Spatial variability of aboveground net primary production for a forested landscape in northern Wisconsin

S.N. Burrows, S.T. Gower, J.M. Norman, G. Diak, D.S. Mackay, D.E. Ahl, and M.K. Clayton

Abstract: Quantifying forest net primary production (NPP) is critical to understanding the global carbon cycle because forests are responsible for a large portion of the total terrestrial NPP. The objectives of this study were to measure aboveground NPP (NPP_A) for a land surface in northern Wisconsin, examine the spatial patterns of NPP_A and its components, and correlate NPP_A with vegetation cover types and leaf area index. Mean NPP_A for aspen, hardwoods, mixed forest, upland conifers, nonforested wetlands, and forested wetlands was 7.8, 7.2, 5.7, 4.9, 5.0, and 4.5 t dry mass·ha^{-1}·year^{-1}, respectively. There were significant ($p = 0.01$) spatial patterns in wood, foliage, and understory NPP components and NPP_A ($p = 0.03$) when the vegetation cover type was included in the model. The spatial range estimates for the three NPP components and NPP_A differed significantly from each other, suggesting that different factors are influencing the components of NPP. NPP_A was significantly correlated with leaf area index ($p = 0.01$) for the major vegetation cover types. The mean NPP_A for the 3 km × 2 km site was 5.8 t dry mass·ha^{-1}·year^{-1}.

Résumé : La quantification de la production primaire nette (PPN) des forêts est primordiale pour comprendre le cycle global du carbone parce que les forêts sont responsables d'une forte proportion de la PPN terrestre totale. Les objectifs de cette étude consistaient à mesurer la PPN épigée (PPN_E) pour un territoire du Nord du Wisconsin, à examiner le comportement spatial de la PPN_E et de ses composantes et à corréler la PPN_E au type de couvert végétal et à l'indice de surface foliaire. La PPN_E moyenne pour la forêt de peuplier, la forêt feuillue, la forêt mélangée, les conifères sur hautes terres, les terrains marécageux sans arbres et les terrains marécageux boisés était respectivement de 7,8, 7,2, 5,7, 4,9, 5,0 et 4,5 t·ha^{-1}·an^{-1} de matière anhydre. Il y avait des variations spatiales significatives ($p \leq 0,01$) dans les composantes bois, feuillage et sous-étage de la PPN et dans la PPN_E ($p \leq 0,03$) lorsque le type de couvert végétal était inclus dans le modèle. Les estimations de l'intervalle de variation spatiale pour les trois composantes de la PPN et pour la PPN_E étaient significativement différentes les unes des autres, indiquant que différents facteurs influencent les composantes de la PPN. La PPN_E était significativement corrélée avec l'indice de surface foliaire ($p \leq 0,01$) dans le cas des principaux types de couvert végétal. La PPN_E moyenne pour le site de 3 km × 2 km était de 5,8 t·ha^{-1}·an^{-1} de matière anhydre.

[Traduit par la Rédaction]

Introduction

Quantifying terrestrial carbon accumulation is critical to understanding the global carbon cycle because terrestrial ecosystems contain nearly three times as much carbon as the atmosphere (Schlesinger 1997). Changes in this balance could have global consequences. Forested ecosystems are important because they occupy 33% of the Earth's surface area (Schlesinger 1997) and have moderate net primary production (NPP) (Landsberg and Gower 1997). Temperate forests, in particular, have been suspected of being large carbon sinks (Barford et al. 2001). NPP in forests is the net difference between gross primary production of plants and the autotrophic respiration.

Field-based measurements of aboveground NPP (NPP_A) and carbon allocation are needed to understand ecosystem structure and function. NPP components, such as wood NPP (NPP_W), foliage NPP (NPP_F), and understory NPP (NPP_U), have different residence times and decomposition rates (Landsberg and Gower 1997). If the vegetation has different

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spatial patterns of NPP$_W$ to NPP$_F$ to NPP$_U$, observed net ecosystem exchange estimates from eddy flux towers and ecosystem process models will differ across a landscape.

Previous studies (Whittaker and Niering 1975; Runyon et al. 1994) have shown significant NPP differences among terrestrial ecosystems along transects traversing large environmental gradients. However, few studies have examined spatial patterns of NPP within a landscape and attempted to quantify the variability and causes of the observed patterns (Kimball et al. 1999; Hansen et al. 2000). No geostatistical field studies, to our knowledge, have been performed to assess the spatial variation in NPP and its components on extents from 25 m to 3 km. These distances are important for several reasons: human forest management activities occur at these scales (U.S. Forest Service, unpublished data), soil and topographic gradients occur at these scales, several remote sensing platforms measure on scales ranging from 25 m (Landsat) to 500 m (MODIS), and many mesoscale ecosystem process models simulate ecosystem structural and functional characteristics at these scales (Mackay and Band 1997; Kimball et al. 1999).

Spatial patterns in NPP$_A$ should follow those in leaf area index (LAI) if NPP$_A$ and LAI are highly correlated. NPP$_A$ has been correlated with LAI for forests in the upper Great Lakes region (Fassnacht and Gower 1997) and in the forests of the western United States (Gholz 1982; Gower et al. 1992). Measurements of NPP$_A$ in the upper Great Lakes region are different among vegetation cover types (Fassnacht and Gower 1997; S.T. Gower, K.S. Fassnacht, D.J. Mladenoff, and S.N. Burrows, unpublished data). NPP$_A$ is also positively correlated with water and nutrient availability (Fassnacht and Gower 1997; S.T. Gower, K.S. Fassnacht, D.J. Mladenoff, and S.N. Burrows, unpublished data).

The objectives of this study were to (1) measure NPP$_A$ for the land surface around a very tall eddy flux tower in northern Wisconsin, (2) relate these measurements to vegetation cover types and LAI, and (3) quantify the spatial patterns found for individual NPP$_A$ components and NPP$_A$.

Methods

Site description

The study site was located in northern Wisconsin near Park Falls (45.9458°N, 90.2723°W). The study area is a NASA Earth Observing System Core Validation Site (NASA, MODIS land discipline Web site 2002: http://modis-land. gsfc.nasa.gov/), which includes a 447 m tall communication tower that is instrumented with eddy covariance systems to measure energy, water, and carbon exchange between the forest landscape and the atmosphere (Berger et al. 2001). The tower is located in the Chequamegon–Nicolet National Forest on the Northern Highlands physiographic province (a southern extension of the Canadian Shield). The bedrock is composed of Precambrian metamorphic and igneous rock, and is overlain by 8 to 90 m of glacial and glaciofluvial material deposited approximately 10 000 – 12 000 years before present. Topography is slightly rolling, varying by 45 m between highest and lowest elevations within the study area. Outwash, pitted outwash, and moraines are the dominant geomorphic landforms. The growing season is short and the

winters are long and cold. Mean annual July and January temperatures are 19 °C and –12 °C, respectively.

