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Improved Allometric Equations for Black Locust (*Robinia pseudoacacia*) in the Coweeta Basin

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Abstract

Allometric equations are widely used to estimate forest aboveground biomass (AGB). However, their development rarely includes the oldest and largest trees, leading to estimation errors. Black locust (*Robinia pseudoacacia*) is an early successional nitrogen-fixing tree, native to the Eastern United States. It is widespread, often the dominant tree following disturbance, and can be a significant source of new nitrogen to recovering forests. Here we developed allometric equations for black locust to predict AGB and leaf area based on diameter at breast height (DBH). We compiled existing data from our study site and sampled new trees, ranging in size from 6.0–58.5 cm DBH. Destructively harvested new trees were measured for foliage, branch, and bole dry biomass and carbon and nitrogen concentrations. Parameters for our predictive equations were lower than those previously published; existing equations applied to these largest individuals resulted in overestimates of bole and branch biomass on average by 33.6 and 325.3 percent, respectively. We also found that foliage and woody nitrogen concentrations declined with age, together suggesting age-related declines in black locust are greater than other co-occurring species. Our equations significantly improved accuracy of AGB predictions and will aid in site-specific forest biomass estimates and new nitrogen inputs.

Keywords: Allometry, aboveground biomass, black locust, Coweeta Hydrologic Laboratory, nitrogen fixation, yellow locust.

Acknowledgments

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Introduction

Black locust (*Robinia pseudoacacia* L.), also known as yellow locust, is an early successional tree, native to the Eastern United States and also found in southern Canada and parts of Europe and Asia (Huntley 1990). Widespread, particularly following disturbance (Elliott and others 2016, 2019), it is the most abundant nitrogen (N)-fixing tree in eastern U.S. forests (Staccone and others 2020) and provides a significant source of new N to recovering forests (Boring and Swank 1984a). Although N fixation rates may change over the tree's lifespan, they are estimated to be as high as 30 kg N ha^{-1} yr^{-1} in young, dense stands (Boring and Swank 1984a). Black locust is also functionally important because it has conservative water use relative to other early successional trees such as tulip poplar (*Liriodendron tulipifera*) (Wurzburger and Miniat 2014). Because many of these tree-based processes scale with age and size, accurate models are needed to predict black locust aboveground biomass (AGB).

Multiple studies provide allometric equations for young and small-diameter black locust (Boring and Swank 1984b, Elliott and Clinton 1993, Minucci and others 2019), which can account for as much as 71 percent of basal area in young stands (Boring and Swank 1984b). Although black locust is generally a short- to medium-lived tree, its lifespan is significantly longer and diameter significantly larger than the oldest trees of previous studies (38 years old and 30 cm diameter at breast height [DBH]; Boring and Swank 1984a, 1984b). It would not be uncommon to find black locust trees in Southern Appalachian forests exceeding 30 years of age and 40 cm in DBH. Thus, estimating AGB in older forests requires equations which are not biased towards young trees, considering that the majority of forests in the Eastern United States are >20 years (Pan and others 2011). Therefore, our objective was to extend the inference range of predicting AGB (foliage, branch, and bole) and carbon (C) and N concentrations of all woody and foliar tissues for black locust trees at peak seasonal biomass.

Materials and Methods

Study location and sample selection

We conducted our study at the U.S. Department of Agriculture Forest Service, Southern Research Station, Coweeta Hydrologic Laboratory in western North Carolina, USA (fig. 1). Climate is mild and humid with mean annual temperature of 12.6 °C and ca. 1800 mm of rainfall (Burt and others 2017). Forests are mixed deciduous with high richness and diversity (Elliott and Swank 2008). Sample trees were selected to be greater than the diameters of sampled trees used in existing allometric equations, 0.9–30.6 cm (Boring and Swank 1984b, Elliott and others 2002). In total, three canopy-dominant black locust trees between 39.4–58.5 cm DBH were identified in reference watersheds with no forest management manipulations since the Coweeta Basin was partially cut in the early 1900s (fig. 1). Care was taken to ensure that trees were accessible but not along roads so that trees would represent those growing in interior forest conditions.

