

forest management

Biomass Estimates of Small Diameter Planted and Natural-Origin Loblolly Pines Show Major Departures from the National Biomass Estimator Equations

Jamie Schuler, Don C. Bragg, and Kristin McElligott

As southern pine forests (both planted and naturally regenerated) are more heavily used to provide biomass for the developing energy sectors and carbon sequestration, a better understanding of models used to characterize regional biomass estimates is needed. We harvested loblolly pines (*Pinus taeda* L.) between 0.5 and 15 cm dbh from several plantations and naturally regenerated stands in southeastern Arkansas to evaluate allometric relationships based on stand origin. In this process, each pine was separated into stemwood, branches + foliage, and taproot biomass components. Although the differences changed with dbh, loblolly pines from planted stands generally had greater percentages of biomass allocated to foliage + branches and taproots, whereas those from natural-origin stands had greater amounts in stemwood, aboveground, and total biomass. National Biomass Estimator (NBE) high-specific gravity pine equations predicted natural-origin aboveground biomass reasonably well. However, the same NBE model underpredicted aboveground biomass for small (<5 cm) diameter planted pine and overpredicted planted pines between 7 and 15 cm dbh. When scaled to stand-level estimates, the NBE models resulted in estimates for average stand diameters of 5, 10, and 15 cm that ranged from –18.6 to 2.1% for natural stands and from –21.9 to 62.8% for planted stands.

Keywords: National Biomass Estimators; biomass allocation; *Pinus taeda*

In the southeastern United States, total forest cover has changed remarkably little over the last 60 years. However, the upland forests of this region have dramatically increased in pine dominance, largely due to increases in pine plantations (Wear and Greis 2002, Hartsell and Conner 2013) via the conversion of naturally regenerated (also called “natural-origin” or “natural”) pine, pine-hardwood, and upland hardwood forests (Hartsell and Conner 2013). For example, between 1952 and 2010, the area in the southeastern United States occupied by natural-origin pine forest has dropped from 29.1 million to less than 12.5 million ha, while the acreage of planted pine has grown from 747,000 to almost 16 million ha (Hartsell and Conner 2013). Indeed, across the southeastern United States, loblolly pine (*Pinus taeda* L.) has become the major commercial tree species over the past half-century, with a number of historical factors driving the explosive growth of planted loblolly pine (Carter et al. 2015).

Most of these large-scale forest-type conversions reflect changes in the silvicultural preferences of private landowners. Although the efficacy of even-aged or uneven-aged silvicultural practices in loblolly pine-dominated stands of natural origin has been repeatedly shown over the decades (e.g., Guldin and Baker 1988, Farrar et al. 1989, Cain and Shelton 2001), this has not slowed the conversion of southern landscapes. Under current conditions, few other silvicultural systems in southern uplands match the income potential of short-rotation loblolly pine plantations (Yin and Sedjo 2001, Cubbage et al. 2007, Fox et al. 2007). Increasingly, intensive treatments such as site preparation, competition control, optimized stand densities, and improved genetics have led to considerably faster and more substantial volume growth, especially with planted loblolly, and, to a lesser extent, slash (*Pinus elliotii* Engelm.) pine (Fox et al. 2007).

Changes in the composition and structure of forests across the southeastern United States have major implications for land

Manuscript received August 9, 2016; accepted December 30, 2016; published online February 16, 2017.

Affiliations: Jamie Schuler (jamie.schuler@mail.wvu.edu), West Virginia University, Morgantown, WV. Don C. Bragg (dbragg@fs.fed.us), USFS Southern Research Station. Kristin McElligott (kmc2@vt.edu), Virginia Polytechnic Institute and State University.

Acknowledgments: We thank the following individuals for their contributions: Kirby Sneed and Rick Stagg (USDA Forest Service); Jonathan Hartley (University of Arkansas-Monticello); and Conner Fristoe (Weyerhaeuser Company). This research was supported by Agriculture and Food Research Initiative Competitive Grant 2009-35103-05356 from the USDA National Institute of Food and Agriculture, the Southern Research Station of the USDA Forest Service, and the Arkansas Forest Resources Center.

managers and policymakers. The silviculturally driven loss of natural-origin pine stands is of increasing concern to many agencies and conservation organizations (e.g., South and Harper 2016), prompting some to engage in campaigns to protect remaining areas of this kind of forest. For example, most of the major forest sustainability certification bodies now prohibit or greatly limit a participating landowner's ability to convert naturally regenerated forests into pine plantations (Forest Stewardship Council 2010, Sustainable Forestry Initiative 2015). Others have sought to counter the loss of natural stands by promoting increased management intensity of natural stands. Many landowners assume that only short-rotation pine plantations are profitable or that natural stands do not adequately respond to treatment; however, years of research have shown that more intensive management of natural-origin loblolly pine stands can greatly improve their yields and financial returns (e.g., Balmer et al. 1978, Nelson and Bragg 2016). The lower stand establishment costs associated with natural stands are especially attractive if landowners prefer longer rotation lengths. Emerging opportunities in carbon storage markets, bioenergy, or other nontraditional ecosystem services may further alter the calculus of southern pine silvicultural practices. As an example, developing markets for biofuel feedstocks by converting nonmerchantable residues (e.g., tops) or submerchantable products (precommercial thinnings) into merchantable products (e.g., pellets) may help close the gap in the investments and returns needed to make natural-origin pine-dominated stands more economically appealing to landowners.

Not surprisingly, then, the need for accurate large-scale estimates of forest biomass is becoming increasingly important as broad management and policy decisions are often made based on these estimates. Yet we know remarkably little about how existing biomass models behave under circumstances experienced in the field, even for well-described cover types such as loblolly pine. For instance, numerous biomass equations have been developed specifically for commercial-size loblolly pine trees grown in plantations or natural stands (e.g., Van Lear et al. 1986, Baldwin 1987, Clark and Saucier 1990, Adegbi et al. 2002, Jenkins et al. 2003, Posey 2003, Doruska and Patterson 2006, Gonzalez-Benecke et al. 2014). However, none of these were developed to compare natural and planted stands for size classes traditionally considered precommercial. Furthermore, very few models have been developed with the specific intention of describing loblolly pine biomass attributes or projecting biomass trends for regional to national scales. Rather, they were designed to address fine-scale ecological or silvicultural questions.

At the regional or national scales, US forest biomass and carbon stocks are usually estimated by coupling easy-to-use single-parameter biomass equations (e.g., those in the National Biomass Estimator [NBE] Library) (Jenkins et al. 2004, Chojnacky et al. 2014) with data from the publicly available Forest Inventory and Analysis (FIA) program (e.g., Smith et al. 2013). However, a number of articles have already discussed the limitations of the NBE (and similar) equations: notably the lack of taxonomic specificity, site-specific attributes, and a paucity of models for belowground estimates (Temesgen et al. 2015, Weiskittel et al. 2015). Even though the latest iteration of the NBE (Chojnacky et al. 2014) attempts to address some of these limitations, challenges remain. As an example, silvicultural practices are known to significantly affect biomass production patterns in individual loblolly pine trees (e.g., Albaugh et al. 1998). As loblolly pine forests are managed more intensively, treatments such as site preparation, fertilization, and vegetation control can alter allocation patterns to harvestable (aboveground) tissues

(e.g., Borders and Bailey 2001). Hence, even within a known, clearly defined species such as loblolly pine, biomass predictions using designs such as the NBE may prove unreliable across multiple scales if not properly evaluated. This is particularly true for southern forest landscapes that are increasingly dominated by young stands of planted pine, which may prove allometrically different from the natural-origin trees that preceded them.

Since the nature of southeastern United States forests continues to change dramatically, our objectives were 2-fold. First, we sought to assess the influences of different management approaches on biomass allocation patterns in young loblolly pine. Are there differences in biomass for planted loblolly pines growing on sites that were mechanically prepared versus those that were not? Does biomass allocation differ between naturally regenerated and planted loblolly pine of the same bole size? If so, how will differences influence model predictions? Second, we compared our locally derived biomass models for small-diameter loblolly pine with the relevant NBE pine models. How well does the NBE predict the biomass of individual pines in different silvicultural systems? What are the implications of applying NBE versus local biomass models at larger scales? To address these questions, we evaluated the effects of three management scenarios (planted without mechanical site preparation, planted on bedded sites, and naturally regenerated pine) on allocation patterns for the various biomass components for loblolly pine. We then developed local equations to predict oven-dry biomass for loblolly pine using destructively sampled small diameter stems and compared these local models to the published NBE equations used for developing regional biomass assessments.

Methods

Field Sampling

Between June 2011 and January 2012, 99 loblolly pines were destructively harvested on or near the US Department of Agriculture (USDA) Forest Service's Crossett Experimental Forest (CEF) in Ashley County, Arkansas. Samples consisted of 61 naturally regenerated pines from the CEF and 38 stems from several planted stands on nearby (within 10 km) corporate lands. The trees from privately owned properties were selected for site conditions and landforms similar to those found on the CEF. In this portion of Ashley County, most upland soils are somewhat poorly drained silt loams (alfisols) with a natural-origin loblolly pine site index of 25 to 30 m (50-year base age) (Gill et al. 1979). The gently undulating terrain of the CEF varies between 35 and 50 m above sea level, with local elevation differences rarely exceeding 3 m.

