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Allometric equations for young northern hardwoods: the importance of age-specific equations for estimating aboveground biomass

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Abstract: Estimates of aboveground biomass and nutrient stocks are commonly derived using equations that describe tree dimensional relationships. Despite the widespread use of this approach, there is little information about whether equations specific to stand age are necessary for accurate biomass predictions. We developed equations for small trees (2–12 cm diameter) of six species in four young northern hardwood stands. We then compared our equations with equations used frequently in the literature that were developed in mature stands (Whittaker et al. 1974. Ecol. Monogr. **44**: 233–252). Our equations for yellow birch (*Betula alleghaniensis* Britt.) predicted 11%–120% greater stem wood for individual trees compared with the equations from Whittaker et al. and, on average, 50% greater aboveground yellow birch biomass in the four stands that we studied. Differences were less pronounced for sugar maple (*Acer saccharum* Marsh.) and American beech (*Fagus grandifolia* Ehrh.); our equations predicted, on average, 9% greater aboveground stand biomass for sugar maple and 3% lower biomass for American beech compared with Whittaker et al. Our results suggest that stand age may be an important factor influencing the aboveground allometry and biomass of small yellow birch trees in these developing northern hardwood stands.

Résumé : Des estimations de la biomasse aérienne et de la quantité de nutriments sont souvent calculées à l'aide d'équations décrivant des relations tridimensionnelles. Malgré l'utilisation généralisée de cette approche, il y a peu d'information concernant la nécessité d'utiliser des équations qui tiennent compte de l'âge du peuplement pour obtenir des prévisions précises de la biomasse. Nous avons mis au point des équations pour les petits arbres (de 2 à 12 cm de diamètre) de six espèces provenant de quatre jeunes peuplements de feuillus nordiques. Nous avons ensuite comparé nos équations à celles qui sont fréquemment utilisées dans la littérature et qui ont été mises au point à partir de peuplements matures (Whittaker et al. 1974. Ecol. Monogr. **44** : 233–252). Dans le cas du bouleau jaune (*Betula alleghaniensis* Britt.), nos équations prédisaient 11 % à 120 % plus de bois de tronc par arbre que les équations de Whittaker et al. et, en moyenne, 50 % plus de biomasse aérienne de bouleau jaune dans les quatre peuplements étudiés. Ces différences étaient moins prononcées dans le cas de l'érable à sucre (*Acer saccharum* Marsh.) et du hêtre à grandes feuilles (*Fagus grandifolia* Ehrh.); en effet nos équations prédisaient, en moyenne, 9 % plus de biomasse aérienne du peuplement pour l'érable à sucre et 3 % moins de biomasse pour le hêtre à grandes feuilles que les équations de Whittaker et al. Nos résultats indiquent que l'âge du peuplement est un facteur qui peut avoir un effet important sur l'allométrie et la biomasse aérienne des bouleaux jaunes de petite taille dans ces jeunes peuplements de feuillus nordiques.

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Introduction

Accurate descriptions of aboveground forest biomass are essential for characterizing ecosystem function and accounting for terrestrial C stocks. Estimates of forest biomass are commonly derived from allometric equations that relate the biomass of an individual tree to its diameter at 1.37 m (diameter at breast height (DBH)) or parabolic volume (PV) (Jenkins et al. 2004). Allometric estimates of forest biomass have been used to help assess the impacts of forest management (Leighty et al. 2006), land-use change (Ouimet et al. 2007), increases in atmospheric CO_2 (Norby et al. 2002), and the potential of forests to offset anthropogenic C emissions (Canadell and Raupach 2008). Biomass estimates derived from allometric equations are also an integral component of nutrient budgets (e.g., Likens et al. 1998) because the biomass of individual tree components (e.g., stem wood, branches, stem bark, foliage, roots, etc.) are multiplied by average tissue nutrient concentrations to estimate nutrient content.

Developing allometric equations requires felling trees of a range of sizes and obtaining their mass by component. Mathematical models are then used to describe the relationships between component dry mass and the DBH or PV of the trees sampled. In practice, allometric equations are often applied to tree populations distinct from the population in which they were developed (e.g., Nowak and Crane 2002), which assumes that species-specific dimensional relationships are invariant across space and time. Yet there is evidence that contradicts this assumption. Tree allometry sometimes varies with site quality (Koerper and Richardson 1980; Gargaglione et al. 2010), and dimensional relationships for a species can change over the course of a rotation (Vanninen et al. 1996; Lehtonen et al. 2004). If allometric equations do not appropriately describe the dimensional relationships of the population to which they are being applied, these equations can be a significant source of error (up to 20%) in aboveground biomass estimates (Chave et al. 2004).

Second-growth forests in North America are a patchwork of stands of different ages ranging from early-successional young stands to late-successional mature stands. The influence of stand age on allometric estimates of biomass warrants attention as a potential source of error in estimates of biomass and nutrient stock in these ecosystems. Stand age might be expected to affect tree allometry through its influence on stem density, canopy structure, and tree growth patterns. Small trees in young developing stands hold dominant or codominant positions in the canopy and thus have more access to light than trees of the same size in the understory of mature stands. In dense young stands, trees can outcompete neighbors by growing in height (Beaudet and Messier 1998) and expanding crown area to shade out competitors. Under these conditions, increased allocation of biomass to branch and leaf (Porté et al. 2002) and stem height (Messier and Nikinmaa 2000) may confer a competitive advantage.

There is evidence that aboveground biomass allocation patterns and tree allometry vary with stand age for some tree species (Peichl and Arain 2007), but the degree of plasticity in biomass allocation may depend on the ecological niche and shade tolerance of the species (DeLucia et al. 1998; Ray et al. 2011). Competition for canopy dominance may cause trees to allocate more photosynthate to shoot extension in-

stead of radial growth (Waring 1987). For example, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) trees were found to be taller relative to their diameter in young stands than in mature stands (Knowe 1994). Canopy loblolly pines (*Pinus taeda* L.) allocated a smaller percentage of total aboveground biomass to stem wood but a greater percentage to branch tissues compared with subcanopy trees of the same diameter (Naidu et al. 1998). A study of red maple (*Acer rubrum* L.) in the Great Lakes region that compared slopes and intercepts for allometric equations based on DBH for stands 40 and 70 years old did not reveal a significant effect of stand age on allometric equations (Crow 1983). Information from trees of additional species and stand ages can help determine under what conditions equations specific to stand age are required.

