

## ***A Call to Improve Methods for Estimating Tree Biomass for Regional and National Assessments***

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biomass, carbon & bioenergy

# A Call to Improve Methods for Estimating Tree Biomass for Regional and National Assessments

Aaron R. Weiskittel, David W. MacFarlane, Philip J. Radtke, David L.R. Affleck, Hailemariam Temesgen, Christopher W. Woodall, James A. Westfall, and John W. Coulston

Tree biomass is typically estimated using statistical models. This review highlights five limitations of most tree biomass models, which include the following: (1) biomass data are costly to collect and alternative sampling methods are used; (2) belowground data and models are generally lacking; (3) models are often developed from small and geographically limited data sets; (4) simplistic model forms and predictor variables are used; and (5) variation is commonly averaged or grouped rather than accounted for. The consequences of these limitations are highlighted and discussed. Several recommendations for future efforts are presented including the following: (1) collection of field measurements of tree biomass using consistent protocols; (2) compilation of existing data; (3) continued evaluation and improvement of existing models; (4) exploration of new models; and (5) adoption of state-of-the-art analytical and statistical techniques. Given the increasing importance of accurately estimating forest biomass, there is a critical need to understand, evaluate, and improve current tree biomass prediction methods.

**Keywords:** forest biomass, statistical equations, tree measurements

Measuring the status of and change in forest biomass (total dry organic matter) is critical to the establishment of sound national policies regarding the management and care of forest resources across large spatial scales (McKinley et al. 2011). The status of and change in forest resources are affected by a suite of human activities and ecological conditions. Forest growth, natural disturbances, and management actions are

among the factors that influence the amounts of forest biomass and carbon on landscapes and their changes over time (Powell et al. 2014). Relevant human activities include land-use conversion, greenhouse-gas-related climate change, and the introduction of non-native and invasive species (Thompson et al. 2009). Key natural disturbance agents include fire, insects, pathogens, and wind (Environmental Protection Agency 2013).

Over time, the effects of both human activities and natural agents may change. For example, Dale et al. (2001) suggested that the intensity, timing, and duration of forest disturbances are being affected by a changing climate. In addition, recent policy and market shifts have influenced the amount and type of forest material harvested as well as how that material is used (Guo et al. 2011, Sikkema et al. 2011). Consequently, accurate monitoring of forest biomass is an important part of programs tasked with ensuring long-term viability and sustainability of forest resources on regional to national and international scales, particularly when it comes to carbon and greenhouse gas accounting (Miner et al. 2014). Monitoring can also aid in understanding the implications of policy actions, changes in demands on raw materials, and how climate change may affect sustainability (Birdsey et al. 2006). For example, recent conflicting reports on forests as significant carbon sources versus sinks (McKinley et al. 2011) are probably influenced by the qual-

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ity, scale, and scope of the data used (e.g., Hayes et al. 2012). Similarly, recent findings about the rate of carbon accumulation in large trees were based almost entirely on predictions from biomass models developed with data from comparatively small trees (Stephenson et al. 2014).

Lu (2006) identified three inventory data types for forest biomass estimation: ground-based inventory (e.g., Pan et al. 2011); inventory via remote sensing (e.g., Tollefson 2009); or a combination of both methods (e.g., Ducey et al. 2009). Traditional field-based measurement methods, i.e., forest inventories, are considered to be more accurate than remote-sensing based estimates, as long as sample sizes are sufficiently large. Remote sensing can be more cost-effective, especially over large areas including rugged or inaccessible terrain. Regardless of the data collection method, accurate tree- or stand-level models are necessary to translate field measurements or remotely sensed data into estimates of forest biomass. The most commonly used models rely on traditional forest inventory measurements, such as tree dbh and total height, as predictors in equations that estimate tree biomass. Tree-based estimates are then summed on inventory plots and applied to larger land areas using probability and area-based expansion factors. Tree carbon is commonly assumed to equal one-half of tree dry mass (Lamtom and Savidge 2003). This simple assumption can result in systematic biases of approximately 1.6–5.8% with variation attributable to a range of sources (Thomas and Martin 2012).

Ver Planck and MacFarlane (2014) define three major methods for estimating tree biomass: direct estimation of tree biomass from predictor variables; estimation of biomass from tree volume; or simultaneous estimation of both biomass and volume. Direct prediction of biomass is probably the most accurate, but involves the costly process of felling and weighing of trees of different sizes and species to generate the data. Further, as in any model-based estimation scheme, it assumes the relevant properties (size, density, and form) of the trees selected in developing prediction equations are representative of the larger populations for which predictions will be made. Translating stem volume inventory data to biomass is accomplished through some form of biomass expansion factor, assuming a constant or variable density within trees and between species (Domke et al. 2012). The latter

method is cost-efficient but may be subject to errors if the density conversion factors are inaccurate. The simultaneous method seeks to avoid such errors by accounting for the variation in both volume and wood density in tree models (Ver Planck and MacFarlane 2014). Regardless of the method, empirical data are needed to calibrate and test models.

Because tree biomass models are applied at different spatial scales including local (e.g., Nelson et al. 2014), regional (e.g., Jenkins et al. 2004), national (e.g., Jenkins et al. 2003), and international (e.g., Pilli et al. 2006) scales, application of these models to populations other than the ones for which they were developed can result in significant errors, some reportedly as high as 240% (Wang et al. 2002, Nelson et al. 2014). Such errors are further compounded when combined with the measurement and sampling errors inherent in any field-based or remote sensing-derived inventory data. In some cases, sampling and measurement errors may even exceed the size of errors caused by extrapolation (e.g., Ståhl et al. 2014).

This article reviews important limitations for accurately estimating tree biomass from forest inventory data and proposes strategies for improving methodologies. We hope to communicate the importance and relevance of these estimates to a broad audience ranging from forest managers to policymakers, planners, and investors, along with various other stakeholders, across both private and public sectors. Recently, the Forest Inventory and Analysis (FIA) program of the US Department of Agriculture (USDA) Forest Service, which is responsible for esti-

imating the amount of carbon stored in US forests, changed the methodology used to estimate forest biomass. This change considerably reduced the national estimate of forest carbon stocks (Domke et al. 2012), which has significant financial implications (Box 1). Large changes in estimates resulting from changes in methodology are not uncommon and should not be surprising because the various sources of uncertainty associated with estimating tree- and forest-level biomass and carbon are rarely fully accounted for.

In particular, this article is focused on the application of tree-level biomass equations to large, national-scale inventories like the FIA in the United States. National-scale estimates of forest biomass require accuracy in two key components. One is the extensive network of field-based inventory plots linked with remote sensing data for scaling to landscape levels. The other is the method for translating inventory measurements into estimates of tree volume, biomass, and carbon contents. Considerable attention has been given to inventory design, for example, the US FIA program characterized tolerances and allowable errors in measurements and inventory estimates in great detail (Gillespie 1999, McRoberts 2005, Pollard et al. 2006). However, much less attention has been given to reviewing the characteristics of data and models that transform inventory data into quality estimates of forest biomass (Sileshi 2014) and carbon (Thomas and Martin 2012). Although quantifying the carbon contents of standing trees is important and deserving of attention, this review focuses primarily on biomass estimation be-

## Management and Policy Implications

Forest biomass and carbon are becoming central themes for both management and policy decisions, given the increasing interest in biofuels, greenhouse gas neutrality, and carbon sequestration. For example in the United States, the Environmental Protection Agency is mandated to report an annual national greenhouse gas inventory to the United Nations, which includes estimates of forest carbon stock changes over time, both for those that release CO<sub>2</sub> and for those that sequester it. Biomass inventories are also used by industrial manufacturers of forest products and bioenergy for assessments of resource availability and location of production facilities. Typically these estimates are generated by using models to convert forest inventory data into tree biomass and carbon, but the limitations of these models are rarely acknowledged or fully understood. This review highlights some of the key limitations of the estimation process and provides suggestions for future efforts concentrated on improving estimation of tree biomass. In general, better quantifying tree biomass will help improve forest management and policy decisions. Providing better information and educating model users should prevent some incorrect applications in scenarios where they may not be well suited. Better information should lead to more credible applications of tree biomass models to real-world problems.

cause of its essential role in carbon assessments and because reviews of carbon content in wood and other tree tissues have been presented elsewhere (e.g., Lamtom and Savidge 2003, Thomas and Martin 2012). Temesgen et al. (2015) present a detailed review and assessment of tree-level biomass models.

