



## Comparing tree foliage biomass models fitted to a multispecies, felled-tree biomass dataset for the United States



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### ABSTRACT

Estimation of live tree biomass is an important task for both forest carbon accounting and studies of nutrient dynamics in forest ecosystems. In this study, we took advantage of an extensive felled-tree database (with 2885 foliage biomass observations) to compare different models and grouping schemes based on phylogenetic and geographic variation for predicting foliage biomass at the tree scale. We adopted a Bayesian hierarchical statistical framework, first to compare linear models that predict foliage biomass directly to models that separately estimate a foliage ratio as a component of total aboveground biomass, then to compare species specific models to both 'narrow' and 'broad' general biomass models using the best fitted functional form. We evaluated models by simulating new datasets from the posterior predictive distribution, using both summary statistics and visual assessments of model performance. Key findings of our study were: (1) simple linear models provided a better fit to our data than component ratio models, where total biomass and the foliar ratio are estimated separately; (2) species-specific equations provided the best predictive performance, and there was no advantage to narrow species groupings relative to broader groups; and (3) all three model schemes (i.e., species-specific models versus narrow or broad groupings proposed in national-scale biomass equations) tended to over-predict foliage biomass and resulted in predictions with very high uncertainty, particularly for large diameter trees. This analysis represents a fundamental shift in carbon accounting by employing felled-tree data to refine our understanding of uncertainty associated with component biomass estimates, and presents an ideal approach to account for tree-scale allometric model error when estimating forest carbon stocks. However, our results also highlight the need for substantial improvements to both available fitting data and models for foliage biomass before this approach is implemented within the context of greenhouse gas inventories.

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### 1. Introduction

Estimation of live tree biomass from forest inventory data, typically using regression models with individual tree measurements as covariates, is important for both forest carbon accounting and studies of nutrient flows across whole ecosystems (Houghton, 2003; Jenkins et al., 2003; Schroeder et al., 1997). While many models have been developed for total tree biomass, it is often desirable to have individual estimates of particular biomass components (e.g. leaves, branches, and roots) as these stocks play key roles in many ecosystem processes (Chapin et al., 2002). For example, the bulk of a tree's nitrogen is found in foliage (Wirth et al., 2004) while fine

roots are involved in the exchange of both nutrients and carbon at the plant–soil interface (Bardgett et al., 2014). However, empirical observations of tree component biomass stocks are costly and difficult to collect in the field, let alone during a systematic inventory of forests at scales ranging from an individual stand to national efforts (e.g., IPCC, 2006). Models that provide reliable estimates with realistic uncertainty bounds are necessary for forest ecosystem research, monitoring, and reporting of national greenhouse gas inventories (Baker et al., 2010).

Despite the need, a consistent methodology for estimating biomass components from forest inventories is lacking. Felled-tree data are required to estimate parameters in biomass models, but studies that have accurately sampled biomass components are rare relative to those that have sampled whole trees (Jenkins et al., 2003; Zianis et al., 2005). In addition, component stocks are often highly variable. Foliage is particularly dynamic, varying both across space

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(i.e., individual tree sizes) and time (i.e., leaf longevity). Tree foliage biomass is influenced by a host of factors including but not limited to: genetic variation, climate, geography, stand dynamics, and disturbance events (Niinemets, 2001; Reich et al., 2014; Wirth et al., 2004). Understanding these dynamics requires models tailored to biomass components to both improve predictive accuracy and to understand the scale of uncertainty in component stocks relative to that of whole tree estimates.

Thus far, two general frameworks have been proposed for modeling foliage biomass (Bartelink, 1998). One approach involves the relationship between the area of conductive tissue located in the tree stem at the base of the crown and the amount of leaf biomass it supports (Mäkelä, 1986; Shinozaki et al., 1964; Valentine et al., 1985). This approach has been used to construct models that directly estimate leaf biomass based on stem cross section (Robichaud and Methven, 1992; Waring et al., 1982; Wirth et al., 2004; Zellers et al., 2012):

$$\ln(BM_{fol}) = \alpha + \beta * \ln(d) \quad (1)$$

where  $BM_{fol}$  is foliage biomass,  $d$  is a proxy of sapwood area (typically diameter at breast height; dbh), and  $\alpha$  and  $\beta$  are model parameters. Although the parsimonious nature of these models is attractive, their application may be limited due to poor relationships between dbh and the area of conductive tissue higher up the stem (Bartelink, 1996; Bond-Lamberty et al., 2002; Laubhann et al., 2010).

