

Testing a new component ratio method for predicting total tree aboveground and component biomass for widespread pine and hardwood species of eastern US

Brian J. Clough^{1*}, Grant M. Domke², David W. MacFarlane³, Philip J. Radtke⁴, Matthew B. Russell¹
and Aaron R. Weiskittel⁵

¹Department of Forest Resources, University of Minnesota, St. Paul, MN 55108, USA

²US Forest Service Northern Research Station, St. Paul, MN 55108, USA

³Department of Forestry, Michigan State University, East Lansing, MI 48824, USA

⁴Department of Forest Resources and Environmental Conversation, Virginia Polytechnic Institute, Blacksburg, VA 24061, USA

⁵School of Forest Resources, University of Maine, Orono, ME 04468, USA

*Corresponding author. E-mail: brian@silviaterra.com

Received 8 February 2017

The US National Greenhouse Gas Inventory uses the component ratio method (CRM), a volume conversion approach that incorporates models for tree biomass components, for forest carbon assessments. However, the performance of the CRM relative to other methods, as well as influences on its accuracy and precision, must be evaluated. We constructed a data-driven CRM (n-CRM), used it to predict total tree and component biomass for six US tree species, and compared this approach to a reference allometric model. We also assessed the influence of size, crown dynamics, and stem growth on the performance of both methods. Results show that the n-CRM was more accurate for four species, resulting from the inclusion of more predictor variables. Both methods had high uncertainty, but the precision of n-CRM predictions was two to eight times higher for small diameter trees (<10 cm) across all species. Accuracy and precision of the crown component models (i.e. branches and foliage) was low, though better for pines than for hardwoods. Species-level analysis suggests that poor precision is influenced by crown traits and the size distribution of fitting datasets. Our results highlight needed improvements to the n-CRM, and motivate further development of data that facilitate predictive evaluation of biomass models.

Introduction

For the US, Canada and many other nations with national forest inventory (NFI) systems, individual tree measurements form the basis for the monitoring, management and projection of forest biomass stocks (Lambert *et al.*, 2005; Woodall *et al.*, 2011; Neumann *et al.*, 2016). Many different methods for tree biomass prediction have been proposed, but they can generally be broken down into three classes: (1) biomass equations that predict total tree or tree component biomass directly from tree measurements, typically stem diameter at breast height (dbh); these are often referred to as ‘allometric’ equations (Sileshi, 2014); (2) ‘biomass expansion factor’ (BEF) approaches that convert tree total or merchantable stem volume into total tree biomass by integrating wood density with the stem volume estimates to predict stem mass and the total tree mass (Segura and Kanninen, 2005; Westfall, 2012); and (3) ‘hybrid’ approaches that use some elements of the previous two classes (i.e. a BEF for bole volume and biomass, allometric models for belowground and crown components; e.g. Ver Planck and MacFarlane, 2015).

The Forest Inventory and Analysis (FIA) program in the US utilizes a hybrid biomass estimation approach referred to as the component ratio method (CRM; Woodall *et al.*, 2011; Domke *et al.*, 2012). In the CRM, inside bark bole biomass is estimated by expanding predictions from an allometric stem volume model with species-specific estimates of wood density. Stump and crown components are then directly estimated using additional allometric models (Raile, 1982; Jenkins *et al.*, 2003), and bark biomass is calculated using published bark ratio and bark specific gravity values for North American tree species (Woodall *et al.*, 2011). The CRM has the advantage of providing biomass estimates that are consistent with volume estimates calculated from FIA data, but is limited in that it makes strict assumptions about several parameters that will affect total tree biomass estimates, including: (1) wood and bark specific gravity; (2) average bark to wood ratio of the stem; and (3) allometric scaling coefficients of branch and foliage biomass models. While previously these assumptions were necessary to ensure consistent biomass estimates within FIA, new datasets, coupled with data-driven methods for fitting models such as Bayesian estimation

techniques, provide an opportunity to expand the CRM to better account for among and within species heterogeneity in overall biomass assessments.

A key issue for any biomass estimation approach is accurately predicting total tree biomass, which is important for verifiable national forest carbon inventories. However, an ideal biomass estimation method should also accurately predict biomass components, as these are relevant to the valuation of wood products and usage of the tree (Domke *et al.*, 2012; MacFarlane, 2015). However, for hybrid approaches such as the CRM simultaneously estimating total and component biomass with sufficient accuracy and precision is challenging. Using a single allometric equation to directly estimate total biomass generally gives better results than adding up the sum of predicted components (e.g. stems, branches, leaves), because of the additive errors of each of the predicted components (Parresol, 2001; MacFarlane, 2015). BEFs extrapolate total biomass from the stem, so their total mass estimation is limited by the accuracy of the underlying stem volume equations, which are not necessarily well correlated with the volume and biomass of crown components. A recent analysis by Radtke *et al.* (2017) showed that the CRM underestimates live tree biomass in the eastern US by ~6–17 per cent and that direct estimation via species-specific allometric models was more accurate than any of the volume conversion methods they considered. Similar discrepancies between volume conversion and allometric modeling approaches have been observed for population-level biomass estimates in the US (Domke *et al.*, 2012), as well as in Scandinavia (Jalkanen *et al.*, 2005). While small, this body of evidence corroborates a recent review of biomass methods by Weiskittel *et al.* (2015) who suggested that allometric models are ‘probably’ more accurate; at least for total biomass estimates. However, given that NFIs are typically used for both volume and biomass stock assessments, BEFs and hybrid approaches, such as the CRM, as well as models used by most European nations (Neumann *et al.*, 2016), have become common and relatively widespread. Ensuring consistency between biomass and volume stock assessments is a great benefit of these methods, as it facilitates the accounting of carbon fluxes related to harvested wood products (Domke *et al.*, 2012).

Given the competing these needs (e.g. consistency between bole biomass and volume estimates, accurate estimation of components), hybrid approaches such as the CRM are a good compromise solution. Separate estimation of branch and foliage components via allometric models allows for greater flexibility in predicting these biomass pools, which is preferable given the variable nature of tree crowns. However, in order to guarantee accurate and precise estimation of both total and component biomass, the performance of these sub-models must be carefully evaluated when embedded into a hybrid approach such as the CRM. Currently, the CRM uses component ratio equations developed based on biomass ‘pseudodata’ by Jenkins *et al.* (2003), yet previous work has shown that this approach exhibits significant bias and uncertainty in the prediction of crown components (MacFarlane, 2015; Clough *et al.*, 2016a, b). Further, the impact of component models on the overall accuracy and precision of total biomass estimates from hybrid approaches is unknown. Since hybrid approaches are likely to remain commonplace for NFIs that report both carbon and volume estimates, addressing these methodological gaps is an important priority.

Recent advances in forestry data science present the opportunity to revisit the CRM, with the aim of addressing these important issues. These include the compilation of new datasets that allow for direct evaluation of both total and component biomass models (Radtke *et al.*, 2017), as well as the proliferation of new computational approaches that allow for prediction uncertainty to be conditioned on these data. Bayesian estimation techniques provide a particularly convenient framework for integrating the uncertainty of component models as in a hybrid biomass estimation approach and, when specified with ‘weakly informative’ priors (Gelman *et al.*, 2003), allow these uncertainty estimates to be largely informed by the fit of component models to the best available data.

