

biometrics

Equations for Estimating Biomass, Foliage Area, and Sapwood of Small Trees in the Southern Appalachians

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Small trees and shrubs play an important role in forest diversity and regeneration and may contribute substantially to ecosystem fluxes of carbon and water; however, relatively little attention is given to quantifying the contribution of small trees to forest processes. One reason for this may be that the allometric equations developed for large trees tend to systematically underestimate structural variables such as biomass and foliage area when applied to small trees, both on an individual tree level and at the stand level. To test this hypothesis, we developed allometric equations for trees <10 cm dbh (D) for seven dependent variables (woody, foliage, and total biomass; woody, foliage, and whole-plant surface area; and sapwood area) and compared these new equations with the existing equations for large trees. We found significant differences between small tree and large tree equations for most variables and showed that equations for large trees tend to underestimate the structural characteristics of small trees. When we applied new size-specific equations to forest survey data representing a chronosequence of forest development, estimates of small tree biomass increased 30–73% and estimates of foliage area increased 72–142% compared with results using only equations for large trees. These results suggest that small trees can contribute substantially to forest structure and associated ecosystem fluxes, especially in stands with a large proportion of small trees. However, size-specific equations for small trees did not substantially change the estimates of forest biomass in these stands, and the need to develop size-specific equations may depend on the variables of interest.

Keywords: allometric equations, forest regeneration, forest understories, leaf area index, plant surface area, sapwood area

Small trees and shrubs, defined here as individual stems having overbark dbh (D , 1.37 m) <10 cm, may contribute substantially to ecosystem structure and function (Nilsson and Wardle 2005, Donato et al. 2012). In undisturbed temperate forests, understory trees and shrubs create important wildlife habitat and may contribute substantially to biodiversity (Gilliam and Roberts 2003, Donato et al. 2012). Forest understories also facilitate growth of shade-tolerant species and drive changes in forest composition and structure as understory trees mature and replace aging canopy trees (Nilsson and Wardle 2005, Donato et al. 2012). Although the economic value of wood products and the ecosystem services provided by dominant canopy tree species have caused the majority of research to focus on large canopy trees, small trees and shrubs may also contribute substantially to important forest ecosystem fluxes such as carbon and water. For example, the forest under-

story can account for between 25 and 50% of total forest transpiration, and a dense shrub understory has been shown to reduce streamflow in headwater catchments (Johnson and Kovner 1956, Hamada et al. 2004). In addition, research that focuses primarily on the structure and function of canopy trees in mature undisturbed forests does not account for a significant portion of the overall forest landscape in both current and future forests (Elliott and Vose 2011, Huggett et al. 2011). Forests regenerating after disturbances are naturally dominated by small stem size classes, which contribute to foliage area recovery and to the resulting recovery of important ecosystem processes such as transpiration (Boring and Swank 1986, Ford et al. 2011, Brantley et al. 2013).

To quantify understory carbon pools and scale ecosystem fluxes adequately, tree and shrub structural variables, e.g., biomass, foliage area, and sapwood area (A_{SW}), must be accurately characterized;

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Table 1. List of species and their name abbreviations, sample sizes, and size ranges used to develop allometric equations.

Species (family)	Abbreviation	<i>n</i>	<i>D</i> (cm)		<i>H</i> (m)	
			Minimum	Maximum	Minimum	Maximum
Understory trees						
<i>Acer rubrum</i> L. (Aceraceae)	ACRU	7	1.10	7.70	2.45	11.80
<i>Betula lenta</i> L. (Betulaceae)	BELE	7	1.01	7.40	2.40	13.25
<i>Carya</i> spp. Nutt. (Juglandaceae)	CASP	6	1.15	5.92	3.05	8.21
<i>Kalmia latifolia</i> L. (Ericaceae)	KALA	11	1.20	6.00	2.08	6.16
<i>Liriodendron tulipifera</i> L. (Magnoliaceae)	LITU	7	1.25	7.40	2.20	13.10
<i>Quercus alba</i> L. (Fagaceae)	QUAL	7	1.16	6.50	2.60	9.60
<i>Quercus rubra</i> L. (Fagaceae)	QURU	7	1.19	7.28	2.90	9.80
Sun trees						
<i>Acer rubrum</i> L. (Aceraceae)	ACRU	7	1.15	6.81	1.90	9.00
<i>Liriodendron tulipifera</i> L. (Magnoliaceae)	LITU	7	1.21	6.17	2.50	6.50
<i>Quercus rubra</i> L. (Fagaceae)	QURU	7	1.48	6.97	2.50	9.60

however, collecting these data is labor intensive and requires destructive sampling. Thus, developing predictive equations that use quickly and easily measured tree variables such as *D* and/or tree height (*H*) to estimate these harder-to-obtain, but more ecologically meaningful structural variables, is an economical route (e.g., Whittaker et al. 1974, Martin et al. 1998, Fatemi et al. 2011). Examples of structural variables that can be estimated using allometric equations include woody biomass, foliage mass and area, sapwood volume and area, and wood surface area (e.g., Vertessy et al. 1995, Martin et al. 1998). These values can then be used to scale to ecosystem-level processes, such as sap-flux measurements to tree-level transpiration (Granier 1987, Vertessy et al. 1995) and carbon efflux to tree-level respiration (Clark and Schroeder 1986, Ryan and Waring 1992, Ryan et al. 1997).