### Major Limitations

Notable limitations in common estimation techniques for tree biomass can be expressed in terms of four tree mass derivatives: (1) volume, (2) density, (3) biomass, and (4) carbon (Table 1). For discussion, these limitations can be generally categorized as the following: (1) tree biomass data are costly to collect and employ a variety of sampling methods for estimating total biomass and its components, which may not be compatible; (2) belowground data and models are generally lacking, and certain relationships must be assumed; (3) models are developed from small and geographically limited data sets; (4) simplistic model forms and predictor variables are used; and (5) variation across forest subpopulations is averaged or grouped rather than explicitly accounted for. These limitations are discussed below and have important implications for estimating forest biomass and carbon.

### Data Limitations

Collection of tree biomass data is difficult, expensive, and time-consuming, because it requires the felling of trees for detailed measurement (Figure 1). Sample trees

### Box 1. Economic Significance of Accurate Forest Carbon Stock Estimation.

In 2012, forested lands in the United States sequestered 866.5 Tg of CO<sub>2</sub>e (Environmental Protection Agency 2014). Given an average value of \$7.8 per ton of CO<sub>2</sub>e for forest carbon offsets in 2012 (Peters-Stanley et al. 2013), this has an approximate financial value of \$6.7 trillion. In this context, an apparent 16% decrease in US forest carbon stocks, associated with moving from one estimation method to another (as observed by Domke et al. 2012), might represent a \$1 trillion change in value. In contrast, the total annual budget for the USDA Forest Service FIA program charged with reporting this carbon pool in 2012 was about \$69.1 million, with only a small fraction devoted to the national greenhouse gas inventory (USDA Forest Service 2013). It is important to note that the magnitude of this disparity depends on the value of carbon, and the assumed \$7.8 per ton of CO<sub>2</sub>e is likely on the low end. For example, a mean price of \$13.55 per ton of CO<sub>2</sub>e with a range between \$11.34 and \$50.00 per ton of CO<sub>2</sub>e was recently observed at a California Air Resources Board quarterly auction in May 2014<sup>1</sup> and future projections show additional increases in value. In contrast, the USDA Forest Service FIA budget in 2013 actually decreased by 5% from the previous year with a concomitant limitation on staffing for improving estimation of forest carbon and greenhouse gases.

must be sectioned into their components including foliage, branches, wood, bark, and belowground tissues. Finally, sample tissues must be collected, weighed, and analyzed to determine properties such as moisture content and density that are needed to quantify the total biomass contents. As a result of the effort required to collect sample data, along with structural differences in different types of trees, felled-tree studies often vary in how they actually sample for biomass. Even in felled-tree studies, data collection schemes often differ in terms of the measurements made, types and amounts of tissues collected, and analyses used. These differences lead to contrasting levels of accuracy in the biomass data collected (e.g., Schlecht and Affleck 2014), particularly for foliage (Te-

mesgen et al. 2011) and belowground tissues, which can both be prohibitively expensive to collect and analyze. Because of the varying moisture content in different tissue types (Shottafer and Brackley 1982) and the dynamic nature of moisture content over time, tree weights are commonly recorded in terms of dry biomass rather than green weight, with the former sometimes referred to as “oven-dry” or “bone-dry” weight and the latter sometimes called “fresh” weight. To obtain both green and dry weights along with the often-needed conversion factors between the two, sample specimens must be weighed immediately after felling and again after oven-drying.

For some tree components, especially bolewood, standardized methods exist for

**Table 1. Summary of key limitations associated with tree biomass and carbon modeling in comparison to bole volume and wood density modeling efforts.**

Limitation	Tree biomass	Tree carbon	Tree bole volume	Wood density
Sampling methods	Highly varied and not all components are consistently measured	Infrequent and only select components are measured (e.g., foliage)	Standardized methods with volume generally derived from multiple stem diameter and height measurements	Standardized methods that differ in resolution (whole-tree versus disc versus ring) and basis (green or dry)
Data scope	Generally small and geographically limited data sets	Very limited	Generally large and geographically extensive data sets available, with limitations in some regions	Smaller than tree volume, but more extensive than tree biomass and carbon
Belowground	Rarely available; multiplier approach (belowground weight = 0.3 × aboveground weight)	Rarely included in measurements	Stump weight information seldom collected	Rarely considered
Modeling considerations	Relatively simple model forms that are primarily a function of tree dbh and height	Conversion factor approach (carbon weight = 0.5 × dry weight)	Varied, sometimes complex equations that use both dbh and height along with some other variables (e.g., form factor)	Average values by species with detailed equations relatively rare
Grouping variation	Common groupings include multiple sites or species to increase sample size and simplify application	Routinely assume fixed value (0.5) for all species and components	Often species- and region-specific; some grouping of species to simplify application	Species specific with some geographic differentiation





**Figure 1.** USDA Forest Service measurement specialists weighing stem sections at a Check-Cruiser workshop on the Tahoe National Forest in California, October 2014. Photo by Ruth Rieper.

collecting volume, weight, and density data (Table 1), making reliable determination of inside-bark green weight, biomass, density, and moisture content relatively straightforward. Although there are multiple ways to determine the density of wood specimens, they are not all equal in terms of their accuracy or even the basis for how “density” is defined (Williamson and Wiemann 2010). A commonly used alternative is to adopt published values of wood and bark densities and other wood properties from standard reference materials (Miles and Smith 2009, Forest Products Laboratory 2010) to obtain biomass information from volumetric mea-

surements. This can result in significant biases (e.g., Mavouroulou et al. 2014) because wood properties can vary widely both within and among trees of the same species (e.g., Jordan et al. 2008), in some cases related to site, genetic, or silvicultural effects (e.g., Tassisa and Burkhart 1998). Systematic variation in wood properties has also been noted across geographic gradients in some species (Chave et al. 2009).

Volumes for components such as branches can be particularly difficult to estimate and can have densities that are distinctly different from that of the stem (Swenson and Enquist 2008). A similar statement can also be

made for roots (see below). In summary, sampling for tree biomass is an expensive, difficult, and tedious process with a variety of approaches used. This introduces unknown uncertainty into estimates of tree biomass and effectively limits sample sizes.

### Lack of Belowground Measurements and Models

Prediction of belowground biomass still remains problematic and difficult. Only 8% of the 607 models reviewed in Zianis et al. (2005) provided predictions of total root biomass. Given the expense and level of error in collecting this information, the relative lack of models for the majority of species, and the overall importance of this biomass pool, an alternative approach is often needed. For example, a linear relationship between stand total aboveground and belowground biomass (e.g., Ranger and Gelhaye 2001) or aboveground net primary productivity and total belowground carbon flux (e.g., Litton et al. 2007) has generally been found useful. Similar linear and positive relationships for fine root and foliage biomass may also exist (e.g., Vanninen and Mäkelä 1999). These relationships would probably hold at the tree level and could be constrained to ensure compatibility (e.g., Chojnacky et al. 2013). At the tree level, Enquist and Niklas (2002) indicated that the relationship between aboveground and belowground biomass scale universally irrespective of species, ecological factors, and plant height. However, these relationships need to be further evaluated, which will be rather difficult and costly to accomplish.

Beyond the difficulty of sampling belowground biomass, its relationship to aboveground biomass may be governed by factors that are not commonly included in the estimation process. For example, Russell et al. (2015) recently found a systematic bias in estimating belowground biomass using a static equation and suggested that climatic information be used to adjust estimates. This type of approach will probably become more important as climate change has the potential to alter assumed tree form relationships (Box 2). Consequently, estimates of belowground biomass will continue to be an important source of uncertainty in forest-level estimates of total biomass or carbon.