This study presents a new, modified version of the CRM (n-CRM) and compares this hybrid approach to a standard allometric approach for estimating total tree biomass, with the overall goal of understanding how aboveground components of the hybrid approach (branch, foliage, stump and bark) contribute to the error in total mass estimation. We perform this analysis for six common, widespread species of the eastern US (three hardwoods and three conifers), and we adopt a Bayesian simulation approach that allows us to access estimates of prediction accuracy and uncertainty at the tree scale. The specific objectives of the study were to: (1) develop and parameterize the n-CRM and compare it to total mass allometric models for each of the six study species; (2) analyze a suite of individual traits to determine which factors have the largest influence on the accuracy (i.e. residual error between predicted and observed biomass) and precision (i.e. relative uncertainty estimates) for each species; and (3) assess differences among species and/or taxa (hardwoods vs. conifers) to formulate recommendations for further improvements of the n-CRM approach.

Methods

Data

Data for this study were drawn from the US Forest Service legacy biomass database, a repository of more than 250 000 individual tree attribute records that has been collated from published and unpublished sources, for the purposes of developing and calibrating tree-scale biomass and volume models (LegacyTreeData, 2016), along with data from an ongoing project to enhance the legacy database (Radtke *et al.*, 2017). The key data for constructing and fitting the n-CRM were: (1) bole volume to a 10 cm top; (2) wood specific gravity; (3) bark ratio (i.e. bark volume as a fraction of wood volume) of the bole; (4) bark specific gravity; and (5) aboveground biomass and component biomass (i.e. stem, branch, foliage) data. Wood specific gravity, bark specific gravity and bark ratio data were used to estimate both stem and stump biomass. Total aboveground biomass, dbh and total height measurements for the trees were used for fitting the standard allometric model. The legacy database is a data compilation, so while it is the best resource available for fitting models of US tree species, it is not a systematic sample of tree attribute data. Consequently, we confined our analyses to six species in the dataset, three hardwood species (red maple (*Acer rubrum* L.), sweetgum (*Liquidambar styraciflua* L.), and white oak (*Quercus alba* L.)) and three pine species (loblolly pine (*Pinus taeda* L.), slash pine (*Pinus elliotii* Engelm.) and longleaf pine (*Pinus palustris* Mill.)). Each of these species had reasonable samples (i.e. >100 observations of each attribute) of the aforementioned variables across a range of tree sizes and locations (Table 1).

Table 1 Summary statistics for fitting and validation datasets.

CRM datasets								
	Bole volume					Bark specific gravity		
	N	Volume (m ³)		dbh ² h (cm ² *m)		N	Mean	SD
		Mean	SD	Mean	SD			
Red maple	137	0.34	0.29	12 272.98	10 451.93	193	0.52	0.05
Sweetgum	470	0.44	0.5	16 064.42	17 248.41	732	0.37	0.07
White oak	236	0.57	0.6	20 339.48	20 894.66	297	0.53	0.07
Loblolly pine	567	0.87	0.66	25 063.26	18 731.39	1808	0.32	0.1
Longleaf pine	449	0.69	0.5	22 662.05	15 817.77	625	0.38	0.1
Slash pine	469	0.46	0.5	15 710.22	15 414.63	831	0.35	0.05
	Wood specific gravity			Bark ratio				
	N	Mean	SD	N	Mean	SD		
Red maple	233	0.49	0.06	348	0.13	0.03		
Sweetgum	745	0.47	0.02	745	0.14	0.04		
White oak	306	0.64	0.03	333	0.14	0.04		
Loblolly pine	3814	0.46	0.05	567	0.19	0.06		
Longleaf pine	626	0.56	0.07	799	0.14	0.07		
Slash pine	1723	0.51	0.06	1114	0.22	0.09		
	Branch biomass (kg)		Foliage biomass (kg)		dbh (cm)			
	N	Mean	SD	Mean	SD	Mean	SD	
Red maple	142	86.98	245.93	6.02	7.35	20.82	9.44	
Sweetgum	323	46.38	55.72	3.86	4.55	21.02	8.9	
White oak	199	135.65	167.12	15.04	18.06	24.12	11.32	
Loblolly pine	531	38.23	39.15	9.51	9.83	21.63	10	
Longleaf pine	159	66.34	78.51	13.63	13.95	23.5	11.41	
Slash pine	409	30.34	28.78	9.45	9.65	18.94	7.5	
Allometric model and validation data								
Fitting datasets								
	Total biomass (kg)			dbh (cm)				
	N	Mean	SD	Mean	SD			
Red maple	142	269.75	485.57	20.82	9.44			
Sweetgum	323	239.11	278.51	21.02	8.9			
White oak	199	467.78	534.65	24.12	11.32			
Loblolly pine	531	241.57	331.92	21.63	10			
Longleaf pine	159	348.53	349.13	23.5	11.41			
Slash pine	409	190.75	253.3	18.94	7.5			
Validation datasets								
Red maple	58	311.95	855.96	17.28	14.43			
Sweetgum	155	526.85	723.34	27.11	14.9			
White oak	48	1372.14	1747.97	36.58	19.73			
Loblolly pine	369	184.8	270.46	19.98	7.87			
Longleaf pine	95	600.77	455.15	29.05	10.75			
Slash pine	152	260.25	381.67	20.68	10.3			

Note that the CRM utilizes several data sources (stem volume, wood and bark specific gravity, biomass components) while the allometric model uses only total aboveground biomass.

Modeling approach

The first step was to construct a data-informed hybrid model, modified from the currently used CRM approach, which follows Woodall *et al.* (2011). In brief, Woodall *et al.*'s (2011) approach uses standard regional volume equations and species-specific tree density estimates within a BEF approach to estimate bole biomass (Domke *et al.*, 2012), with separate estimates for wood and bark density, as well as a model for stump volume, based on the volume equations of Raile (1982). These are expanded to give total biomass and then other component biomass pools are estimated via component ratio models developed by Jenkins *et al.* (2003) which predict the fraction in each pool from dbh. For more complete details on the CRM approach, refer to Woodall *et al.* (2011).

The n-CRM employed in our study followed the protocols outlined in Woodall *et al.* (2011), but with several important differences. Of course, the most important is that rather than using fixed scaling coefficients and expansion factors, we allow all n-CRM parameters to follow statistical distributions, and therefore reflect the uncertainty of each component in biomass estimates. Under the standard CRM approach, wood and bark specific gravity are fixed values, drawn from published tables (Miles and Smith, 2009) and the bark ratios are predicted from allometric models using dbh (Jenkins *et al.*, 2003). In n-CRM, we allowed the latter parameters to vary, following a statistical distribution derived from the legacy data. Additionally, we also adopted some changes to the component allometric models used in CRM. Specifically, n-CRM used allometric models that estimate stem, branch and foliage biomass directly, rather than using the component models of Jenkins *et al.* (2003), since Clough *et al.* (2016a, b) suggest that this is a more accurate approach for predicting biomass components. Each of these components was predicted from tree dbh and height. Finally, the CRM applies an additional adjustment when predicting sapling biomass, but given that we have observed biomass data across a range of tree sizes we did not adopt this approach in n-CRM. Since the legacy data do not possess observations of stump volume, we follow the CRM in calculating the volumes of stump wood and bark empirically using models defined by Raile (1982). Table 2 outlines the set of component models used within n-CRM.

Total tree biomass was predicted as a function of dbh (cm) and total tree height (m) to provide a reference model to compare the n-CRM to (Table 2). Both the dependent and independent variables were log transformed and then to fit a linear function. Several authors have suggested that a log-linear specification reduces residual error in total tree biomass predictions (Sileshi, 2014; Radtke *et al.*, 2017).

Model fitting

We adopted a Bayesian inferential framework for model fitting. Bayesian inference integrates prior information with likelihood functions drawn

from models fitted to the data, allowing for generation of posterior predictive distributions for independent observations (i.e. validation data; Gelman *et al.*, 2003). In this way, Bayesian models naturally account for uncertainty resulting from the model as well as data-level variance, and are an ideal system for assessing the precision of different elements of the biomass models.