Many allometric equations exist for estimating structural variables for large stems (>10 cm *D*) (e.g., Whittaker et al. 1974, Clark and Schroeder 1986, Martin et al. 1998), and additional sources can be found to estimate variables for seedlings (e.g., Elliott and Clinton 1993). However, equations developed for large trees (e.g., Whittaker et al. 1974, Martin et al. 1998) often underestimate structural variables for small trees (Fatemi et al. 2011, Fonseca et al. 2012) and may return values near zero for the smallest stems, even when correction factors are applied (Sprugel 1983). Whereas others have developed equations for small trees in other regions and/or for other species (e.g., Fatemi et al. 2011, Fonseca et al. 2012), a considerable gap exists in the literature for common subcanopy tree species in southern Appalachian forests.

The purpose of this study was to test the effect of size-specific allometric equations on several important stand-level structural variables across a chronosequence of forest development in southern Appalachians. Specifically, we addressed two primary questions: Do allometric relationships developed for large trees underestimate the same variables for small trees? Does the use of equations developed for large trees underestimate the contributions of small trees to various forest structural variables at the stand level? To answer these questions, we developed new allometric equations for individual trees between 1.0 cm and 10.0 cm *D* with heights between ~2 and 15 m (henceforth *small stems*). Target taxa in forest understories included red maple (*Acer rubrum* L.), sweet birch (*Betula lenta* L.), pignut and mockernut hickories (*Carya* spp.), mountain laurel (*Kalmia latifolia* L.), yellow-poplar (*Liriodendron tulipifera* L.), white oak (*Quercus alba* L.), and northern red oak (*Quercus rubra* L.). We also developed equations for three of the same species (*A. rubrum*, *L. tulipifera*, and *Q. rubra*) in a recently logged site where trees were

exposed to full or near-full sunlight to determine whether allometric equations for small trees differ between sites with different light regimes. Predictor variables were *D* and *H*, and response variables of interest were woody, foliage, and total biomass; foliage, woody, and whole-plant surface area; and sapwood area. We then applied both our new size-specific equations for small stems and existing allometric equations for large stems (McGinty 1972, Martin et al. 1998, B.D. Kloeppel, unpublished data) to a forest survey data set to determine the importance of developing size-specific equations for these variables.

Methods

Study Site

The study was conducted at two sites in the Nantahala National Forest of western North Carolina, USA. The region is mountainous and heavily forested with a mix of cove hardwood, northern hardwood, oak, and oak-pine communities (Day et al. 1988). Understory (henceforth *shade*) samples were collected from second-growth, cove hardwood forest within the boundaries of Coweeta Hydrologic Laboratory (CWT) (35°03'N and 83°25'W) of the US Department of Agriculture Forest Service. Basal area at the CWT site was ~30 m² ha⁻¹ and was dominated by *Liriodendron tulipifera*, *Q. alba*, and a diverse assemblage of codominant hardwoods and evergreen shrubs as represented by the species listed in Table 1. Elevation at these sites varied from 685 to 900 m above mean sea level (ASL). Soils are highly variable but dominated by fine loamy Typic Hapludults mapped in either the Cowee-Evard or Fannin series. Open-canopy (henceforth *sun*) samples were collected in a second site ~20 km from the CWT site (35°06'N and 83°38'W) where a shelterwood harvest (SWH) was conducted 4 years before initiation of the current study. Preharvest basal area data was unavailable, but postharvest basal area was ~10 m² ha⁻¹. Although light levels were never measured directly, we observed that all sampled trees received direct sunlight for most of the day. Elevation of the SWH sampling site is 1,200–1,300 m ASL, and species composition represented a transition zone between cove hardwood forest and oak-dominated hardwoods with relatively greater dominance of *Q. rubra* than on the CWT site (Day et al. 1988). Soils at the SWH site are Typic Dystrochrepts mapped in the Edneyville-Chestnut complex. Soil texture is coarse loamy. Soils at both sites are generally very deep (solum layer >1 m) and well drained (Thomas 1996). Climate in the region is classified as marine, humid temperate (Swift et al. 1988). Mean annual temperature ranges from 12.8° C at lower elevations (685 m ASL) to 9.8° C at higher elevations (1,398 m

Table 2. Specific foliage area for six tree and one shrub species in the southern Appalachian forests ($n = 20$ for each species and exposure class).

Species	Specific foliage area ($\text{cm}^2 \text{g}^{-1}$) (SE)
Understory	
ACRU	280.1 (7.8) ^{bc}
BELE	472.4 (18.4) ^e
CASP	310.6 (7.7) ^{cd}
KALA	140.0 (4.8) ^a
LITU	332.6 (11.7) ^d
QUAL	284.0 (9.9) ^{bc}
QURU	263.4 (7.1) ^b
Mean	323.8 (7.8)
Sun	
ACRU	126.5 (3.1) ^a
LITU	190.1 (8.8) ^b
QURU	130.8 (6.2) ^a
Mean	149.1 (5.3)

Data are partitioned by light environment for the species sampled. Mean values for understory trees exclude the evergreen shrub *Kalmia latifolia* (KALA). Superscript letters represent significant differences among species within the same exposure class. See Table 1 for species abbreviations.