### Limitations in Data Scope

The significant cost and effort required to obtain field measurements of

## Box 2. Tree Volume Estimation in the Context of Contemporary and Projected Future Climates.

Given that climate is one factor that affects tree form and function, changes in climate could broadly influence tree form and, hence, tree biomass and carbon. Currently, each individual tree sampled by the FIA program is assigned to a volume model based on its region (Woodall et al. 2011), which is then translated into total tree biomass and carbon. At present, there are more than 20 unique volume modeling regions in the United States that generally follow political (e.g., southern states) and geophysical (e.g., eastern versus western Cascades) boundaries, with regions spanning 1–10 Köppen climatic zones (Rubel and Korteck 2010) (Figure B1). Projecting Köppen climatic zones in the years 2076–2100 (A1F1 climatic scenario) (Intergovernmental Panel on Climate Change 2013) suggests that a majority of volume modeling regions will contain novel climates (Figure B1). Volume modeling regions across the Rocky Mountains may have up to four novel climates within their boundaries, whereas the eastern Cascades and central/northeastern states are projected to have no novel climates. Changes in the frequency and types of tree injury (e.g., top damage, breakage) as well as shifts in tree allometry can be anticipated in response to these and other projected climate changes across the United States (Melillo et al. 2014). As such, tree height, vigor, and form should be measured to reduce the uncertainty associated with tree volume, biomass, and carbon in a changing climate.

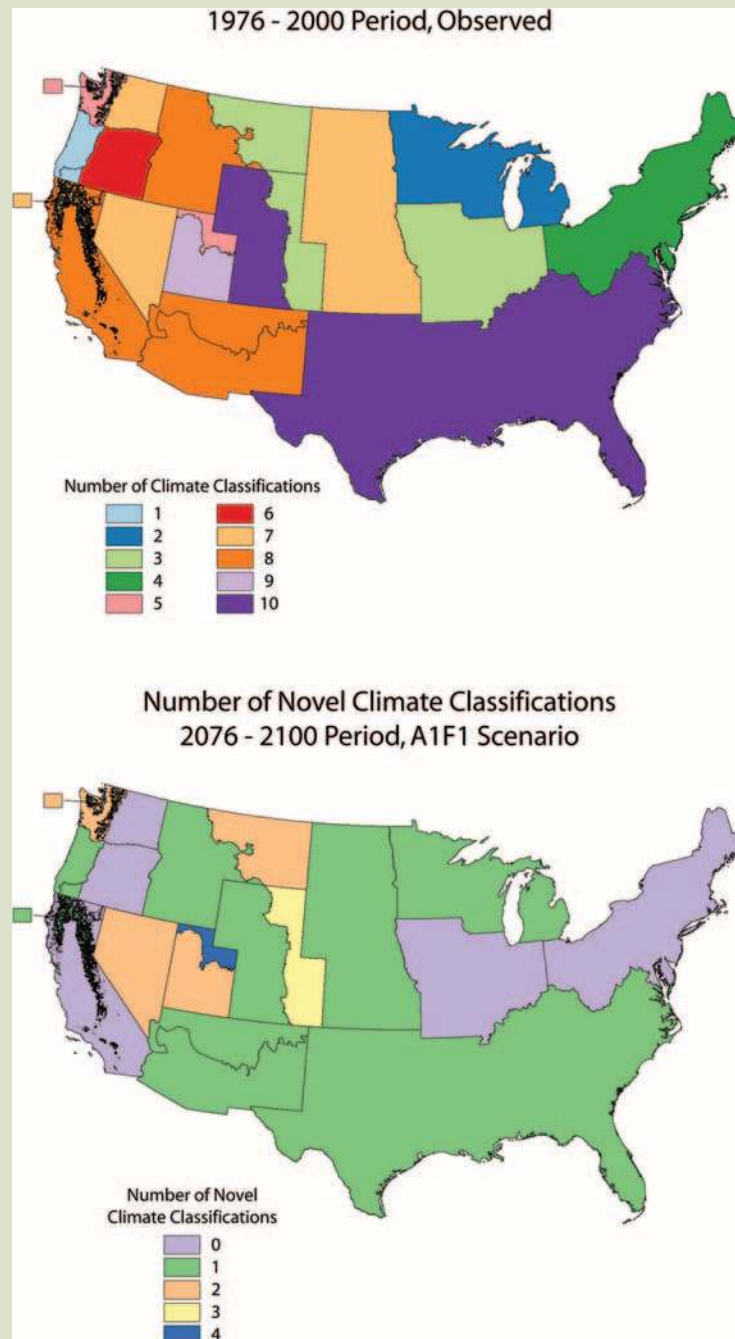


Figure B1. FIA volume model regions with the number of contemporary (1976–2000) (top) and projected novel (2076–2100, A1F1 scenario) (bottom) Köppen climatic zones occurring within each volume model region.



tree component weights dictate that data sets are often limited in size and scope. For example, Zianis et al. (2005) found that more than 75% of biomass studies in Eu-

rope had sample sizes of fewer than 50 individual trees. This affects the suitability of the data for developing models to be applied over large spatial domains. In the

United States, the mean sample size for 2,642 biomass equations summarized by Jenkins et al. (2004) was 41 individual trees. Nearly half of the studies had sample sizes of 20 trees or less, mainly because they were intended for local use in specific stands or under a narrow range of conditions. As a result, many biomass studies focused on small geographic areas (Figure 2) with samples spanning a narrow range of tree sizes, species, or growing conditions (Figure 3). Subsequent needs for regional and national scale estimators motivated the application of local-scale equations or data to geographically broader scopes (Jenkins et al. 2004, Chojnacky et al. 2013). As a result, studies are often limited to specific geographic areas (Figure 2) and do not cover a full range of observed tree diameters (Figure 3).

Because the costs of felling, measuring, and collecting specimens on trees grows rapidly with tree size, relatively few studies have looked at trees larger than approximately 50 cm dbh, despite the potentially important roles of large trees in estimating forest-level biomass stocks. Any large trees measured probably exert undue influence in tree biomass equations, especially at the upper end

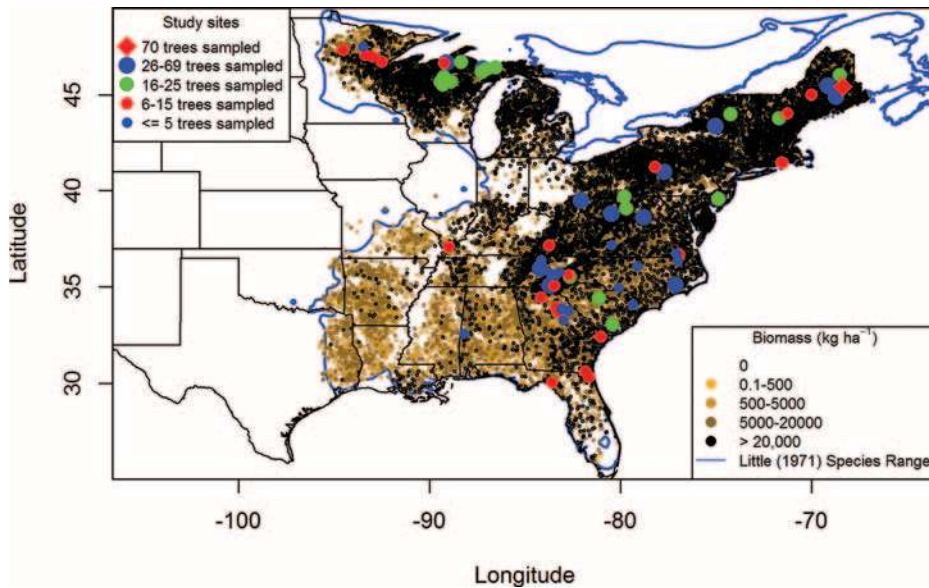


Figure 2. Map showing the species range of red maple (*Acer rubrum* L.), current estimated red maple biomass based on 2007–2011 USDA FIA plots, and the location of compiled felled tree biomass legacy data sets by sample size.