Allometric equations were developed for five species in a mature northern hardwood forest by Whittaker et al. (1974) and corrected by Siccama et al. (1994) based on trees measured in the Hubbard Brook Experimental Forest. These equations have been validated for aboveground biomass (Arthur et al. 2001) and refined for root biomass (Vadeboncoeur et al. 2007) and are often applied to estimate northern hardwood biomass at other sites (e.g., Magill et al. 1996; Park et al. 2008). However, the accuracy of these equations in predicting aboveground biomass in young stands has never been tested.

The objective of this study was to examine the importance of stand age on allometric predictions of biomass for small trees (2–12 cm DBH) of northern hardwood species. We first developed species-specific allometric equations for trees in young (<30 years old), even-aged northern hardwood stands. Three of the six species that we studied are also described by allometric equations in Whittaker et al. (1974) from mature stands. The Whittaker equations describe a much broader range in tree DBH than our equations do, but include small trees. To investigate how stand age can influence tree allometry, we compared our biomass equations with the Whittaker equations. We hypothesized that our equations would predict greater branch and foliage biomass for small trees because they occupy a more dominant position in the canopy of our young stands compared with subdominant positions in mature stands. We also expected our equations to predict greater stem wood biomass and height at a given DBH because stem height growth can confer a competitive advantage where there is high competition for canopy light in young, dense stands. Finally, we assessed whether differences in equations from this study and the Whittaker equations were important for calculating total aboveground biomass in four developing northern hardwood stands.

Methods

Site description

We studied four young, even-aged stands (14–30 years after clearcut) located in and around the Bartlett Experimental Forest in the White Mountain National Forest of New Hampshire (Table 1). All stands are located in the Bartlett Experimental Forest, except for C1, which is located just outside the official boundary. The climate is characterized by a short growing season with a frost-free period of 120 days. Precipitation averages 120–140 cm/year and is well distrib-

Table 1. General location and site characteristics for the four young northern hardwood stands that we sampled, each located in a designated compartment (Cmpt) in the Bartlett Experimental Forest, with the exception of C1.

Stand	Age (years)	Location in the Bartlett Experimental Forest	Latitude, longitude	Approximate elevation (m)	Basal area (m²/ha)	Stem density (no./ha)	Dominants
C1	14	Southwest of Cmpt 32	44°02′N, 71°19′W	570	12	12 982	Pin cherry, white birch, American beech
C2	16	Cmpt E2	44°04′N, 71°16′W	340	14	12 776	American beech, pin cherry, white birch
C4	26	Cmpt E3	44°03′N, 71°16′W	410	25	8 463	White birch, American beech, bigtooth aspen
C6	29	Cmpt E5	44°02′N, 71°16′W	460	29	6 224	Yellow birch, American beech, red maple

Note: Stem density describes only stems ≥2 cm DBH. Species are listed in order of abundance by contribution to basal area. "Age" describes years post-harvest in 2004 when all species except sugar maple were sampled.

uted throughout the year with about one third in the form of snow (Smith and Martin 2001). Soils are mostly well-drained coarse-loamy, mixed, frigid Typic Haplorthods derived from granitic till (Leak 1991).).

Sampling methods

Trees were measured in four 30 m × 30 m plots in each stand in 2004. All trees ≥10.0 cm DBH were identified by species and DBH was recorded. In five 5 m × 5 m subplots within each plot, we identified and recorded all trees 2.0–9.9 cm DBH. We sampled the most abundant species based on their contribution to basal area: yellow birch (*Betula alleghaniensis* Britt.), American beech (*Fagus grandifolia* Ehrh.), red maple, white birch (*Betula papyrifera* Marsh.), and pin cherry (*Prunus pensylvanica* L.f.). We also sampled sugar maple (*Acer saccharum* Marsh.), which was not one of the six most abundant species but is an important species in many northern hardwood ecosystems and was also sampled by Whittaker et al. (1974). Trees were uniformly sampled across the 2–12 cm DBH range for all species except American beech (2–8 cm) because beech trees >8 cm DBH were seldom found in these stands. Beech bark disease was prevalent and severe in some of these stands, but we did not sample trees with significant, visible damage from insect or fungal infestation. For all tree species, we selected single-stem trees that appeared to have good vigor, without obvious disease or damage. Twelve trees per species were sampled, including three individuals per species per stand, with the exception of American beech, for which we sampled only two individuals in stand C6 for a total of 11 trees. Field samples were collected between 22 July and 24 August in 2004 for all species except sugar maple, which was sampled between 22 July and 12 August in 2005.

Trees were cut ≤16 cm above the ground. Trees were separated into stem wood, branches, and foliage components. Each component was weighed in the field and subsampled for determination of moisture content. If a clear main stem could not be identified, we defined stem wood as the largest, most central branch of the tree. The main stem was cut into separate logs of ~2 m in length. After logs were weighed, we cut disks ~2 cm thick from the end of each log; disks were returned to the laboratory for determination of moisture content.

The portion of the main stem <2 cm diameter was considered to be part of the branches. Branches were divided into three size classes based on average branch basal diameter: small (<1 cm), medium (1–2 cm), and large (>2 cm). Subsamples of branch material were taken from these size classes proportionately by contribution to total branch mass for a total subsample mass of 200 g to determine moisture content. Because total branch mass depended on the size of the tree, the actual percentage of total branch mass that was subsampled from the tree varied widely: <10% for the largest trees and >50% for the smallest trees. Dead branches, encountered on only a few of the larger trees, were weighed in the field along with live branches but were not subsampled separately for moisture content. We estimated that dead branches accounted for <5% of total dry branch mass when present.

Foliage was sampled in the field by dividing the tree crown into four vertical segments of equal length along the

main stem. Foliage, including the petioles, was removed from the branches, weighed, and subsampled proportionately by contribution of each vertical segment to total canopy mass. A standard total subsample mass of 30 g was used for determination of moisture content. Because total foliage mass depended on the size of the tree and position in the canopy, the actual percentage of total foliage mass that was subsampled from the tree also varied widely: <1% for the largest trees and >20% for the smallest trees.

For pin cherry, yellow birch, and white birch, it would have been prohibitively time-consuming to separate all foliage from the fine twigs (shoots <5 mm in diameter). For these species, fine twigs were weighed with foliage. For sugar maple, red maple, and American beech, whose foliage was easy to remove, fine twigs were weighed with branches. Whittaker et al. (1974) also measured twigs with foliar biomass and reported that twigs comprised only ~5% of total foliage and twig mass.

In the laboratory, bark was removed from stem disks and all samples (foliage, branches, stem wood, and stem bark) were weighed before and after oven-drying to constant mass at 60 °C. We did not remove the bark from branch subsamples. Component dry mass was estimated by application of the ratio of dry to fresh mass obtained from subsamples to component fresh mass determined in the field.