Diameters at ground height and DBH were recorded. Trees were directionally felled with a chainsaw, minimizing canopy damage. We then measured stump height, bole length to the base of live crown (BLC), and diameters at mid-bole and BLC. Using a chainsaw, we cut one cross-sectional disc from the top of each above-mentioned section, including the top of the bole. Average disc height, bark depth, and sapwood depth were measured using calipers and used to estimate wet volume of each disc (V_d) assuming discs were cylindrical. We measured all live canopy branches and implemented randomized branch sampling for three or four representative branches to harvest (Sollins and Anderson 1971). For one tree, we harvested the entire crown due to extensive branch breakage upon felling to avoid errors in matching branches and foliage. Sample branches were excised, separated into foliage or wood, and bagged. All field masses (M_f, kg) of foliage, branch wood, and bole discs were measured using a 10-kg,

Left: Black locust, 44.8 cm DBH and 95 years old, selected prior to felling. Right: A cross-sectional disc from a black locust >110 years old, sanded smooth for determining age, shows advanced heart rot. (USDA Forest Service photos by Joel Scott)

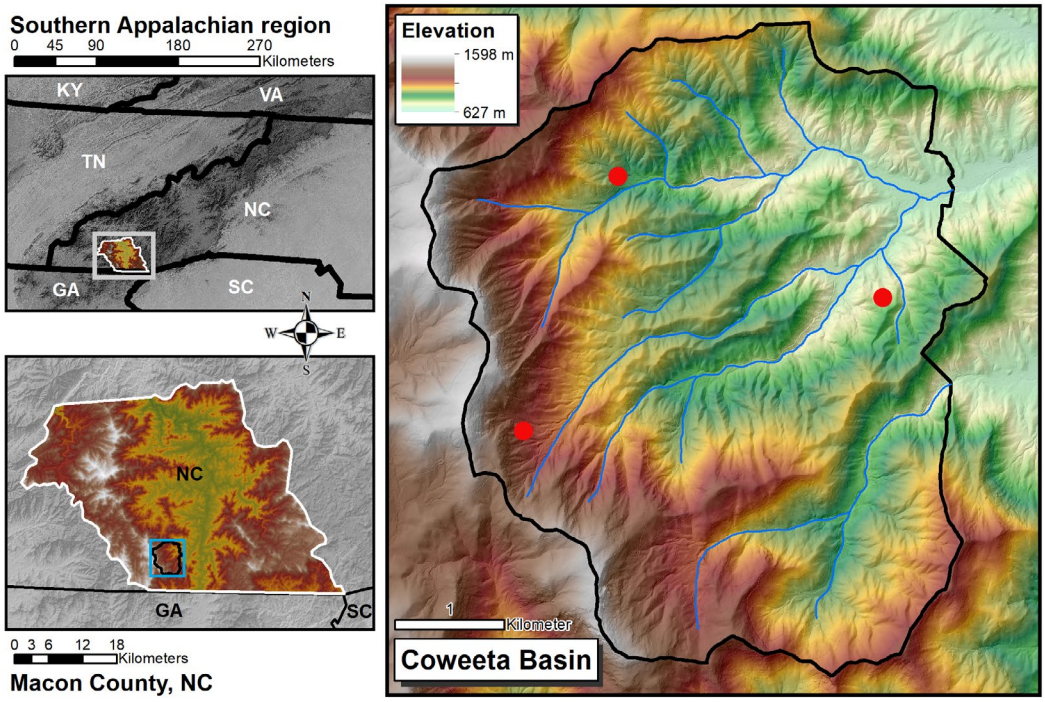

Figure 1—The Coweeta Basin study site and location of sampled trees. From left to right, trees were 44.8, 58.5, and 39.4 cm diameter at breast height (DBH).

calibrated, hanging scale (Intercomp® Model ST2000), dried at 65 °C until a constant weight was achieved (Sheldon SM028-2), and weighed to the nearest 0.1 kg.