Red pine (*Pinus resinosa* Ait.) and jack pine (*Pinus banksiana* Lamb) are the dominant species on excessively drained, sandy soils derived from glacial outwash. Northern hardwood forests, composed of sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.), green ash (*Fraxinus americana* Marsh.), yellow birch (*Betula alleghaniensis* Britt.), and basswood (*Tilia americana* L.), occur on the finer-textured soils derived from moraines and drumlins. Soils of intermediate texture support a wide variety of broadleaf deciduous tree species, such as paper birch (*Betula papyrifera* Marsh.), quaking aspen (*Populus tremuloides* Michx.), bigtooth aspen (*Populus grandidentata* Michx.), red maple, and evergreen needle-leaf trees such as red and white pine (*Pinus strobus* L.). The poorly drained organic soils are dominated by eastern white-cedar (*Thuja occidentalis* L.), balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana* (Mill) BSP), tamarack (*Larix laricina* (Du Roi) Koch.), and speckled alder (*Alnus regosa* (Du Roi) Spreng.). The species composition and structure of the forest are influenced by landform and management activities such as thinning and harvesting (Fassnacht and Gower 1997, 1999).

The site is very heterogeneous in nature with small topographic changes resulting in large vegetation changes from nonforested wetlands to upland conifer stands with less than 10 m change in elevation. The site has also been heavily managed in the late 19th and 20th centuries and has a median stand age between 50 and 60 years with very few stands older than 100 years (Burrows 2002). This is in contrast to presettlement estimates of stand age using General Land Office data to estimate disturbance rates where the mean stand age was much greater than 100 years (Schulte 2002). The site is currently under active management by the U.S. Forest Service, and there have been recent (<5 years) thinning and clearing activities throughout the site (Burrows 2002).

Sampling design

A cyclic sampling design was used because it is more efficient than random or systematic designs for measuring vegetation characteristics in situ (Burrows et al. 2002). The cyclic sampling design uses a repeating pattern over the landscape that optimizes spatial sampling by minimizing the redundant pairs of points measured at different distances. The design is based on a cycle that equally samples distances within each cycle while allowing for additional sample pairs to be analyzed across cycles as effectively (Burrows et al. 2002). These cycles are extended across the landscape, with each cycle using the other cycles to distribute the sampling effort across the study site. Two inefficiencies in the design are redundant lag pairs created at the cycle length and extra lag pairs created on the diagonals of the x–y plane. A detailed description of this methodology can be found in Burrows et al. (2002).

Three hundred and twelve plots were established in a 3 km × 2 km area centered on the flux tower. We selected a 3 km × 2 km study area because it would contain several of NASA's Moderate Resolution Imaging Spectroradiometer (MODIS) sensor pixels while keeping the field measurements within logistical constraints. Each plot was geolocated

to within 0.5 m using a real-time kinematic global positioning system (RTK GPS, Ashtech, Inc., Sunnyvale, Calif.). Basic stand structural characteristics (basal area, species composition, recent management activities) were measured in all 312 plots in 1998 using variable-radius subplots. Each plot was classified using a species-specific cover-type class and generalized into one of seven site-specific land-cover-type schemes: aspen, forested wetlands, hardwoods, mixed, nonforested wetlands, red pine, and upland conifers.

Aboveground net primary production

Aboveground net primary production (NPP_A) is the sum of the annual aboveground biomass production of wood (stem + branches), foliage, and understory:

$$[1] \qquad NPP_A = NPP_W + NPP_F + NPP_U$$

where NPP_W is aboveground wood NPP (e.g., stem + branches), NPP_F is foliage NPP, and NPP_U is understory NPP. Loss of NPP due to herbivory is generally less than 10% in forest ecosystems (Schowalter et al. 1986) and was ignored in this study. NPP_A and its components were estimated for 3 years (1998–2000). All values are expressed as metric tons of dry biomass per hectare per year.

Aboveground net primary production was measured at 100 "intensive" plots in three of the nine cyclic blocks. These three blocks were chosen because they were independent of each other based on a priori remote sensing estimates of spatial autocorrelation, and they adequately sampled all of the major vegetation cover types (Burrows et al. 2002).

Annual radial increment was measured from tree increment cores taken in October 2000. At each plot center, a variable-radius plot was established using metric basal area factor prisms (1–4 $m^2 \cdot ha^{-1}$). The prism size was chosen to ensure that typically 10 trees (greater than 2.5 cm DBH) were in each plot. Two increment cores were taken 90° from each other at DBH from each tree in all 100 plots for a total of 1033 trees cored. Annual radial increments were measured using the WinDENDRO tree ring analysis system (Regent Instruments, Québec, Que., 2000). Each core was scanned, and annual radial increments were measured for the last 10 years. Tree diameters were estimated for each year based on the DBH measured in 2000 and the radial increment measured for each tree. Aboveground biomass for each year was calculated based on published allometric equations (Appendix A) for each tree species wood components (stem wood, stem bark, branches) (Young et al. 1980; Hocker and Earley 1983; Freedman 1984; Ker 1984; Harding and Grigal 1985; Perala and Alban 1994). Development of site-specific equations for each of the 35 tree species was not possible because of practical considerations; this would have required the harvesting and measuring of several hundred trees. While generalized published allometric equations may introduce errors, the errors are acceptable for woody components (Gower et al. 1999; C. Wang, S.T. Gower, E.V. Nordheim, B. Bond-Lamberty, and J.M. Norman, unpublished analysis). NPP_W for each year was calculated by subtracting the prior year's biomass from the current year's biomass. The number of trees per hectare (TPH) was calculated using eq. 2:

$$[2] \qquad TPH = BAF/(0.000\ 0785\ 3 \times DBH^2)$$

where BAF is the metric basal area factor of the prism used for the plot, and DBH is the diameter at breast height of the tree. NPP_W for each plot was calculated as the product of $NPP_W \times TPH$ for each tree and summing for each plot.

NPP_F was estimated from leaf litterfall using five 0.6 m × 0.4 m baskets in each intensive plot. The baskets were placed in a cross or "X" pattern in each plot with one basket at the center of the "X", and one basket located at each of the four ends of the "X" at 45°, 135°, 225°, 215°, 9 m from the center (Burrows et al. 2002). Approximately 15% of the baskets were disturbed by bears and unusable. Litterfall samples were collected in the fall of 1998 and 1999, dried at 70 °C, and weighed to obtain the total mass of the sample. The five subsamples for each plot were combined and then separated into alder, aspen, northern hardwoods, and conifer foliage and woody material, bark, and reproductive tissues. Each sample set was dried at 70 °C to a constant mass and weighed to obtain the masses of the components.