We restricted our sampling to small diameter (0.5–15 cm dbh) loblolly pines because equipment limitations constrained our ability to measure and weigh entire trees (including the taproot). All trees were selected at random from stands chosen to fall into one of several management strategies (see the following paragraphs). Individuals that were forked or those with obvious aboveground physical damage (e.g., ice breakage), decay, or cankers were avoided. In those cases, the next nearest individual was selected. Naturally regenerated loblolly pines were harvested from a number of different management compartments on the CEF, using compartments that were well stocked and representative of natural-origin pine-dominated stands in the region. The younger age classes of these stands had not received any postestablishment competition control, as is typical for natural pine stands in this area. Pines selected from these natural stands were not aged before harvest. Because of the detailed records kept by the private landowner, we were able to select loblolly pine

plantations across a range of ages to help ensure a good sample of diameters (again, from 0.5 to 15 cm dbh). Planted loblolly pines ranged between 1 and 7 years of age, were of improved genetic stock, and had received initial competition control, but were not yet thinned (commercially or otherwise) or fertilized. Prescribed planting densities were 1,384 trees/ha. We randomly selected two pines from stands without mechanical site preparation before planting (“flat-planted”; 9 stands) and from stands that were bedded before planting (10 stands).

Smaller sample trees were collected using a tractor with a hydraulic boom extension lift to pull the entire tree (taproot included) from the ground once the soil was loosened with hand tools. Larger samples that could not be lifted from the ground were partially excavated with a backhoe and hand tools, and any uncollected fragments of the taproot were removed using hand tools. We chose to only extract the taproot to simplify root sampling (i.e., no lateral or fine roots were collected). Although loblolly pine root morphology can vary dramatically based on soil conditions, tree genetics, and a number of other factors (Harrington et al. 1989), we found that the pines we sampled (regardless of stand origin) had distinctive taproots. After collection, each tree was separated into three biomass components: stemwood, combined branch and foliage, and taproot. The taproot component included the 15.2-cm-tall stump and the entire taproot (the main unbranched portion of each root system to 0.5-cm root diameter). All biomass components were dried in a forced air oven at 90° C to a constant weight (oven-dry), and were weighed to the nearest 0.01 kg using a standard laboratory balance. Tree age was estimated by counting the number of rings on a disk removed from each tree near the root collar. Although this was only an approximation of actual tree age, the sampled pines had clear rings, with no sign of false or missing rings, so this age estimate should be accurate to ± 1 year. Planted tree ages were validated using company establishment records.

Data Analysis and Model Development

A statistical analysis package (Statistica; StatSoft, Inc., Tulsa, OK) was used to develop predictive equations for each biomass component. The following nonlinear allometric equation was used to fit data from each stand type:

$$Y = a + bD^c$$

where Y is the oven-dry biomass component in kg, D is dbh in cm, and a , b , and c are regression coefficients. Although there have been recent criticisms of using constant allometric equations (Picard et al. 2015, Temesgen et al. 2015), power functions tend to dominate the tree biomass literature (e.g., Zianis et al. 2005), and a simple power function with an intercept is more directly interpretable than more complicated designs (Sileshi 2014). The positive intercept ensured that even the smallest diameter pines (those approaching 0 dbh) had some biomass; the fitting process with weighted least-squares regression (using the inverse of squared dbh) addressed the increasing heteroscedasticity typically found in biomass data. Differences between allometric models (e.g., planted versus natural) were assessed using the sum of squares reduction test. Significance was assessed at $P \leq 0.05$.

We compared our new biomass equations with those of the NBE for their pine “pseudospecies,” which includes loblolly pine. The NBE equations were originally developed to provide large-scale woody biomass estimates for North America (Jenkins et al. 2003,

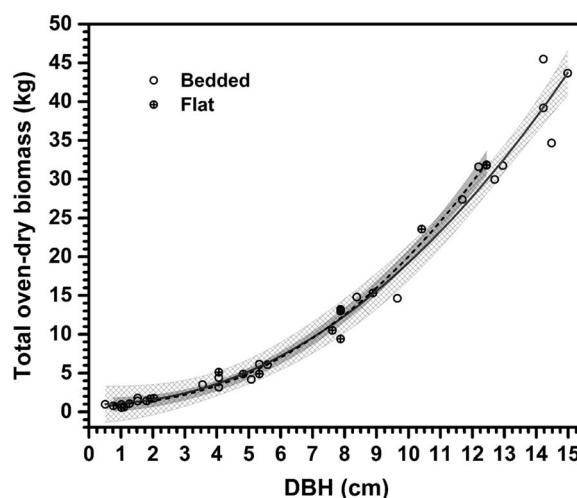


Figure 1. Overlay of bedded and flat-planted small diameter loblolly pines from young plantations in the proximity of the CEF in southern Arkansas. The shaded areas associated with the fitted curves represent 95% confidence intervals.

2004). Recent modifications to the NBE pine model have split this pseudospecies into two categories for low- and high-specific gravity (SG) pines (Chojnacky et al. 2014). All three pine NBE models (the original Jenkins et al. equations, as well as the low-SG [$SG < 0.45$] and high-SG [$SG \geq 0.45$] equations of Chjonakcy et al.) were used to evaluate the oven-dry biomass predictions of our equations. Furthermore, we then made stand-level comparisons of predicted total aboveground biomass (stemwood and branches + foliage) for both natural and planted stands using our natural and planted equations, as well as the NBE equation for high-SG pine. Stand biomass was estimated by multiplying aboveground biomass and a corresponding stand density estimate (assuming that all trees have the same diameter). Natural stand density estimates (between 1,853 and 4,695 stems/ha, depending on mean diameter) were adapted from values obtained in USDA Miscellaneous Publication 50 (USDA 1976). We assumed a planting density of 1,483 stems/ha. This planting density is comparable to that used by many landowners in the study region interested in generating high stand-level volume production while encouraging good individual tree diameter growth (e.g., Zhao et al. 2011).

Results

Pine Comparisons by Management Type

One of the initial questions was whether there were statistically significant differences in biomass accumulation between plantation establishment (bedded versus flat-planted) approaches. However, when we plotted the distribution of the 20 loblolly pines from bedded stands and the 18 loblolly pines from our flat-planted stands, it was apparent that there was virtually no difference in biomass as a function of dbh (Figure 1). This indicated that all planted loblolly pines from our sample could be aggregated into a single planted category to compare with natural-origin loblolly pine. Hereafter, all comparisons involve planted pines as one category, with natural-origin pines as the contrast.

Our sampling design ensured a relatively even distribution of natural and planted pines. Across the range of diameters sampled, there were significant differences in bole length (roughly analogous to tree height) as a function of stand origin (Figure 2A).

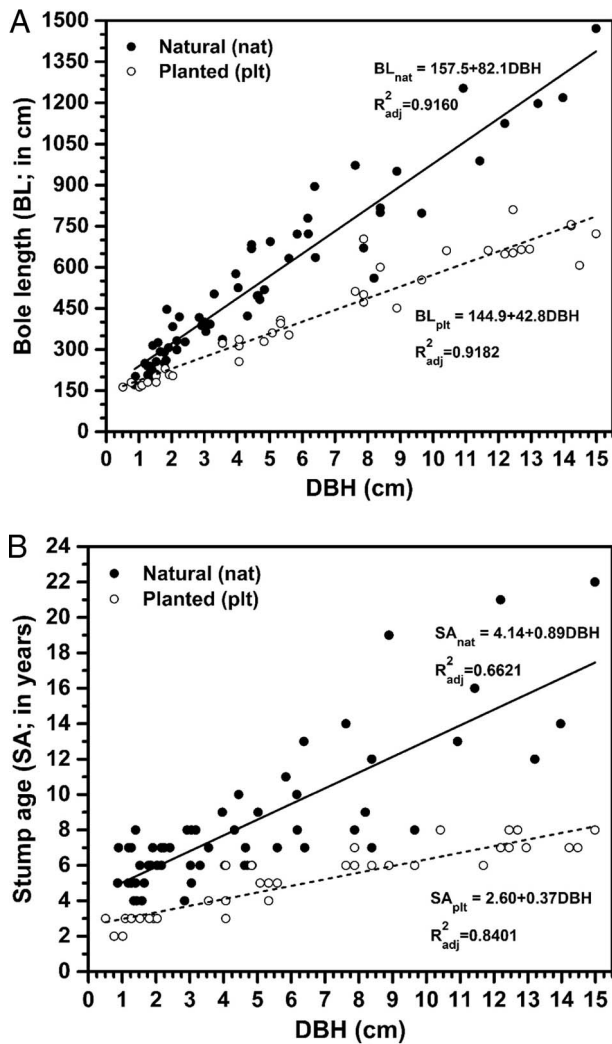


Figure 2. Bole length (A) and age (stump ring counts) (B) as a function of dbh from loblolly pines in natural or planted stands on or near the CEF. In each of the respective graphs, the linear ordinary least-square regressions were all significantly different (*F*-tests, $P < 0.05$) from each other.