Trees were aged by counting the annual rings of the oldest disc where they could be visualized to the pith under 40x magnification (Olympus SZ40) after surfacing with a belt sander. In some cases, heart rot (caused by *Phellinus robiniae*) prevented aging the lowest disc, and thus ages are approximate and not actual.

Tissue analysis

Dried foliage, branch, and disc tissues were subsampled from each bag, coarsely ground (Wiley Laboratory Mill 3375-E15), then finely ground to pass through a 0.5-mm mesh (Retsch® ZM200). Ground tissue was composited across bags for each tissue category, and a 5-mg subsample analyzed for C and N content (Thermo Electron Corp. Flash EA 1112 NC) following the Dumas method (USDA Forest Service 2017) and expressed as percent concentration of dry mass.

Scaling to crown and tree biomass

To estimate crown biomass, we used data from the harvested branches to fit a polynomial model between branch foliage dry mass ($M_{foliage}$, kg) and branch diameter (d, cm), and branch wood dry mass (M_{wood}, kg) and d, with a 0 intercept. These relationships then predicted $M_{foliage}$ and M_{wood} of all canopy branches based on each branch's d. All predicted and measured biomass was then summed to estimate crown mass. Leaf area (A_{leaf}) was estimated by multiplying $M_{foliage}$ by specific leaf area (238.77 $cm^2\ g^{-1}$) reported in Wurzburger and Miniat (2014).

To estimate bole volume (V_b), we used data from the discs and their sample heights and assumed the volume of bole sections could be approximated by a frustum. Disc density (ρ_d) was estimated as disc M_f divided by V_d. The disc dry mass fraction (f_d) was estimated as 1 minus the ratio of the water mass in the disc to the M_f. Biomass of bole sections was estimated as the product of V_d, average disc f_d, and average ρ_d. Bole sections were summed to estimate total bole biomass.

Statistical analysis

Across all samples from this and two additional studies (table 1), we log transformed the biomass data for tree total foliage, branches, bole (M_{bole}), and total AGB, then fit linear regressions to biomass or A_{leaf} as a function of log transformed overbark diameter at DBH. We also fit linear regressions of nitrogen concentration ([N]) of tree components as a linear function of tree age. Best fit equations were selected using the best R^2 value, and significance was tested at $\alpha = 0.05$ level.

Table 1—Data used for developing allometric equations for black locust

DBH	AGB[a]	Foliage biomass	Branch biomass	Bole biomass	Leaf area	Source
cm			*kg*		*m²*	
6.0	6.36	0.31	1.05	5.01	7.44	Elliott and others (2002)
8.4	16.43	0.48	3.90	12.05	11.46	Boring and Swank (1984b)
9.0	26.16	1.16	4.37	20.63	27.70	Boring and Swank (1984b)
9.0	21.55	1.18	3.73	16.64	28.17	Boring and Swank (1984b)
9.1	22.48	1.41	2.97	18.10	33.71	Elliott and others (2002)
10.4	32.30	1.36	7.29	23.65	32.47	Boring and Swank (1984b)
10.5	33.70	1.66	4.44	27.59	39.75	Elliott and others (2002)
17.0	109.40	4.20	27.71	77.49	100.28	Boring and Swank (1984b)
18.2	126.48	5.31	23.77	97.40	126.79	Boring and Swank (1984b)
18.5	137.58	4.64	41.83	91.11	110.79	Boring and Swank (1984b)
27.1	332.54	5.67	31.37	295.49	135.49	Elliott and others (2002)
29.0	630.42	10.50	98.54	521.38	250.71	Boring and Swank (1984b)
30.6	629.00	7.06	59.98	561.96	168.57	Boring and Swank (1984b)
39.4	869.47	4.42	40.52	824.10	105.51	This study
44.8	1464.37	3.07	72.83	1388.48	73.21	This study
58.5	1509.83	6.39	46.28	1457.16	152.56	This study

AGB = aboveground biomass; DBH = diameter at breast height.