ASL) (Laseter 2012). Mean annual precipitation at the study sites ranges from $\sim 1,800 \text{ mm year}^{-1}$ at the CWT site to $\sim 2,060 \text{ mm year}^{-1}$ at the SWH site and averages $>100 \text{ mm}$ during all months (Laseter 2012, C.R. Ford, unpublished data).

Harvesting and Processing

We selected trees of each species to represent a range in D between 1.0 and 10.0 cm ($n = 6\text{--}11$) (Table 1). All trees were selected outside of, but adjacent to, the established study plots described below. We selected only healthy trees with single, straight main stems (for tree species), typical shapes, and no visual evidence of disease, crown damage, or other deformation. After recording D to the nearest 0.1 cm, the individual was cut at the base using a hand-saw, and H was measured to the nearest 0.1 m as the distance from the base of the main stem(s) to the most distant branch in the upper canopy. Biomass was separated into three categories: leaves and petioles (henceforth foliage mass), small stems and branches ($<3.0 \text{ cm}$ diameter), and large stems and branches ($>3.0 \text{ cm}$ diameter). All biomass was placed in bags and dried to a constant mass at 60°C and weighed to the nearest 0.1 g. Specific foliage area (SLA) ($\text{cm}^2 \text{g}^{-1}$) was determined on a separate set of freshly harvested leaves ($n = 20$) for sun and shade leaves of each species. Projected foliage area (cm^2) was measured (LI-3100; Li-Cor Biosciences, Lincoln, NE) for individual leaves, and then mass (to the nearest 0.001 g) was recorded after drying at 60°C to a constant weight. Because trees at each of the two sites were fairly uniform in their light exposure (either all sun or all shade), values of SLA developed for shade leaves were used for all leaves from the CWT site and values for sun leaves were applied to all leaves from the SWH site.

Total aboveground biomass was determined by summing foliage and wood mass. Foliage mass was converted to one-sided area using species and site-specific values for SLA (Table 2). Surface area (A_{woody}) of large stems was estimated from stem diameter (d) and length (l):

$$A_{\text{woody}} = \pi \times d \times l \quad (1)$$

Small stem surface area was estimated by diameter size class: 0–0.5 cm, 0.5–1.0 cm, 1.0–2.0 cm, and 2.0–3.0 cm. Each size class was

weighed, and five representative pieces of each size class were measured for diameter and length to develop a mass-to-surface area conversion factor for each species using Equation 1. Small and large stem surface areas were summed to determine whole-tree woody surface area.

To determine sapwood area for species with diffuse-porous xylem, discs were cut from the stem of each sample tree and bark/sapwood/heartwood boundaries were determined visually using differences in wood color and appearance to indicate either sapwood (lighter in color and density) or heartwood (darker and denser). Average disc diameter was estimated from two perpendicular measurements. Average bark thickness and sapwood depth were estimated from four measurements approximately 90° apart. All measurements were taken to the nearest 0.01 cm with dial calipers. Heartwood area was determined by subtracting the area of bark and sapwood from the total basal area of the stem, all assumed to approximate a circle.

To determine the sapwood area of species with ring-porous xylem, i.e., *Quercus*, the width of hydroactive xylem was determined by stain injection into active xylem of a set of healthy trees of both *Q. alba* ($n = 7$) and *Q. rubra* ($n = 6$). An $\sim 8\text{-mm}$ hole was drilled into the trunk at $\sim D$, and the tree was immediately injected with a 0.5% aqueous solution of indigo carmine from a collapsible bottle attached to the tree above the injection site. Injections were carried out near the end of the growing season on days with high potential transpiration (i.e., midday vapor pressure deficit $>1.0 \text{ kPa}$ and photosynthetic photon flux density $>1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$). Stems were allowed to absorb/transport the stain for 3–4 hours and were destructively sampled by cutting the bole 2–4 cm above the injection site. The width of hydroactive xylem was measured to the nearest 0.01 mm and compared across tree sizes and species. There was no significant difference in sapwood depth between *Q. rubra* and *Q. alba* ($t = 1.007$, $P = 0.325$), so data were pooled before further analysis. In addition, sapwood depth did not increase with D on these small trees and shrubs; therefore, all sapwood width measurements were averaged (mean sapwood depth = 0.456 cm) and used with D and bark widths to determine the inner (r) and outer radii (R) of sapwood area (A_{SW}):

$$A_{\text{SW}} = \pi(R^2 - r^2) \quad (2)$$

Statistical Analysis

Simple linear, multiple linear, and nonlinear regression equations were used with both untransformed and log-transformed data to relate D (cm) or both D and H (m) to the following response variables (Y): woody biomass (kg), foliage biomass (g), total biomass (kg), foliage area (L , one-sided; m^2), sapwood area (cm^2), and woody surface area (m^2). We evaluated the following equations:

$$Y = a \times D + b \quad (3)$$

$$Y = a \times D + b \times H + c \quad (4)$$

$$\log_{10} Y = a \times \log_{10} D + b \quad (5)$$

$$\log_{10} Y = a \times \log_{10} D + b \times \log_{10} H + c \quad (6)$$

$$Y = a \times D^b \quad (7)$$

For predicting L when A_{SW} (m^2) is known, we also considered the equation:

Table 3. Coefficients for allometric regression equation 7 ($Y = a \times D^b$) for predicting woody biomass, total biomass, woody surface area, and sapwood area for understory trees in intact forests.