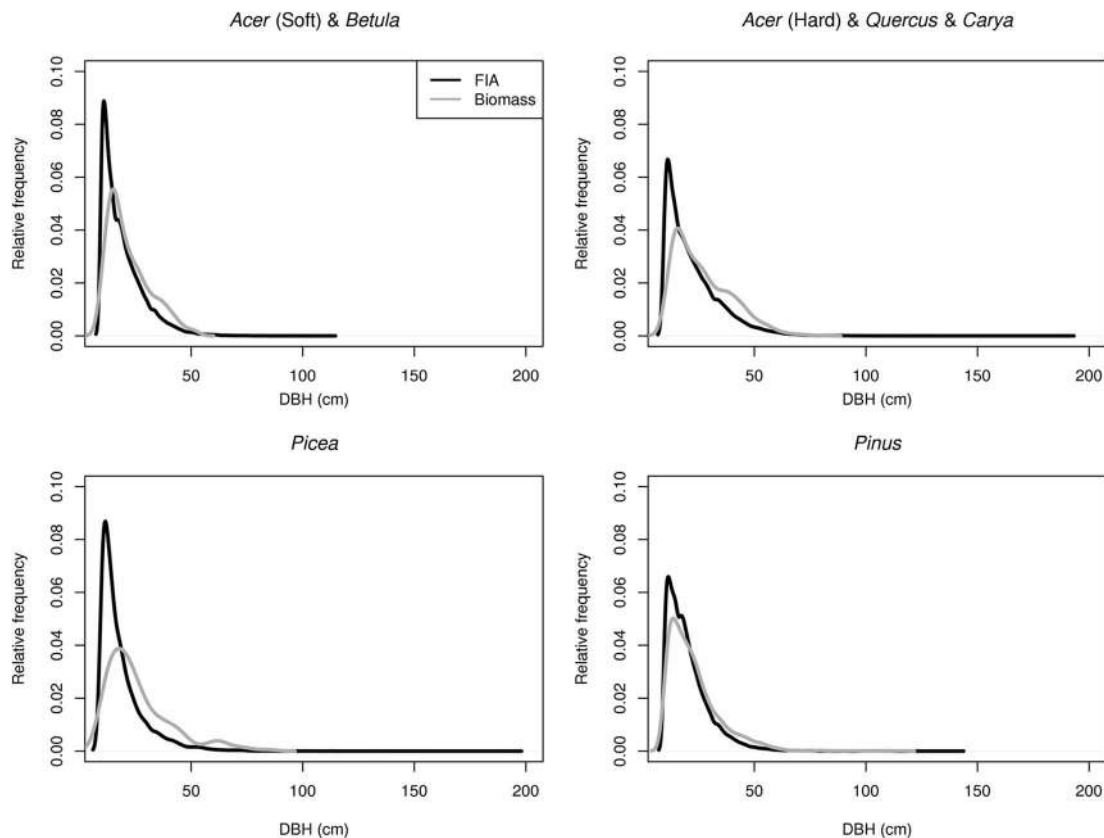
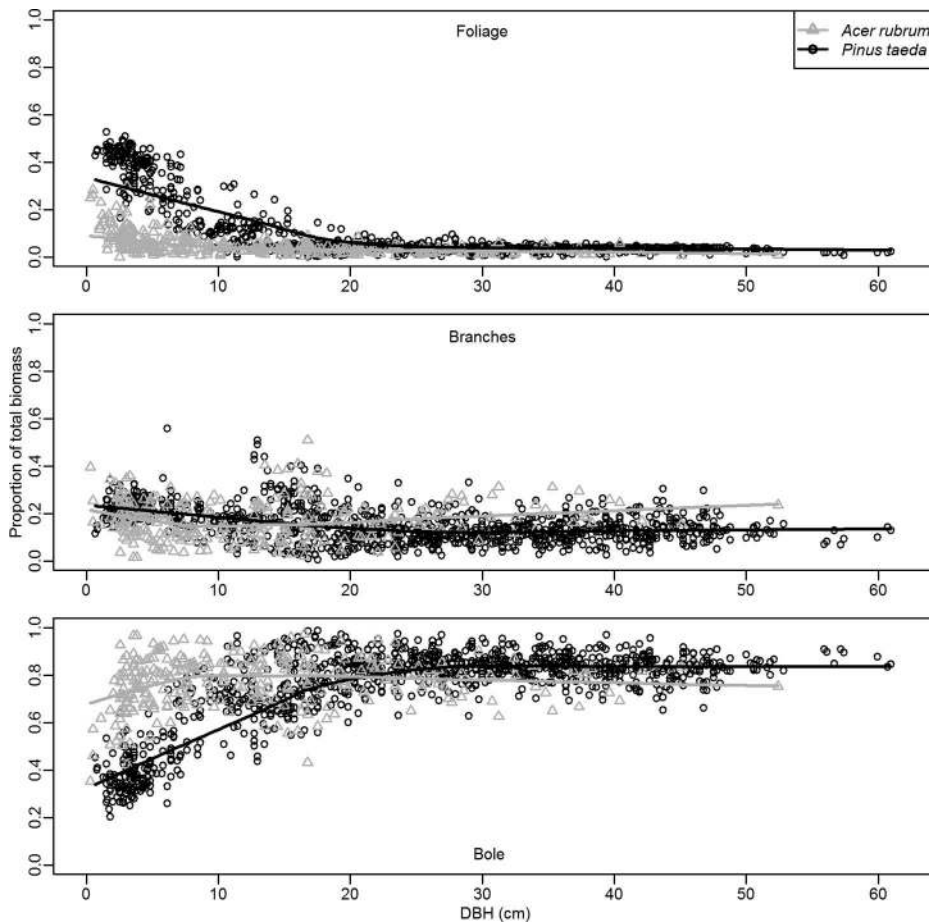


Figure 3. Relative distributions of observed dbh (cm) based on the 2007–2011 USDA FIA national inventory (black line) and a compiled felled tree biomass legacy database (gray line) for four common species groups. Note that the gray line rarely fully overlaps the black line and does not extend to the largest dbh classes.



**Figure 4.** Comparison of observed proportion of total biomass by component including foliage (a), branch (b), and bole (c) for loblolly pine (*Pinus taeda* L.) and red maple (*Acer rubrum* L.) with a lowess regression fit by species. Observations were obtained from a compiled database of existing tree biomass data collected in the United States.

of the range in tree sizes where any predictions are made. Further, trees that appear to be healthy, sound, and of good form are much more frequently selected in model-development samples than trees that are unhealthy, have signs of decay, or exhibit poor form. Interestingly, Westfall (2008) found that a field estimate of percent cull in a stem was the most important factor influencing observed differences between measured and predicted stem volume. A similar conclusion would probably extend to tree biomass estimates derived from tree volume without accounting for missing or decaying volume. Taken together, these factors suggest that many biomass equations will perform poorly when applied to populations that are broader than the sample tree collections from which they were developed, which will generally be the case.