[a] The percentage of the canopy sampled from the three black locust trees harvested for this study was 20, 38, and 100 percent in order of appearance in the last three rows of the table. Average carbon concentrations (percent) for the three trees in order of foliage, branch, and bole, were 47.96, 46.56, and 47.64; 45.16, 47.76, and 48.07; and 47.23, 47.02, and 47.62, respectively.

Results

Branch biomass increased with branch diameter (fig. 2). Polynomial models predicting branch foliage dry mass and branch wood dry mass from branch diameter were significant ($M_{foliage}$: $F_{1,6} = 43.35$, $P < 0.001$; M_{wood}: $F_{1,6} = 582.05$, $P < 0.0001$). The fit for branch dry mass was stronger than foliage dry mass. The one tree that required sampling the entire crown strengthened model fits because it increased the range of the branch diameters sampled. Excluding data from that tree did not alter the significance for the relationship with M_{wood} ($F_{1,5} = 48.9$, $P = 0.001$) but did for $M_{foliage}$ ($F_{1,5} = 0.66$, $P = 0.45$).

Aboveground biomass and leaf area increased with tree diameter (fig. 3). Across all trees from this and two additional studies shown in table 1, bole, foliage, and AGB increased with DBH ($\log_{10}(M_{bole})$: $F_{1,14} = 1120.6$, $P < 0.0001$, $R^2 = 0.99$ $\log_{10}(M_{foliage})$: $F_{1,14} = 32.68$, $P < 0.0001$, $R^2 = 0.70$; $\log_{10}(AGB)$: $F_{1,14} = 1089.5$, $P < 0.0001$, $R^2 = 0.99$). Our analysis indicates an increase in leaf area with DBH ($\log_{10}(A_{leaf})$: $F_{1,14} = 32.68$, $P < 0.0001$, $R^2 = 0.70$), but the relationship was less strong than the equations predicting biomass. For the larger trees sampled in this study, previously established equations overestimated both bole and branch biomass on average by ~33.6 and ~325.3 percent, respectively (table 2).

Mean foliar [N] was at least four times higher than bole [N] and generally declined with tree age (table 3, fig. 4). Foliar [N] averaged 2.9 percent, while branch and bole [N] were 1.7 and 0.4 percent, respectively. Compared to younger/smaller trees sampled at this site previously (Boring and Swank 1984b), the older/larger trees from this study had significantly lower tissue [N]. Across both studies, age was a strong predictor of tissue [N]; the older the tree, the lower the [N]. As trees aged, foliar [N] declined by 0.02 percent per decade, while bole [N] declined by 0.04 percent.

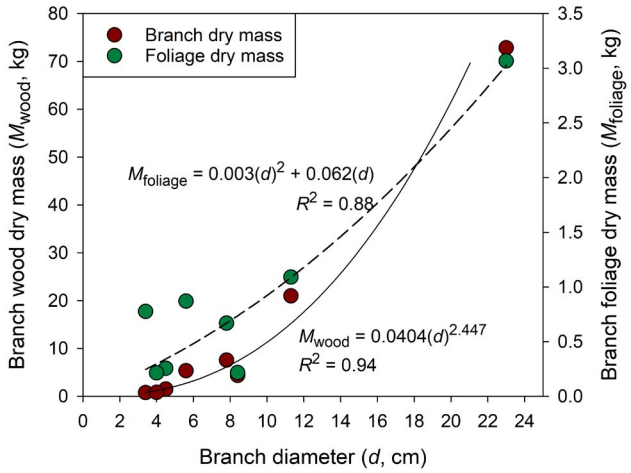

Figure 2—Branch wood and foliage dry mass as a function of branch diameter for the three black locust trees sampled in this study. Predictive equations used to estimate branch and foliage biomass for unsampled branches in the crown are shown with fit statistics (P <0.05 for both).