Although there was virtually no difference in bole length between the naturally regenerated and planted loblolly pines at the smallest dbh, planted pines were consistently shorter and exhibited greater taper (not measured directly, but interpreted as shorter trees with the same diameter) as dbh increased. For example, 1-cm dbh pines from both stand types had bole lengths of approximately 2 m, whereas 15-cm dbh natural-origin pines had boles about 13.9 m long compared with approximately 7.9 m for the planted pines (Figure 2A).

For the stem sizes sampled, stump age varied from 4 to 22 years for natural pines and from 2 to 8 years for planted pines (Figure 2B). Natural-origin stems consistently showed greater variability, especially for larger diameter individuals. Similar-sized stems of planted pine were consistently much younger than their natural-origin counterparts, regardless of bole diameter. As an example, 1-cm dbh loblolly pines were between 2 and 3 years old in planted stands, compared with 4 to 8 years old in natural stands. This disparity increased with increasing dbh: 15-cm dbh pines were 6–8 years old in planted stands versus 14–22 years old in natural stands.

Regression Outcomes

Biomass model fit statistics were generally high (coefficients of determination of 0.88–0.99) for all biomass models (Table 1). The lowest nonlinear R^2 for the branch + foliage component of natural pines probably reflects the more inconsistent environment, including localized differences in tree stocking and competition and a greater chance of damage from outside factors (e.g., ice, wind, and animals) experienced by these older saplings. All other coefficients of determination exceeded 0.94, and most were greater than 0.97 (Table 1).

Although the models, as a whole, were statistically different, taproot biomasses were similar for stems ≤ 8 cm dbh (Figure 3). For larger diameter trees, however, natural-origin pine had greater biomass allocated to taproots. The overall allocation of taproot biomass as a percentage of total biomass was relatively consistent (Table 2), averaging about 16% regardless of origin. Branch and foliage biomass varied by pine origin (Figure 3). Planted pines had more branch and foliage biomass for a given dbh than natural pines. Apart from the smallest individuals, branch and foliage biomass contributed roughly 50 and 25% to the total biomass for planted and natural pines, respectively (Table 2). Stemwood biomass equations differed between natural and planted pines. Above 6 cm dbh, natural-origin pines accumulated more stem biomass than planted pines (Figure 3). In fact, stemwood biomass was consistently the largest contributor to total biomass of natural origin pines, contributing 55–65%. In contrast, the contribution of stemwood biomass to total biomass for planted pines increased with increasing dbh, with only the largest stems approaching an even split between bole biomass and the other biomass components (Table 2).

Total tree (taproot + branch and foliage + stemwood) oven-dry biomass for pines 0.5–15 cm dbh ranged between 0.3 and 71.9 kg for natural-origin and between 0.5 and 45.5 kg for planted loblolly pines, respectively (Figure 3). Biomass estimates are similar for stems less than 8 cm regardless of origin. For larger diameter stems, natural-origin pines had greater total biomass accumulation relative to that of the planted pines. Much of this difference in total biomass was due to greater accumulation of stemwood biomass on the larger natural stems (Figure 3; Table 2). Stemwood comprised roughly 64% of the total biomass for stems > 10 cm dbh, while accounting for only 43% for planted stems (Table 2). Aboveground biomass represents the harvestable portion of each stem between natural and planted stems (Table 2). Like the total biomass equations, the natural origin and planted pine aboveground biomass models showed significant departures as stem diameter increased. Both models were relatively consistent through 6 cm dbh. After that point, the natural origin pine model showed much greater biomass for a given dbh than planted pine (Figure 4). For example, 10- and 15-cm natural origin pine stems have 35 and 59% more biomass per stem than planted pines of the same dbh (Table 2).

When a series of tree component biomass equations is developed, it is desirable that the modeled estimates of the components sum to the predicted total tree estimate (Parresol 2001). The additivity of the individual biomass components (i.e., taproot + branch + foliage + stemwood) demonstrated excellent agreement with aboveground and total biomass models. With the use of 1-, 5-, 10-, and 15-cm stems for comparison, neither aboveground nor total biomass equations deviated more than 0.35% from the added predictions of each component (Table 2). Interestingly, the aboveground equations showed the smallest departures for the planted stems,

Table 1. Weighted least-squares regression parameter estimates for oven-dry biomass as a function of dbh by stand origin and tree components for loblolly pines sampled on or near the CEF.

Stand origin tree component (Y)	Y = a + bD ^c submodel	Parameter	Estimate	SE	95% confidence limits		R ^{2*}
					Lower	Upper	
Natural-origin pine stands							
Taproot	1	a	0.0495	0.0155	0.0184	0.0806	0.9786
		b	0.0139	0.0029	0.0081	0.0198	
		c	2.4574	0.0850	2.2872	2.6276	
Stemwood	2	a	0.1638	0.0521	0.0595	0.2681	0.9802
		b	0.0442	0.0084	0.0274	0.0610	
		c	2.5661	0.0766	2.4129	2.7194	
Branch + foliage	3	a	0.0825	0.0369	0.0086	0.1564	0.8803
		b	0.0276	0.0085	0.0106	0.0446	
		c	2.2935	0.1265	2.0403	2.5467	
Aboveground only†	4	a	0.2469	0.0618	0.1232	0.3707	0.9821
		b	0.0703	0.0110	0.0482	0.0924	
		c	2.4899	0.0635	2.3628	2.6169	
Total tree†	5	a	0.2965	0.0668	0.1628	0.4303	0.9868
		b	0.0842	0.0120	0.0601	0.1083	
		c	2.4848	0.0577	2.3692	2.6004	
Planted pine stands							
Taproot	6	a	0.0586	0.0188	0.0205	0.0967	0.9676
		b	0.0473	0.0108	0.0255	0.0692	
		c	1.8220	0.0917	1.6359	2.0081	
Stemwood	7	a	0.1375	0.0465	0.0432	0.2318	0.9429
		b	0.0616	0.0187	0.0236	0.0996	
		c	2.1247	0.1206	1.8798	2.3696	
Branch + foliage	8	a	0.6085	0.0629	0.4808	0.7361	0.9655
		b	0.0553	0.0267	0.0010	0.1096	
		c	2.1238	0.1918	1.7343	2.5132	
Aboveground only†	9	a	0.7460	0.0790	0.5856	0.9063	0.9761
		b	0.1169	0.0327	0.0506	0.1832	
		c	2.1243	0.1108	1.8993	2.3492	
Total tree†	10	a	0.8067	0.0830	0.6381	0.9753	0.9826
		b	0.1609	0.0367	0.0864	0.2354	
		c	2.0662	0.0908	1.8818	2.2506	

All parameters were significant (P value < 0.05).

* Nonlinear coefficient of determination.

† Aboveground only = stemwood + branch + foliage; total tree = taproot + stemwood + branch + foliage.

whereas total biomass equations were more closely aligned with the summed component equations for natural stems.

We also merged the natural and planted aboveground live biomass samples and fit a single regression line to explore what happened if a management system was not used to discriminate between the data. The net result was a model that does a reasonably good job of explaining the variation in this aggregated data set, with a coefficient of determination just over 0.92. However, examination of bias when actual measurements for either stand type were compared with the combined model presented a noticeably different picture (Figure 5). With the exception of a small zone of relative agreement (from about 4 to 6 cm dbh), the combined model yielded biased results for both natural and planted loblolly pines. For stems greater than 6 cm dbh, this combined model overpredicted planted pine biomass and underpredicted biomass for natural-origin pines (Figure 5). These bias trends were reversed for small diameter stems, with natural-origin pines experiencing dramatic (>70%) overestimation bias below 2 cm dbh (Figure 5). These results suggest that the merger of discrete (silviculturally defined) data sets may be less desirable than retaining separate stand origin-based regressions if highly precise and accurate estimates of individual stem biomass are required. Others have addressed similar issues in the design of allometric models using other statistically robust approaches such as mixed-effects models (e.g., Zhang and Borders 2004, Meng et al.

2007, Fu et al. 2014). Because our data were more limited in scope, there was no advantage to taking this more complicated analysis approach; however, a mixed-effects design may offer a better solution to regionalized biomass models if the management strategy can be reliably applied as a random effect.