Fitting of both the n-CRM and the allometric model was accomplished using Stan (Stan Development Team, 2015), based on 1000 Markov chain Monte Carlo iterations following a 'warm up' period of 1000 iterations from four Markov chains (i.e. a total of 2000 iterations). To develop posterior predictive biomass estimates for the n-CRM approach, we generated 2000 posterior simulations of the following attributes for each observation in the validation datasets: (1) bole volume; (2) bark ratio; (3) wood specific gravity; (4) bark specific gravity; (5) bole biomass; (6) branch biomass; and (7) foliage biomass. In addition, we generated posterior simulations of total aboveground biomass using the standard allometric model described above and in Table 2. This approach resulted in tree-scale posterior predictive distributions (i.e. 2000 posterior simulations per tree) for the validation datasets of each study species, generated using both n-CRM and allometric modeling approaches. We summarized these distributions into mean estimates and posterior uncertainty interval ranges (i.e. 95% uncertainty interval of each posterior predictive distribution), which were used both to compare overall performance of the two approaches for each species by root mean squared percentage error and percent mean bias. We use these relative measures to allow for better comparisons across species, where the datasets differed in tree size distribution. Additionally, model residuals and relative uncertainties for each prediction were saved for the traits-based analysis aimed at assessing sources of uncertainty in each method.

Model validation and accuracy assessment

The summary output from the fitted n-CRM and allometric models was used to obtain tree-scale estimates of accuracy (residuals between posterior predicted means and observed values in the validation data) and precision (relative uncertainty, defined as the ratio of the posterior 95% uncertainty interval and the posterior predicted mean) for all six species.

We assessed the role of five traits available from the validation data in accounting for the accuracy and precision of the n-CRM and allometric approaches: crown ratio (CR); ratio of foliage biomass to total aboveground biomass (FR); ratio of leaf biomass to stem area at dbh (FSR); total height (ht; m); and diameter at breast height (dbh; cm). We included the crown characteristics, in addition to height and diameter, because the n-CRM separately estimates crown components (i.e. branches, foliage) and because we expected large uncertainties associated with predicting these pools (Wirth *et al.*, 2004; Wutzler *et al.*,

Table 2 Equations, and relevant references, related to the tree attributes that were simulated based on legacy data for each approach.

CRM	Attribute	Equation	References
	Bole volume	$\ln(\text{Vol}) = \alpha + \beta \ln(\text{dbh}^2 \text{ht}) + \epsilon$	Woodall <i>et al.</i> (2011)
	Stump volume	$S_{\text{vol}} = \frac{\pi (\text{dbh})^2}{4(144)} \left[(\alpha - \beta)^2 + 11\beta(\alpha - \beta)^2 \ln(\text{ht} + 1) - \frac{30.25}{h+1} \beta^2 \right] \frac{\alpha}{\beta}$	Raile (1982)
	Wood specific gravity	$\text{WSG} \sim \text{Weibull}(\mu, \tau)$	n/a
	Bark specific gravity	$\text{BSG} \sim \text{Weibull}(\mu, \tau)$	
	Bark ratio	$\text{BR} \sim \text{Weibull}(\mu, \tau)$	
	Biomass components (stem, branch, foliage)	$\ln(\text{BM}) = \alpha + \beta_1 \ln(\text{dbh}) + \beta_2 \ln(\text{ht}) + \epsilon$	Clough <i>et al.</i> (2016a, b)
Allometric model	Total aboveground biomass	$\ln(\text{BM}) = \alpha + \beta_1 \ln(\text{dbh}) + \beta_2 \ln(\text{ht}) + \epsilon$	Jenkins <i>et al.</i> (2003)

For details on the conversion of n-CRM attributes to aboveground biomass estimates, see Woodall *et al.* (2011) and Appendix A.

2008; Clough *et al.*, 2016a, b) to have a relatively large effect on overall performance of the n-CRM, particularly in the case of small trees (<10 cm diameter at breast height (dbh)).

We used a random forests (RF) analysis to assess the impact of individual tree measurements and traits on the performance of n-CRM and the standard allometric model. We simulated 1000 trees from the RF algorithm implemented in the ‘randomForest’ package for R (Liaw and Wiener, 2002), and evaluated the influence of each trait on the percent increase in mean squared error associated with each variable left out of the selected model. This approach provided a quantitative assessment of the relative impacts of different explanatory variables (i.e. tree size (dbh and ht)) vs traits such as wood density or crown characteristics) on the accuracy and precision of the n-CRM. This approach has been previously used to assess the influence of both plant functional traits and climate variables on forest productivity in the eastern US (Weiskittel *et al.*, 2011; Russel *et al.*, 2014).

We withheld independent datasets from the available aboveground biomass data in the legacy data repository for model validation. In general, we selected datasets that were totally independent (i.e. collected by different authors at different locations) from the fitting data. Since the n-CRM uses different attributes than those used for fitting allometric models and validating predictive performance (i.e. volume, specific gravity and component biomass datasets vs total aboveground biomass), this ‘hold-out’ predictive approach was necessary. Since all of the relevant variables are not available for every tree used in our analysis, testing on separate datasets rather than doing ‘pseudo out-of-sample’ assessments via cross validation procedures is necessary (Vehtari and Ojanen, 2012). Using fully independent validation data represents a strong test of predictive performance (Vehtari and Ojanen, 2012), although in this case it also required that inferences were made on a small number of datasets.

Results

Performance of n-CRM and allometric models for predicting total tree biomass

Overall, our results suggest that the n-CRM tended to provide more accurate predictions of total tree biomass, as evaluated with root mean squared error (RMSE, see Table 3), in comparison with species-specific allometric models. The n-CRM was more accurate for four species (longleaf pine, slash pine, sweetgum and white oak), with fairly large differences in accuracy for the two pines (i.e. 20–30 per cent relative improvement) and much narrower gains for the hardwood species (i.e. ~3 per cent). The allometric model performed better for loblolly pine and red maple, although for red maple the result was heavily influenced by greater under-prediction of one large (~6 000 kg) tree in the

Table 3 Root mean squared percentage error and percent mean bias for n-CRM and allometric models applied to each of the study species.

	CRM (%)		Allometric (%)	
	RMSE	Mean bias	RMSE	Mean bias
Loblolly pine	29.82	8.42	23.67	-2.41
Slash pine	18.31	-7.95	23.31	-13.29
Longleaf pine	19.74	-4.88	29.51	7.94
Red maple	19.74	-4.88	29.51	7.94
Sweetgum	72.71	-17.23	47.10	-8.71
White oak	27.91	-5.88	28.70	3.52

validation dataset (Figure 1). In general, prediction performance of both methods was poor for large (>1000 kg) red maples, although only three such individuals were available for fitting models. In the case of loblolly pine, the difference in RMSE between the two methods was narrower, mainly arising from a tendency of the n-CRM to over-predict the biomass of small trees (Table 4). Most species showed opposing signs in bias estimates for the n-CRM and allometric models, though these trends were not consistent across species. For example, the n-CRM showed a negative bias and the allometric model a positive bias for slash pine, but the opposite was true of loblolly pine. In the case of longleaf pine both methods under-predicted observed values (Table 4), though the bias was less severe for the allometric model. White oak showed similar bias between the two methods for smaller trees, but a greater tendency of the n-CRM to underestimate large individuals. White oak and sweetgum exhibited poorer accuracy by either method when compared to the remaining four species.