Species	<i>a</i> (SE)	<i>b</i> (SE)	<i>R</i> ²
Woody biomass (kg)			
ACRU	0.0152 (0.0066)	3.4349 (0.2145)	0.995
BELE	0.0610 (0.0116)	2.8874 (0.0983)	0.998
CASP	0.1214 (0.0254)	2.5563 (0.1220)	0.996
KALA	0.2036 (0.0711)	1.9162 (0.2190)	0.918
LITU	0.0490 (0.0106)	2.6962(0.1121)	0.997
QUAL	0.2116 (0.0772)	2.1552 (0.2076)	0.985
QURU	0.1683 (0.0235)	2.3599 (0.0729)	0.982
All trees*	0.1101 (0.0401)	2.4829 (0.1913)	0.913
Total biomass (kg)			
ACRU	0.0511 (0.0366)	3.0440 (0.3800)	0.974
BELE	0.0787 (0.0153)	2.7725 (0.1004)	0.997
CASP	0.1205 (0.0205)	2.6130 (0.0995)	0.998
KALA	0.2196 (0.0753)	1.9215 (0.2151)	0.919
LITU	0.0581 (0.0145)	2.6205 (0.1288)	0.996
QUAL	0.2215 (0.0818)	2.1473 (0.2103)	0.984
QURU	0.2054 (0.0280)	2.2859 (0.0714)	0.984
All trees*	0.1305 (0.0472)	2.4158 (0.1907)	0.908
Woody surface area (m²)			
ACRU	0.0322 (0.0092)	2.3748 (0.1454)	0.992
BELE	0.1003 (0.0284)	1.8152 (0.1525)	0.980
CASP	0.0725 (0.0124)	1.8597 (0.1034)	0.992
KALA	0.0811 (0.0212)	1.9427 (0.1635)	0.948
LITU	0.1025 (0.0448)	1.7727 (0.2332)	0.966
QUAL	0.0756 (0.0227)	1.7563 (0.1736)	0.980
QURU	0.1241 (0.0182)	1.8202 (0.0790)	0.978
All trees*	0.0650 (0.0158)	2.0232 (0.1306)	0.926
Sapwood area (cm²)			
ACRU	0.5973 (0.0414)	2.0743 (0.0375)	0.999
BELE	0.6062 (0.0263)	2.0476 (0.0243)	0.999
CASP	0.4770 (0.0255)	2.1974 (0.0326)	0.999
KALA	0.8818 (0.0641)	1.8548 (0.0489)	0.996
LITU	0.8086 (0.2110)	1.8331 (0.1332)	0.991
QUAL	0.8531 (0.0883)	1.2000 (0.0628)	0.992
QURU	0.7856 (0.1182)	1.2110 (0.0900)	0.978
Diffuse-porous	0.8198 (0.0702)	1.8635 (0.0474)	0.987
Ring-porous	0.8239 (0.0806)	1.2024 (0.0590)	0.983

See Table 1 for species abbreviations.

* Data for KALA were excluded when coefficients for equations for all trees are calculated.

$$\log_{10} L = a \times \log_{10} A_{SW} + b \quad (8)$$

The best-fit equations were selected for each variable based on examination of *R*² and mean square error values, residuals and visual examination of each relationship. For shade trees, we analyzed pooled data for each variable using species as a dummy variable to determine whether a single equation could be used for all species. After finding significant effects of species for all variables, we built additional models with pairwise contrast statements to detect significant differences in each model parameter among species. We then repeated this analysis for sun trees. We also used a separate set of analyses of covariance to detect differences between sun and shade trees for each species common to both sites. We used one-way analysis of variance to test for differences in SLA among species at each site ($\alpha = 0.05$). All analyses were done using either the PROC GLM or PROC NLIN procedure in SAS version 9.3 (SAS Institute, Cary, NC).

To examine the effects of using size-specific equations for small trees, we applied either a single equation (Martin et al. 1998, C.R. Ford, unpublished data) or a pair of size-specific equations (the large tree equations and the newly derived equations) to all stems >1.0 cm dbh in a forest survey data set that represented a chronosequence

Table 4. Coefficients for allometric regression equation 7 ($Y = a \times D^b$) for predicting woody biomass, total biomass, woody surface area, and sapwood area for trees exposed to full sunlight.