Allometric analysis

Ordinary least-squares regression was used to develop equations for each species relating tree component and total aboveground biomass to DBH and PV (independent variable). PV was calculated using the following formula: $1/2\pi \times (DBH/2)^2 \times HT$, where DBH is measured in centimetres and HT is tree height (centimetres). Allometric equations are presented in the following form:

$$[1] \qquad \log_{10}(Y) = a + b \log_{10}(X)$$

where Y is biomass (grams) or height (centimetres), X is tree DBH (centimetres) or PV (cubic centimetres), and a and b are the regression coefficients. Dependent variables modeled include the dry masses of total aboveground biomass, stem wood, branches, stem bark, and foliage. To check for homogeneity of variance in the data for each regression model, we used White's (1980) test. Using $\alpha = 0.05$ for this test, all of our data conformed to the assumption of homogeneity of variance.

Ordinary least-squares regression of log-transformed data was chosen because of its simplicity, ubiquity in the literature, and the high correlation coefficients achievable with this method. However, the logarithmic transformation can lead to a bias towards underestimating biomass (Baskerville 1972; Beauchamp and Olson 1973). To correct for this effect, we calculated a correction factor, the quasi-maximum likelihood estimator (Smith 1993) (QMLE):

$$[2] \qquad QMLE = e^{(MSE/2)}$$

where MSE is the mean-squared error of the regression model. To compare biomass estimates derived from equations from this study and those from Whittaker et al. (1974), we

calculated 95% confidence intervals based on the standard error of the mean of Y at a specified value of X (Snedecor and Cochran 1989, p. 162; Yanai et al. 2010). This error parameter (ε) is calculated as

$$[3] \qquad \varepsilon = MSE\sqrt{\frac{\frac{1}{n} + (x - \bar{x})^2}{SSD}}$$

which incorporates the MSE of the regression equation, the number of trees used to derive the regression equations (n), the $\log_{10}$(DBH) of a given tree (x), the mean $\log_{10}$(DBH) of the trees used to derive the regression equation ($\bar{x}$), and the sum of squared deviations (SSD) of the $\log_{10}$(DBH) of the trees used to develop the regression model. To calculate the error on the Whittaker regression equations, we used the antilog of the error term "E" published in Whittaker et al. (1974) to obtain the MSE. We used unpublished data from that study to obtain values for $\bar{x}$ and the SSD.

Biomass comparisons

We compared allometric equations developed from American beech, sugar maple, and yellow birch trees in this study with equations from Whittaker et al. (1974). Whittaker et al. (1974) sampled trees from the lower and middle elevations of the area just west of Watershed 6 at the Hubbard Brook Experimental Forest, approximately 55 years after the forest was selectively logged. We graphed biomass predictions from our equations and the Whittaker equations and restricted analysis to the size range that we sampled (2–12 cm for sugar maple and yellow birch and 2–8 cm for American beech). To determine whether estimates of biomass or height from our equations were significantly different from Whittaker's estimates, we compared the 95% confidence intervals on these equations. We focus on describing the differences in biomass predictions based on DBH because it is widely used to estimate biomass (Jenkins et al. 2004). We also provide our PV equations because they are more accurate in cases where tree heights are known.

We compared total aboveground biomass in our four stands by calculating the sum of component biomass equation estimates instead of total aboveground biomass equations because component equations are necessary for constructing nutrient budgets. We calculated total aboveground biomass by component using two different approaches. The "Fatemi and Whittaker" approach relies on equations developed for this study for trees <12 cm DBH but equations from Whittaker et al. (1974) for trees ≥12 cm DBH and for trees species not described by our equations (striped maple (*Acer pensylvanicum* L. and red spruce (*Picea rubens* Sarg.)). In the "Fatemi and Whittaker" approach, we used the Whittaker equations for approximately 1% of the total basal area in stands C1 and C2 because they do not contain many trees ≥12 cm DBH. The other stands that we studied contained more trees ≥12 cm DBH, and the Whittaker equations were used to estimate biomass for 62% and 48% of the total basal area in C4 and C6, respectively. In the "Whittaker" approach, we used only the Whittaker equations for sugar maple, American beech, yellow birch, striped maple, and red spruce to estimate aboveground biomass.

Table 2. Regression coefficients (*a* and *b*) derived from equations of the following form: $\log_{10}(\text{biomass (g) or height (cm)}) = a + b \log_{10}(X)$, where (*X*) is either tree DBH (cm) or PV (cm^3).

	Regressions on DBH				Regressions on PV			
	a	*b*	R^2	RMSE	*a*	*b*	R^2	RMSE
Total aboveground biomass								
A. rubrum	2.130	2.237	0.988	0.0548	0.170	0.921	0.995	0.0341
A. saccharum	2.180	2.416	0.997	0.0365	0.337	0.897	0.995	0.0531
B. alleghaniensis	2.260	2.513	0.972	0.0666	0.366	0.931	0.987	0.0707
B. papyrifera	1.990	2.538	0.990	0.0621	−0.384	1.048	0.986	0.0749
F. grandifolia	2.342	2.155	0.959	0.0936	0.683	0.817	0.955	0.1037
P. pensylvanica	1.833	2.597	0.872	0.2140	0.187	0.899	0.836	0.2429
Stem wood biomass								
A. rubrum	1.860	2.492	0.970	0.0920	−0.218	0.973	0.985	0.0651
A. saccharum	1.921	2.512	0.991	0.0691	−0.005	0.935	0.992	0.0664
B. alleghaniensis	1.978	2.752	0.988	0.0948	−0.102	1.023	0.988	0.0680
B. papyrifera	1.739	2.638	0.979	0.0948	−0.753	1.096	0.986	0.0769
F. grandifolia	2.029	2.307	0.957	0.1017	0.254	0.876	0.947	0.1141
P. pensylvanica	1.659	2.694	0.988	0.0738	−0.499	1.030	0.876	0.2369
Stem bark biomass								
A. rubrum	1.166	2.266	0.983	0.0629	−0.708	0.881	0.988	0.0523
A. saccharum	1.231	2.284	0.985	0.0807	−0.516	0.849	0.983	0.0859
B. alleghaniensis	0.846	2.665	0.862	0.2457	−1.227	1.005	0.897	0.2126
B. papyrifera	0.823	2.711	0.934	0.1693	−1.627	1.010	0.963	0.1268
F. grandifolia	0.890	2.297	0.906	0.1551	−0.865	0.869	0.889	0.1688
P. pensylvanica	0.104	3.311	0.929	0.2141	−2.304	1.168	0.793	0.3631
Branch biomass								
A. rubrum (plus twigs)	1.611	2.079	0.882	0.0927	−0.106	0.808	0.961	0.0886
A. saccharum (plus twigs)	1.386	2.460	0.941	0.1771	−0.473	0.909	0.926	0.1979
B. alleghaniensis	1.941	1.566	0.819	0.1696	0.831	0.562	0.760	0.1950
B. papyrifera	1.476	2.195	0.925	0.1527	−0.495	0.886	0.876	0.1963
F. grandifolia (plus twigs)	1.945	1.890	0.897	0.1343	−0.822	1.114	0.797	0.3070
P. pensylvanica	1.956	1.484	0.837	0.1610	0.992	0.512	0.584	0.3631
Foliage biomass								
A. rubrum	0.526	2.653	0.640	0.4091	−1.427	0.969	0.584	0.3631
A. saccharum	1.585	1.539	0.882	0.1615	0.404	0.573	0.884	0.1602
B. alleghaniensis (plus twigs)	1.572	1.250	0.582	0.2383	0.682	0.455	0.542	0.2494
B. papyrifera (plus twigs)	0.622	2.485	0.764	0.3338	−1.482	0.972	0.672	0.3935
F. grandifolia	1.527	1.500	0.836	0.1392	0.427	0.554	0.779	0.1620
P. pensylvanica (+twigs)	0.812	1.851	0.619	0.2924	−0.753	0.739	0.654	0.3466
Tree height								
A. rubrum	2.539	0.561	0.763	0.0650				
A. saccharum	2.468	0.682	0.943	0.0483				
B. alleghaniensis	2.449	0.682	0.829	0.0714				
B. papyrifera	2.622	0.475	0.648	0.0809				
F. grandifolia	2.459	0.589	0.711	0.0780				
P. pensylvanica	2.301	0.807	0.790	0.0893				