Examining RMSE and bias for the component models used in the n-CRM showed a negative bias for branch biomass and positive bias for foliage, with some exceptions (i.e. foliage biomass for loblolly pine; Table 4). Bias of stem components was negative for the three pine species and positive for the three hardwoods. Comparing RMSEs to mean observed component biomass for the validation data showed much poorer prediction accuracy for the branch and foliage biomass models when compared to the stem biomass model. However, accuracy of the branch models for the three hardwood species was generally poorer than those fitted to the pines. The same was true of the foliage biomass models for loblolly and longleaf pine, though the foliage biomass model for slash pine had higher error.

Influence of individual traits on accuracy and precision of n-CRM and allometric models

For the most part, the traits we considered explained little or no variance for the residuals of both the n-CRM and allometric model (Table 5). The exception was loblolly pine, where a moderate degree of variation was explained for both n-CRM and allometric model residuals (47 and 29 per cent, respectively). For this species, CR had the highest importance score for n-CRM residuals while DBH had the highest for allometric residuals. Additionally, while the remaining residuals models explained little or no variance, the highest ranking variables were either related to foliage biomass (FR, FSR) or overall tree size (DBH, HT).

Precision of the n-CRM predictions (i.e. relative uncertainties, Table 5) was well explained by the traits, with these models accounting for 54–92 per cent of the variance across all species. In all cases, the most important variables were some combination of CR, DBH and HT. The size variables were the most important for longleaf pine and the three hardwood species, while DBH and CR were most important for loblolly and slash pine. Allometric model relative uncertainty was generally not explained by the traits we considered, though a little more than half of the variance for red maple was accounted for by size (DBH, HT).

To better understand the nature of the relative uncertainties they were plotted against dbh for each species (Figure 2). In all cases, the n-CRM displayed poor precision relative to the allometric model for small individuals (<10 cm dbh), but these differences disappeared for larger trees where the precision of

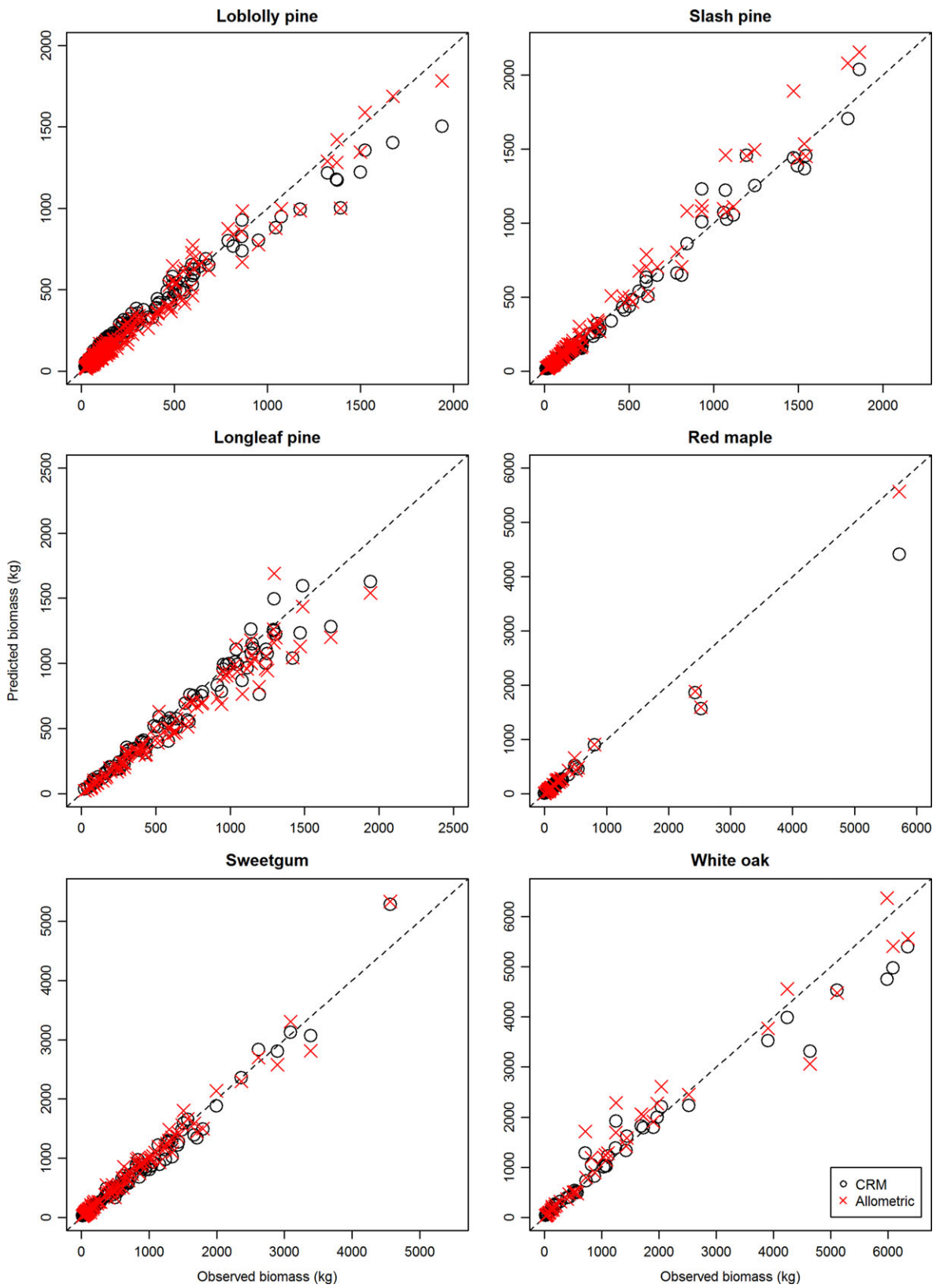


Figure 1 Predicted vs observed biomass for the CRM and allometric models.

Table 4 Root mean squared percentage error and percent mean bias for biomass components (stem, branch, foliage) according to the component models used in n-CRM approach.

	Stem (%)		Branch (%)		Foliage (%)	
	RMSE	Mean bias	RMSE	Mean bias	RMSE	Mean bias
Loblolly pine	25.1	-2.3	66.0	4.2	50.6	-3.0
Longleaf pine	21.3	-13.8	59.5	-11.0	46.0	-16.0
Slash pine	17.2	-1.0	92.1	-21.4	185.8	72.6
Red Maple	58.8	0.1	289.1	-52.2	127.7	27.7
Sweetgum	19.8	5.0	107.3	-35.1	75.5	16.0
White oak	20.9	5.5	105.5	-42.0	262.7	161.4

both approaches is generally comparable. This trend is particularly apparent for red maple, where relative uncertainties were very high (up to 700 per cent) for small trees, which agreed with the finding that dbh and ht influenced prediction precision for red maple even if size did not have a large impact for other hardwoods. In slash pine and red maple, the n-CRM maintains a small but notable higher uncertainty even for larger individuals, while the remaining species show comparable performance between the two methods. Note however that the validation dataset contains only four red maples >1000 kg in biomass. In all cases, the relative uncertainties for the n-CRM method exceed that of the allometric models, indicating greater precision with the allometric approach. However, the relative uncertainties were generally large (greater than 75 per cent, and in most cases greater than 100 per cent) across all species, indicating very poor precision in these data-fitted models regardless of whether a n-CRM or allometric equation is used.

Since the n-CRM also gives component biomasses, in addition to total biomass, we were also able to examine how the parts contributed to prediction of the whole for this method. Examining the same relationships (i.e. posterior relative uncertainty plotted against dbh) for aboveground biomass components provides further context for the patterns in overall biomass uncertainty (Figure 3). In components the uncertainty/size relationship was less severe, with the exception of branch and foliage biomass for red maple, which showed a relationship between relative uncertainty and dbh. Hardwoods showed generally higher relative uncertainty in branch and foliage predictions when compared with the three pine species. In particular, red maple and sweetgum show relative uncertainties >200 per cent for foliage biomass, and uncertainties between 150–200 per cent for branch biomass. By contrast relative uncertainties for foliage were lower for softwoods, although both branch and foliage relative uncertainty were comparable to that of white oak. Relative uncertainty of the stem model was fairly comparable across all six species, although in loblolly pine the relative uncertainty of all three components was similar and higher than stem relative uncertainty in the other species.