Comparisons with the NBEs

The comparison of all three pine NBE models (original, low SG, and high SG) with our natural-origin, planted, and combined pine models produced interesting results (Figure 4). All but the planted and combined pine models yielded similar trajectories across the range of diameters compared. The planted pine and combined models (based on the field samples we collected) departed from these general trends at approximately 7 cm dbh and increasingly differed to 15 cm dbh (dashed line in Figure 4). Our natural pine model predicted that a 15-cm dbh loblolly pine would have an aboveground oven-dry biomass of 59.9 kg, our planted pine model forecasted the same-sized loblolly pine to be 37.6 kg, and the combined model predicted 45.8 kg, compared with the 57.6–61.3 kg estimated by the NBEs (Figure 4; Table 3). Note that the NBE models, regardless of the particular one used, were decidedly higher in their estimates of loblolly pine biomass for 15-cm dbh trees. This is important, because it suggests that the NBE models for small diameter

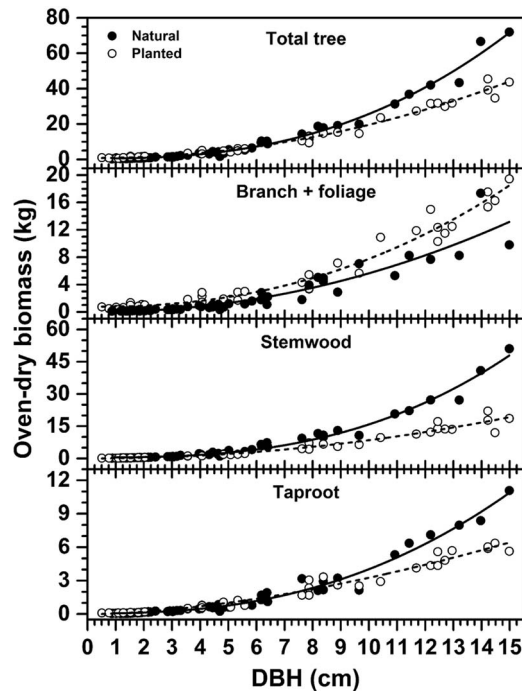


Figure 3. Comparison of oven-dry biomass by tree component between natural- and planted-origin loblolly pine, showing allometric equations fit to the data (model parameters and fit statistics are given in Table 1).

pine may fail to account for the differences in biomass as a function of stand origin.

Other potentially significant differences become apparent when the model outcomes are segregated into 5-cm dbh segments (Figures 6A–C). For the smallest dbh segment (Figure 6A), the NBE aboveground biomass models showed the smallest stems having zero biomass, our natural-origin pine model had close to zero biomass, and the planted stem model had 2–3 times the biomass of the natural

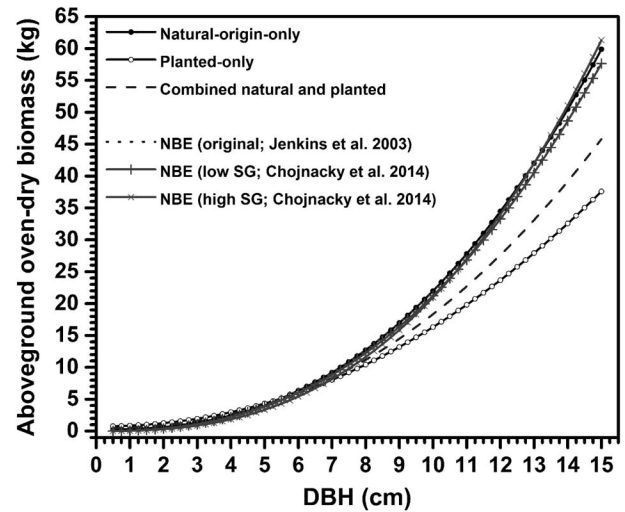


Figure 4. The lines fitted in this study (solid and short dashes) compared with the predictions of the original NBE of Jenkins et al. (2003) for their pine pseudospecies and the high- and low-SG pine pseudospecies of Chojnacky et al. (2014).

stems. Not surprisingly, as the pines increased in size, they were also more variable in their oven-dry biomass. So, as average stem size approached 5 cm dbh, all but the high-SG NBE model converged in their predictions of biomass. Even the high-SG NBE predictions fell only slightly below the 95% confidence intervals for either of our regression equations at 5 cm dbh (Figure 6A). Because of the model form and coefficients used, the high-SG NBE equation consistently predicted lower oven-dry biomass than the low-SG NBE equation between 0.5 and 10.5 cm dbh.

For the 5- to 10-cm dbh segment (Figure 6B), the aboveground biomass predictions for the natural-origin, original NBE, and low-SG NBE models remained similar, and the high-SG NBE model gradually began to conform to the 95% confidence interval for the natural-origin pine data. At approximately 7 cm dbh, the

Table 2. Estimated oven-dry biomass components for natural-origin and planted loblolly pines of 1, 5, 10, and 15 cm dbh on or near the CEF.

Stand origin tree component (submodel)	1 cm dbh (kg)	% of total	5 cm dbh (kg)	% of total	10 cm dbh (kg)	% of total	15 cm dbh (kg)	% of total
Natural origin pine stands								
Taproot (1)	0.06	15.8	0.78	15.9	4.04	15.6	10.85	15.3
Stemwood (2)	0.21	55.3	2.91	59.6	16.44	63.3	46.23	65.2
Branch + foliage (3)	0.11	28.9	1.19	24.3	5.50	21.2	13.82	19.5
Sum aboveground only (2 + 3)	0.32		4.10		21.94		60.05	
Sum total components (1 + 2+3)	0.38		4.88		25.98		70.91	
Aboveground model in kg (4)	0.32		4.11		21.97		59.87	
Percent difference*	0.24		-0.35		-0.14		0.30	
Total tree model in kg (5)	0.38		4.89		26.01		70.73	
Percent difference†	0.19		-0.29		-0.12		0.26	
Planted pine stands								
Taproot (6)	0.11	11.3	0.95	18.1	3.20	16.4	6.64	15.0
Stemwood (7)	0.20	20.6	2.02	38.4	8.35	42.8	19.56	44.2
Branch + foliage (8)	0.66	68.0	2.30	43.7	7.97	40.9	18.02	40.8
Sum aboveground only (7 + 8)	0.86		4.32		16.31		37.58	
Sum total components (6 + 7+8)	0.97		5.26		19.51		44.22	
Aboveground model in kg (9)	0.86		4.32		16.31		37.58	
Percent difference*	0.00		0.00		-0.01		-0.01	
Total tree model in kg (10)	0.97		5.28		19.54		44.11	
Percent difference†	0.13		-0.32		-0.16		0.24	

* Difference between the sum of the aboveground components as predicted by their individual component models compared with the aboveground-only model fit to all of the aboveground components (2 + 3 versus 4 and 7 + 8 versus 9).

† Difference between the sum of the total tree components as predicted by their individual component models compared with the total tree only model fit to all of the tree components (1 + 2+3 versus 5 and 6 + 7+8 versus 10).

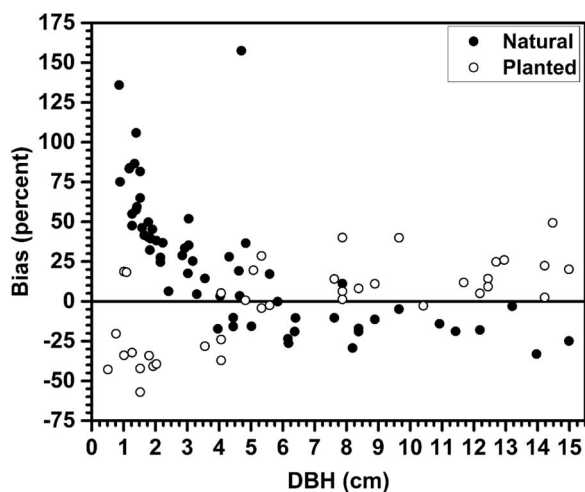


Figure 5. Bias (in terms of percentage) patterns resulting from a combined model developed by merging all field data and then individually comparing the actual natural and planted loblolly pine biomass values.

planted stems began a substantial departure from the natural-origin pine data, and by about 8 cm dbh there was virtually no overlap between their 95% confidence intervals (Figure 6B). At 10 cm dbh, the planted pine model estimate was about 30% lower than the other models. In other words, our data and planted pine equation showed a 10-cm dbh loblolly pine to have just over 16 kg in above-ground oven-dry live biomass compared with about 21 kg as predicted by the low-SG and high-SG NBE equations (Figure 6B; Table 3).

Once stem diameter exceeded 10 cm, the models continued to show only very modest differences between the three NBE and natural pine estimates to 15 cm dbh (Figure 6C). At about 11.5 cm dbh, the high-SG and low-SG NBE models finally diverged in an expected pattern, with the low-SG model predicting lower oven-dry aboveground biomass than the high-SG model. By 13 cm dbh, the low-SG NBE model fell below the 95% confidence interval of our natural pine model, although considerable variability in actual tree biomass probably implies that this slight departure is not particularly meaningful. For all models, aboveground biomass predictions were approximately 60% greater than the planted pine model estimate.

These model differences were even more apparent when extrapolated to stands. According to our assumed stand densities and using our natural-origin biomass equation, stand-level aboveground biomass estimates ranged from about 19 to 111 Mg ha⁻¹ for natural-

origin pine stands with average dbh of 5 to 15 cm (Table 3). With application of the high-SG NBE to these same, small diameter natural pine stands, stand-level biomass estimates were 3.6 Mg ha⁻¹ lower (for 5 cm dbh average), 3.3 Mg ha⁻¹ lower (for 10 cm dbh average), and 2.4 Mg ha⁻¹ higher (for 15 cm dbh average). Inappropriately applying our planted pine equation to these natural-origin stands produced departures of +1.0, -17.5, and -41.3 Mg ha⁻¹ for stands with average diameters of 5, 10, and 15 cm dbh, respectively. For planted loblolly pine stands averaging 5, 10, and 15 cm dbh, the NBE high-SG equation produced departures of -1.4, +6.8, and +35.0 Mg ha⁻¹, respectively. Misapplying our natural origin biomass equation to these planted stands yielded departures similar to those of the NBE equation (Table 3).