Note: RMSE, root mean-squared error.

Species substitutions

The stands in this study included species not described by our equations or by those from Whittaker et al. (1974). For these species, we substituted equations based on similarities in growth form to species for which we had equations following Vadeboncoeur et al. (2007). In the "Fatemi and Whittaker" approach, we used substitutions for all species but the six that we sampled. In the "Whittaker" approach, we used substitutions for all species but the five that were published in Whittaker et al. (1974).

The American beech equation was used for white ash (*Fraxinus americana* L.) and northern red oak (*Quercus rubra* L). The sugar maple equation was used for red maple, striped maple, and basswood (*Tilia americana* L.). The yellow birch equation was used for white birch, aspens (*Populus* spp.), and pin cherry. The percentage of trees that we used substitutions for in these stands in the "Fatemi and Whittaker" approach was 5% for C1, 8% for C2, 33% for C4, and 30% for C6. For the "Whittaker" approach, there was a much larger proportion of individual trees that required substitutions: 69% for C1, 56% for C2, 59% for C4, and 47% for C6. This is because these stands include a high proportion of pin cherry and red maple not described by Whittaker's equations.

Uncertainty in stand-level biomass estimates

We used a Monte Carlo approach implemented in Microsoft Excel 2008 (Yanai et al. 2010) to estimate the uncertainty associated with stand-level biomass calculated using allometric equations. This approach estimates the statistical distribution of the output of a calculation through multiple iterations in which the input data are chosen randomly based on their known underlying distributions. In this case, we accounted for model uncertainty associated with the regression equations by adding randomly selected error terms (mean = 0, standard deviation = ε; eq. 3) to each regression equation (not for each tree) for each iteration. We used 200 iterations to derive our uncertainty estimates, which is twice the number of iterations required to estimate mean biomass and the standard deviation with an uncertainty of about 1% of the mean (Yanai et al. 2010).

Results

Biomass equations and estimates for individual tree species

Among the biomass equations that we developed, the regression models for total aboveground and stem wood biomass explained more variability in the data than equations for smaller components did. Equations for aboveground biomass and stem wood biomass had R^2 values ranging from 0.88 to 0.99 (Table 2), depending on the species. Stem bark biomass equations had R^2 values ranging from 0.71 to 0.99. Our regression models had the lowest R^2 values for tree height ($R^2 = 0.65–0.94$), branch biomass ($R^2 = 0.58–0.94$), and foliage biomass ($R^2 = 0.56–0.88$). Correction factors for all biomass and height equations are listed in Table 3.

Equations developed from young stands in this study predicted greater total aboveground biomass than those developed in mature stands by Whittaker et al. (1974) for sugar maple and yellow birch (Fig. 1). This difference was more pronounced for yellow birch than for sugar maple. Our total aboveground yellow birch biomass equation predicts 10%–30% greater biomass for yellow birch and 0%–15% greater biomass for sugar maple for trees ranging from 2 to 12 cm DBH, depending on the size of the tree (the discrepancy increases with tree DBH) (Fig. 1).

The magnitude of individual component biomass as predicted by our equations, in some cases, is different from that predicted by the equations from Whittaker et al. (1974). Stem wood biomass of yellow birch is predicted to be 11%–120% higher using the equation from this study compared with the Whittaker equation; this difference is also most pronounced for larger trees. Sugar maple wood biomass predicted by the Whittaker equation is 4%–26% greater than predicted by our equation. Whittaker's equation for yellow birch branches predicts 1%–200% greater biomass compared with our equation, while our equation for sugar maple predicts greater branch biomass (47%–260%). Foliar biomass was predicted to be 10%–120% higher for sugar maple by our equation compared with the Whittaker equation, but this difference is only significant for trees <7 cm DBH where 95% confidence intervals do not overlap.

Equations from this study predicted greater heights for trees of the same diameter than those from Whittaker et al. (1974), but these differences were not significant based on

Table 3. Correction factors for biomass regressions (the corresponding equation coefficients are listed in Table 2).

	Aboveground		Stem wood		Stem bark		Branch		Foliage		Height
	DBH	PV	DBH	PV	DBH	PV	DBH	PV	DBH	PV	Height, DBH
A. rubrum	1.002	1.001	1.004	1.002	1.002	1.001	1.004	1.004	1.004	1.004	1.002
A. saccharum	1.001	1.001	1.002	1.002	1.003	1.004	1.016	1.020	1.016	1.020	1.001
B. alleghaniensis	1.002	1.003	1.005	1.002	1.031	1.023	1.014	1.019	1.014	1.019	1.003
B. papyrifera	1.002	1.003	1.005	1.003	1.014	1.008	1.012	1.019	1.012	1.019	1.003
F. grandifolia	1.004	1.005	1.005	1.007	1.012	1.014	1.009	1.048	1.009	1.048	1.003
P. pensylvanica	1.023	1.030	1.003	1.028	1.023	1.068	1.013	1.068	1.013	1.068	1.004

Note: DBH, equations using diameter at breast height (cm) as the independent variable; PV, equations using parabolic volume (cm^3) as the independent variable.