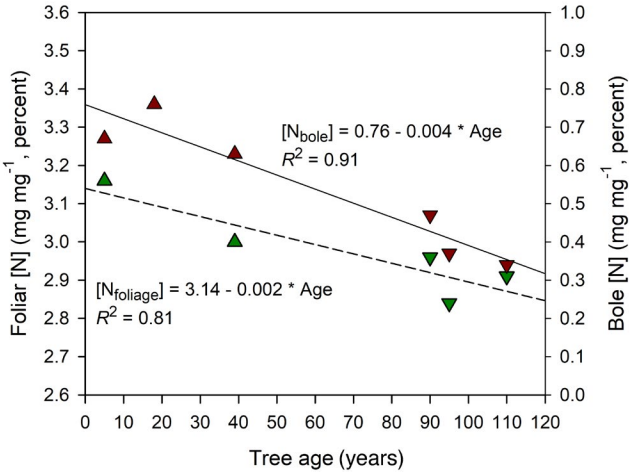

Figure 4—Nitrogen concentration [N] of foliage (in green) and bole (in red) tissue ($[N_{foliage}]$ and $[N_{bole}]$, respectively) as a function of tree age for the three black locust trees sampled in this study (downward triangles) and those in Boring and Swank (1984b) (upward triangles) (table 3). Parameters and fit statistics given for each relationship (P <0.05 for both).

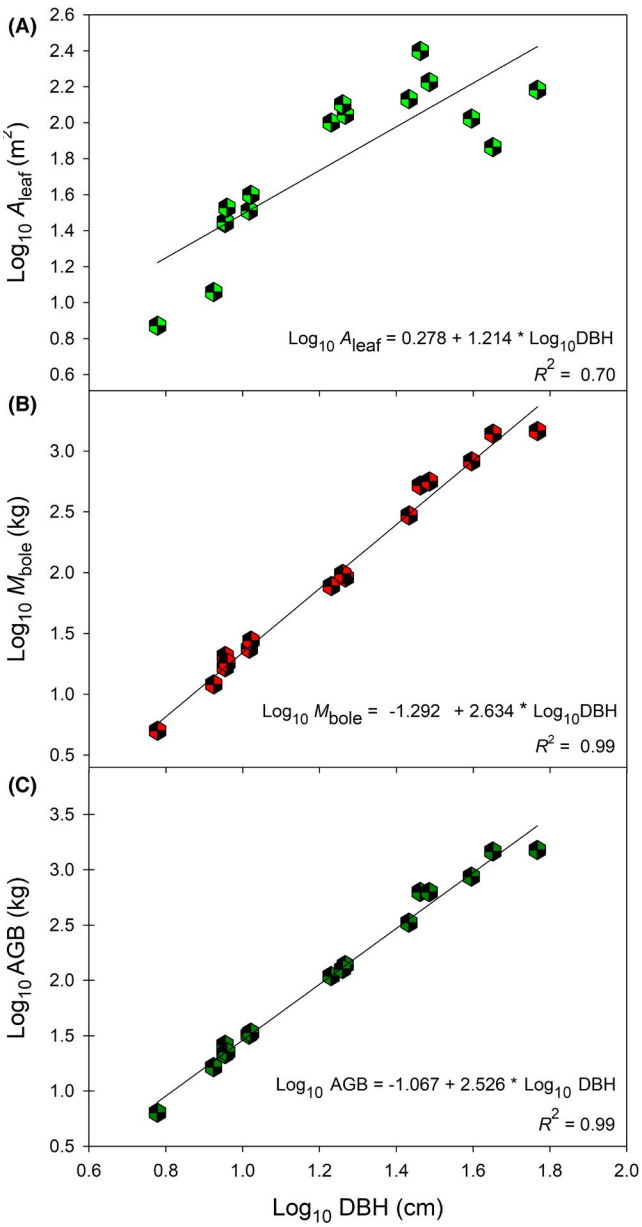

Figure 3—Log transformed total tree leaf area (A_{leaf}) (A), bole biomass (M_{bole}) (B), and aboveground biomass (AGB) (C) versus log transformed tree diameter at breast height (DBH). Lines, parameters, and coefficient of determination (R^2) shown for linear regressions (P <0.05 for all). Slope and intercept for log transformed leaf biomass (kg) versus log transformed DBH (cm) equation are 1.212 and -1.100, respectively (not shown).