NPP_U was measured in August of 1999 and 2000 by clipping all understory (including woody material up to 2.5 cm DBH) in five 0.25-m^2 subplots in each of the 100 plots, for a total of 500 samples per year. Each subplot was located adjacent to a litterfall basket. Samples were separated into new and old tissue in 1999. Additionally, in 2000, the samples were separated into different plant functional groups (i.e., grasses, forbs, woody material, and ferns). Each sample was dried at 70 °C to a constant mass and weighed to obtain the mass of the sample. Since it was only collected in August of each year, there could be some errors introduced into the total estimates owing to the appearance and disappearance of ephemerals earlier in the season.

Since the only year all three components of NPP_A (NPP_U, NPP_W, NPP_F) were measured simultaneously was 1999, all analyses in this paper were based on 1999 data, except where noted.

Leaf area index field measurements

Leaf area index (LAI) was measured using direct (allometry and leaf litterfall) and optical approaches (LI-COR LAI 2000 Plant Canopy Analyzer, LI-COR Inc., Lincoln, Nebr.), with the direct measurements restricted to the 100 intensive plots (Burrows et al. 2002). At the 100 NPP plots, LAI was measured directly using three methods: the application of allometric equations, the collection of litterfall, and optical methods. Litterfall was collected as described in the NPP_F methods presented above. A specific leaf area for each plant functional group was applied to calculate the leaf area based on the mass of the dry leaves, which was scaled by the ground area sampled by the litter traps (Fassnacht and Gower 1997; S.T. Gower, K.S. Fassnacht, D.J. Mladenoff, and S.N. Burrows, unpublished data). LAI was estimated indirectly using the LI-COR LAI-2000 plant canopy analyzers (Gower and Norman 1991; Fassnacht et al. 1994; Chen et al. 1997). All optical estimates of LAI were obtained using one above-canopy unit and several below-canopy units. Light transmission was measured at five subplot locations within each plot using the LAI-2000, where three under-canopy measurements were made at each subplot for a total of 15 measurements per plot. The optical measurements were made in June 1999, July 1999, June 2000, and July 2000. A detailed summary of the methods used to correct raw LAI-

Table 1. Mean (±1 SE) aboveground net primary production (NPP) estimates (t dry mass·ha^{-1}·year^{-1}), using the geostatistical model, by component measured for the major cover types in 1999.

Cover type	NPP$_U$	NPP$_W$	NPP$_F$	NPP$_F$/NPP$_W$
Aspen	0.7 (0.1)	4.6 (0.4)	2.8 (0.2)	0.61
Forested wetlands	0.4 (0.2)	2.4 (0.4)	2.5 (0.2)	1.04
Hardwoods	0.9 (0.2)	3.4 (0.5)	3.2 (0.2)	0.94
Mixed	1.6 (0.5)	1.8 (1.1)	2.6 (0.6)	1.44
Nonforested wetlands	3.9 (0.3)	0.1 (0.8)	0.5 (0.5)	na*
Red pine	0.6 (0.3)	2.3 (0.8)	2.3 (0.3)	1.00
Upland conifer	0.8 (0.3)	2.0 (0.8)	2.0 (0.4)	

Note: Estimates were derived using the spatial autocorrelation estimates from Fig. 1. NPP$_U$, understory NPP; NPP$_W$, wood NPP; NPP$_F$, foliar NPP.

*Nonforested wetlands are excluded from this column because most of their production comes from herbaceous plants.

2000 measurements is provided by Burrows et al. (2002). A detailed description of the field methodology is provided by Campbell et al. (1999).

Geostatistics

Structural and functional characteristics of forests are often correlated, and the correlation can be modeled as a function of the distance between sample locations. Sample locations that are closer to each other are likely to be more similar than sample locations that are farther apart. The spatial variability of structures can be quantified with a variogram (Cressie 1993), which quantifies variability as a function of distance between sample locations (eq. 3).

Gamma (γ) is defined as

$$[3] \qquad \gamma(h) = \frac{1}{2|N(h)|} \sum_{N(h)} (z_i - z_j)^2$$

where $N(h)$ is the set of all pairs of observations, such that the distance between i and j is h. $|N(h)|$ is the number of such pairs (i, j), and z_i and z_j are data values at locations i and j, respectively.

The $\lim_{h \to 0} \gamma(h)$ is referred to as the nugget, which is the estimate of the variance when distance h approaches 0 (the y intercept). The $\lim_{h \to \infty} \gamma(h)$ is referred to as the sill and represents the variance (σ^2) of the random field (the study area as a whole). Finally, the distance above which data are no longer autocorrelated is referred to as the range (Kaluzny et al. 1998).

Statistical analyses

Statistical analyses were performed using S-Plus 2000 (Mathsoft 1999a), the S+Spatial Module version 1.5 (Mathsoft 1999b), and the NLME Library version 3.3 (Pinheiro and Bates 2000). Geostatistical regression and ANOVAs were performed using SAS's PROC MIXED procedure (SAS Institute Inc. 2001). Variograms were used because they can easily be integrated into the covariance structure of mixed-effects models. Geostatistical covariance structural parameters (range, sill, nugget) were estimated using the GLS and LME procedures in S-Plus (Pinheiro and Bates 2000) when they could not be estimated with SAS. SAS's PROC MIXED procedure allowed for a mixed-effect model to be built with geostatistical covariance structures.

Fig. 1. Spherical variogram models of the different components of net primary production (NPP).
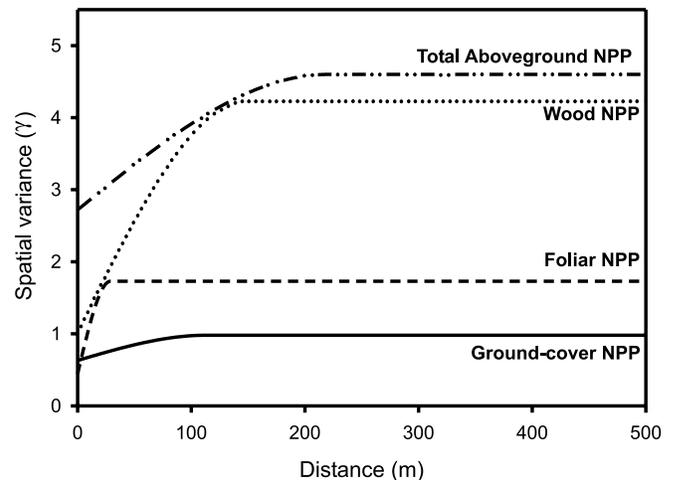
A geostatistical model for each NPP component was fit with a spherical variogram integrated into the covariance structure. Since this model incorporates local information as a function of the spatial model, more detailed information can be used to estimate the means and variance. An ANOVA test between the geostatistical and nongeostatistical models was performed in S-Plus to determine if the geostatistical model was significantly different from the nongeostatistical model (Pinheiro and Bates 2000).