Species	<i>a</i> (SE)	<i>b</i> (SE)	<i>R</i> ²
Woody biomass (kg)			
ACRU	0.0938 (0.0122)	2.5613 (0.0698)	0.998
LITU	0.3287 (0.2334)	1.6144 (0.4183)	0.843
QURU	0.1034 (0.0169)	2.6051 (0.0873)	0.997
All trees	0.0924 (0.0198)	2.6258 (0.1137)	0.982
Total biomass (kg)			
ACRU	0.1193 (0.0271)	2.4962 (0.1221)	0.994
LITU	0.4558 (0.3468)	1.5895 (0.4491)	0.816
QURU	0.1220 (0.0190)	2.5683 (0.0833)	0.997
All trees	0.1375 (0.0300)	2.4750 (0.1194)	0.977
Woody surface area (m²)			
ACRU	0.1170 (0.0279)	1.7559 (0.1341)	0.978
LITU	0.2952 (0.2394)	1.2491 (0.4948)	0.665
QURU	0.0779 (0.0196)	2.0635 (0.1381)	0.985
All trees	0.1326 (0.0398)	1.7646 (0.1732)	0.894
Sapwood area (cm²)			
ACRU	0.6072 (0.0228)	2.0816 (0.0207)	0.999
LITU	0.5490 (0.0414)	2.1003 (0.0440)	0.999
QURU	0.7926 (0.0487)	1.2392 (0.0367)	0.996
Diffuse porous	0.5474 (0.0455)	2.1214 (0.0470)	0.997

See Table 1 for species abbreviations.

of forest regeneration. These stands were 4, 14, 37, and 87 years old (time since harvest), and we also included a previously unharvested forest with many trees >200 years old (hereafter *200-year-old*). The 4- and 14-year-old stands were shelterwood harvests (leaving $\geq 15\%$ residual basal area), whereas the 37-year-old stand was clearcut and the 87-year-old stand was high graded, taking all merchantable trees >38 cm at the stump (Douglass and Hoover 1988). In each stand, two 20 × 40-m plots were established, and all stems >10 cm were identified to species and measured for *D* to the nearest 0.1 cm. In each stand, 10–12 additional 5 × 5-m subplots were surveyed for stems in the 1–10 cm *D* range.

We estimated error in stand-level variable estimates using a Monte Carlo simulation approach similar to that detailed in Yanai et al. (2010) and Fatemi et al. (2011). This approach used multiple iterations of stand-level variable estimates to account for model uncertainty in regression Equations 5 and 7. Each iteration used a randomly selected error term with a mean value of 0 and a distribution based on the SD of the parameter for each model. We implemented this approach for 200 iterations using the PROC MODEL function in SAS version 9.3, which provided both a mean value for each stand-level variable and 95% confidence intervals for the estimate.

Results

The best fit between dependent and independent variables was generally obtained using Equation 5 ($\log_{10} Y = a \times \log_{10} D + b$) or Equation 7 ($Y = a \times D^b$), depending on the response variable. When *H* was included with *D* in multiple linear regression analyses, it generally did not improve on models using *D* alone, with two exceptions, which are discussed below. Regressions between *D* and both woody and total biomass using Equation 7 had high coefficients of determination with an *R*² value for all models of 0.91 and 0.98 for understory and sun trees, respectively, and *R*² values for individual species all falling above 0.84 (Tables 3 and 4). Woody surface area and sapwood area were also best predicted by Equation 7 (Tables 3 and 4) and had *R*² values >0.90 for all species except *L*.

Table 5. Coefficients for allometric regression equation 5 ($\log_{10} Y = a \times \log_{10} D + b$) for predicting foliage mass, foliage area, and plant surface area for understory trees in intact forests.

Species	<i>a</i> (SE)	<i>b</i> (SE)	<i>R</i> ²
Foliage mass (g)			
ACRU	1.8253 (0.3457)	1.1027 (0.1843)	0.818
BELE	2.1321 (0.4491)	1.0079 (0.2485)	0.782
CASP	2.0596 (0.2931)	1.2759 (0.1440)	0.906
KALA*	1.1319 (0.4091)	1.6376 (0.1986)	0.400
LITU	0.9987 (0.2540)	1.5164 (0.1480)	0.707
QUAL*	1.4055 (0.4012)	1.3064 (0.2238)	0.653
QURU	1.9943 (0.1366)	1.3869 (0.0709)	0.973
All trees†	1.6997 (0.1631)	1.2681 (0.0883)	0.729
Foliage area (m ²)			
ACRU	1.8238 (0.3480)	-0.4495 (0.1855)	0.815
BELE	2.1309 (0.4482)	-0.3172 (0.2480)	0.783
CASP	2.0596 (0.2931)	-0.2341 (0.1434)	0.906
KALA*	1.1239 (0.4073)	-0.2124 (0.1977)	0.398
LITU	0.9987 (0.2547)	0.0379 (0.1484)	0.706
QUAL*	1.4108 (0.4022)	-0.2448 (0.2243)	0.653
QURU	1.9943 (0.1366)	-0.1931 (0.0709)	0.973
All trees†	1.7050 (0.1624)	-0.2335 (0.0879)	0.732
Plant surface area (m ²)			
ACRU	1.6625 (0.1492)	-0.9957 (0.0796)	0.954
BELE	1.7414 (0.2523)	-0.9727 (0.1396)	0.886
CASP	1.6985 (0.1115)	-1.0449 (0.0546)	0.979
KALA*	1.4735 (0.1437)	-0.8291 (0.0698)	0.912
LITU	1.8301 (0.0902)	-1.0438 (0.0525)	0.986
QUAL	1.6148 (0.2195)	-1.0508 (0.1224)	0.899
QURU	1.8888 (0.1153)	-0.9552 (0.0599)	0.978
All trees†	1.7342 (0.0771)	-1.0066 (0.0417)	0.927

See Table 1 for species abbreviations.

* Alternate coefficients for use in equation 4 are shown in Table 6.