Table 2—Bole and branch biomass estimates and percent error (%Error) for three sampled black locust trees using previously published equations for smaller/younger trees

DBH	Actual bole biomass	Actual branch biomass	Estimated bole biomass	Estimated branch biomass	%Error bole	%Error branch
cm	---------- *kg* ----------					
39.4[a]	824.10	40.52	819.70	131.10	-0.5	223.5
44.8[a]	1388.48	72.83	1145.26	181.50	-17.5	149.2
58.5[a]	1457.16	46.28	2294.26	356.74	57.4	670.8
					Average: 13.1	**Average: 347.9**
39.4[b]	824.10	40.52	1046.01	124.21	26.9	206.5
44.8[b]	1388.48	72.83	1518.30	167.35	9.4	129.8
58.5[b]	1457.16	46.28	3292.45	310.86	125.9	571.7
					Average: 54.1	**Average: 302.7**

DBH = diameter at breast height.

[a] Equations used for estimated biomass are $\log_{10y} = a + b \log 10x$ where y = dry weight (g) and x = DBH (cm). For the purposes of this study, g were converted to kg. Bole: a = 1.75911, b = 2.60392; branch: a = 1.07682, b = 2.53262 (Elliott and others 2002).

[b] Equations used for estimated biomass are $\log_{10y = a + b} \log 10x$ where y = dry weight (kg) and x = DBH (cm). Bole: a = -1.609, b = 2.901; branch: a = -1.609, b = 2.321 (Boring and Swank 1984b).

Table 3—Mean (SE) nitrogen concentration ([N]) of foliage, branch, and bole tissues for black locust trees differing in DBH and age sampled in this study and those reported in Boring and Swank (1984b)

			[N] (mg mg^{-1}) (percent)		
DBH	Age	Tissue type	Mean	SE	Source
cm	*years*				
8.9[a]	<5	foliage	3.16[b]	0.05	Boring and Swank (1984b)
		branch	1.13[b]	0.10	
		bole	0.67[b]	0.04	
17.9[a]	<18	foliage	—	—	Boring and Swank (1984b)
		branch	—	—	
		bole	0.76[b]	0.08	
28.9[a]	<39	foliage	3.00[b]	0.09	Boring and Swank (1984b)
		branch	1.47[b]	0.17	
		bole	0.63[b]	0.07	
39.4	>90	foliage	2.96	0.12	This study
		branch	1.32	0.12	
		bole	0.47	0.12	
44.8	95	foliage	2.85	NA	This study
		branch	1.96	NA	
		bole	0.37	0.12	
58.5	>110	foliage	2.91	0.16	This study
		branch	1.77	0.15	
		bole	0.34	0.18	

DBH = diameter at breast height; SE = standard error.

[a] Average DBH for trees in this age class.

[b] Averaged [N] for multiple trees in this age class.

— = Data missing from Boring and Swank (1984b).

NA = Foliage and branch SE for 44.8 cm DBH tree not shown as the entire crown was sampled.

Discussion

We sought to improve allometric relationships for black locust by reanalyzing previously published data with additional data from older/larger trees. Parameters for our predictive equations were lower than those previously published, indicating that AGB rates slow as black locust gets older and larger. Previously published equations were derived from samples acquired from young, early successional forests which rapidly produce biomass. Although most tree species display declines in growth rate and physiological activity (Bond 2000, Gower and others 1996), our findings suggest a stronger decline in black locust than many co-occurring trees. Comparing allometric equation coefficients to those of 10 co-occurring species (Martin and others 1998), we estimate that although young/small black locust trees initially have a 17 percent greater AGB (i.e., intercept), the increase in total AGB over time is 5 percent slower (i.e., slope). Similarly, young/small black locust trees initially have a 93 percent greater foliar biomass than that of 10 co-occurring species combined, but the increase in foliar biomass over time is 67 percent slower. This pattern of a lower rate of AGB and foliar biomass increase over time might be explained by high levels of stem-boring insects, heart rot, and herbivory, which were apparent on all harvested trees in this study. Indeed, we found that disc density (ratio of dry mass to wet volume) declined with age/size by 11 percent dm^{-1}, possibly indicating heart rot in the older portions of the tree or older trees.