Results and discussion

Understory net primary production (NPP$_U$)

Mean understory net primary production varied significantly ($p = 0.01$) by 10-fold among vegetation cover types and ranged from 0.4 t·ha^{-1}·year^{-1} for forested wetlands to 3.9 t·ha^{-1}·year^{-1} for nonforested wetlands (Table 1). NPP$_U$ had significant ($p = 0.001$) spatial patterns when vegetation cover type was used as an independent variable. The spherical variogram model had a range of 113 m, a sill of 0.98, and a nugget of 0.63 (Fig. 1). The mean NPP$_U$, using the geostatistical model, for the study site was 1.26 t·ha^{-1}·year^{-1} (Table 1).

Fig. 2. Interannual variability in wood net primary production (NPP_W) from 1998 to 2000 ($p < 0.01$).
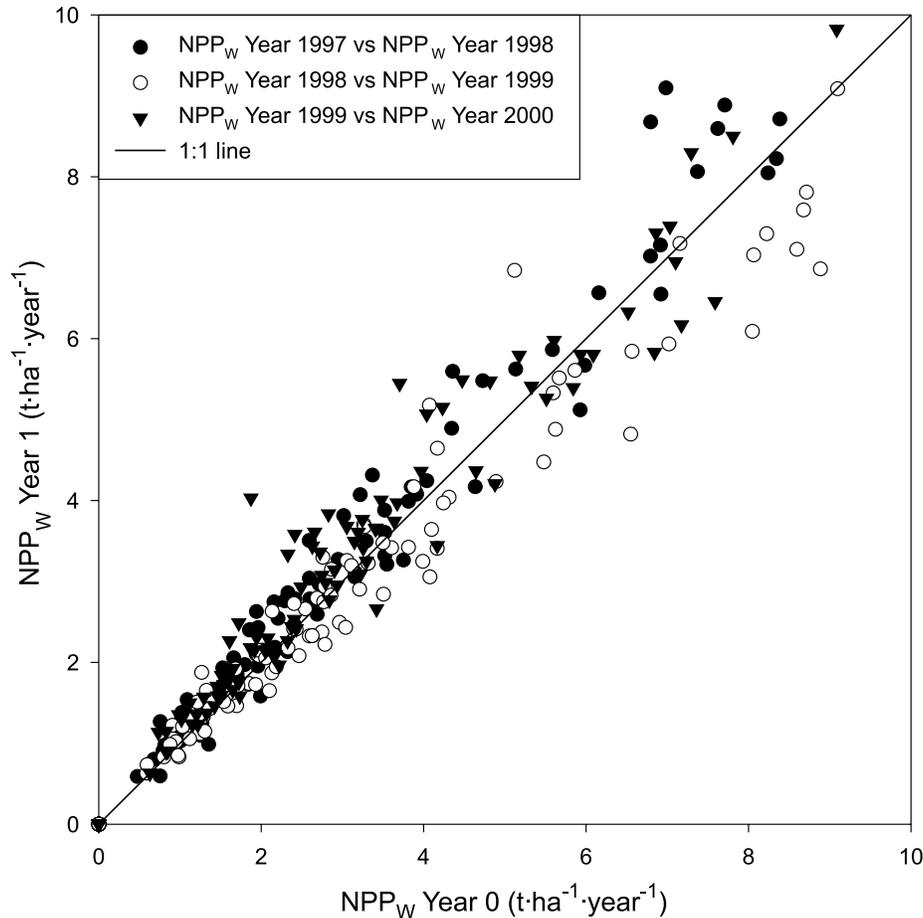
Wood net primary production (NPP_W)

Wood net primary production differed significantly ($p = 0.01$) among the vegetation cover types. NPP_W was lowest for the nonforested wetland (0.1 $t·ha^{-1}·year^{-1}$). It ranged from 1.8 $t·ha^{-1}·year^{-1}$ for mixed forests to 4.6 $t·ha^{-1}·year^{-1}$ for aspen (Table 1) in the forest cover types. NPP_W had significant ($p = 0.04$) spatial patterns when vegetation cover type was used as a independent variable. The spherical model had a range of 150 m, a sill of 4.23, and a nugget of 1.00 (Fig. 1). The mean NPP_W, using the geostatistical model, was 2.6 $t·ha^{-1}·year^{-1}$ for the study site (Table 1).

Wood net primary production differed significantly ($p = 0.01$) among the 4 years (Fig. 2), but there was no consistent positive or negative trend over the 4 years. The observed increase in NPP_W of 7% from 1999 to 2000 was consistent with the previously reported 17% increase in LAI measure at the same site (Burrows 2002).

Foliage net primary production (NPP_F)

Foliage net primary production differed significantly ($p = 0.001$) among the vegetation cover types and ranged from 0.5 $t·ha^{-1}·year^{-1}$ for nonforested wetlands to 3.2 $t·ha^{-1}·year^{-1}$ for hardwoods (Table 1). NPP_F had a significant ($p = 0.001$) spatial pattern when the vegetation cover type was used as an independent variable. The spherical model had a range of 28 m, a sill of 1.73, and a nugget of 0.44 (Fig. 1). The mean NPP_F, using the geostatistical model, was 2.26 $t·ha^{-1}·year^{-1}$ for the study site (Table 1).

Table 2. Aggregated aboveground net primary productivity (NPP_A) estimates (t dry mass·$ha^{-1}·year^{-1}$) derived from plot-level estimates for each NPP component for the dominant vegetation cover types, and the NPP_A estimates from summing the spatial estimates of the three aboveground biomass components.

Cover type	Aggregate NPP_A	NPP_A from spatial components
Aspen	7.8 (0.4)	7.5 (0.7)
Forested wetlands	5.0 (0.5)	4.4 (0.8)
Hardwoods	7.2 (0.6)	7.7 (0.9)
Mixed	5.7 (1.4)	6.4 (2.2)
Nonforested wetlands	4.5 (0.9)	4.4 (1.6)
Red pine	4.9 (0.9)	5.5 (1.4)
Upland conifer	4.9 (1.0)	4.9 (1.5)

Note: Values are means with SEs in parentheses. There are no significant differences using a paired t test ($p = 0.26$) between the aggregate means and the means from the sum of the three different spatial means of the components.