An alternative approach is to estimate total tree biomass as well as a component ratio for foliage using models dependent on tree component and region (Domke et al., 2012). An estimate of foliage biomass (or other tree components) can then be obtained for an individual tree by multiplying these two quantities together, which relies on consistent patterns of resource allocation within species functional groups. The component ratio method (CRM) is currently used by the United States (U.S.) Forest Service to estimate biomass components in the national Forest Inventory and Analysis (FIA) program (Woodall et al., 2011). This approach is appealing because in that patterns of resource allocation vary in response to predictor variables (e.g., tree size, climate, geography; Reich et al., 2014). However, most published regression equations for these foliar components are based on small datasets, while patterns of biomass allocation across species remain poorly understood (Chojnacky et al., 2013).

Beyond establishing an appropriate functional form for foliage biomass, it is also important to consider how tree species will be grouped to develop general biomass equations. An obvious approach is to use species-specific models, but this may present some disadvantages. Because felled-tree data are generally required to parameterize biomass models, the absence or underrepresentation of a particular species in such datasets can hinder the development of species-specific models. Combining multiple species into functional groups, such as those proposed by Jenkins et al. (2003) and Chojnacky et al. (2013), can address this issue by allowing analysts to obtain biomass estimates using data from species assumed to be similar to those absent in observed datasets (Weiskittel et al., 2015). The determination of such functional groups is often subjective. The method of grouping may successfully categorize the most common species into unique groups, but determining how rare and/or infrequent species are accounted for remains an open question (Picard et al., 2010). For instance, the 10 species groups proposed by Jenkins et al. (2003) were based on coarse geographic and taxonomic factors, while the 35 groups established by Chojnacky et al. (2013) considered more refined phylogenetic and allometric relationships. It is important to note that neither of these studies were based on actual biomass observations but instead used pseudodata simulated from a range of published biomass models. This highlights the need for empirical

observations of felled-tree total and foliar biomass data to inform component biomass models.

Given that model development has primarily focused on total biomass, there is a clear need for a consistent methodology for estimating component biomass stocks that has been validated using felled-tree datasets. This includes both establishing an appropriate model functional form as well as ideal groupings for nationally consistent component biomass equations. In this study, we used an extensive database of felled tree data compiled from previous published and unpublished work to compare multiple models for tree foliage biomass for the primary species occurring across the U.S. We focused on foliage since it is a highly dynamic yet poorly understood carbon pool that is an important parameter in numerous nutrient budget models (e.g., PnET, CENTURY). Our specific objectives were to: (1) develop and compare multiple functional models for foliage biomass (i.e., simple models and component ratio models) at the species level; and (2) assess the performance of species-specific equations versus the broad species grouping proposed by Jenkins et al. (2003) and the narrower grouping of Chojnacky et al. (2013) (hereafter referred to as “broad” and “narrow” groupings, respectively) when fit to observed foliage biomass data.

## 2. Methods

### 2.1. Study area

Data used in our study were collected at 130 locations in the U.S. and Canada (Fig. 1). The majority of the sampling locations were in the southeast U.S., though data were also used from the northern states, at several locations from the western U.S. and Canada, and from one location in interior Alaska. Since previously published biomass data were employed, it should be noted that the number of species and sample sizes at each location varied widely.

### 2.2. Legacy biomass database

For our analysis, we used an extensive database of felled-tree biomass estimates, hereafter referred to as “legacy data,” that has been assembled as part of ongoing efforts to improve the volume, biomass, and carbon models used by FIA for conducting forest resource inventories (Weiskittel et al., 2015). The database contains original records of felled tree data, from both published and unpublished work, collected between 1960 and 2013. For our modeling work we only retained observations where leaf biomass, dbh, and total height were measured. We excluded individuals that were smaller than 12.7 cm dbh, as biomass allocation patterns in seedlings and saplings differ from that of mature trees and are typically modeled separately (Jenkins et al., 2003; Nelson et al., 2014). We also removed any species with fewer than four observations to maintain as much diversity as possible within the broad and narrow species groups we considered. These filters resulted in a final sample of 2885 observations from 49 studies. A total of 65 species, 24 of the 35 Chojnacky et al. (2013) narrow species groups, and all 10 Jenkins et al. (2003) broad species groups are represented in this sample (Fig. 2; A1).

### 2.3. Design of Bayesian hierarchical model

Bayesian hierarchical models are useful for the development of multispecies tree component biomass models because they account for the richness in correlation structures needed in such analyses, and the analysis of posterior distributions naturally allows for a complete assessment of uncertainty in biomass predictions (Finley et al., 2008; Green et al., 1999). In our analysis, we used the same error structure for each model we considered, so

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