant and Soil* **42**:629–651.
- Woudenberg, S. W., and T. O. Farrenkopf. 1995. The West-wide Forest Inventory Data Base: user's manual. General Technical Report INT-GT-317. USDA Forest Service Intermountain Research Station, Ogden, Utah, USA.
- Xiao, X., J. Melillo, D. Kicklighter, A. McGuire, R. Prinn, C. Wang, P. Stone, and A. Sokolov. 1998. Transient climate change and net ecosystem production of the terrestrial biosphere. *Global Biogeochemical Cycles* **12**:345–360.
- Young, H. E., J. H. Ribe, and K. Wainwright. 1980. Weight tables for tree and shrub species in Maine. Miscellaneous Report 230. University of Maine Life Sciences and Agriculture Experiment Station, Orono, Maine, USA.
- Young, H., L. Strand, and R. Altenberger. 1964. Preliminary fresh and dry weight tables for seven tree species in Maine. Technical Bulletin 12. Maine Agricultural Experiment Station, Orono, Maine, USA.

APPENDIX A

A table reporting aboveground tree dry-mass regression coefficients for key species is available in ESAs Electronic Data Archive: *Ecological Archives* A011-016-A1.

APPENDIX B

Assignment of tree species to key species for biomass determination and species groups for calculation of mean annual diameter increment is available in ESAs Electronic Data Archive: *Ecological Archives* A011-016-A2.

APPENDIX C

Ratios used to find foliage and (stump + root) biomass of other tree components are available in ESAs Electronic Data Archive: *Ecological Archives* A011-016-A3.

APPENDIX D

Equations used to predict stump diameter from dbh and specific gravity values used to convert stump volume to biomass are available in ESAs Electronic Data Archive: *Ecological Archives* A011-016-A4.

APPENDIX E

Parameters for algorithms used to predict dbh (t_0) from dbh (t_1) for ingrowth, ongrowth, and nongrowth stems are available in ESAs Electronic Data Archive: *Ecological Archives* A011-016-A5.