Aboveground net primary production (NPP_A)

Aboveground net primary production differed significantly ($p = 0.01$) across the vegetation cover types and ranged from 4.5 $t·ha^{-1}·year^{-1}$ for nonforested wetlands to 7.8 $t·ha^{-1}·year^{-1}$ for aspen (Table 2). NPP_A had a significant spatial pattern ($p = 0.03$); the overall mean NPP_A was 5.7 $t·ha^{-1}·year^{-1}$ for the

Fig. 3. Exponential rise to maximum relationship between foliage (NPP$_F$) and wood (NPP$_W$) net primary production. The exponential rise to maximum regression model is significant at $p < 0.001$. Symbols represent the different vegetation cover types.
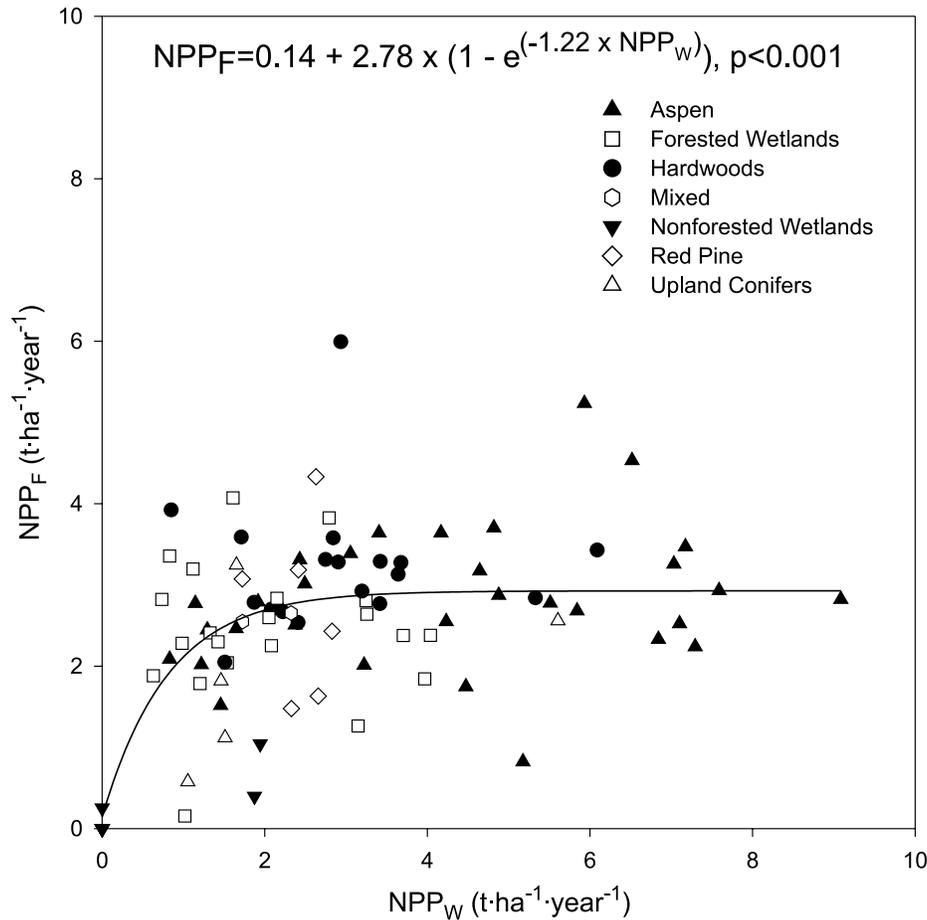
site. The spherical model had a range of 221 m, a sill of 4.60, and a nugget of 2.72 (Fig. 1). These estimates were calculated by aggregating the components (wood, foliage, understory) for each plot and then using the geostastical model to analyze plot-level sums as a single value. NPP$_A$ ranged from 4.4 to 7.7 t·ha^{-1}·year^{-1} with an overall spatially weighted mean of 5.8 t·ha^{-1}·year^{-1} for the study site when the spatial patterns of each component were taken into account. This was accomplished by using the geostatistical results of the component estimated and then summing up the components after accounting for the spatial variance (Table 2). The two estimates of NPP$_A$ for the study site did not differ significantly ($p = 0.26$). Additional comments and the relationships between NPP$_A$ and its components can be found later in this section.

Comparisons between NPP$_A$ estimates and previous studies

NPP$_A$ estimates from this study were very similar to those from a previous study that was conducted in the Chequamegon and Nicolet National Forests (Fassnacht and Gower 1997). Our estimates were slightly higher, which can partially be explained by the fact that we measured NPP$_U$ in addition to NPP$_W$ and NPP$_F$. On average, NPP$_U$ was 18% of NPP$_A$. Our NPP$_A$ estimate for red pine (4.9 t·ha^{-1}·year^{-1}) was similar to previously reported estimates in northern Wis-

consin of 4.0–5.1 t·ha^{-1}·year^{-1} (Fassnacht and Gower 1997). Our estimate of NPP$_A$ for aspen was approximately 25% lower than previously measured estimates in northern Wisconsin (Crow 1978), and our estimate of NPP$_U$ in aspen was approximately 50% lower (Crow 1978). Our estimate of northern hardwood NPP$_A$ was similar to those found by Crow (1978). Our estimate of NPP$_W$ was higher than those recently measured in a hardwood stand in Massachusetts (Barford et al. 2001). There are several possible reasons for the observed differences in NPP. Recent forest thinning and harvesting activities in the past 5 years decreased LAI (Burrows 2002). Since LAI is positively correlated with NPP (Fassnacht and Gower 1997; this study, next section), the decrease in LAI may be the cause for lower NPP. Aspen and red pine forests received the greatest thinning and showed the largest differences in NPP$_A$ from previous studies. NPP$_W$ also varied among years, but the difference averaged less than 10%.

Associations among the NPP components

The three NPP components showed significant relationships with each other. NPP$_W$ and NPP$_F$ were significantly positively correlated with each other with a nonlinear relationship ($p = 0.001$; Fig. 3). NPP$_U$ was inversely related to both NPP$_W$ and NPP$_F$ ($p = 0.0001$ and $p = 0.0001$, respectively, Figs. 4 and 5). The NPP$_F$/NPP$_W$ ratio was very similar