### Modeling Considerations

Major limitations in tree biomass model development are the cost and feasibility

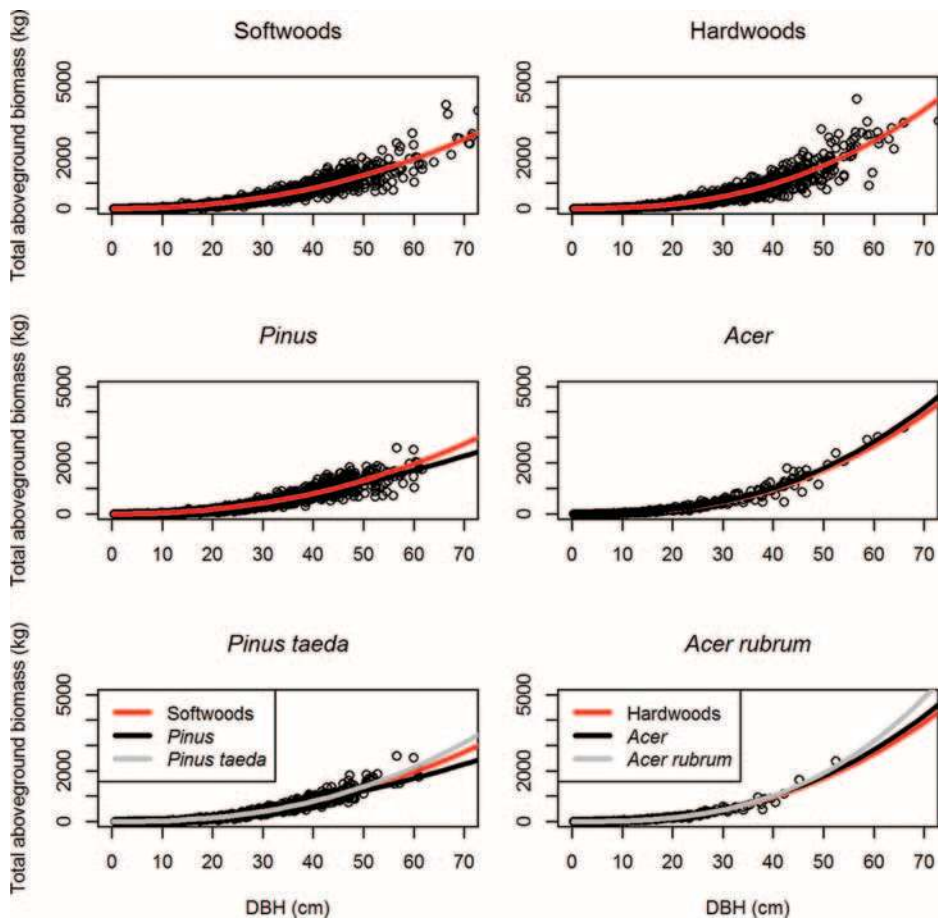
of tree measurements as described above and limitations on model form, with the latter in part being constrained by the former. Sileshi (2014) recently provided a detailed critical review of these modeling considerations; only the most relevant issues are discussed here.

Because of the strong nonlinear relationship between biomass and tree dbh and the ubiquity, low cost, and accuracy of measuring dbh, the majority of biomass models are formulated as a simple power function,  $\text{biomass} = a\text{DBH}^b$ , with  $a$  and  $b$  being coefficients or a linearized version employing logarithmic data transformations of mass and dbh with the latter introducing transformation bias. Zianis et al. (2005) found that more than two-thirds of the European biomass models they examined were solely a function of dbh. Although dbh is well correlated with tree height and volume, the use of dbh alone assumes that the underlying allometric relationships are static, which is

often not the case, especially when spatial scale is increased and managed stands are included. Ducey (2012) recently found evidence against the notion of a universal scaling exponent governing the relationship between tree dbh and height for 86 species in the northeastern United States where there was considerable variation in diameter-height relationships between species and geographic locations. Nonetheless, the added expense and uncertainties associated with tree height measurements as biomass model predictors may negate any gains in predictive accuracy, especially when models for use over a narrow range of conditions are developed (Temesgen et al. 2015).

Including additional variables in biomass prediction equations can improve model precision, but it also increases the cost of both model development and subsequent forest inventory. Because the predictors in a volume or biomass equation (the variables measured and to be entered on the right-hand side of the equation) have a direct impact on the cost of the inventory effort, a tradeoff between accuracy and affordability exists. When planning inventories, this tradeoff must be considered in the selection of an appropriate equation (Packard and Radtke 2007). Lambert et al. (2005) found that including tree height measurements in forest inventories allowing for tree volume in addition to dbh typically reduces the root mean squared error of total tree biomass predictions by approximately 8 and 25% for hardwood and softwood species groups, respectively. Goodman et al. (2014) found that using crown radius in addition to dbh and height further reduced a bias by 11–14% for total aboveground biomass. These or other additional predictors could be even more important in the estimation of the various components of biomass, given the generally poor relationship between dbh and biomass component fractions (Figure 4). More recently suggested predictors of tree biomass components, such as the diameter of the largest branch in a tree, put forward by MacFarlane (2011) as a promising predictor of branch volume and mass, need to be further evaluated. More accurate prediction of tree biomass components should not only improve tree biomass estimation but also improve understanding of the proper utilization of tree biomass (Ver Planck and MacFarlane 2014).





**Figure 5.** Influence of grouping by taxonomy, genus, and species on the relationship between total aboveground dry biomass (kg) and dbh (cm) based on a compiled database of existing tree biomass data from the United States.

### Grouping Variation

Variation in tree biomass and its allocation to components is commonly found in comparisons among individuals, stands, geographic regions, and species. However, despite many of the issues identified above, it is common to group disparate observations to increase sample size and reduce complexity. For example, the total aboveground biomass estimators intended for the US national inventory classify all tree species into 10 distinct groups, whereas the sub-models for estimating the various biomass components only distinguish between hardwood and softwood species (Jenkins et al. 2003). The latter were recently revised to include 35 distinct groupings based on taxonomy and wood specific gravity (Chojnacky et al. 2013), but yielded estimates similar to the those for the initial Jenkins et al. (2003) approach when applied to the larger population.

Species groupings and other forms of aggregation can be advantageous because increased sample sizes generally allow for more

accurate characterization of the relationships between standing tree dimensions and volume or biomass. However, as the amount of grouping increases, the accuracy of predictions for various subpopulations is likely to decrease, particularly when the various components of aboveground biomass are examined. For example, a model fitted to data from all pine (*Pinus*) species may provide adequate predictive accuracy across all pines but may behave poorly for any particular pine species. This example is illustrated in Figure 5 where a model (red line) is fitted to data combined from several softwood genera (top, left), another model (black line) is fitted to the single genus *Pinus* (middle, left), and a third model (gray line) is fitted to the single species loblolly pine (*Pinus taeda* L.) (bottom, left). The three models all diverge over some portion of the range of data shown, a pattern also noted for models fitted to several hardwood genera (top, right), the genus *Acer* (middle, right), and the species red maple (*Acer rubrum* L.) (bottom, right; Figure 5). Assuming that the species models

(gray lines) are the most accurate for loblolly pine and red maple, in the bottom left and right panels (Figure 5), respectively, using either of the softwood/hardwood or genera models will result in biased predictions for either of these species, which can be quite significant when scaled to a landscape level.

With questions of precision and accuracy aside, the primary driver for creating groups is usually cost. It is rare that financial resources exist to obtain sufficient samples by species across large areas such that the numerous sources of variation can be assessed. Often, empirical relationships such as biomass are grouped by species characteristics such as shade tolerance, evergreenness, and wood density, but these factors usually explain a limited amount of the variation at the individual level (e.g., Ducey 2012). In contrast, comparable results can be obtained from using species groups compared with a species-specific approach if these models are applied at rather broad geographic scales and there is a strong underlying relationship ( $R^2 = >0.95$ ) (McRoberts and Westfall 2014). However, McRoberts and Westfall (2014) made this conclusion based on examining the variation in the prediction of stem volume and not tree biomass, which could be much more variable for all the reasons given above.

### Implications for Prediction of Forest Biomass and Carbon

Each of the limitations described above has a significant influence on how and where tree biomass and carbon prediction models can be applied. For example, a common application of tree biomass equations is to estimate aboveground net primary production (ANPP) using forest inventory data. In this application, ANPP is estimated by applying biomass prediction equations to inventory data collected at two points in time (e.g., Lavigne et al. 2005) and subtracting to obtain an estimate of the biomass accumulated per unit area, per year. Especially for shorter intervals (<5 years), this approach can be rather problematic because the prediction errors at either measurement point are likely to be greater than the actual biomass change. Thus, estimated trends in ANPP might simply be due to the choice of model and the scope of data used in its development.

Another major problem is that equations for some species or geographic regions are simply not available where they are needed. In such cases, practitioners are faced with choosing the best available equation,

despite having limited information available that could be used to choose between alternative models. Appreciable error can result from this and other forms of model extrapolation. To address this limitation, model averaging of disparate equations may be used (e.g., Picard et al. 2012), but it does not address the larger issues of sparse observed values or assessments of prediction bias. A related concern is that the predicted values of forest biomass, whether for single trees or for areas of interest as large as states or nations, are generally reported without any statement of their estimated uncertainty. This is particularly problematic when the predictions are based on model averages or pseudodata (see the cover of Jenkins et al. 2004) because the uncertainty of such predictions would probably be larger than that in applications for which statistical models were available.