Black locust foliage and bole [N] declined with age. Because photosynthetic rate highly correlates with foliar [N] (Field and Mooney 1986, Reich and others 1995), we might expect reductions in productivity as foliar [N] declines (table 3). However, it is not clear why black locust bole tissue [N] declined with age. In other species, [N] was not related to diameter at this site (Martin and others 1998). Further, aboveground primary productivity and leaf litter [N] have increased at this site over the last 20 years (Knoepp and others 2018), coinciding with chronic atmospheric N deposition (Burns and others 2011). Therefore, there is little evidence for increasing N limitation over time at this site. Perhaps foliage and bole tissue [N] declines over tree age as black locust shifts its reliance from fixation to soil to fulfill its N demands.[1] Older black locust trees (>75 years) rarely nodulate, and those that do have low tree-specific fixation rates.[1] Therefore, decreases in [N] may signal a shift in black locust N economy as trees age.

Predicting age-related declines in AGB growth rate and tissue [N] requires our improved equations that include older/larger black locust trees. Because of its prevalence in disturbed sites (Boring and Swank 1984b; Elliott and others 2016, 2019) and its ability to increase N availability (Boring and Swank 1984a, 1984b; Minucci and others 2019), our ability to more accurately predict AGB will improve ecosystem-level estimates of N fixation, aboveground C stock, and forest change in the Southern Appalachians.

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University of Georgia graduate students Jessie Motes and Sarah Ottinger sort leaf biomass from a black locust tree. The mass of these leaves will be used to broaden existing allometric equations to include older age classes of black locust. (USDA Forest Service photo by Joel Scott)

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Left: Branch biomass is cut to fit into bags for weighing. Right: Each branch is measured and randomized branch sampling implemented (Sollins and Anderson 1971) before sampling cross-sectional discs and foliage for weighing and analysis. (USDA Forest Service photos by Joel Scott)

Scott, Joel L.; Miniat, Chelcy F.; Motes, Jessie; Ottinger, Sarah L.; Wurzburger, Nina; Elliott, Katherine J. 2021. Black locust allometric equations: improved allometric equations for black locust (*Robinia pseudoacacia*) in the Coweeta Basin. Res. Pap. SRS-64. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 8 p. https://doi.org/10.2737/SRS-RP-64.

Allometric equations are widely used to estimate forest aboveground biomass (AGB). However, their development rarely includes the oldest and largest trees, leading to estimation errors. Black locust (*Robinia pseudoacacia*) is an early successional nitrogen-fixing tree, native to the Eastern United States. It is widespread, often the dominant tree following disturbance, and can be a significant source of new nitrogen to recovering forests. Here we developed allometric equations for black locust to predict AGB and leaf area based on diameter at breast height (DBH). We compiled existing data from our study site and sampled new trees, ranging in size from 6.0–58.5 cm DBH. Destructively harvested new trees were measured for foliage, branch, and bole dry biomass and carbon and nitrogen concentrations. Parameters for our predictive equations were lower than those previously published; existing equations applied to these largest individuals resulted in overestimates of bole and branch biomass on average by 33.6 and 325.3 percent, respectively. We also found that foliage and woody nitrogen concentrations declined with age, together suggesting age-related declines in black locust are greater than other co-occurring species. Our equations significantly improved accuracy of AGB predictions and will aid in site-specific forest biomass estimates and new nitrogen inputs.

Keywords: Allometry, aboveground biomass, black locust, Coweeta Hydrologic Laboratory, nitrogen fixation, yellow locust.

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