Discussion

Local Biomass Model Outcomes

The biomass models developed for flat-planted trees and trees planted on beds did not differ meaningfully (Figure 1). Whereas previous studies have shown that bedding treatments result in greater growth and survival (Rahman et al. 2006) in the Upper West Gulf Coastal Plain, the increased growth rate was probably due to more efficient carbon sequestration rather than to changes in biomass allocation patterns. Allometric relationships for loblolly pine have not shown changes in biomass allocation even when subjected to a wide range of site preparation intensities (Will et al. 2002), consistent with our results comparing flat-planted and bedded treatments. However, the distribution of biomass between planted and natural-origin stems as related to diameter was substantial, especially for stems greater than 6 cm diameter. Similar effects of stem origin on volume equations for pulpwood and small sawtimber-sized trees have been shown in the southeastern United States (Amateis and Burkhardt 1987).

The greater quantity of branch and foliage components in planted stands reflects the openness of plantations (Subedi et al. 2012) and has also been noted for open-grown trees in agricultural lands (Zhou et al. 2015). Although specific comparisons are lacking in the literature, crown-based ideotypes have become a point of emphasis in recent years (e.g., Martin et al. 2001, Villacorta et al. 2015) and might lead to structural departures that should be accounted for in equations designed to predict biomass accumulation for natural- and planted-origin loblolly pine stands. In addition to obvious localized stocking impacts on branchiness and foliage retention, the natural-origin pines were primarily in understory positions and had variable overstory cover (i.e., seed trees) that may have

Table 3. Estimated stand-level aboveground oven-dry biomass for well-stocked young loblolly pine stands in southern Arkansas with average stem diameters of 5, 10, and 15 cm using our models and the most recent version of the NBE.

c	Stem density (no./ha)*	Natural stand			Planted stand			
		Oven-dry biomass			Oven-dry biomass			
		NAT	PLNT	NBE	Stem density (no./ha)	NAT	PLNT	NBE
	(Mg/ha).....						
5 cm	4,695	19.3	20.3	15.7	1,483	6.1	6.4	5.0
10 cm	3,089	67.9	50.4	64.6	1,483	32.6	24.2	31.0
15 cm	1,853	110.9	69.6	113.3	1,483	88.8	55.7	90.7

Natural-origin biomass (NAT) and planted biomass (PLNT) models (submodels 4 and 9) from this article; NBE from Chojnacky et al. (2014) using the high-SG pine model coefficients.

* Data from USDA (1976).

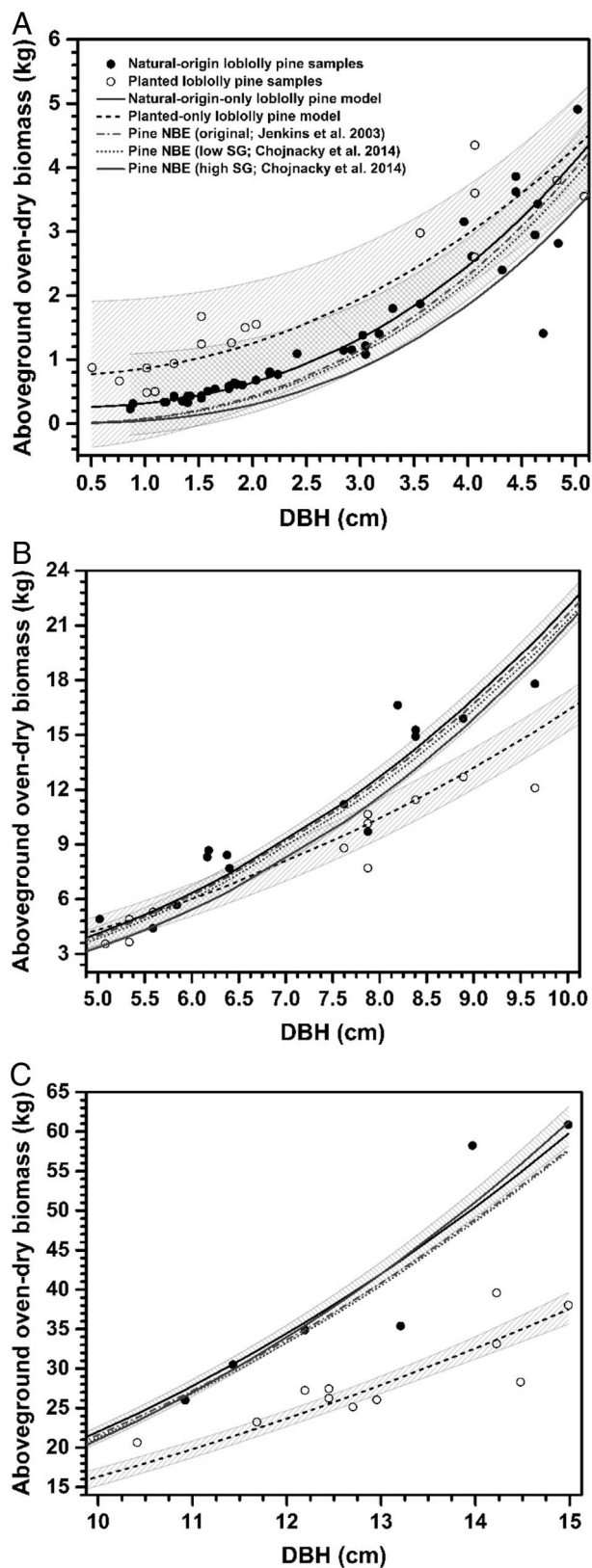


Figure 6. Decomposition of aboveground biomass models into three different 5-cm-wide segments (A–C) with the actual data points plotted with the fitted curves. The shaded areas associated with the fitted curves represent 95% confidence intervals.

influenced their ability to retain foliage and branches (Naidu et al. 1998). In addition, their greater ages made it more likely that they experienced crown damage from weather events (e.g., ice or wind storms) that periodically affect the study area, although saplings with obvious impacts were excluded from sampling.

Similar to other studies (e.g., Retzlaff et al. 2001), our data found loblolly pine taproots to contribute approximately 15% of the total biomass. The effects of stem origin on taproot biomass emerged for stems greater than 8 cm dbh (Figure 3). Although not specifically assessed in this study, others have noted morphological differences in root systems between planted and naturally seeded loblolly pine (Harrington et al. 1989). Most of the sampled loblolly pines in this study had dominant, unforked tap roots. The additional biomass in taproots of natural-origin stems may have implications for carbon storage. Taproots, which represent the largest root fraction (Retzlaff et al. 2001), are slow to decay (Van Lear and Kapeluck 1995, Ludovici et al. 2002). Increasing management of natural forests to decrease rotation lengths will increase carbon stocks sequestered in taproot biomass (Johnsen et al. 2001).

Likely Origins of Model Differences

The models presented in this study should not be construed to suggest that natural-origin loblolly pine trees are inherently more productive. Over the short term, stand-level biomass production is greater for plantations than for naturally regenerated stands (Stan-turf et al. 2003). The greater yield associated with natural stands highlighted in Table 3 resulted from greater stem densities over longer time frames. Whereas natural-origin pines of similar dbh had significantly greater individual stem biomass, they were also nearly twice as old, and this difference in biomass was largely attributable to greater bole lengths (Figure 3). Southern pine plantations may have lower standing carbon stocks than naturally regenerated hardwood and pine stands (e.g., Sohngen and Brown 2006) because of differences in wood density and stand stocking. In addition to greater taper, planted pines also had a substantially higher proportion of lower SG juvenile wood than older, slower grown, less-tapered natural-origin loblolly pines.

Because loblolly pine production and allocation are affected by factors such as stand age, soils, climate, genetics, and silvicultural treatments (Allen et al. 1990, Gower et al. 1994, Aspinwall et al. 2013), a number of equations have been developed for predicting pine biomass and volume across the various regions in the southern United States. Our data and models are most applicable to the Upper West Gulf Coastal Plain of southern Arkansas and northern Louisiana—a southward-sloping plain of gently rolling hills with ancient marine sediments sometimes capped by late Pleistocene loess. The aboveground oven-dry biomass models presented here predict less biomass for young (small diameter) planted loblolly pines than other published equations (Adegbidi et al. 2002, Chojnacky et al. 2014). Regionally, these differences can be attributed in part to factors such as site conditions (large-scale soil patterns), genetics, and regional differences in climate that influence allocation patterns and wood characteristics (Zobel and Talbert 1984, Albaugh et al. 1998, King et al. 1999, Jordan et al. 2008, Stovall et al. 2012). It is also likely that planting stock provenance may have influenced biomass accumulation in our stands through its impact on wood SG (e.g., Zobel and McElwee 1958, Mitchell and Wheeler 1959).

Although there are a number of factors that may contribute to the observed differences in plantation versus natural stand models,

stand densities may be an underlying driver for the observed relationships rather than stem origin. A number of planting density studies have shown differences in biomass allocation over time. Wide spacings in young planted stands result in increased foliage (Burkes et al. 2003) and branch and stem biomass per stem (Zhao et al. 2011). However, when allometric relationships are compared (i.e., as a function of dbh), these patterns may not be as pronounced or even exist.