In summary, limitations in existing biomass models, data sets, and estimation procedures hinder the ability to provide accurate and consistent assessments of forest biomass and its changes over time. Considerable knowledge exists for leveraging future research and development aimed at reducing these challenges; however, given the complexity and breadth of the problem, a plan of action is warranted. Future advances should address current limitations facing biomass estimation at the regional and national scales without succumbing to pitfalls that have affected some past efforts. With these goals in mind, the following recommendations are presented for ongoing and future efforts that aim to address knowledge gaps in the practice of estimating whole-tree biomass for regional and national assessments.

## Recommendations

Moving forward, it is critical to recognize and understand the current limitations of individual tree biomass models as outlined above and by Temesgen et al. (2015). An ideal solution to this issue will probably never emerge, but recommendations for future efforts include the following (in order of importance):

1. New regional or national efforts to collect biomass data in a consistent manner are necessary worldwide. Although expensive and time-consuming, this type of work would allow for the minimization of methodological differences, more effective comparisons between nations, regions, or ecological zones, and the modification of existing models or the

development of new ones. Recently, the USDA Forest Service FIA program has led a collaborative effort between academics, industry, and state and federal agencies for collecting detailed tree-level biomass data for the primary commercial species across the United States (see Westfall et al. 2014).

2. Compile existing and new collections of volume, biomass, carbon, and wood density data into a documented, quality-tested, transparent, harmonized, and openly accessible electronic database. An example of such an effort is represented by the Food and Agriculture Organization of the United Nations GlobAllomeTree project.<sup>2</sup> The GlobAllomeTree project facilitates the appropriate use and dissemination of biomass equations, much like the collections of volume and biomass equations for North American species compiled in the USDA Forest Service National Volume and Biomass Estimator Libraries.<sup>3</sup> Collections like these do not purport to compile and share actual measurements of field or laboratory sample specimens, nor do they attempt to solve problems brought about by model averaging or pseudodata-based approaches that attempt to simulate the information contained in existing models. A repository of original data sets would obviate the need for duplicating data collection efforts previously carried out while ensuring that existing data would remain available for reuse as new modeling tools and techniques become available. A recent effort led by the USDA Forest Service FIA program has compiled biomass and volume data for more than 15,000 and 100,000 individual trees, respectively, from past studies carried out across the United States. These numbers will probably increase as greater attention and resources are directed to efforts like this.
3. Use one or more comprehensive collections of individual tree biomass data like those described above to make greater use of statistical validation tools to evaluate and compare biomass models. This should help promote the use of consistent and measurable accuracy standards that relate to the expected accuracy of models when applied to various forest populations. Adopt tools that make use of both analytical (e.g., Afleck and Turnquist 2012, Nelson et al. 2014) and empirical (e.g., Domke et al. 2012, Westfall 2012) solutions, striving to

provide generalized assessments of prediction errors and uncertainties, while discovering the underlying sources of errors and their possible solutions.

4. Explore new model forms and incorporate additional predictor variables, some of which may be obtained using emerging technologies like terrestrial light detection and ranging (LiDAR) (e.g., Henning and Radtke 2006, Kaasalainen et al. 2014). In particular, it is important to evaluate potential gains in precision and bias reduction relative to the feasibility and costs of obtaining new predictors. This is illustrated in the recent works of Chave et al. (2014) and Goodman et al. (2014). In addition, compatibility between tree volume, biomass, and density estimates should be ensured (e.g., Jordan et al. 2008, Ver Planck and MacFarlane 2014), which may allow for further leveraging of existing information or legacy data sources.
5. Employ emerging mathematical and statistical methods for improving predictions and characterizing uncertainty in the estimates. This recommendation has multiple dimensions including the following:
  - a. Recognize and quantify the uncertainty of model predictions by incorporating variation from model parameter errors, overall prediction errors, and other uncertainties, e.g., how biomass attributes are affected by geographic and/or genetic factors (e.g., Breidenbach et al. 2014). Simulation based methods show particular promise in providing more realistic assessments of uncertainty. These approaches ensure that a range of plausible values is presented and evaluated rather than a single value. However, one source of uncertainty that may be difficult to quantify is the measurement and sampling error associated with alternative methods of determining felled tree biomass given the general need for subsampling. This is probably an important topic for future research.
  - b. Explore the use of new statistical methods for improving prediction. For example, fitting regional or national biomass models using hierarchical or mixed models allows the sources of variation to be better identified (e.g., Dietze et al. 2008) and the potential for local calibration if observations are available (e.g., deMiguel et al. 2014). In addition, assessing and utilizing the spatial dependence between observations can be useful for improving predictions (e.g., Babcock et al. 2012). Finally, nonparametric methods

from fields such as data mining and artificial intelligence may be useful for addressing problems in model selection and form or for extracting useful predictive information from complex and increasingly large data sets (Breiman 1996).

- c. Develop techniques for maximizing utilization of existing information (e.g., fitted models and wood density data). For example, an improvement in predictions has been observed using approaches as simple as a geometric mean of multiple predictions (e.g., Li and Weiskittel 2010) or as sophisticated as Bayesian model averaging (e.g., Picard et al. 2012, Zapata-Cuartas et al. 2012). The effectiveness of these approaches may be limited when actual data or model fit statistics are unavailable, but it is evident that the increasing importance of forest biomass warrants the use of modeling techniques that can leverage strength from all existing forms of information.

## Endnotes

1. Please visit [www.arb.ca.gov/cc/capandtrade/auction/may-2014/results.pdf](http://www.arb.ca.gov/cc/capandtrade/auction/may-2014/results.pdf) for more information.
2. For more information, see [www.globallometree.org/](http://www.globallometree.org/).
3. For more information, see [www.fs.fed.us/fmsc/measure/volume/nvel/index.php](http://www.fs.fed.us/fmsc/measure/volume/nvel/index.php) and [www.fs.fed.us/fmsc/measure/biomass/index.shtml](http://www.fs.fed.us/fmsc/measure/biomass/index.shtml).