Fig. 1. Comparison of biomass predictions for three tree species based on equations from this study and those from Whittaker et al. (1974). The 95% confidence intervals are represented by the shaded areas around each equation. Points represent individual trees that were sampled in this study.
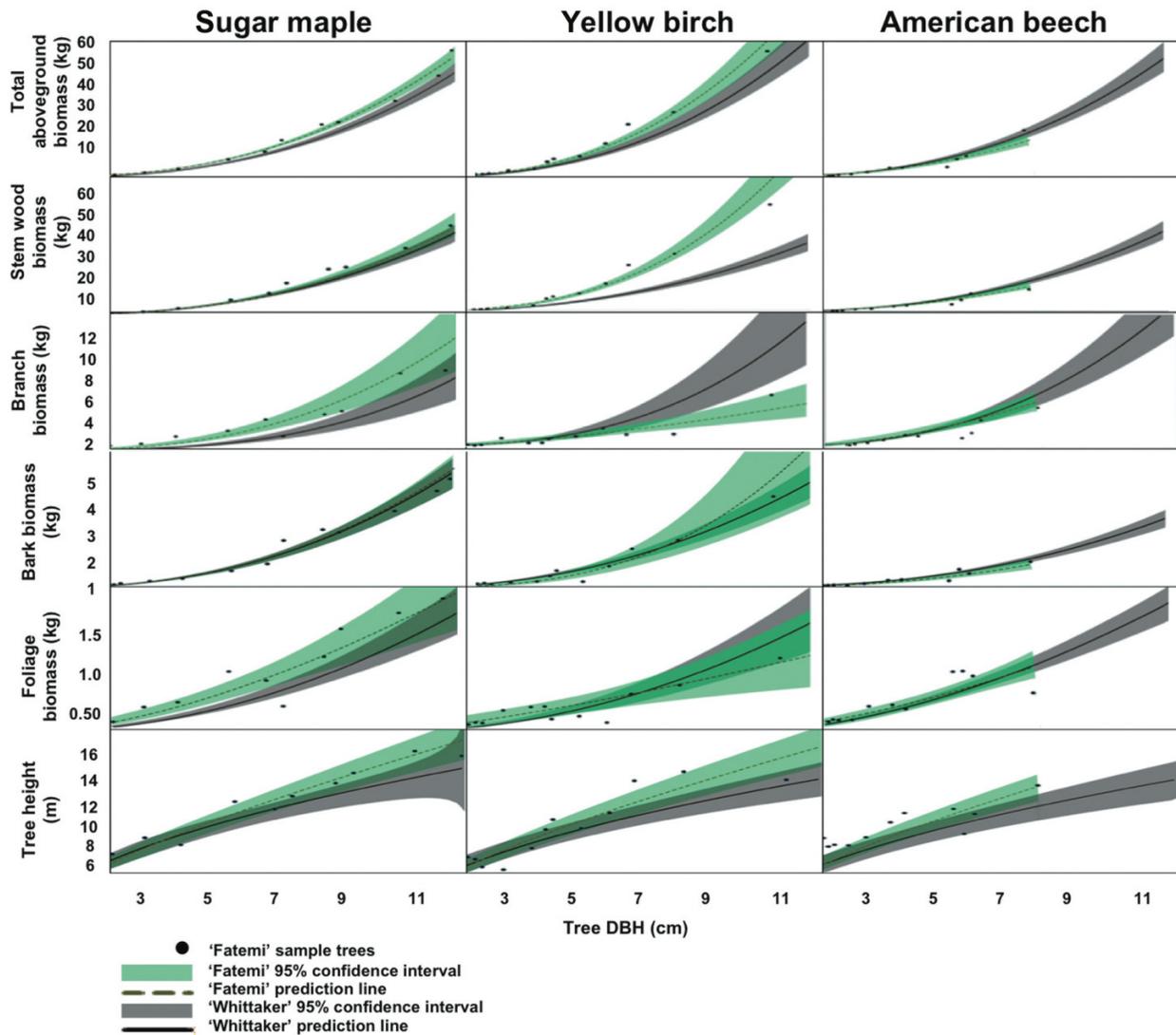
comparison of 95% confidence intervals (Fig. 1). Our equation for sugar maple height predicted trees to be 1%–21% taller and our equation for yellow birch predicted trees to be 1%–28% taller than predicted using the Whittaker equations.

Stand aboveground biomass estimates

To determine how much the source allometric equation mattered for estimates of biomass at the stand scale, we calculated total aboveground biomass in our four stands for the species that were sampled both in this study and by Whittaker et al. (1974): sugar maple, American beech, and yellow birch (Table 4). We used our equations in one estimate and the Whittaker equations in another estimate, and we included only trees 2–12 cm DBH. The magnitude of the difference between these two estimates was greatest for yellow birch: our equations predict 35%–72% greater aboveground biomass in our stands than the Whittaker equations. On average, our equations estimated 50% greater aboveground biomass for

yellow birch, 9% greater aboveground stand biomass for sugar maple, and 3% lower biomass for American beech compared with Whittaker's equations. There were also some important differences for other species in how the source equations estimated biomass distribution in these stands. For instance, although the estimate for aboveground biomass for sugar maple trees in stand C1 using our equations (18 g/m^2) was similar to the estimate made using Whittaker's equations (17 g/m^2), branch biomass by our estimate was 17% of total biomass compared with only 6% estimated by Whittaker's equations. However, Whittaker's equations estimate a greater percentage of sugar maple biomass to be in bark and wood tissues than our equations do, offsetting this difference in branch biomass relative to the aboveground biomass sum.

When we included all species in our analyses, total aboveground biomass estimated using the "Fatemi and Whittaker" approach (Fig. 2) was 39 Mg/ha for C1 (standard errors from the Monte Carlo estimates are not symmetrical: +3.2, –2.5),

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Table 4. Aboveground biomass (g/m²) in each stand by component for trees 2–12 cm DBH of the three species that we compared.