Fig. 4. The inverse exponential relationship between wood (NPP_W) and understory (NPP_U) net primary production ($p < 0.0001$). Symbols represent the different vegetation cover types.
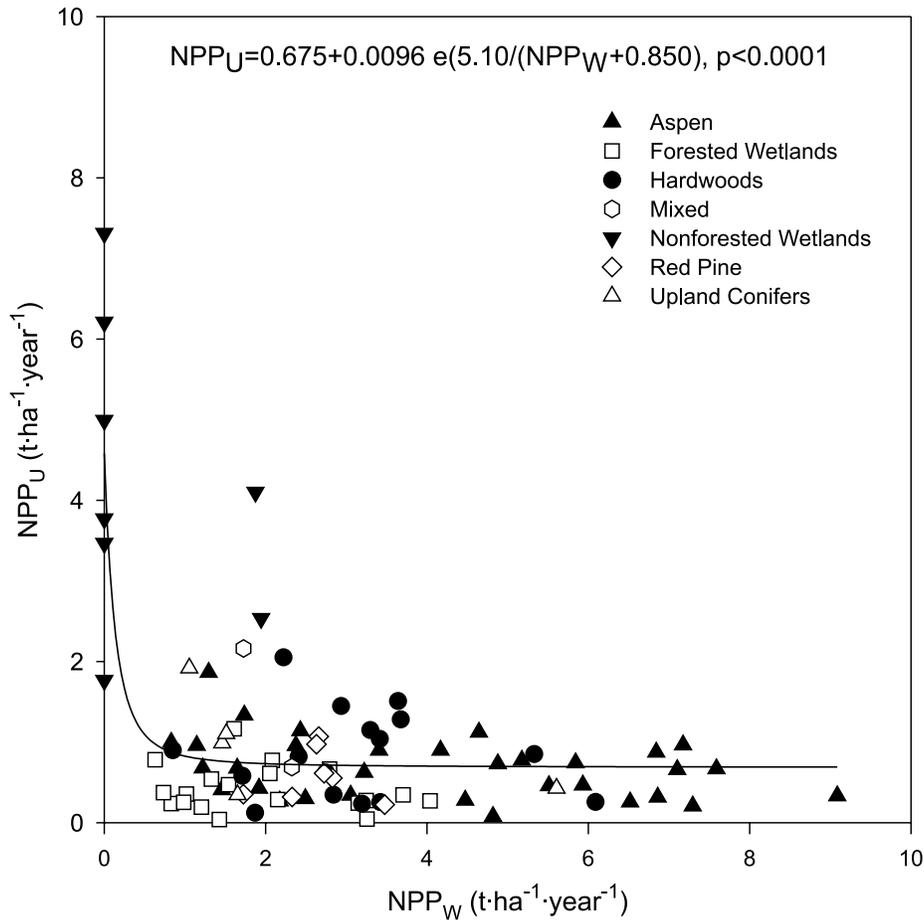
for the upland conifers, northern hardwoods, and the forested wetlands (0.91 to 1.04) but was smaller for the aspen (0.61) and larger for mixed forests (1.44) (Table 1).

The inverse relationship between NPP_U and NPP_F or NPP_W was a key indicator as to why spatial patterns found in the NPP components are different from those found in the overall NPP_A estimates. Depending on the vegetation cover type, most of NPP_A either occurred on the ground (e.g., nonforested wetlands) or in the canopy (e.g., hardwoods and lesser so in the other forested vegetation cover types). This is manifested as spatial patterns found in the components, but the overall NPP_A spatial pattern was smoothed out by the compensatory production of the components (e.g., when the overstory productivity ($NPP_F + NPP_W$) is high, the understory productivity is low). Looking at the variance estimates (represented by the sill in Fig. 1), the variance for NPP_A was not the sum of $NPP_U + NPP_F + NPP_W$. Since the three components were not independent (e.g., correlated), the variance of NPP_A was less than the sum of the variances of the three components.

The different spatial patterns found among the components (NPP_U, NPP_F, NPP_W) of NPP_A are very interesting. If the inverse relationship between foliage and understory was linear, the spatial range of autocorrelation would be the same because as NPP_F would increase, NPP_U would decrease at the same rate. However, because of the highly nonlinear re-

lationship found, there is a strong disconnect between the spatial patterns of these two components. Similar reasons for the differences in spatial patterns between all three components are observed in the nonlinear relationships found between these components (Figs. 3–5). The results are interesting in that NPP_W has the longest range and highest sill, NPP_F has the shortest range and intermediate sill, and NPP_U has an intermediate range and the smallest sill (Fig. 1). It would seem that since both foliage and wood come from the overstory that they should be more correlated with each other spatially than with the understory component. However, since they are not, there could be other factors (such as site conditions, stand history) that are influencing the patterns observed.

Relationship between NPP_A and LAI

NPP_A was positively correlated with LAI for all five vegetation cover types (Fig. 6) as well as when all vegetation cover types were composited ($p = 0.01$, Fig. 6). The relationships, however, were not as strong as those previously reported for evergreen and deciduous forests in the same area (Fassnacht and Gower 1997). Also, the LAI-to-NPP_A slope for northern hardwoods in this study was 45% greater than the value reported for northern hardwoods in northern Wisconsin by Fassnacht and Gower (1997). The difference can be explained by two factors. NPP_U was included in this

Fig. 5. The inverse exponential relationship between foliage (NPP_F) and understory (NPP_U) net primary production ($p < 0.0001$). Symbols represent the different vegetation cover types.
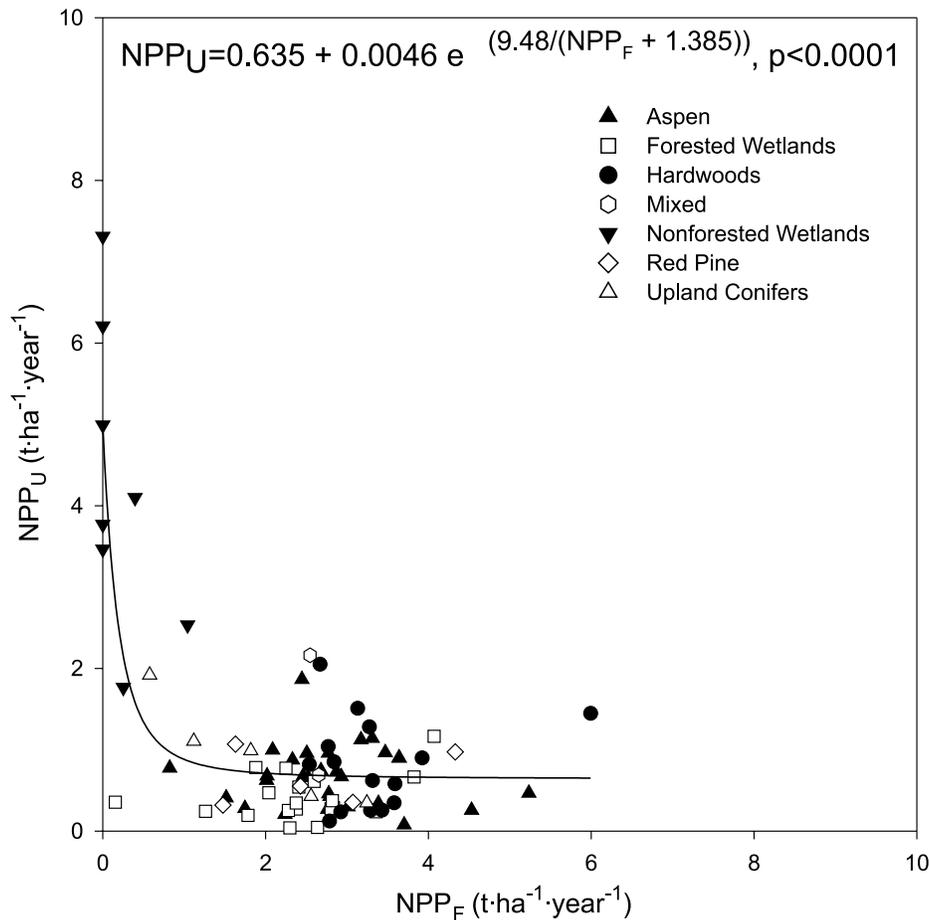
study but not by Fassnacht and Gower (1997). When understory was removed from the equation, the slope of the fitted line was reduced by 12%. The steeper slope reported in this study was likely because many of the stands were thinned, and thinning is known to increase wood production per unit leaf area (Waring and Pitman 1985).