## Literature Cited

- AFFLECK, D.L.R., AND B.R. TURNQUIST. 2012. Assessing the accuracy of crown biomass equations for the major commercial species of the interior northwest: Study plan and preliminary results. P. 247–254 in *Monitoring across borders: 2010 joint meeting of the Forest Inventory and Analysis (FIA) symposium and the Southern Mensurationists*, McWilliams, W., and F.A. Roesch (eds.). USDA For. Serv., e-Gen. Tech. Rep. SRS-157, Southern Research Station, Asheville, NC.
- BABCOCK, C., J. MATNEY, A.O. FINLEY, A. WEISKITTEL, AND B.D. COOK. 2012. Multivariate spatial regression models for predicting individual tree structure variables using LiDAR data. *IEEE J. Sel. Top. Appl. Earth Obs. Remote Sens.* 6:6–14.
- BIRDSEY, R., K. PREGITZER, AND A. LUCIER. 2006. Forest carbon management in the United States: 1600–2100. *J. Environ. Qual.* 35:1461–1469.
- BREIDENBACH, J., C. ANTÓN-FERNÁNDEZ, H. PETERSSON, R.E. MCROBERTS, AND R. ASTRUP. 2014. Quantifying the model-related variability of biomass stock and change estimates in the Norwegian National Forest Inventory. *For. Sci.* 60:25–33.
- BREIMAN, L. 1996. Heuristics of instability and stabilization in model selection. *Ann. Stat.* 24: 2350–2383.
- CHAVE, J., D. COOMES, S. JANSEN, S.L. LEWIS, N.G. SWENSON, AND A.E. ZANNE. 2009. Towards a worldwide wood economics spectrum. *Ecol. Lett.* 12:351–366.
- CHAVE, J., M. RÉJOU-MÉCHAIN, A. BÚRQUEZ, E. CHIDUMAYO, M.S. COLGAN, W.B.C. DELITTI, A. DUQUE, ET AL. 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. *Glob. Change Biol.* 20:3177–3190.
- CHOJNACKY, D.C., L.S. HEATH, AND J.C. JENKINS. 2013. Updating generalized biomass models for North American tree species. *Forestry* 87:129–151.
- DE-MIGUEL, S., L. MEHTATALO, AND A. DURKAYA. 2014. Developing generalized, calibratable, mixed-effects meta-models for large-scale biomass prediction. *Can. J. For. Res.* 44:648–656.
- DALE, V.H., L.A. JOYCE, S. McNULTY, R.P. NEILSON, M.P. AYRES, M.D. FLANNIGAN, P.J. HANSON, ET AL. 2001. Climate change and forest disturbance. *BioScience* 51:723–734.
- DIETZE, M.C., M.S. WOLOSIN, AND J.S. CLARK. 2008. Capturing diversity and interspecific variability in allometries: A hierarchical approach. *For. Ecol. Manage.* 256:1939–1948.
- DOMKE, G.M., C.W. WOODALL, J.E. SMITH, J.A. WESTFALL, AND R.E. MCROBERTS. 2012. Consequences of alternative tree-level biomass estimation procedures on US forest carbon stock estimates. *For. Ecol. Manage.* 270:108–116.
- 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.
- DUCEY, M.J., D. ZHENG, AND L.S. HEATH. 2009. Creating compatible maps from remotely sensed and forest inventory data using radial basis functions. In *Proc. of Extending forest inventory and monitoring over space and time*, 2009 May 19–22, Quebec City, QC, Canada. International Union of Forest Research Organizations.
- ENQUIST, B.J., AND K.J. NIKLAS. 2002. Global allocation rules for patterns of biomass partitioning in seed plants. *Science* 295:1517–1520.
- ENVIRONMENTAL PROTECTION AGENCY. 2013. *Inventory of US greenhouse gas emission and sinks: 1990–2011*. EPA 430-R-13-001, Environmental Protection Agency, Washington, DC. 503 p.
- ENVIRONMENTAL PROTECTION AGENCY. 2014. Land use, land-use change, and forestry. Chapter 7 in *US Environmental Protection Agency, inventory of US greenhouse gas emissions and sinks: 1990–2012*. EPA 430-R-14-003. Available online at [www.epa.gov/climatechange/Downloads/ghgemissions/US-GHG-Inventory-2014-Main-Text.pdf](http://www.epa.gov/climatechange/Downloads/ghgemissions/US-GHG-Inventory-2014-Main-Text.pdf); last accessed Nov. 17, 2014.
- FOREST PRODUCTS LABORATORY. 2010. *Wood handbook: Wood as an engineering material*. USDA For. Serv., Gen. Tech. Rep. FPL-GTR-190, Forest Products Laboratory, Madison, WI. 508 p.
- GILLESPIE, A.J.R. 1999. Rationale for a national annual forest inventory program. *J. For.* 97:16–20.
- GOODMAN, R.C., O.L. PHILLIPS, AND T.R. BAKER. 2014. The importance of crown dimensions to improve tropical tree biomass estimates. *Ecol. Applic.* 24:680–698.
- GUO, Z., D.G. HODGES, AND T.M. YOUNG. 2011. Woody biomass utilization policies: State rankings for the US. *For. Policy Econ.* 21:54–61.
- HAYES, D.J., D.P. TURNER, G. STINSON, A.D. MCGUIRE, Y. WEI, T.O. WEST, L.S. HEATH, B. JONG, B.G. MCCONKEY, AND R.A. BIRDSEY. 2012. Reconciling estimates of the contemporary North American carbon balance among terrestrial biosphere models, atmospheric inversions, and a new approach for estimating net ecosystem exchange from inventory-based data. *Glob. Change Biol.* 18:1282–1299.
- HENNING, J.G., AND P.J. RADTKE. 2006. Detailed stem measurements of standing trees from ground-based scanning lidar. *For. Sci.* 52:67–80.
- INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE. 2013. *Scenario data for the atmospheric environment*. Available online at [www.ipcc-data.org/sres/ddc\\_sres\\_emissions.html](http://www.ipcc-data.org/sres/ddc_sres_emissions.html); last accessed Nov. 17, 2014.
- 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.* 49:12–35.
- 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 For. Serv., Gen. Tech. Rep. NE-319, Northeastern Research Station, Newtown Square, PA. 45 p.
- JORDAN, L., A. CLARK, 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.* 38:698–710.
- KAASALAINEN, S., A. KROOKS, J. LISKI, P. RAUMONEN, H. KAARTINEN, M. KAASALAINEN, E. PUTTONEN, K. ANTTILA, AND R. MAKIPAA. 2014. Change detection of tree biomass with terrestrial laser scanning and quantitative structure modeling. *Remote Sens.* 6:3906–3922.
- LAMBERT, M.-C., C.-H. UNG, AND F. RAULIER. 2005. Canadian national tree aboveground biomass models. *Can. J. For. Res.* 35:1996–2018.
- LAMLON, S.H., AND R.A. SAVIDGE. 2003. A reassessment of carbon content in wood: Variation within and between 41 North American species. *Biomass Bioenergy* 25:381–388.
- LAVIGNE, M.B., R.J. FOSTER, G. GOODINE, P.Y. BERNIER, AND C.-H. UNG. 2005. Alternative method for estimating aboveground net primary productivity applied to balsam fir stands in eastern Canada. *Can. J. For. Res.* 35:1193–1201.
- LI, R., AND A.R. WEISKITTEL. 2010. Comparison of model forms for estimating stem taper and volume in the primary conifer species of the North American Acadian Region. *Ann. For. Sci.* 67:302.
- LITTON, C.M., J.W. RAICH, AND M.G. RYAN. 2007. Carbon allocation in forest ecosystems. *Glob. Change Biol.* 13:2089–2109.
- LU, D. 2006. The potential and challenge of remote sensing-based biomass estimation. *Int. J. Remote Sens.* 27:1297–1328.
- MACFARLANE, D.W. 2011. Allometric scaling of branch volume in hardwood trees in Michi-