Discussion

Our analyses revealed several important trends related to tree biomass estimation via n-CRM relative to a standard allometric

approach which only uses dbh and height. First, our results show that n-CRM can at least provide comparable predictive performance to standard allometric approaches for predicting total tree biomass, and for some species may offer improvements in prediction accuracy. However, it also needs to be recognized that the n-CRM uses considerably more information to do so (Table 2). Both the n-CRM and the allometric models here used height and dbh as baseline predictors, but the n-CRM also used wood density, which has been shown to improve both component and total tree mass estimation (MacFarlane, 2015). Though less accurate in four of six cases, the allometric models had lower uncertainty overall and a generally constant invariance over the size range. This suggests that standard allometric models are more precise than the n-CRM-type approaches, particularly for small trees, but may have greater bias. This bias likely comes with the assumption of constant scaling across size, which is a hallmark of allometric scaling theory (Enquist and Niklas, 2001), although our results indicate that these trends may be less consistent for crown components.

Second, the crown component (branches, foliage) models used in the n-CRM showed poor prediction accuracy and precision (relative uncertainty) when compared to stem biomass, particularly for hardwood species. Previous work by Clough *et al.* (2016a, b) highlighted substantial uncertainties that arise when predicting component biomass pools such as foliage with hierarchical models fitted to biomass data, and application of similar component biomass models within the CRM in this analysis fits with this pattern. Crown components occupy a much larger proportion of total biomass at smaller size classes, so uncertainty in foliage and branch biomass accounts for the much poorer precision of the CRM when applied to smaller diameter trees. This effect is particularly apparent for red maple, which was also the only species to show substantial size dependence (i.e. poorer precision for small trees) in the relative uncertainty of its biomass components as well.

Third, results of posterior predictive assessment show size dependence in precision of CRM predictions across all species, which is linked to both dimensional and crown attributes by the RF analysis. The pattern of exponentially decreasing relative uncertainty across size from the CRM, with constant relative uncertainty from the allometric model, is particularly striking. These results agree with a stand-level comparison of BEFs and allometric models conducted by Jalkanen *et al.* (2005), who found that BEFs produced higher relative standard errors than allometric models across all age classes, with generally poorer precision of both methods among younger trees. However, unlike Jalkanen *et al.* (2005), we found that the relative precision of the two approaches were strongly size dependent (i.e. Figure 2). This disagreement is probably explained by methodological differences: their study used a BEF to convert stem volume to total aboveground biomass, while our approach followed Woodall *et al.* (2011) in using a BEF to calculate bole biomass and separate allometric equations for crown components. Thus, while our results generally confirm the CRM as a comparable method for biomass estimation of major North American tree species, they also reveal important gaps in the CRM, such as the very poor precision of predictions for small diameter trees relative to standard allometric models. Such issues influence the overall precision of biomass stock assessments calculated from NFIs, but also highlight the role of predictive model assessment for improving forest biomass estimation procedures.

Table 5 Variable importance scores (%IncMSE) and fit statistics (R²; MSE) for the residuals for the full model and two variable models fit with the RF algorithm.

	Variable importance (% increase in MSE)			
	n-CRM residuals	n-CRM relative uncertainty	Allometric residuals	Allometric relative uncertainty
Loblolly pine				
CR	22.3*	34.5**	16.7	16.7*
FR	18.7	19.8	22.2**	15.6
FSR	17.78	23.2	18.2	5.8
HT	19.57**	29.4	16.1	15.7**
DBH	14.22	39.1*	31.4*	11.9
R2	0.47	0.92	0.29	-13.71
MSE	562.8	0.002	1166.2	9.00E-04
Longleaf pine				
CR	3.4	14.3	3.9	9.3
FR	13.4**	11.6	10.4	12.1**
FSR	19.8*	9.5	12.1**	8.7
HT	10.3	28.3*	12.7*	8.1
DBH	7.9	28.1**	8	13*
R2	8.57	85.86	4.66	1.92
MSE	7020.1	2.00E-03	9068.2	1.00E-04
Slash pine				
CR	6.4	25.8**	5	9.6
FR	9.1**	14.4	11.6**	9.9
FSR	10.2*	13.4	9.1	2.8
HT	1.7	25.1	12.3*	10**
DBH	-3.9	29.6*	9.4	13.6*
R2	-5.61	93.85	-5.3	-16.03
MSE	2611.8	2.00E-03	3925.9	2.00E-04
Red maple				
CR	9.5*	11.5	5.5	9.5
FR	3.2	14.2	2.4	13.4
FSR	8**	10.7	8.8*	8.8
HT	1.7	14.6**	6.5**	15.7**
DBH	1.3	17.2*	-1.7	17.4*
R2	-19.74	54.22	-14.27	54.9
MSE	5122.3	5.00E-04	16 284.9	5.00E-04
Sweetgum				
CR	6.8	28.5	2.2	10.5
FR	11.1**	15	12.2*	7.8
FSR	12.6*	13.9	10.8**	2.9
HT	2.9	29.7**	-4.7	11.2*
DBH	10.2	30.8*	0.7	12.5*
R2	-0.17	94.55	-27.43	-25.06
MSE	10 541	2.00E-03	14 841.9	3.00E-04
White oak				
CR	2.52	15.5	-2.5	1.2
FR	-1	12.3	-2.9	8.9
FSR	-1.6	5.7	-3.8	10.2**
HT	9.7**	20.7**	14.1*	5.7
DBH	17.6*	21.5*	13.6**	12.7*
R2	-5.94	87.9	-10.63	2.66
MSE	51 795	0.01	140 989	2.00E-04

Separate models are presented for n-CRM and allometric model, as well as the relative uncertainties, for each of the study species. * Indicates the most important variable of the two variable model and ** indicates the second variable.