Unlike Fassnacht and Gower (1997), we found a moderately significant relationship between LAI and NPP_A for the conifers (red pine and upland conifers) owing to a limited range in LAI values sampled (Fig. 6). This is most likely due to site history. Almost all conifers were planted within the last 70 years (Burrows 2002), so all of the red pine plots measured were of the same age-class. However, sections of the plantations have received different management treatments in the past 5 to 10 years, leading to the increase in variation that we observed.

The implications of spatial patterns in the components of NPP should not be overlooked. Mean residence times and decomposition rates differ by several orders of magnitude among the biomass components. For example, NPP_W is the component with the longest mean residence time (Landsberg and Gower 1997), and the range estimate for wood NPP was 150 m. The range was 28 m for NPP_F. This means that there is less spatial correlation found in foliage production compared with wood production in the same area. Previous studies (Kimball et al. 1999; Ahl 2002) have found significant variation in NPP estimates based on the spatial scale at which

ecosystem process models are run. The results from this paper show that the components of NPP_A are operating at different scales and are also correlated with each other. Process-based models should take this factor into account when developing estimates of NPP_A and NEE.

While this study was one of the larger spatial studies of NPP_A to date, future studies designed to look at the causes of spatial patterns of NPP_A will require even greater sample sizes to both estimate the spatial structure and measure the potential underlying causes. A companion study (Burrows 2002) using all 312 plots to analyze the correlation of spatial patterns of LAI with anthropogenic and abiotic site conditions was adequately sampled, but the 100 plots used for NPP_A were not large enough to be used for the same type of analysis that was used to relate the ecological mechanisms behind the patterns. Since there is a positive relationship between LAI and NPP_A (Fig. 6), we can use the correlation of LAI and the spatial patterns found in Burrows (2002) to extrapolate some of the anthropogenic and abiotic site conditions that could influence NPP_A. They include interannual variation, elevation, cover type, management activity, slope, aspect, soil texture, and several interactions between these main effects (Burrows 2002).

Unfortunately this study does not look at the spatial patterns of belowground NPP. This is not to say that the authors did not value the importance of belowground measurements, but rather the collection and analysis of belowground NPP

Fig. 6. Regressions between aboveground net primary productivity (NPP_A) and leaf area index (LAI) measured in 1999 by vegetation cover type. All regressions are positively correlated.
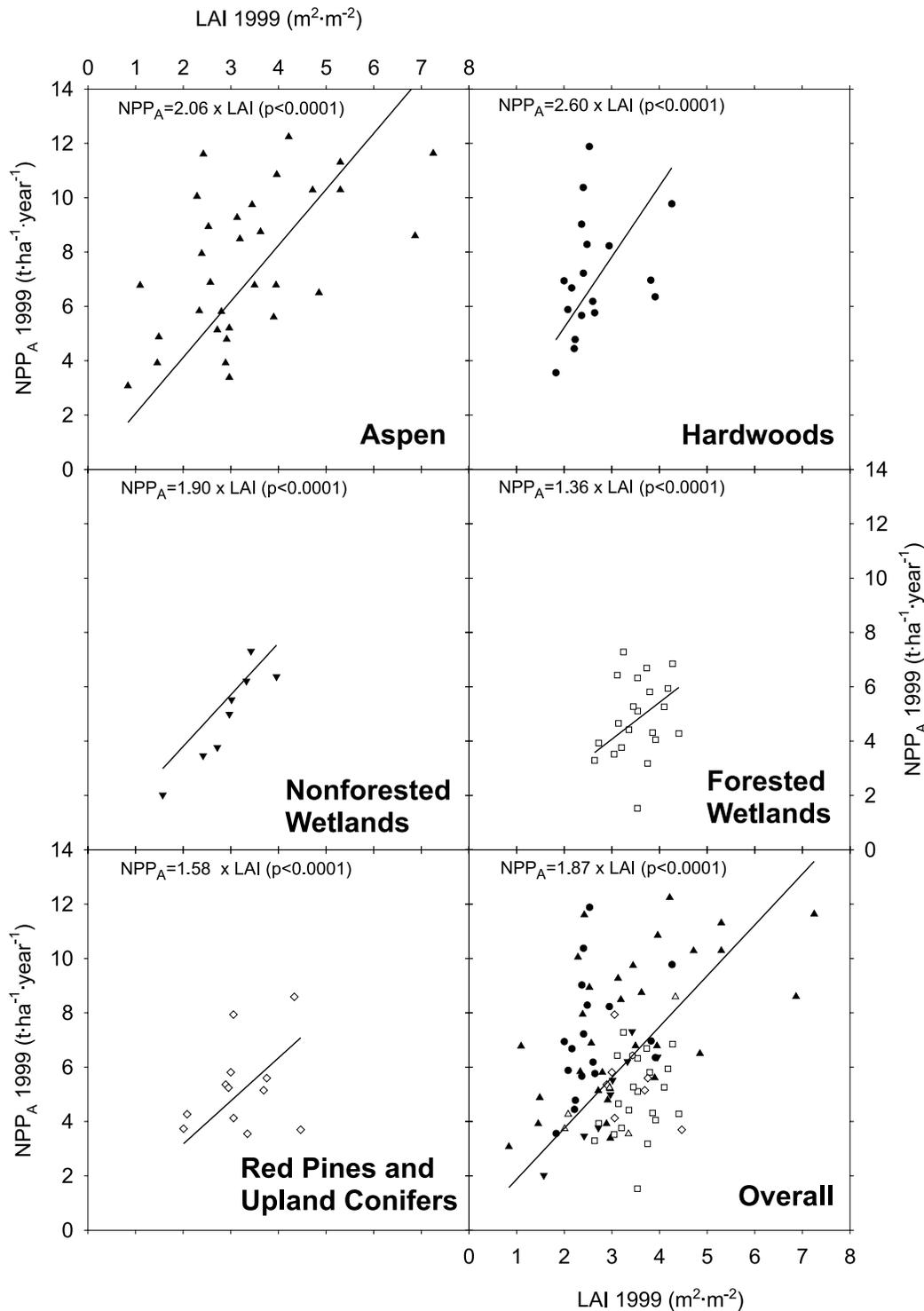
data were both very difficult to perform, and the accuracy of belowground measurement techniques are highly variable in their results. Belowground allocation of C in the different cover types found on the study site could easily influence C cycling patterns and could easily be different than those observed in the aboveground NPP components. The authors highly recommend future studies to look at the spatial pat-

terns of belowground NPP so that a more complete look at spatial patterns of NPP can be conducted.