Site	Equation	Sugar maple					Yellow birch					American beech				
		Wood	Bark	Branch	Foliage	Sum	Wood	Bark	Branch	Foliage	Sum	Wood	Bark	Branch	Foliage	Sum
C1	Fatemi	11	2	3	2	18	203	14	41	12	270	336	24	177	45	582
	Whittaker	13	2	1	<1	17	137	24	30	9	199	350	33	118	46	547
C2	Fatemi	9	2	3	2	15	189	13	38	11	251	900	65	418	95	1478
	Whittaker	10	2	<1	<1	14	127	23	27	8	185	971	86	342	102	1501
C4	Fatemi	0	0	0	0	0	2025	124	203	51	2403	1108	80	477	102	1767
	Whittaker	0	0	0	0	0	1014	162	292	54	1522	1219	104	441	111	1875
C6	Fatemi	128	17	34	11	190	1977	116	139	32	2264	1056	76	428	87	1647
	Whittaker	130	19	18	7	174	857	130	284	41	1312	1180	99	436	96	1811

Note: We used equations from this study for the "Fatemi" estimate and equations from Whittaker et al. (1974) for the "Whittaker" estimate.

46 Mg/ha (+3.0, –2.4) for C2, 134 Mg/ha (+7.0, –6.4) for C4, and 143 Mg/ha (+6.4, –4.8) for C6. There were also some differences in the biomass distribution by component predicted by the "Fatemi" versus the "Fatemi and Whittaker" approach. For example, in stand C1, our equations for small trees predicted 55% of stand biomass was wood and 22% bark, but the equations from Whittaker et al. (1974) predict 70% wood and 11% bark. However, our total aboveground biomass estimates were all within 7% of the estimates based on Whittaker's equations and were indistinguishable from Whittaker's predictions based on 95% confidence intervals (Fig. 2).

Discussion

The log-transformed linear regression models that we developed had lower variance for aboveground biomass, stem wood, and bark biomass than for foliage or branch biomass. Foliage and branch components have been reported by others to have higher variation than other components (Martin et al. 1998; Bond-Lamberty et al. 2002), probably because they respond more to local conditions such as canopy position and light availability. In general, R^2 values for foliage and branch regressions were lower than reported by some authors in the region (Whittaker et al. 1974; Young et al. 1980) but within the range reported by others (Jenkins et al. 2004). The R^2 values for all of our component equations are consistently lower than the R^2 values reported by Whittaker et al. (1974), despite the fact that our sample size ($n = 11$–12) is not much smaller than that used by Whittaker et al. (1974) ($n = 14$). Our sample population probably varied more than the population sampled by Whittaker et al. (1974) because we sampled four separate stands that varied in age and species composition, while the trees sampled by Whittaker et al. (1974) came from a single catchment with common land-use history. Because of the large size of the trees, Whittaker's approach required more subsampling, subsidiary regressions, and subjective selection of representative components. In addition, Whittaker et al. (1974) sampled a much wider range in tree size (1–63 cm DBH), so random noise should have a smaller effect on R^2 values than in our study where the range of tree size was much smaller (2–12 cm DBH).

Differences other than stand age could have contributed to the differences observed between our biomass equations and those of Whittaker et al. (1974). Because of climate change, N deposition, and elevated CO_2, our young stands, sampled in 2004–2005, developed in a different environment than the 55-year-old stand that Whittaker et al. (1974) sampled in 1965. However, these differences are unlikely to have produced significant changes in the aboveground allometry of trees (Grier et al. 1984; Norby et al. 2001; Calfapietra et al. 2003). More importantly, inconsistencies in component definitions or sampling methods could contribute to the observed differences in biomass estimations between our equations and Whittaker's equations. For instance, Whittaker et al. (1974) sampled foliage by dividing the tree crown into five height ranges and choosing a live and dead branch from each fifth. Leaves and twigs were then separated to determine dry mass. We sampled foliage and branches by completely delimbing the crown, and because our trees were small, we were able

Fig. 2. Total aboveground biomass for the four stands sampled in this study. Estimates were made using equations developed primarily in young stands for small trees in the "Fatemi and Whittaker" approach. Only equations developed in mature stands in the "Whittaker" approach. Error bars represent 95% confidence intervals derived from Monte Carlo iterations. Site name and corresponding stand age are shown above each set of bars.
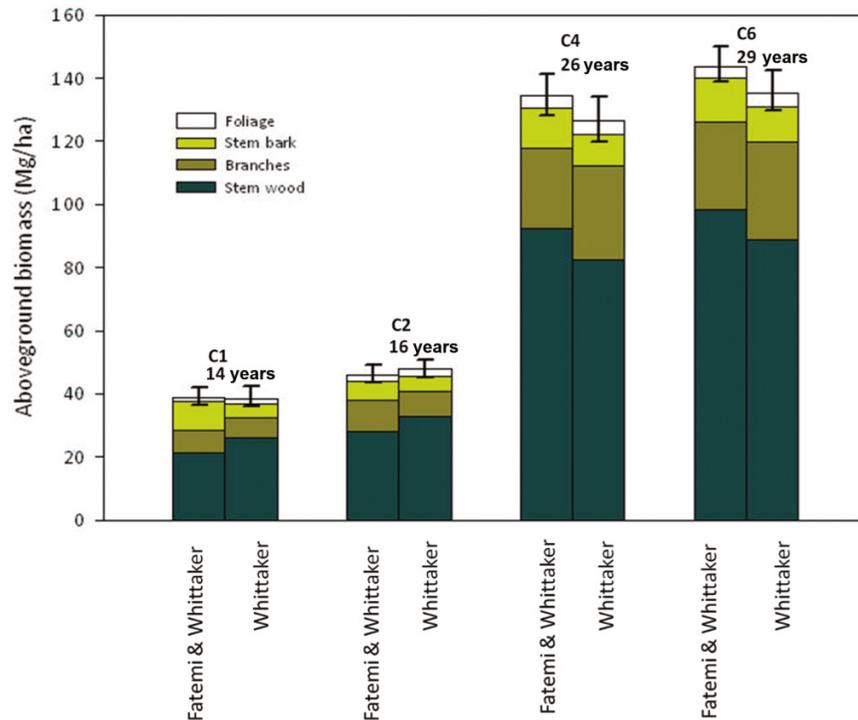
to weigh the entire mass. For this reason, our method should more accurately characterize variability in branch mass.

The differences between the biomass distribution by tree component estimated by equations from this study and equations from Whittaker et al. (1974) are particularly relevant for estimating nutrient stocks. Foliage and branch components are nutrient rich and accounted for 48%–67% of N, P, K, Mg, or Ca in Whittaker's stands (Whittaker et al. 1979). Our equations may be more suitable for describing biomass and nutrient content in young stands that contain mostly small trees because our sample size in the small tree range is much larger ($n = 11$–12) compared with the number of small trees that Whittaker et al. (1974) sampled ($n = 2$–4). Stump and root sprouting was also probably more prevalent in the young stands that we sampled compared with the mature stands that Whittaker et al. (1974) sampled; this could affect tree allometry by alleviating the need for sprouted trees to allocate resources to support root growth, thereby enhancing shoot growth.