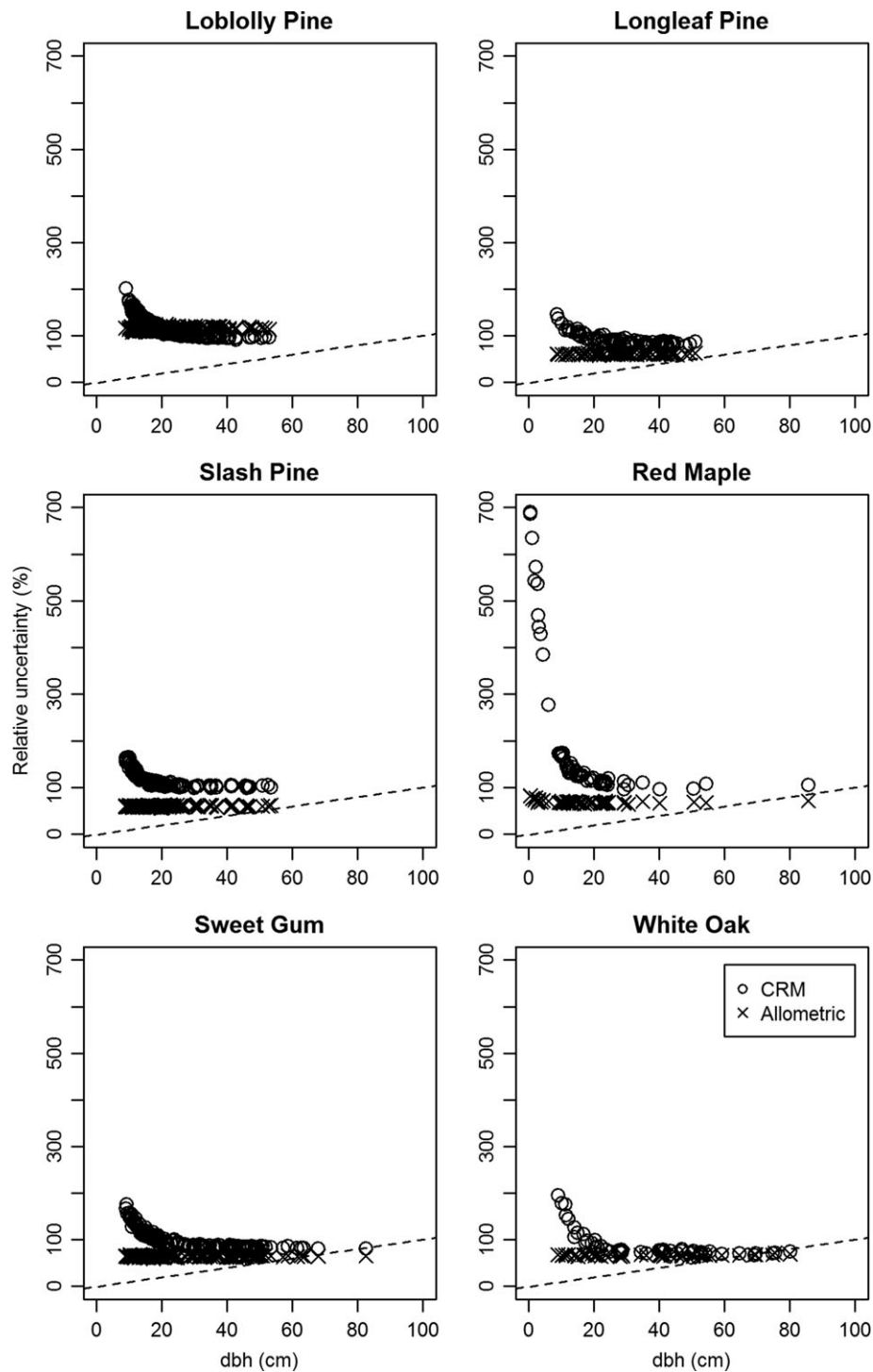


Figure 2 Relative uncertainty of biomass predictions (posterior 95% uncertainty interval/posterior mean) vs diameter at breast height (dbh) for the component ratio model (CRM) and allometric model (Allometric).

Species-related influences on results

The species-level traits that influenced performance of both the CRM and allometric models highlight possible ways to improve the overall accuracy of biomass stock assessments.

The differences in accuracy and precision of component biomass models between pine and hardwood species may be related to general differences in whole-tree architecture and growth between the two taxa. Conifers tend to have an

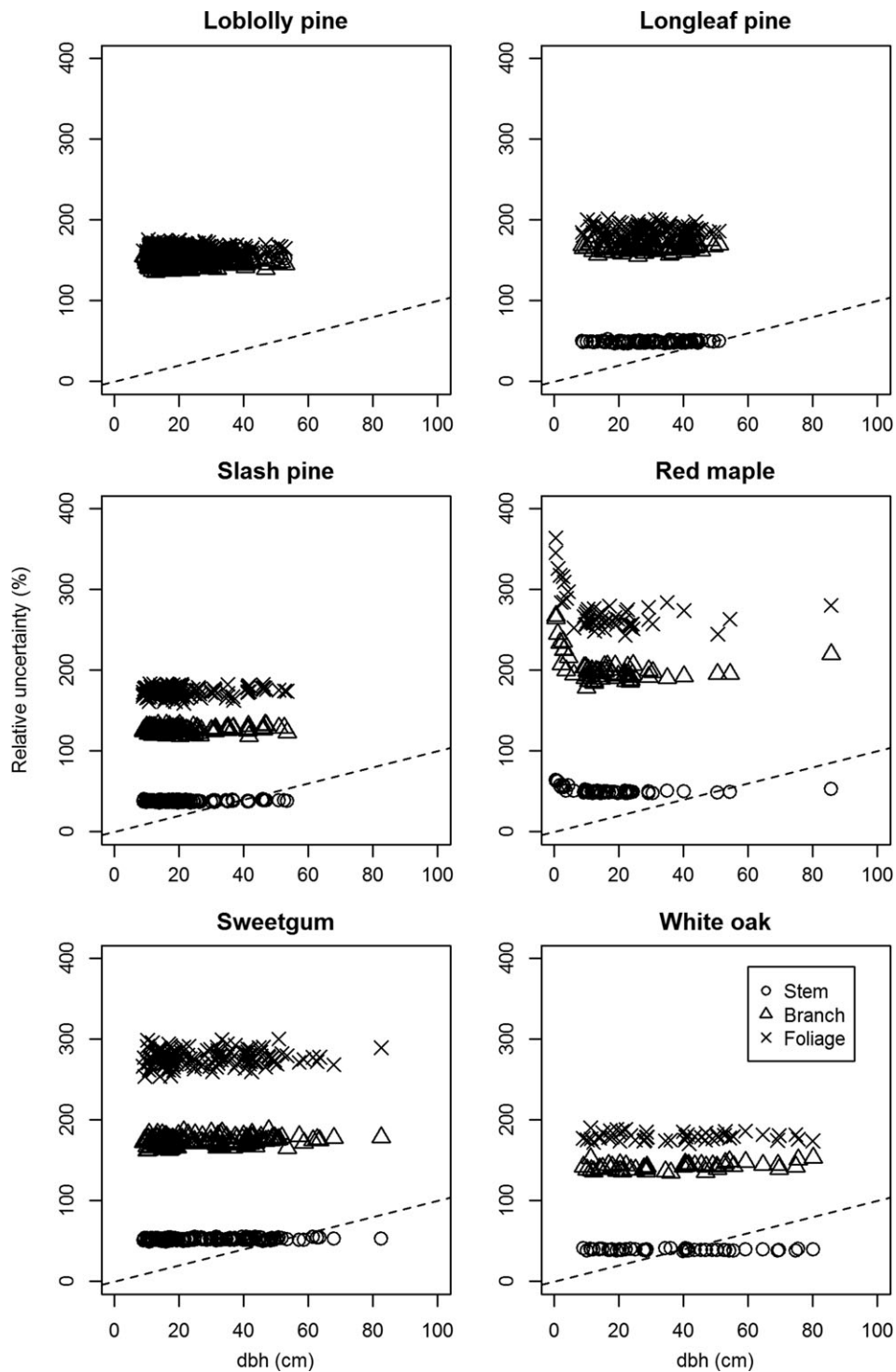


Figure 3 Relative uncertainty of component biomass predictions (95% posterior uncertainty interval/posterior mean) vs dbh.

excurrent, vertical crown structure (i.e. low width and but relatively high depth in the canopy) and strong vertical growth, which distributes branch and foliage biomass along a similar vertical axis to stem biomass. By contrast hardwood tree species typically exhibit decurrent crowns where most or all of the crown biomass arises from a single plane at the top of the stem

and large branches may account for a significant proportion of the overall tree biomass (MacFarlane, 2010). These differences have been previously noted as reasons why incorporating crown dimensions into models of bole volume might be less effective for conifers than for hardwoods (Thomas and Paresol, 1991; Valentine and Gregoire, 2001). In conifers, crown dimensions

are generally proportional to overall tree size, so they add little new information to a bole model (MacFarlane, 2010). However, a more uniform crown structure should mean that allometric functions for predicting crown components based on tree size should perform better for conifers than for hardwoods. Our results provide some indication of this, at least when comparing the pine and hardwood species considered by our study. The better prediction accuracy of the component models for the pine species suggests that separately modeling biomass components as in the CRM might be a better approach for conifers than for hardwoods. It should also be noted that all three hardwoods we analyzed are at least relatively shade tolerant species, which may have denser wood and shorter boles that can support large crowns, even in sub-canopy positions (Ninements and Valladares, 2006). However, the legacy data we employed are a compilation of studies collected from multiple locations, so disentangling the effects of management (i.e. plantation vs natural stands), competition and other site-specific factors which many influence biomass allocation to crowns is challenging and beyond the scope of our study. So, while our results point to some general patterns, fully evaluating whether these results generalize to other sites and/or species requires a more diverse sample of crown biomass data.