† Data for KALA were excluded when calculating coefficients for equations for all trees.

tulipifera woody surface area in the 4-year-old stand, with an *R*² of 0.67.

Foliage area and total surface area were generally predicted best by Equation 5. Even with log-log transformation in Equation 5, *R*² values were generally lower for variables related to foliage than for those related to wood (Tables 5 and 6). *R*² values also varied more among species, especially for foliage biomass and foliage area, but were mostly >0.70. However, understory *K. latifolia* and *Q. alba* had *R*² values for foliage mass and foliage area below 0.70 (Table 6), and these were the only species for which using *H* substantially improved *R*² values (Table 7). Equation 4 ($Y = a \times D + b \times H + c$) best explained variation in foliage mass for *K. latifolia* and *Q. alba*, where *R*² values improved from 0.40 and 0.65 to 0.71 and 0.86 for *K. latifolia* and *Q. alba*, respectively (Table 7).

For all variables, species had a significant effect on model parameters (Tables 3, 4, 5, and 6). A notable exception was the total biomass equations for *B. lenta*, *Carya* spp., and *L. tulipifera*, which did not differ significantly from one another (Table 3). Although model parameters were not significantly different among species in all pairwise comparisons, we report equations for each species separately and we exclude any notation of significant differences in the interest of brevity (Tables 3, 4, 5, and 6). Model coefficients also differed between small tree equations and large tree equations for most species. Notable exceptions to this were observed for shade *A. rubrum* and sun *Q. rubra*, for which we developed foliage area models nearly identical to those published in Martin et al. (1998) (Table 5; Figures 1 and 2). Model coefficients also varied between sun and shade trees of the same species for most variables (*P* < 0.05) with one major exception: sapwood area did not vary between sun and

Table 6. Coefficients for allometric regression equation 4 ($Y = a \times D + b \times H + c$) for predicting foliage mass, foliage area, and plant surface area in trees exposed to full sunlight.

Species	<i>a</i> (SE)	<i>b</i> (SE)	<i>R</i> ²
Foliage mass (g)			
ACRU	1.2338 (0.3146)	2.0006 (0.1549)	0.706
LITU	2.1496 (0.3197)	1.6484 (0.1627)	0.881
QURU	1.9194 (0.1816)	1.5235 (0.0997)	0.949
All trees	1.7294 (0.1929)	1.7465 (0.0998)	0.799
Foliage area (m ²)			
ACRU	1.2380 (0.3176)	0.1016 (0.1564)	0.703
LITU	2.1496 (0.3197)	-0.0716 (0.1627)	0.881
QURU	1.9194 (0.1883)	-0.3637 (0.1033)	0.945
All trees	1.7143 (0.2284)	-0.0814 (0.1181)	0.735
Plant surface area (m ²)			
ACRU	1.9657 (0.1565)	-1.0538 (0.0770)	0.963
LITU	1.8587 (0.2535)	-0.9478 (0.1290)	0.898
QURU	1.7079 (0.1074)	-0.8670 (0.0589)	0.977
All trees	1.8633 (0.1034)	-0.9682 (0.0535)	0.942

See Table 1 for species abbreviations.

shade trees for any of the species that we compared (Tables 3 and 4). Specific foliage area varied among species within both sun (*F* = 88.97, *P* < 0.001) and shade leaves (*F* = 30.43, *P* < 0.001). SLA also varied significantly by site for all species (all *P* < 0.001) with sun leaves weighing more per unit area than understory leaves.

In all instances, using equations developed for large stems on small stems resulted in lower estimates of forest structural characteristics than using equations developed specifically for small stems (Figure 3). However, the relative importance of using size-specific equations to estimate stand structure varied among characteristics. Even with the increased understory biomass estimates observed when size-specific equations were used to estimate stand biomass, biomass at all sites was dominated by stems ≥10 cm *D* in all sites (Figure 3). The contribution of small stems to stand sapwood area and foliage area was much greater than their contribution to biomass (Figure 3). Using equations for small stems increased estimates of sapwood area and foliage area significantly for all variables in most stands, but the changes were particularly large in the two stands with the greatest number of small stems. In the data set we used, the 4-year-old stand had a low density of small stems because regeneration had not yet produced high stem density and the 37- and 200-year-old sites had relatively sparse understories. The 14- and 87-year-old stands had high densities of either small trees (14-year-old) or shrubs (87-year-old). In both instances, use of equations developed for larger stems for stems <10 cm significantly underestimated both foliage area and sapwood area (Figure 3).

Discussion

We demonstrate that equations for predicting forest structural characteristics for large trees cannot be applied across all tree size classes without the risk of significantly underestimating important structural variables such as sapwood area and foliage area. Equations for large stems nearly always underestimated values for structural variables of small stems, even when published correction factors were applied. When Equation 5 was used, coefficients for small stems developed in the current study generally had steeper slopes and/or less negative intercepts than equations developed for large trees of the same species. As a result, use of the large stem equations led to lower values for these variables. Such errors may be particularly large in stands with a high density of small stems, such as regenerating stands, for which relatively small errors for individual

Table 7. Coefficients for allometric regression equation 4 ($Y = a \times D + b \times H + c$) for predicting foliage mass and foliage area for understory *K. latifolia* and *Q. alba*.