Stand density can also contribute to differences in stem taper: the typically higher stocking of natural-origin stands generally reduces stem taper more than that associated with pine plantations (Van Lear et al. 1986) and wood formation. When controlled for age, the faster growing pines in lower stem density plantations tend to have a considerably higher proportion of juvenile wood, which has inherently lower SG than mature wood (e.g., Taylor and Burton 1982, Megraw 1985) relative to trees in natural-origin stands. Generally, the demarcation of juvenile and mature wood ranges from 10 to 13 years (Tasissa and Burkhart 1998, Jordan et al. 2008), although this can vary based on a number of factors (Megraw 1985, Zobel and van Buijtenen 1989); Jordan et al. (2008) and Clark et al. (2006) describe an extended juvenile-to-mature transitional period (from ages 4 to 13) in loblolly pine plantations. In our study, all of the trees sampled from plantations were less than 10 years old, suggesting that they had not yet begun generating much mature wood. Conversely, a large proportion of the loblolly pines we sampled from natural-origin stands (especially those over 6 cm dbh) were older than 10 years of age (Figure 2B), indicating that they probably had a greater fraction of mature wood. This 6-cm threshold also coincides with divergences in the stemwood and aboveground biomass model predictions (Figures 3 and 4). Planted pines, when density is regulated to ensure greater diameter growth, also tend to have a higher earlywood/latewood ratio, given the dramatically lower SG of earlywood (Megraw 1985), which translates to a lower wood density and thus lower oven-dry biomass.

Scaling Up: Implications of Simulations

There are two direct implications of this study: first, modeling the oven-dry biomass of young loblolly pines regardless of stand origin and silvicultural treatment can be problematic; second, the newer, more refined NBE equations may not be appropriate when applied to young southern pines such as loblolly pine, particularly if these equations do not account for ontogenetic variation in tree SG or bole form. As currently designed, the new NBE applies an SG cutoff of 0.45 (Chojnacky et al. 2014), which will often be interpreted at the species level (for mature trees) rather than at a weighted developmental condition level (i.e., by wood “juvility”). Recent reviews and modeling efforts integrating whole trees (e.g., Pilli et al. 2006, Jordan et al. 2008, Ducey 2012, Ver Planck and MacFarlane 2015) have recognized differences in wood density and, hence, oven-dry biomass estimates as a function of tree developmental stage (juvenile versus mature versus old), suggesting that the applications of biomass model systems need to be more flexible. This is especially important for young planted loblolly pines at current levels of genetic improvement, which tend to have a much lower SG. For example, one major loblolly pine seedling producer reported the wood SG of a number of their preferred varieties at 5 years of age as ranging from 0.393 to 0.430 (ArborGen n.d.).

Related to these specific, fine-scale outcomes, there are other potential implications of this work for broader resource issues. As Table 3 clearly shows, proper model selection is vital when stand-

regional-level biomass estimates are derived, as even subtle differences in predictions are magnified as the number of trees is scaled upwards. Other researchers have found similar disparities; for example, Zhou et al. (2015) reported significant underestimates of biomass when forest-derived equations are used for open-grown trees, largely due to the higher SG found in open-grown specimens. Hence, large-scale assessments and modeling exercises designed to consider the role of silvicultural practices on carbon sequestration over large (especially regional or national) spatial extents may be particularly sensitive to the issues raised by this research. For example, Sohngen and Brown (2006) considered how the conversion of natural-origin hardwood and pine forests to loblolly pine plantations may affect carbon sequestration and other ecosystem services over a three-state area. In their models, they assumed that natural and planted pines would have the same carbon density and that any differences in carbon storage would arise solely from differences in stocking and tree size. Our model results call that assumption into question, particularly for younger stands dominated by small diameter southern pines.

Given that 19% of the forestland in the southeastern United States is classified as pine plantation (Wear and Greis 2012), much of which is loblolly pine, improper upscaling of individual tree biomass equations may yield problematic regional biomass totals. Table 3 also demonstrates the consequences of inappropriately applied biomass models to conditions for which they were not derived. Although a universal equation applicable to most species in most locations has considerable appeal, under most circumstances such models rarely perform as well as ones fitted to actual local data. This is clearly the case in this project; equations fit to young loblolly pines (both of natural and planted origins) generally outperformed the broader NBE models.

Conclusions

Silvicultural decisions must be based on the best information available; this includes the applied statistical models derived from biomass research. Unfortunately, most tree species do not have locally based equations for biomass, necessitating the use of less desirable alternatives. Simple designs, especially those with more universal application (both in spatial scale as well as taxonomic coverage) have considerable appeal for their ease of implementation, but this may lead to additional challenges. The fact that diameter-only based biomass models developed for young loblolly pine stands of natural and planted origin in southern Arkansas departed substantially suggests that regional estimates should be reexamined in light of the considerable acreage converted to pine plantations in the southern United States. This study supports a growing body of evidence (e.g., Zhou et al. 2015) that universally applied biomass models are often unable to account for differences in allometric patterns, growing conditions, and/or genetics/site interactions and thus may not provide the most accurate accounting of biomass.

Such discrepancies have meaningful consequences across a range of scales, from potential underestimates when arranging biomass sales from a particular logging project to regional inaccuracies in determining carbon sequestration or release. Our simulations make it clear that at least for the circumstances we evaluated, inappropriately applying a universal equation (such as the NBE) or applying an inappropriate local equation (such as one developed from natural-origin trees) to young loblolly pine plantations can lead to significant overestimates of oven-dry biomass on a fine scale. Given that most regional carbon assessments simply scale-up stand-level biomass by multiplying biomass per

unit area by the total area in that forest category, fine-scale errors increase dramatically in their influence and be promulgated into less-than-ideal policy decisions, especially if one considers that planted pine forests are expected to account for 24–34% of the forestland by 2060 (Wear and Greis 2012). At this point, it is unclear if such fine-scale errors can or should be treated as offsetting or compensatory. Some of our simulations noted that both under- or overestimations were possible, depending on tree size; discrepancies between exact model forms do not present consistent biases that could be adjusted or factored out (sensu Zhou et al. 2015).