In addition to accounting for general differences in tree architecture, directly modeling biomass components may account for other methodological gaps as well. Allometric scaling theory assumes that branching networks such as tree crowns are volume filling, but the pine species we studied can exhibit substantial variation in relationships between crown volume and tree size (Chmura *et al.*, 2007). Additionally, branch senescence, which is common in pines, is poorly accounted for by allometric models, unless they incorporate an auxiliary variable such as CR (Mäkelä and Valentine, 2006). In these cases, directly predicting component biomass with their own allometric relationships (i.e. dbh-branch; dbh-foliage), rather than integrating these into a whole-tree biomass estimate, may represent a more accurate approach. This notion is partly validated by our comparison of total aboveground biomass predictions for the CRM and allometric model, where the former tended to perform better for the pine species. The exception is loblolly pine where the allometric model showed a modest relative improvement in accuracy that seems to be related to lower bias in predicting small diameter trees. However, given the broad morphological and biological similarities between these three pine species, this difference likely arises from broad differences in site level factors such as management regime.

Future application of n-CRM in the US' NFI

The CRM is the current approach for quantifying forest biomass in the US National Greenhouse Gas Inventory (EPA, 2016), and our results highlight a need for model improvements to increase the precision of overall biomass stock assessments. Most importantly, our results provide both an overall assessment of the uncertainty in biomass CRMs, as well as some indication of the most important contributors to overall error. Taken together, these results present a case for both data-driven approaches to biomass estimation, as well as the 'hybrid' estimation approach relative to allometric models. However, they also indicate

specific methodological improvements to the current CRM that may improve the accuracy of biomass predictions.

The scale of prediction uncertainty from n-CRM, as well as the distribution of precision estimates among species and size classes, is perhaps the most important finding of our work in that it presents a strong case for utilizing data-driven approaches to estimate biomass within NFIs. The current CRM method assumes that both BEFs as well as allometric scaling coefficients are fixed (Woodall *et al.*, 2011), which does not allow for prediction uncertainty to be directly assessed at the tree scale. By contrast, n-CRM uses the Legacy Tree Database to fit models via Bayesian estimation techniques, which naturally allow for posterior uncertainty assessments that capture both model and residual error to be derived. This is advantageous over CRM because accurate quantification of error in biomass stock assessments is part of the United States' reporting commitments under the United Nations' Framework Convention on Climate Change (EPA, 2016), and the current CRM approach ignores tree-scale model error (Clough *et al.*, 2016a, b). Of course other the n-CRM approach could be adopted to other statistical frameworks, particularly when point estimation is the main goal and uncertainty assessments are not necessary. However even in these cases the Bayesian framework is useful for continuous updating of models, where previous predictions and parameter estimates act as priors for updates to n-CRM. This feature provides a convenient workflow for continuously expanding models (Gelman *et al.*, 2003), which is useful since the Legacy data and other data resources will grow as additional sampling efforts are undertaken.

From the perspective of obtaining accurate biomass estimates, our results provide some evidence to prefer component ratio approaches over allometric models. Overall, we demonstrate that the n-CRM is capable of producing better or comparable accuracy to allometric models, but exhibits poor precision when predicting biomass of smaller trees across a range of softwood and hardwood species. The trait analysis we conducted, along with the posterior uncertainties of branch and foliage biomass, indicates that this pattern is driven by large posterior prediction uncertainties in crown components, particularly foliage biomass, which make up a large proportion of overall biomass in smaller trees. The models in our CRM implementation use dbh and height as predictors, but our trait analysis supports the inclusion of auxiliary variables such as crown diameter (MacFarlane, 2015) or metrics (potentially drawn from remote sensing datasets; e.g. Jucker *et al.*, 2017) to increase both precision and accuracy. However, while precision of CRM predictions was explained by some of the traits we considered, model residuals were generally not well accounted for, suggesting additional factors which influence the accuracy of the CRM approach. In general, our results suggest that standard allometric modeling approaches may be suboptimal for addressing the overall architecture and variation in crown biomass in conifers, particularly pines, and that therefore n-CRM is likely to produce better component biomass estimates. Given that n-CRM also provides the advantage of consistent biomass and volume assessments, and that accuracy was better or comparable to allometric models for the six species we assessed, our results provide support for the application of component ratio approaches within NFIs.

However, our work also suggests that improvements are needed to the CRM method if it is to be applied for developing national biomass stock assessments. In particular, our posterior

analysis suggests that substantial improvements to crown component models are necessary if the CRM is to be relied upon for producing accurate, precise biomass predictions within national forest inventories. In particular improvements to crown component models are necessary, and more flexible approaches for modeling stem biomass may help reduce prediction uncertainty in hardwoods and small stems. [Radtke et al. \(2017\)](#) also demonstrate significant gains via alternative model formulations with the CRM, though ultimately conclude that allometric models still provide more accurate biomass stock assessments. The methodological changes considered in their study should be considered for implementation, and our work extends these results by arguing for additional exploration of key plant traits which may account for variation in component ratio models. While the inferences in our study are based on a small number of validation datasets owing to the hold-out predictive approach necessitated by the CRM/allometric model comparison, the trends across hardwood and softwood species in our study suggest that future work should seek to understand how these patterns generalize for larger, more representative biomass datasets. The 'out of sample' prediction we performed is akin to applying fitted models to independent tree measurements within NFIs, so our results indicate that the largest expected influences would be for early successional forests and resource-limited ecosystems, where trees maintain small stature such as the 'pine barrens' forest types found throughout the Atlantic coastal plain in the eastern US.

Finally, these analyses would not be possible without large, independent data resources such as the legacy tree data repository used here. These are invaluable for conducting robust predictive evaluation, and for critiquing the performance of different models as we do here. As data for more species and sampling locations are added worldwide (e.g. [Jucker et al., 2017](#)), additional inferences on traits driving variation in biomass stock estimation procedures, as well as more robust comparisons of alternative biomass model formulations, will be possible. Additionally, the overall large relative uncertainties we observed (i.e. greater than 75 across all species regardless of the method applied) indicate that, regardless of the approach, allometric model error requires consideration as a source of uncertainty when predicting biomass at stand to regional levels. Resources such as the legacy data are crucial for ensuring that these uncertainties are accurately captured and accounted for in biomass stock assessments.

Acknowledgements

Data compilation for the legacy data and the independent validation datasets, as well as B. Clough's time, were funded by the USDA Forest Service Forest Inventory and Analysis Program, Northern Region. Additional funding and support was available from the Minnesota Agricultural Experiment Station. Part of D.W. MacFarlane's time was supported with funds from Michigan AgBioResearch through the USDA National Institute of Food and Agriculture.

Conflict of interest statement

None declared.