Species	<i>a</i> (SE)	<i>b</i> (SE)	<i>c</i> (SE)	<i>R</i> ²
Foliage mass (g)				
KALA	165.191 (40.513)	-83.651 (41.911)	-0.969 (85.221)	0.708
QUAL	97.804 (39.321)	-21.240 (26.078)	-69.618 (50.924)	0.858
Foliage area (m ²)				
KALA	2.311 (0.567)	-1.170 (0.586)	-0.0136 (1.192)	0.708
QUAL	2.768 (1.113)	-0.601 (0.738)	-1.970 (1.441)	0.858

KALA, *Kalmia latifolia*; QUAL, *Quercus alba*.

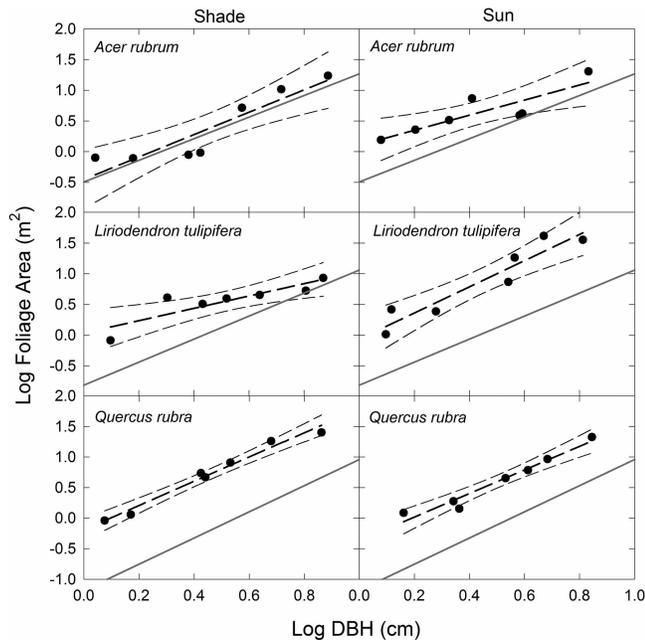


Figure 1. Comparison of allometric models for predicting foliage area of trees < 10 cm dbh (black line) in intact forest understories (Shade) and in a recent harvest site (Sun), with allometric models derived from trees > 10 cm dbh (gray line); 95% confidence limits are shown for small tree models (dashed lines).

stems are magnified by large numbers of stems. Our results further support the results of Fatemi et al. (2011), who previously showed that age-specific equations were important for predicting biomass in the northeastern United States. Similarly, Chaturvedi and Raghubanshi (2015) developed equations for each separate 10-cm size class. We suggest using at least two separate sets of size-specific equations for forested stands: one for large stems (≥ 10 cm *D*) and one for smaller stems (here defined as 1 – 10 cm *D* and with heights generally between ~ 2 and 15 m).

These results also indicate that allometric relationships between *D* and structural variables are actually nonlinear. Our results for variables including biomass, sapwood area, and stem surface area were best explained using species-specific power functions. When allometric equations are developed for large trees, the inherent variation among individual trees contributes to heteroscedasticity and makes it more difficult to detect nonlinear relationships, especially when raw data are log transformed (Martin et al. 1998, Zar 1999). However, when we developed allometric equations for small trees in this study, heteroscedasticity was reduced and the nonlinear nature of the relationship was more apparent when looking at the raw data. The theory that natural patterns often scale with power functions is well established in the literature (e.g., West et al. 1999, Brown et al.

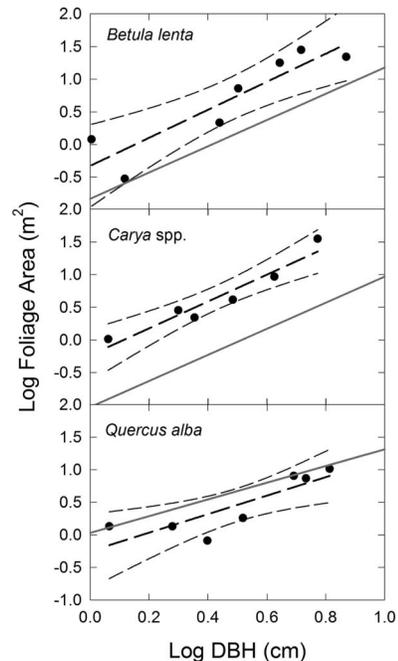


Figure 2. Comparison of allometric models for predicting foliage area of trees < 10 cm dbh (black line) in intact forest understories and allometric models derived from trees > 10 cm dbh (gray line); 95% confidence limits are shown for small tree models (dashed line).

2002). Although attempts have been made to determine a universal scaling constant for tree architecture (Enquist and Niklas 2002), numerous researchers have shown that scaling relationships vary among species (Mencuccini 2002, McCulloh and Sperry 2005, Meinzer et al. 2005). Meinzer et al. (2005) showed that sapwood area scaled with basal area using a power function, but exponents varied among species; our results further support that conclusion. Both Mencuccini (2002) and McCulloh and Sperry (2005) also showed that there was no consistent relationship in hydraulic function and/or architecture among species.