Literature Cited

- ADEGBIDI, H.G., E.J. JOKELA, N.B. COMERFORD, AND N.F. BARROS. 2002. Biomass development for intensively managed loblolly pine plantations growing on Spodosols in the southeastern USA. *For. Ecol. Manage.* 167(1–3):91–102. doi:10.1016/S0378-1127(01)00691-0.
- ALBAUGH, T.J., H.L. ALLEN, P.M. DOUGHERTY, L.W. KRESS, AND J.S. KING. 1998. Leaf area and above- and belowground growth responses of loblolly pine to nutrient and water additions. *For. Sci.* 44(2):317–328. <http://www.ingentaconnect.com/contentone/saf/fs/1998/00000044/00000002/art00016>.
- ALLEN, H.L., P.M. DOUGHERTY, AND R.G. CAMPBELL. 1990. Manipulation of water and nutrients—Practice and opportunity in southern U.S. pine forests. *For. Ecol. Manage.* 30(1–4):437–453. doi:10.1016/0378-1127(90)90153-3.
- AMATEIS, R.L., AND H.E. BURKHART. 1987. Tree volume and taper of loblolly pine varies by stand origin. *South. J. Appl. For.* 11(4):185–189. <http://www.ingentaconnect.com/contentone/saf/sjaf/1987/00000011/00000004/art00008>.
- ARBORGEN. 2014. *Brochures for varietal seedlings AGV105, AGV123, AGV124, AGV125, AGV127*. ArborGen, Inc., Ridgeville, SC.
- ASPINWALL, M.J., J.S. KING, AND S.E. MCKEAN. 2013. Productivity differences among loblolly pine genotypes are independent of individual-tree biomass partitioning and growth efficiency. *Trees* 27(3):533–545. doi:10.1007/s00468-012-0806-4.
- BALDWIN, V.C. 1987. Green and dry-weight equations for above-ground components of planted loblolly pine trees in the West Gulf Region. *South. J. Appl. For.* 11(4):212–218. <http://www.ingentaconnect.com/contentone/saf/sjaf/1987/00000011/00000004/art00014>.
- BALMER, W.E., K.A. UTZ, AND O.G. LANGDON. 1978. Financial returns from cultural work in natural loblolly pine stands. *South. J. Appl. For.* 2(4):111–117. <http://www.ingentaconnect.com/contentone/saf/sjaf/1978/00000002/00000004/art00005>.
- BORDERS, B.E., AND R.L. BAILEY. 2001. Loblolly pine—Pushing the limits of growth. *South. J. Appl. For.* 25(2):69–74. <http://www.ingentaconnect.com/contentone/saf/sjaf/2001/00000025/00000002/art00003>.
- BURKES, E.C., R.E. WILL, G.A. BARRON-GAFFORD, R.O. TESKEY, AND B. SHIVER. 2003. Biomass partitioning and growth efficiency of intensively managed *Pinus taeda* and *Pinus elliotii* stands of different planting densities. *For. Sci.* 49(2):224–234. <http://www.ingentaconnect.com/contentone/saf/fs/2003/00000049/00000002/art00006>.
- CAIN, M.D., AND M.G. SHELTON. 2001. Natural loblolly and shortleaf pine productivity through 53 years of management under four reproduction cutting methods. *South. J. Appl. For.* 25(1):7–16. <http://www.ingentaconnect.com/contentone/saf/sjaf/2001/00000025/00000001/art00001>.
- CARTER, M.C., R.C. KELLISON, AND R.S. WALLINGER. 2015. *Forestry in the US South: A history*. Louisiana State University Press, Baton Rouge, LA. 386 p.
- CHOJNACKY, D.C., L.S. HEATH, AND J.C. JENKINS. 2014. Updated generalized biomass equations for North American tree species. *Forestry* 87(1):129–151. doi:10.1093/forestry/cpt053.
- CLARK, A., III, R.F. DANIELS, AND L. JORDAN. 2006. Juvenile/mature wood transition in loblolly pine as defined by annual ring specific gravity, proportion of latewood, and microfibril angle. *Wood Fiber Sci.* 38(2):292–299. <https://wfs.swst.org/index.php/wfs/article/view/495>.
- CLARK, A., III, AND J.R. SAUCIER. 1990. *Tables for estimating total tree weights, stem weights, and volumes of planted and natural southern pines in the Southeast*. Georgia Forestry Res. Pap. 79. Georgia Forestry Commission, Research Division, Dry Branch, GA. 23 p.
- CUBBAGE, F., P. MACDONAGH, J. SAWINSKI, JR., R. RUBILAR, P. DONOSO, A. FERREIRA, V. HOEFLICH, ET AL. 2007. Timber investment returns for selected plantations and native forests in South America and the southern United States. *New For.* 33(3):237–255. doi:10.1007/s11056-006-9025-4.
- DORUSKA, P.F., AND D.W. PATTERSON. 2006. An individual-tree, merchantable stem, green weight equation for loblolly pine pulpwood in Arkansas, including seasonal effects. *South. J. Appl. For.* 30(2):61–65. <http://www.ingentaconnect.com/contentone/saf/sjaf/2006/00000030/00000002/art00001>.
- DUCEY, M.J. 2012. Evergreenness and wood density predict height-diameter scaling in trees of the northeastern United States. *For. Ecol. Manage.* 279:21–26. doi:10.1016/j.foreco.2012.04.034.
- FARRAR, R.M., T.J. STRAKA, AND C.E. BURKHARDT. 1989. *A quarter-century of selection management on the Mississippi State farm forestry forties*. Tech. Bull. 164, Mississippi Agricultural and Forestry Experiment Station, Mississippi State, MS. 24 p.
- FOX, T.R., E.J. JOKELA, AND H.L. ALLEN. 2007. The development of pine plantation silviculture in the southern United States. *J. For.* 105(7):337–347. <http://www.ingentaconnect.com/contentone/saf/jof/2007/00000105/00000007/art00005>.
- FOREST STEWARDSHIP COUNCIL. 2010. *FSC-US Forest Management Standard*, version 1.0. FSC-US, Minneapolis, MN. Available online at us.fsc.org/download-box.188.htm; last accessed July 11, 2016.
- FU, L., W. ZHANG, H. ZHANG, G. WANG, Y. LEI, AND S. TANG. 2014. Generic linear mixed-effects biomass models for *Pinus massoniana* in southern China. *South. For.* 76(1):47–56. doi:10.2989/20702620.2013.870389.
- GILL, H.V., D.C. AVERY, F.C. LARANCE, AND C.L. FULTZ. 1979. *Soil survey of Ashley County, Arkansas*. USDA Soil Conservation Service and USDA Forest Service, Washington, DC. 92 p.
- GONZALEZ-BENECKE, C.A., S.A. GEZAN, T.J. ALBAUGH, H.L. ALLEN, H.E. BURKHART, T.R. FOX, E.J. JOKELA, ET AL. 2014. Local and general above-stump biomass functions for loblolly and slash pine trees. *For. Ecol. Manage.* 334:254–276. doi:10.1016/j.foreco.2014.09.002.
- GOWER, S.T., H.L. GHOLZ, K. NAKANE, AND V.C. BALDWIN. 1994. Production and carbon allocation patterns of pine forests. *Ecol. Bull.* 43:115–135. <http://www.jstor.org/stable/20113136>.
- GULDIN, J.M., AND J.B. BAKER. 1988. Yield comparisons from even-aged and uneven-aged loblolly-shortleaf pine stands. *South. J. Appl. For.* 12(2):107–114. <http://www.ingentaconnect.com/contentone/saf/sjaf/1988/00000012/00000002/art00010>.
- HARRINGTON, C.A., J.C. BRISSETTE, AND W.C. CARLSON. 1989. Root system structure in planted and seeded loblolly and shortleaf pine. *For. Sci.* 35(2):469–480. <http://www.ingentaconnect.com/contentone/saf/fs/1989/00000035/00000002/art00016>.
- HARTSELL, A.J., AND R.C. CONNER. 2013. *Forest area and conditions: A 2010 update of Chapter 16 of the Southern Forest Resource Assessment*. USDA Forest Service, e-Gen. Tech. Rep. SRS-GTR-174, Southern Research Station, Asheville, NC. 32 p. <https://www.treesearch.fs.fed.us/pubs/43399>.
- JENKINS, J.C., D.C. CHOJNACKY, L.S. HEATH, AND R.A. BIRDSEY. 2003. National-scale biomass estimators for United States tree species. *For. Sci.* 49(1):12–35. <http://www.ingentaconnect.com/contentone/saf/fs/2003/00000049/00000001/art00002>.
- JENKINS, J.C., D.C. CHOJNACKY, L.S. HEATH, AND R.A. BIRDSEY. 2004.