Conclusions

This study examined the relationships among components of aboveground net primary production. There were signifi-

cant relationships found among the three aboveground components of NPP$_A$. Each component's spatial pattern was different from that of the other components in terms of the spatial range, sill, and nugget estimates. There were significant differences among vegetation cover type NPP estimates, and there were significant interannual variations for NPP$_W$.

The spatial patterns found in the NPP components pose interesting questions — how do the patterns observed on the ground influence measurements and interpretations being made by flux towers and remote sensing systems? Are the spatial resolutions of the sensors matched with the spatial frequencies observed on the ground? Also, how do these patterns relate to models being implemented at different spatial and temporal scales that are used to predict both short-term and long-term carbon fluxes from the landscape? This study has taken the first step to answering these questions by quantifying the NPP patterns found on the landscape. Further research is needed to ascertain why NPP patterns occur and how these observed patterns could be incorporated into models to improve accuracy of predictions of local, regional, and global carbon cycles. Quantifying the spatial heterogeneity of NPP$_A$ components will help to characterize the processes and the scales at which they operate in influencing carbon budgets.

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Appendix A

Table A1. Species-specific aboveground biomass equations used to convert tree DBH (centimetres) to tree biomass (kilograms).

Species	Biomass component	Model	a (c^*)	b (d^*)	Min. DBH (cm)	Max. DBH (cm)	N	r^2	Source
Abies balsamea	Branches	α	0.0050	2.4605	3	51	95	0.949	Young et al. 1980
	Stem	α	0.0679	2.4117	3	51	95	0.995	Young et al. 1980
Acer rubrum	Branches	α	0.0223	2.2055	3	66	62	0.966	Young et al. 1980
	Stem	α	0.0787	2.4898	3	66	62	0.996	Young et al. 1980
Acer saccharum	Branches	α	0.0104	2.5515	3	66	42	0.937	Young et al. 1980
	Stem	α	0.1626	2.2894	3	66	42	0.995	Young et al. 1980
Alnus rugosa	Branches	α	0.0617	1.5201	3	9	30	0.879	Young et al. 1980
	Stem	α	0.0463	2.5755	3	9	30	0.967	Young et al. 1980
Betula papyrifera	Branches	α	0.0215	2.3000	0	34	18	0.979	Hocker and Earley 1983
	Stem	α	0.2044	2.1700	0	34	18	0.995	Hocker and Earley 1983
Fraxinus americana	Branches	α	0.0315	2.1935	1	28	46	0.927	Ker 1980
	Stem	α	0.1124	2.3649	1	28	46	0.991	Ker 1980
Larix laricina	Branches	α	0.0436	1.9810	3	51	23	0.960	Young et al. 1980
	Stem	α	0.0762	2.3051	3	51	23	0.995	Young et al. 1980
Picea glauca	Branches	α	0.0248	2.4300	1	33	115	0.900	Harding and Grigal 1985
	Stem	α	0.0397	2.5360	1	33	115	0.950	Harding and Grigal 1985
Picea mariana	Branches	α	0.0287	2.2679	0	37	195	0.895	Ker 1984
	Stem	α	0.0849	2.3130	0	37	195	0.976	Ker 1984
Pinus banksiana	Branches	α	0.0353	2.1113	0	38	195	0.845	Ker 1984
	Stem	α	0.1470	2.1673	0	38	195	0.972	Ker 1984
Pinus resinosa	Branches	α	0.0098	2.5011	3	51	14	0.986	Young et al. 1980
	Stem bark	α	0.0141	2.0900	3	46	69	0.990	Perala and Alban 1994
	Stem wood	α	0.0649	2.3496	3	46	69	na	Perala and Alban 1994
Pinus strobus	Branches	α	0.0030	2.4858	3	66	35	0.953	Young et al. 1980
	Stem	α	0.0404	2.5459	3	66	35	0.988	Young et al. 1980
Populus grandidentata	Branches	α	0.1368	1.7510	1	24	30	0.963	Freedman 1984
	Stem bark	α	0.0333	2.2142	3	45	58	na	Perala and Alban 1994
	Stem wood	α	0.0426	2.5618	3	45	58	na	Perala and Alban 1994
Populus tremuloides	Branches	α	0.0038	2.7680	15	40	9	0.897	Pastor and Bockheim 1981
	Branches	α	0.0065	2.6950	3	15	45	0.982	Ruark et al. 1987
	Stem bark	α	0.0437	2.1460	15	40	9	0.955	Pastor and Bockheim 1981
	Stem bark	α	0.0108	2.5520	3	15	45	0.981	Ruark et al. 1987
	Stem wood	α	0.0407	2.6060	3	15	45	0.993	Ruark et al. 1987
	Stem wood	α	0.1714	2.1990	15	40	9	0.986	Pastor and Bockheim 1981

Table A1 (*concluded*).

Species	Biomass component	Model	a (c*)	b (d*)	Min. DBH (cm)	Max. DBH (cm)	N	r^2	Source
Prunus pensylvanica	Branches	α	0.0406	1.9197	3	24	30	0.932	Young et al. 1980
	Stem	α	0.0951	2.2988	3	24	30	0.991	Young et al. 1980
Prunus serotina	Wood	β	0.0716	2.6174	5	50	26	na	Brenneman et al. 1978
			(–0.0203)	(2.0380)					
Thuja occidentalis	Branches	α	0.0480	1.9110	3	51	39	0.973	Young et al. 1980
Thuja occidentalis	Stem	α	0.0832	2.1300	3	51	39	0.991	Young et al. 1980
	Wood	β	0.0872	2.3539	4	47	31	na	Perala and Alban 1994
			(–0.0049)	(2.0940)					
Tsuga canadensis	Branches	α	0.0062	2.7033	3	51	36	0.960	Young et al. 1980
	Stem	α	0.0649	2.3662	3	51	36	0.983	Young et al. 1980

Note: Model α = $a \times \text{DBH}^b$; model β = $a \times \text{DBH}^b + c \times \text{DBH}^d$.

*Parameters c and d are presented in parentheses when needed for model β.

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