- gan, USA: Implications for improvements in above-ground forest carbon biomass inventories. *For. Sci.* 57:451–459.
- MAVOUROULOU, Q.M., A. NGOMANDA, N.L.E. OBIANG, J. LEBAMBA, H. GOMAT, G.S. MANKOU, J. LOUMETO, ET AL. 2014. How to improve allometric equations to estimate forest biomass stocks? Some hints from a central African forest. *Can. J. For. Res.* 44:685–691.
- MELILLO, J.M., R. TERESE, AND G.W. YOHE (EDS.). 2014. *Climate change impacts in the United States: The third national climate assessment*. US Global Change Research Program, Washington, DC. 841 p.
- McKINLEY, D., M. RYAN, R. BIRDSEY, C. GIARDINA, M. HARMON, L. HEATH, R. HOUGHTON, ET AL. 2011. A synthesis of current knowledge on forests and carbon storage in the United States. *Ecol. Applic.* 21:1902–1924.
- McROBERTS, R.E. 2005. The enhanced Forest Inventory and Analysis program. P. 11–20 in *The enhanced Forest Inventory and Analysis program—National sampling design and estimation procedures*, Bechtold, W.A., and P.L. Patterson (eds.). USDA For. Serv., Gen. Tech. Rep. SRS-GTR-80, Southern Research Station, Asheville, NC.
- McROBERTS, R.E., AND J.A. WESTFALL. 2014. The effects of uncertainty in model predictions of individual tree volume on large area volume estimates. *For. Sci.* 60:34–42.
- MILES, P.D., AND B.W. SMITH. 2009. *Specific gravity and other properties of wood and bark for 156 tree species found in North America*. USDA For. Serv., Res. Note RN-NRS-38, Northern Research Station, Newtown Square, PA. 35 p.
- MINER, R.A., R.C. ABT, J.L. BOWYER, M.A. BUFORD, R.W. MALMSHEIMER, J. O'LAUGHLIN, E.E. ONEL, R.A. SEDJO, AND K.E. SKOG. 2014. Forest carbon accounting considerations in US bioenergy policy. *J. For.* 112:591–606.
- NELSON, A.S., A.R. WEISKITTEL, M.R. SAUNDERS, AND R.G. WAGNER. 2014. Development and validation of small-diameter aboveground biomass models for naturally-regenerated and planted tree species in eastern Maine. *Biomass Bioenergy* 68:215–227.
- PACKARD, K.C., AND P.J. RADTKE. 2007. Forest sampling combining fixed- and variable-radius sample plots. *Can. J. For. Res.* 37:1460–1471.
- PAN, Y., R.A. BIRDSEY, J. FANG, R. HOUGHTON, P.E. KAUPPI, W.A. KURZ, O.L. PHILLIPS, A. SHVIDENKO, S.L. LEWIS, AND J.G. CANADELL. 2011. A large and persistent carbon sink in the world's forests. *Science* 333:988–993.
- PETERS-STANLEY, M., G. GONZALEZ, AND D. YIN. 2013. *Covering new ground: State of the forest carbon markets 2013*. Ecosystem Marketplace, Washington, DC. 80 p.
- PICARD, N., M. HENRY, F. MORTIER, C. TROTTA, AND L. SAINT-ANDRÉ. 2012. Using Bayesian model averaging to predict tree aboveground biomass in tropical moist forests. *For. Sci.* 58: 15–23.
- PILLI, R., T. ANFODILLO, AND M. CARRER. 2006. Towards a functional and simplified allometry for estimating forest biomass. *For. Ecol. Manage.* 237:583–593.
- POLLARD, J.E., J.A. WESTFALL, P.L. PATTERSON, D.L. GARTNER, M. HANSEN, AND O. KUEGLER. 2006. *Forest Inventory and Analysis national data quality assessment report for 2000 to 2003*. USDA For. Serv., Gen. Tech. Rep. RMRS-GTR-181, Rocky Mountain Research Station, Fort Collins, CO. 43 p.
- POWELL, S.L., W.B. COHNEN, R.E. KENNEDY, S.P. HEALEY, AND C. HUANG. 2014. Observation of trends in biomass loss as a result of disturbance in the conterminous US: 1986–2004. *Ecosystems* 17:142–157.
- RANGER, J., AND D. GELHAYE. 2001. Below-ground biomass and nutrient content in a 47-year-old Douglas-fir plantation. *Ann. For. Sci.* 58:423–430.
- RUBEL, F., AND M. KOTTEK. 2010. Observed and projected climate shifts 1901–2100 depicted by world maps of the Köppen-Geiger climate classification. *Meteorol. Z.* 19:135–141.
- RUSSELL, M.B., G.M. DOMKE, C.W. WOODALL, AND A.W. D'AMATO. 2015. Comparisons of allometric and climate-derived estimates of tree coarse root carbon in forests of the United States: Implications for the National Greenhouse Gas Inventory. *Climatic Change*. In press.
- SCHLECHT, R.M., AND D.L.R. AFFLECK. 2014. Branch aggregation and crown allometry condition the precision of randomized branch sampling estimators of conifer crown mass. *Can. J. For. Res.* 44:499–508.
- SHOTTAFER, J.E., AND A.M. BRACKLEY. 1982. *An analysis of moisture content variation in eastern spruce and balsam fir in Maine*. Tech. Bull. 104, University of Maine Life Sciences and Agriculture Experiment Station, Orono, ME. 29 p.
- SIKKEMA, R., M. STEINER, M. JUNGINGER, W. HIEGL, M.T. HANSEN, AND A. FAAIJ. 2011. The European wood pellet markets: Current status and prospects for 2020. *Biofuels Bioprod. Biorefin.* 5:250–278.
- SILESHI, G.W. 2014. A critical review of forest biomass estimation models, common mistakes and corrective measures. *For. Ecol. Manage.* 329:237–254.
- STÄHL, G., J. HEIKKINEN, H. PETERSSON, J. REPOLA, AND S. HOLM. 2014. Sample-based estimation of greenhouse gas emissions from forests—A new approach to account for both sampling and model errors. *For. Sci.* 60:3–13.
- STEPHENSON, N.L., A.J. DAS, R. CONDIT, S.E. RUSSO, P.J. BAKER, N.G. BECKMAN, D.A. COOMES, ET AL. 2014. Rate of tree carbon accumulation increases continuously with tree size. *Nature* 507:90–93.
- SWENSON, N.G., AND B.J. ENQUIST. 2008. The relationship between stem and branch wood specific gravity and the ability of each measure to predict leaf area. *Am. J. Bot.* 95:516–519.
- TASSISA, G., AND H.E. BURKHART. 1998. Modeling thinning effects on ring specific gravity of loblolly pine (*Pinus taeda* L.). *For. Sci.* 44:212–223.
- 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.* doi:10.1080/02827581.2015.1012114.
- TEMESGEN, H., V. MONLEON, A. WEISKITTEL, AND D. WILSON. 2011. Sampling strategies for efficient estimation of tree foliage biomass. *For. Sci.* 57:153–163.
- THOMAS, S.C., AND A.R. MARTIN. 2012. Carbon content of tree tissues: A synthesis. *Forests* 3:332–352.
- THOMPSON, I., B. MACKEY, S. McNULTY, AND A. MOSSELER. 2009. *Forest resilience, biodiversity, and climate change: A synthesis of the biodiversity/resilience/stability relationship in forest ecosystems*. Tech. Ser. 43, Secretariat of the Convention on Biological Diversity, Montreal, ON, Canada. 67 p.
- TOLLEFSON, J. 2009. Satellites beam in biomass estimates. *Nature* 462:834–835.
- USDA FOREST SERVICE. 2013. *Forest Inventory and Analysis fiscal year 2012 business report*. USDA For. Serv., FS-1020, Washington, DC. 72 p.
- VANNINEN, P., AND A. MAKELA. 1999. Fine root biomass of Scots pine stands differing in age and soil fertility in southern Finland. *Tree Phys.* 19:823–830.
- VER PLANCK, N.R., AND D.W. MACFARLANE. 2014. A vertically integrated whole-tree biomass model. *Trees*. doi:10.1007/s00468–014-1123-x.
- WANG, J.R., A.L. ZHONG, AND J.P. KIMMINS. 2002. Biomass estimation errors associated with the use of published regression equations of paper birch and trembling aspen. *North. J. Appl. For.* 19:128–136.
- WESTFALL, J.A. 2008. Differences in computed individual-tree volumes caused by differences in field measurements. *North. J. Appl. For.* 25: 195–201.
- WESTFALL, J.A. 2012. A comparison of above-ground dry-biomass estimators for trees in the northeastern United States. *North. J. Appl. For.* 29:26–34.
- WESTFALL, J.A., J.L. COULSTON, J. SHAW, AND A. GRAY. 2014. *An improved volume, carbon, and thermochemical database for major US tree species: Proc. of the FIA National User Group Meeting, 2014 March 19–22, Salt Lake City, UT*. Available online at [www.ncasi2.org/downloads/BWG/saltlake/docs/Biomass\\_2014.pdf](http://www.ncasi2.org/downloads/BWG/saltlake/docs/Biomass_2014.pdf); last accessed Nov. 17, 2014.
- WILLIAMSON, G.B., AND M.C. WIEMANN. 2010. Measuring wood specific gravity correctly. *Am. J. Bot.* 97:519–524.
- WOODALL, C.W., L.S. HEATH, G.M. DOMKE, AND M.C. NICHOLS. 2011. *Methods and models for estimating aboveground volume, biomass, and carbon for trees in the US forest inventory, 2010*. USDA For. Serv., Gen. Tech. Rep. NRS-88, Northern Research Station, Newtown Square, PA. 30 p.
- ZAPATA-CUARTAS, M., C.A. SIERRA, AND L. ALLEMAN. 2012. Probability distribution of allometric coefficients and Bayesian estimation of aboveground tree biomass. *For. Ecol. Manage.* 277:173–179.
- ZIANIS, D., P. MUUKKONEN, R. MAKIPAA, AND M. MENCUCINI. 2005. Biomass and stem volume equations for tree species in Europe. *Silva Fenn.*, Monogr. 4. 63 p.