For some species, differences between equations from this study and those from Whittaker et al. (1974) support our hypothesis that small trees in young stands differ in allometry from trees of the same size in mature stands. Small yellow birch and sugar maple trees in young stands appear to allocate more resources to woody production via height growth in the stem or branches, possibly driven by competition for canopy light (Knowe 1994; King 1997). The wood biomass and height differences between our equations and Whittaker's for yellow birch are consistent with the significant light response that has been observed for yellow birch saplings (Messier and Nikinmaa 2000). For American beech, which

exhibits slower height growth compared with sugar maple and yellow birch (McClure et al. 2000; Nyland et al. 2004), our equations were generally indistinguishable from Whittaker's. We suggest that species such as yellow birch may be more plastic in their morphological response to canopy light conditions that are influenced by stand age. Additional research is needed in other forest types to determine whether differences in allometry can be predicted by shade tolerance class.

Conclusions

When comparing our allometric equations from young stands with equations from mature stands (Whittaker et al. 1974), we found important differences in the prediction of aboveground biomass for certain tree components and species, but these differences did not significantly impact estimates of total stand aboveground biomass in the mixed-species young northern hardwood stands that we studied. At the species level, our equations predict significantly greater biomass for small yellow birch trees in these stands than Whittaker's equations do. In the northern hardwood forest, allometric equations specific to forest age might be more appropriate in stands that are heavily dominated by small trees of yellow birch but not necessarily for sugar maple or American beech.

Acknowledgements

References

Arthur, M.A., Hamburg, S.P., and Siccama, T.G. 2001. Validating allometric estimates of aboveground living biomass and nutrient contents of a northern hardwood forest. Can. J. For. Res. **31**(1): 11–17. doi:10.1139/cjfr-31-1-11.

Baskerville, G.L. 1972. Use of logarithmic regression in the estimation of plant biomass. Can. J. For. Res. **2**(1): 49–53. doi:10.1139/x72-009.

Beauchamp, J.J., and Olson, J.S. 1973. Corrections for bias in regression estimates after logarithmic transformation. Ecology, **54**(6): 1403–1407. doi:10.2307/1934208.

Beaudet, M., and Messier, C. 1998. Growth and morphological responses of yellow birch, sugar maple, and beech seedlings growing under a natural light gradient. Can. J. For. Res. **28**(7): 1007–1015. doi:10.1139/cjfr-28-7-1007.

Bond-Lamberty, B., Wang, C., and Gower, S.T. 2002. Aboveground and belowground biomass and sapwood area allometric equations for six boreal tree species of northern Manitoba. Can. J. For. Res. **32**(8): 1441–1450. doi:10.1139/x02-063.

Calfapietra, C., Gielen, B., Galema, A.N.J., Lukac, M., DeAngelis, P., Moscatelli, M.C., Ceulemans, R., and Scarascia-Mugnozza, G. 2003. Free-air CO_2 enrichment (FACE) enhances biomass production in a short-rotation poplar plantation. Tree Physiol. **23**(12): 805–814. doi:10.1093/treephys/23.12.805. PMID:12865246.

Canadell, J.G., and Raupach, M.R. 2008. Managing forests for climate change mitigation. Science, **320**(5882): 1456–1457. doi:10.1126/science.1155458. PMID:18556550.

Chave, J., Condit, R., Aguilar, S., Hernandez, A.H., Lao, S., and Perez, R. 2004. Error propagation and scaling for tropical tropical biomass estimates. Philos. Trans. R. Soc. Lond. B Biol. Sci. **359**(1443): 409–420. doi:10.1098/rstb.2003.1425. PMID:15212093.

Crow, T.R. 1983. Comparing biomass regressions by site and stand age for red maple. Can. J. For. Res. **13**(2): 283–288. doi:10.1139/x83-040.

DeLucia, H., Sipe, T.W., Herrick, J., and Maherali, H. 1998. Sapling biomass allocation and growth in the understory of a deciduous hardwood forest. Am. J. Bot. **85**(7): 955–963. doi:10.2307/2446362.

Gargaglione, V., Peri, P.L., and Rubio, G. 2010. Allometric relations for biomass partitioning of *Nothofagus antarctica* trees of different crown classes over a site quality gradient. For. Ecol. Manag. **259**(6): 1118–1126. doi:10.1016/j.foreco.2009.12.025.

Grier, C.C., Lee, K.M., and Archibald, R.M. 1984. Effect of urea fertilization on allometric relations in young Douglas-fir trees. Can. J. For. Res. **14**(6): 900–904. doi:10.1139/x84-160.

Jenkins, J.C., Chojnacky, D.C., Heath, L.S., and Birdsey, R.A. 2004. Comprehensive database of diameter-based biomass regressions for North American tree species. U.S. For. Serv. Gen. Tech. Rep. NE-319. Available at http://www.treesearch.fs.fed.us/pubs/7058.

King, D.A. 1997. Branch growth and biomass allocation in *Abies amabilis* saplings in contrasting light environments. Tree Physiol. **17**(4): 251–258. PMID:14759864.

Knowe, S.A. 1994. Effect of competition control treatments on height–age and height–diameter relationships in young Douglas-fir plantations. For. Ecol. Manag. **67**(1–3): 101–111. doi:10.1016/0378-1127(94)90010-8.

Koerper, G.J., and Richardson, C.J. 1980. Biomass and net annual primary production regressions for *Populus grandidentata* on three sites in northern lower Michigan. Can. J. For. Res. **10**(1): 92–101. doi:10.1139/x80-015.

Leak, W.B. 1991. Secondary forest succession in New Hampshire, USA. For. Ecol. Manag. **43**(1–2): 69–86. doi:10.1016/0378-1127(91)90077-9.

Lehtonen, A., Makipää, R., Heikkinen, J., Sievänen, R., and Liski, J. 2004. Biomass expansion factors (BEFs) for Scots pine. Norway spruce and birch according to stand age for boreal forests. For. Ecol. Manag. **188**(1–3): 211–224. doi:10.1016/j.foreco.2003.07.008.

Leighty, W.W., Hamburg, S.P., and Caouette, J. 2006. Effects of management on carbon sequestration in forest biomass in southeast Alaska. Ecosystems (N.Y.), **9**(7): 1051–1065. doi:10.1007/s10021-005-0028-3.

Likens, G.E., Driscoll, C.T., Buso, D.C., Siccama, T.G., Johnson, C.E., Lovett, G.M., Fahey, T.J., Reiners, W.A., Ryan, D.F., Martin, C.W., et al. 1998. The biogeochemistry of calcium at Hubbard Brook. Biogeochemistry, **41**(2): 89–173. doi:10.1023/A:1005984620681.