Whereas many studies have focused on the species-specific nature of hydraulic architecture (Mencuccini 2002, McCulloh and Sperry 2005, Meinzer et al. 2005), species-specific equations based on power functions may be useful for other variables as well, particularly for common understory tree species. There were many instances for which models were not significantly different among species, suggesting that certain species could be combined, but we also found many differences in model coefficients among species. Furthermore, there was no consistent pattern in shared slopes and/or intercepts among species for all variables. For instance, A_{SW} models were similar for *A. rubrum* and *B. lenta*, but foliage area

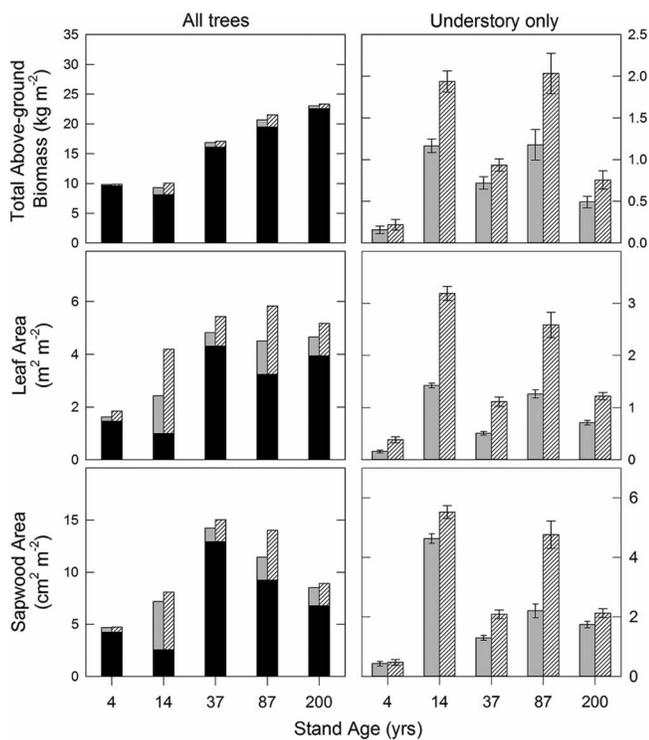


Figure 3. Comparisons of predicted values for structural characteristics of five stands across a chronosequence of forest development using either a single equation developed for large trees or size-specific equations for trees >10 or <10 cm dbh. Left panels show contributions of all trees >1 cm dbh in the stand, and right panels show contributions of trees 1–10 cm dbh only. Black bars are canopy trees, solid gray bars represent the contribution of large trees estimated using equations developed for large trees, and hashed bars represent the contribution of small trees estimated using the newly developed equations for small trees. Error bars in the right panels represent the 95% confidence intervals derived from a Monte Carlo simulation.

models were not. Thus, we chose to report both individual models for all sampled species and general models in which data were combined for groups of species. Generally, we would encourage the use of both species-specific equations to reduce error in estimating structural variables at the stand level where differences in estimates for individual stems are cumulative.

We also found that D was generally the most important measurement to make for estimating forest structure when forest understories were dominated by trees. Although some variables in the current study were best predicted using untransformed D and H , measuring D alone in study plots is generally one of the fastest and most efficient means of accurately surveying relatively large forest plots. Including H in field surveys may be useful for some species, as demonstrated with *K. latifolia* and *Q. alba* in our study, but D can explain most of the variability alone. Although most forest surveys rely heavily on D measurements, D may not be the best predictor for response variables for some shrubs. If shrubs such as *K. latifolia* are a large component of the biomass or are the sole focus of a study, diameter measurements nearer the base of the stem may be preferred because measurement of fewer stems would be faster and would result in less cumulative sampling error (e.g., Elliott and Clinton 1993, Brantley and Young 2007).

Potential applications of these or similar equations include better quantification of stand-level characteristics such as foliage area and

sapwood area and more accurate estimates of associated ecosystem fluxes such as net ecosystem exchange and evapotranspiration. These improvements should be particularly relevant in regenerating stands or other stands with a high density of small stems (Hamada et al. 2004). Forests may have a higher density of small stems for multiple reasons including forest regeneration (recovering after a large-scale disturbance such as logging, fire, or insect attack) or the presence of a large shrub component. Using size-specific equations may be particularly important for structural variables such as sapwood area for which the proportion varies with stem size. For instance, our results indicate that small trees appear to have a higher proportion of sapwood area to basal area because heartwood has not yet developed. More relative sapwood area, in turn, may support higher foliage area and/or higher gas exchange relative to larger trees. This same consideration may apply to the shrub layer in older forests.

Although it would be ideal to develop and use site-specific equations in every study, this is often not practical, and the allometric equations presented here should be a useful addition to the existing literature for forest stands with similar species in the southern Appalachians. Our application of these equations to stand-level biomass also shows that using size-specific allometric equations may not be critical in all circumstances. Whereas certain forest types have a large understory component that can contribute substantially to biomass and productivity (e.g., Mitchell et al. 1999), biomass in many forests is dominated by the wood component in large trees and we show similar results here. Although equations for large trees underestimated biomass in small trees in the sample data set shown here, the resulting difference in overall stand biomass was relatively small for all sites. Thus, research and management programs in similar forests in this region that are focused primarily on standing biomass would not necessarily require more accurate estimates of understory structure, especially in mature, closed-canopy forests where there is little or no shrub layer.

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