- Comprehensive database of diameter-based biomass regressions for North American tree species*. USDA Forest Service, Gen. Tech. Rep. NE-319, Northeastern Research Station, Newtown Square, PA. 45 p. <https://www.treeseearch.fs.fed.us/pubs/7058>.
- JOHNSON, K.H., D. WEAR, R. OREN, R.O. TESKEY, F. SANCHEZ, R. WILL, J. BUTNOR, ET AL. 2001. Meeting global policy commitments: Carbon sequestration and southern pine forests. *J. For.* 99(4):14–21. <http://www.ingentaconnect.com/search/article?option1=tka&value1=Meeting+global+policy+commitments%3a+Carbon+sequestration+and+southern+pine+forests&pageSize=10&index=1>.
- JORDAN, L., A.C. CLARK III, L.R. SCHIMLECK, D.B. HALL, AND R.F. DANIELS. 2008. Regional variation in wood specific gravity of planted loblolly pine in the United States. *Can. J. For. Res.* 38(4):698–710. doi:10.1139/X07-158.
- KING, J.S., T.J. ALBAUGH, H.L. ALLEN, AND L.W. KRESS. 1999. Stand-level allometry in *Pinus taeda* as affected by irrigation and fertilization. *Tree Physiol.* 19(12):769–778. doi:10.1093/treephys/19.12.769.
- LUDOVICI, K.H., S.J. ZARNOCH, AND D.D. RICHTER. 2002. Modeling in-situ pine root decomposition using a 60-year chronosequence. *Can. J. For. Res.* 32(9):1675–1684. doi:10.1139/x02-073.
- MARTIN, T.A., K.H. JOHNSON, AND T.L. WHITE. 2001. Ideotype development in southern pines: Rational and strategies for overcoming scale-related obstacles. *For. Sci.* 47(1):21–28. <http://www.ingentaconnect.com/contentone/saf/fs/2001/00000047/00000001/art00003>.
- MEGRAW, R.A. 1985. *Wood quality factors in loblolly pine*. TAPPI Press, Atlanta, GA., 88 p.
- MENG, Q., C.J. CIESZEWSKI, M. MADDEN, AND B. BORDERS. 2007. A linear mixed-effects model of biomass and volume of trees using Landsat ETM+ images. *For. Ecol. Manage.* 244(1–3):93–101. doi:10.1016/j.foreco.2007.03.056.
- MITCHELL, H.L., AND P.R. WHEELER. 1959. Highlights of Mississippi survey: The search for wood quality. *For. Farmer* 18(4):4–6.
- NAIDU, S.L., E.H. DELUCIA, AND R.B. THOMAS. 1998. Contrasting patterns of biomass allocation in dominant and suppressed loblolly pine. *Can. J. For. Res.* 28(8):1116–1124. doi:10.1139/x98-083.
- NELSON, A.S., AND D.C. BRAGG. 2016. Multidecadal response of naturally regenerated southern pine to early competition control and commercial thinning. *For. Sci.* 62(1):115–124. doi:10.5849/forsci.15-056.
- PARRESOL, B.R. 2001. Additivity of nonlinear biomass equations. *Can. J. For. Res.* 31(5):865–878. doi:10.1139/x98-083.
- PICARD, N., E. RUTISHAUSER, P. PLOTON, A. NGOMANDA, AND M. HENRY. 2015. Should tree biomass allometry be restricted to power models? *For. Ecol. Manage.* 353:156–163. doi:10.1016/j.foreco.2015.05.035.
- PILLI, R., T. ANFODILLO, AND M. CARRER. 2006. Towards a functional and simplified allometry for estimating forest biomass. *For. Ecol. Manage.* 237(1–3):583–593. doi:10.1016/j.foreco.2006.10.004.
- POSEY, T. 2003. *Individual-tree green weight equations and tables for loblolly pine (Pinus taeda L.) sawtimber in the coastal plain of Arkansas*. MSc thesis, Univ. of Arkansas–Monticello, Monticello, AR. 89 p.
- RAHMAN, M.S., M.G. MESSINA, AND R.F. FISHER. 2006. Intensive forest management affects loblolly pine (*Pinus taeda* L.) growth and survival on poorly drained sites in southern Arkansas. *South. J. Appl. For.* 30(2):79–85. <http://www.ingentaconnect.com/contentone/saf/sjaf/2006/00000030/00000002/art00003>.
- RETZLAFF, W.A., J.A. HANDEST, D.M. O'MALLEY, S.E. MCKEAN, AND M.A. TOPA. 2001. Whole-tree biomass and carbon allocation of juvenile trees of loblolly pine (*Pinus taeda*): Influence of genetics and fertilization. *Can. J. For. Res.* 31(6):960–970. doi:10.1139/x01-017.
- SILESHI, G.W. 2014. A critical review of forest biomass estimation models, common mistakes and corrective measures. *For. Ecol. Manage.* 329: 237–254. doi:10.1016/j.foreco.2014.06.026.
- SUSTAINABLE FORESTRY INITIATIVE. 2015. *SFI 2015-2019 standards and rules*. Sustainable Forestry Initiative, Inc., Washington, DC. Available online at www.sfiprogram.org/sfi-standard/guide-to-2015-2019-standards/; last accessed July 11, 2016.
- SMITH, J.E., L.S. HEATH, AND C.M. HOOVER. 2013. Carbon factors and models for forest carbon estimates for the 2005–2011 National Greenhouse Gas Inventories of the United States. *For. Ecol. Manage.* 307:7–19. doi:10.1016/j.foreco.2013.06.061.
- SOHNGEN, B., AND S. BROWN. 2006. The influence of conversion of forest types on carbon sequestration and other ecosystem services in the South Central United States. *Ecol. Econ.* 57(4):698–708. doi:10.1016/j.ecolecon.2005.06.001.
- SOUTH, D.B., AND R.A. HARPER. 2016. A decline in timberland continues for several southern yellow pines. *J. For.* 114(2):116–124. doi:10.5849/jof.15-006.
- STANTURF, J.A., R.C. KELLISON, F.S. BROERMAN, AND S.B. JONES. 2003. Productivity of southern pine plantations: Where are we and how did we get here? *J. For.* 101(3):26–31. <http://www.ingentaconnect.com/contentone/saf/jof/2003/00000101/00000003/art00008>.
- STOVALL, J.P., T.R. FOX, AND J.R. SEILER. 2012. Short-term changes in biomass partitioning of two full-sib clones of *Pinus taeda* L. under differing fertilizer regimes over 4 months. *Trees* 26(3):951–961. doi:10.1007/s00468-011-0673-4.
- SUBEDI, S., M. KANE, D. ZHAO, B. BORDERS, AND D. GREENE. 2012. Cultural intensity and planting density effects on aboveground biomass of 12-year-old loblolly pine trees in the Upper Coastal Plain and Piedmont of the southeastern United States. *For. Ecol. Manage.* 267: 157–162. doi:10.1016/j.foreco.2011.12.008.
- TASSISSA, G., AND H.E. BURKHART. 1998. Juvenile-mature wood demarcation in loblolly pine trees. *Wood Fiber Sci.* 30(2):119–127. <https://wfs.swst.org/index.php/wfs/article/view/64>.
- TAYLOR, F.W., AND J.D. BURTON. 1982. Growth ring characteristics, specific gravity, and fiber length of rapidly grown loblolly pine. *Wood Fiber Sci.* 14(3):204–210. <https://wfs.swst.org/index.php/wfs/article/view/123>.
- TEMESGEN, H., D. AFFLECK, K. POUDEL, A. GRAY, AND J. SESSIONS. 2015. A review of the challenges and opportunities in estimating above ground forest biomass using tree-level models. *Scand. J. For. Res.* 30(4): 326–335. doi:10.1080/02827581.2015.1012114.
- US DEPARTMENT OF AGRICULTURE. 1976. *Volume, yield, and stand tables for second-growth southern pines*. Misc. Publ. No. 50, Washington, DC. 202 p.
- VAN LEAR, D.H., M.A. TARAS, J.B. WAIDE, AND M.K. AUGSPURGER. 1986. Comparison of biomass equations for planted vs. natural loblolly pine stands of sawtimber size. *For. Ecol. Manage.* 14(3):205–210. doi:10.1016/0378-1127(86)90118-0.
- VAN LEAR, D.H., AND P.R. KAPELUCK. 1995. Above- and below-stump biomass and nutrient content of a mature loblolly pine plantation. *Can. J. For. Res.* 25(2):361–367. doi:10.1139/x95-040.
- VER PLANCK, N.R., AND D.W. MACFARLANE. 2015. A vertically integrated whole-tree biomass model. *Trees* 29(2):449–460. doi:10.1007/s00468-014-1123-x.
- VILLACORTA, A.M.G., T.A. MARTIN, E.J. JOKELA, W.P. CROPPER, JR., AND S.A. GEZAN. 2015. Variation in biomass distribution and nutrient content in loblolly pine (*Pinus taeda* L.) clones having contrasting crown architecture and growth efficiency. *For. Ecol. Manage.* 342:84–92. doi:10.1016/j.foreco.2015.01.012.
- WEAR, D.N., AND J.G. GREIS. 2002. Southern forest resource assessment: Summary of findings. *J. For.* 100(7):6–14. <http://www.ingentaconnect.com/contentone/saf/jof/2002/00000100/00000007/art00004>.
- WEAR, D.N., AND J.G. GREIS (EDS.). 2012. *The southern forest futures project: Summary report*. USDA Forest Service, Gen. Tech. Rep. SRS-168, Southern Research Station, Asheville, NC. 54 p. <https://www.treeseearch.fs.fed.us/pubs/42526>.
- WEISKITTEL, A.R., D.W. MACFARLANE, P.J. RADTKE, D.L.R. AFFLECK, H. TEMESGEN, C.W. WOODALL, J.A. WESTFALL, AND J.W. COULSTON.

2015. A call to improve methods for estimating tree biomass for regional and national assessments. *J. For.* 113(4):414–424. doi:10.5849/jof.14-091.
- WILL, R.E., M.J. WHEELER, D. MARKEWITZ, M.A. JACOBSON, AND A.M. SHIRLEY. 2002. II. Early loblolly pine stand response to tillage on the Piedmont and Upper Coastal Plain of Georgia: Tree allometry, foliar nitrogen concentration, soil bulk density, soil moisture, and soil nitrogen status. *South. J. Appl. For.* 26(4):190–196. <http://www.ingentaconnect.com/contentone/saf/sjaf/2002/00000026/00000004/art00003>.
- YIN, R., AND R.A. SEDJO. 2001. Is this the age of intensive management? A study of loblolly pine on Georgia's Piedmont. *J. For.* 99(12):10–17. www.ingentaconnect.com/contentone/saf/jof/2001/00000099/00000012/art00005.
- ZHANG, Y., AND B.E. BORDERS. 2004. Using a system mixed-effects modeling method to estimate tree compartment biomass for intensively managed loblolly pines—An allometric approach. *For. Ecol. Manage.* 194(1–3):145–157. doi:10.1016/j.foreco.2004.02.012.
- ZHAO, D., M. KANE, AND B.E. BORDERS. 2011. Growth responses to planting density and management intensity in loblolly pine plantations in the southeastern USA Lower Coastal Plain. *Ann. For. Sci.* 68(3):625–635. doi:10.1007/s13595-011-0045-7.
- ZHOU, X., M.M. SCHOENENBERGER, J.R. BRANDLE, T.N. AWADA, J. CHU, D.L. MARTIN, J. LI, Y. LI, AND C.W. MIZE. 2015. Analyzing the uncertainties in use of forest-derived biomass equations for open-grown trees in agricultural land. *For. Sci.* 61(1):144–161. doi:10.5849/forsci.13-071.
- ZIANIS, D., P. MUUKKONEN, R. MÄKIPÄÄ, AND M. MENCUCINI. 2005. *Biomass and stem volume equations for tree species in Europe*. Silva Fenn. Monogr. 4. 63 p. Available online at <http://www.silvafennica.fi/pdf/smf004.pdf>.
- ZOBEL, B.J., AND R.L. MCELWEE. 1958. Natural variation in wood specific gravity of loblolly pine, and an analysis of contributing factors. *TAPPI* 41(4):158–161.
- ZOBEL, B., AND J. TALBERT. 1984. *Applied forest tree improvement*. John Wiley & Sons, New York. 505 p.
- ZOBEL, B., AND J.P. VAN BUIJTENEN. 1989. *Wood variation: Its causes and control*. Springer-Verlag, Berlin. 363 p.