Magill, A.H., Downs, M.R., Nadelhoffer, K.J., Hallett, R.A., and Aber, J.D. 1996. Forest ecosystem response to four years of chronic nitrate and sulfate additions at Bear Brooks Watershed, Maine, USA. For. Ecol. Manag. **84**(1–3): 29–37. doi:10.1016/0378-1127(96)03775-9.

Martin, J.G., Kloeppel, B.D., Schaefer, T.L., Kimbler, D.L., and McNulty, S.G. 1998. Aboveground biomass and nitrogen allocation of ten deciduous southern Appalachian tree species. Can. J. For. Res. **28**(11): 1648–1659. doi:10.1139/cjfr-28-11-1648.

McClure, J.W., Lee, T.D., and Leak, W.B. 2000. Gap capture in northern hardwoods: patterns of establishment and height growth in four species. For. Ecol. Manag. **127**(1–3): 181–189. doi:10.1016/S0378-1127(99)00129-2.

Messier, C., and Nikinmaa, E. 2000. Effects of light availability and sapling size on the growth, biomass allocation and crown morphology of understory sugar maple, beech and yellow birch. Ecoscience, **7**(3): 345–356.

Naidu, S., DeLucia, E., and Thomas, R. 1998. Contrasting patterns of biomass allocation in dominant and suppressed loblolly pine. Can. J. For. Res. **28**(8): 1116–1124. doi:10.1139/cjfr-28-8-1116.

Norby, R.J., Todd, D.E., Fults, J., and Johnson, D.W. 2001. Allometric determination of tree growth in a CO_2-enriched sweetgum stand. New Phytol. **150**(2): 477–487. doi:10.1046/j.1469-8137.2001.00099.x.

Norby, R.J., Hanson, P.J., O'Neill, E.G., Tschaplinski, T.J., Weltzin, J.F., Hansen, R.T., Cheng, W., Wullschleger, S.D., Gunderson, C.A., Edwards, N.T., and Johnson, D.W. 2002. Net primary productivity of a CO_2-enriched deciduous forest and the implications for carbon storage. Ecol. Appl. **12**: 1261–1266. doi:10.1890/1051-0761(2002)012[1261:NPPOAC]2.0.CO;2.

Nowak, D.J., and Crane, D.E. 2002. Carbon storage and sequestration by urban trees in the USA. Environ. Pollut. **116**(3): 381–389. doi:10.1016/S0269-7491(01)00214-7. PMID:11822716.

Nyland, R.D., Ray, D.G., and Yanai, R.D. 2004. Height development of upper-canopy trees within even-aged Adirondack northern hardwood stands. North. J. Appl. For. **21**(3): 117–122.

Ouimet, R., Tremblay, S., Périé, C., and Prégent, G. 2007. Ecosystem carbon accumulation following fallow farmland afforestation with red pine in southern Quebec. Can. J. For. Res. **37**(6): 1118–1133. doi:10.1139/X06-297.

Park, B.B., Yanai, R.D., Fahey, T.J., Bailey, S.W., Siccama, T.G., Shanley, J.B., and Cleavitt, N.L. 2008. Fine root dynamics and forest production across a calcium gradient in northern hardwood and conifer ecosystems. Ecosystems (N.Y.), **11**(2): 325–341. doi:10.1007/s10021-008-9126-3.

Peichl, M., and Arain, M. 2007. Allometry and partitioning of above- and belowground tree biomass in an age-sequence of white pine forests. For. Ecol. Manag. **253**(1–3): 68–80. doi:10.1016/j.foreco.2007.07.003.

Porté, A., Trichet, P., Bert, D., and Loustau, D. 2002. Allometric relationships for branch and tree woody biomass of Maritime pine (*Pinus pinaster* Ait.). For. Ecol. Manag. **158**(1–3): 71–83. doi:10.1016/S0378-1127(00)00673-3.

Ray, D.G., Yanai, R.D., and Nyland, R.D. 2011. Canopy growing-space relationships in young even-aged northern hardwood stands. North. J. Appl. For. In press.

Siccama, T.G., Hamburg, S.P., Arthur, M.A., Yanai, R.D., Bormann, F.H., and Likens, G.E. 1994. Corrections to allometric equations and plant tissue chemistry for the Hubbard Brook Experimental Forest. Ecology, **75**(1): 246–248. doi:10.2307/1939398.

Smith, M.L., and Martin, M.E. 2001. A plot-based method for rapid estimation of forest canopy chemistry. Can. J. For. Res. **31**(3): 549–555. doi:10.1139/cjfr-31-3-549.

Smith, R. 1993. Logarithmic transformation bias in allometry. Am. J. Phys. Anthropol. **90**(2): 215–228. doi:10.1002/ajpa.1330900208.

Snedecor, G.W., and Cochran, W.G. 1989. Statistical methods. 8th ed. Iowa State University Press, Ames, Iowa.

Vadeboncoeur, M.A., Hamburg, S.P., and Yanai, R.D. 2007. Validation and refinement of allometric equations for roots of northern hardwoods. Can. J. For. Res. **37**(9): 1777–1783. doi:10.1139/X07-032.

Vanninen, P., Ylitalo, H., Sievänen, R., and Mäkelä, A. 1996. Effects of age and site quality on the distribution of biomass in Scots pine (*Pinus sylvestris* L.). Trees Struct. Funct. **10**(4): 231–238. doi:10.1007/BF02185674.

Waring, R.H. 1987. Characteristics of trees predisposed to die. Bioscience, **37**(8): 569–574. doi:10.2307/1310667.

White, H. 1980. A heteroscedasticity-consistent covariance matrix estimator and direct test for heteroscedasticity. Econometrica, **48**(4): 817–838. doi:10.2307/1912934.

Whittaker, R.H., Bormann, F.H., Likens, G.E., and Siccama, T.G. 1974. The Hubbard Brook ecosystem study: forest biomass and production. Ecol. Monogr. **44**(2): 233–252. doi:10.2307/1942313.

Whittaker, R.H., Likens, G.E., Bormann, F.H., Eaton, J.S., and Siccama, T.G. 1979. The Hubbard Book ecosystem study: forest nutrient cycling and behavior. Ecology, **60**: 203–220. doi:10.2307/1936481.

Yanai, R.D., Battles, J.J., Richardson, A.D., Blodgett, C.A., Wood, D.M., and Rastetter, E.B. 2010. Estimating uncertainty in ecosystem budget calculations. Ecosystems (N.Y.), **13**(2): 239–248. doi:10.1007/s10021-010-9315-8.

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