References

- Chmura, D.J., Rahman, M.S. and Tjoelker, M.G. 2007 Crown structure and biomass allocation patterns modulate aboveground productivity in young loblolly pine and slash pine. *For. Ecol. Manage.* **243**, 219–230.
- Clough, B.J., Russell, M.B., Domke, G.M., Woodall, C.W. and Radtke, P.J. 2016a Comparing tree foliage biomass models fitted to a multispecies, felled-tree biomass dataset for the United States. *Ecol. Modell.* **333**, 79–91.
- Clough, B.J., Russell, M.B., Domke, G.M. and Woodall, C.W. 2016b Quantifying allometric model uncertainty for plot-level live tree biomass stocks with a data-driven, hierarchical framework. *For. Ecol. Manage.* **372**, 175–188.
- Domke, G.M., Woodall, C.W., Smith, J.E., Westfall, J.A. and McRoberts, R.E. 2012 Forest Ecology and Management Consequences of alternative tree-level biomass estimation procedures on U. S. forest carbon stock estimates. *For. Ecol. Manage.* **270**, 108–116.
- Enquist, B.J. and Niklas, K.J. 2001 Invariant scaling relations across tree-dominated communities. *Nature* **410**, 655–660.
- Gelman, A.E., Carlin, J.B., Stern, H.S. and Rubin, D.B. 2003 *Bayesian Data Analysis*. 2nd edn. CRC Press.
- Jalkanen, A., Makipaa, R., Stahl, G., Lehtonen, A. and Petersson, H. 2005 Estimation of the biomass stock of trees in Sweden: comparison of biomass equations and age-dependent biomass expansion factors. *Ann. For. Sci.* **62**, 845–851.
- Jenkins, J.C., Chojnacky, D.C., Heath, L.S. and Birdsey, R.A. 2003 National-scale biomass estimators for United States tree species. *For. Sci.* **49**, 12–35.
- Jucker, T., Caspersen, J., Chave, J., Antin, C., Barbier, N., Bongers, F., et al 2017 Allometric equations for integrating remote sensing imagery into forest monitoring programs. *Glob. Chang. Biol.*, **23**, 177–190.
- Lambert, M.-C., Ung, C.-H. and Raulier, F. 2005 Canadian national tree aboveground biomass equations. *Can. J. For. Res. Can. Rech. For.* **35**, 1996–2018.
- LegacyTreeData: A repository of individual tree measurements of volume, weight, and physical properties (2016). www.legacytreedata.org (accessed on April 2016).
- Liaw, A. and Wiener, M. 2002 Classification and regression by randomForest. *R. News* **2**, 18–22.
- Macfarlane, D.W. 2010 Predicting branch to bole volume scaling relationships from varying centroids of tree bole volume. *Can. J. For. Res.* **40**, 2278–2289.
- MacFarlane, D.W. 2015 A generalized tree component biomass model derived from principles of variable allometry. *For. Ecol. Manage.* **354**, 43–55.
- Miles, P.D. and Smith, B.W. 2009 Specific gravity and other properties of wood and bark for 156 tree species found in North America. US Forest Service Research Note NRS-38.
- Mäkelä, A. and Valentine, H.T. 2006 Crown ratio influences allometric scaling in trees. *Ecology* **87**, 2967–2972.
- Neumann, M., Moreno, A., Mues, V., Härkönen, S., Mura, M., Bouriaud, O., et al 2016 Comparison of carbon estimation methods for European forests. *For. Ecol. Manage.* **361**, 397–420.
- Ninements, U. and Valladares, F. 2006 Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. *Ecol. Monogr.* **76**, 521–547.
- Parresol, B.R. 2001 Additivity of nonlinear biomass equations. *Can. J. For. Res.* **31**, 865–878.
- Radtke, P.J., Walker, D., Frank, J., Weiskittel, A.R., DeYoung, C., Macfarlane, D.W., et al 2017 Improved accuracy of aboveground biomass and carbon estimates for live trees in forests of the eastern United States. *For. An Int. J. For. Res.* **90**, 32–46.

Raile, G.K. 1982 *Estimating Stump Volume*, USDA Forest Service. St. Paul.

Russell, M.B., Woodall, C.W., D'Amato, A.W. and Domke, G.M. 2014 Beyond mean functional traits: influence of functional trait profiles on forest structure, production, and mortality across the eastern US. *For. Ecol. Manage.* **328**, 1–9.

Segura, M. and Kanninen, M. 2005 Models for tree volume and total aboveground biomass in a tropical humid forest in Costa Rica. *Biotropica* **37**, 2–8.

Sileshi, G.W. 2014 A critical review of forest biomass estimation models, common mistakes and corrective measures. *For. Ecol. Manage.* **329**, 237–254.

Stan Development Team. 2017. The Stan Core Library, Version 2.17.0. <http://mc-stan.org>.

Thomas, C.E. and Parresol, B.R. 1991 Simple, flexible, trigonometric taper equations. *Can. J. For. Res.* **21**, 1132–1137.

United States Environmental Protection Agency 2016 *Inventory of U.S. Greenhouse Gas Emissions and Sinks: 1990–2014*. United States Environmental Protection Agency.

Valentine, H.T. and Gregoire, T.G. 2001 A switching model of bole taper. *Can. J. For. Res.* **31**, 1400–1409.

Vehtari, A. and Ojanen, J. 2012 A survey of Bayesian predictive methods for model assessment, selection and comparison. *Stat. Surv.* **6**, 142–228.

Ver Planck, N.R. and MacFarlane, D.W. 2015 A vertically integrated whole-tree biomass model. *Trees Struct. Funct.* **29**, 449–460.

Weiskittel, A.R., Crookston, N.L. and Radtke, P.J. 2011 Linking climate, gross primary productivity, and site index across forests of the western United States. *Can. J. For. Res.* **41**, 1710–1721.

Weiskittel, A.R., Macfarlane, D.W., Radtke, P.J., Affleck, D.L.R., Temesgen, H., Westfall, J.A., et al 2015 A call to improve methods for estimating tree biomass for regional and national assessments. *J. For.* **113**, 414–424.

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.

Wirth, C., Schumacher, J. and Schulze, E.-D. 2004 Generic biomass functions for Norway spruce in Central Europe—a meta-analysis approach toward prediction and uncertainty estimation. *Tree Physiol.* **24**, 121–139.

Woodall, C.W., Heath, L.S., Domke, G.M. and Nichols, M.C. 2011 *Methods and equations for estimating aboveground volume, biomass, and carbon for trees in the U.S. forest inventory, 2010*.

Wutzler, T., Wirth, C. and Schumacher, J. 2008 Generic biomass functions for Common beech (*Fagus sylvatica* L.) in Central Europe – predictions and components of uncertainty. *Can. J. For. Res.* **38**, 1661–1675.

Appendix A

This appendix extends the description of the n-CRM approach in the main body of the paper with additional details related to the computation of total aboveground biomass (AGB). Computing AGB with n-CRM involves separate estimation of tree-scale attributes using several component models, described in Table 2, which are then converted to whole-tree biomass using expansion factor and additive approaches. The n-CRM is closely related to the component ratio method described by Woodall et al. (2011), and computational procedures closely mirror methods used by those authors. For this reason, our treatment here is brief and readers should refer to Woodall et al. (2011) for further background on the component ratio method.

Statistical computing

Before discussing computation of AGB, few additional notes on the statistical methods underlying n-CRM are warranted. As discussed in the Methods section, n-CRM is fit as a Bayesian model in Stan, with each sub-model fit separately and resulting posterior predictions used to general posterior estimates of individual tree total biomass. The specification of a Bayesian model requires the selection of prior distributions for model parameters, and we generally chose ‘weakly informative’ prior distributions that were designed to facilitate efficient Markov chain Monte Carlo (MCMC) sampling without placing any prior information on the posterior parameter estimates, and thus allowing these to be fully informed by the fitting legacy data. For regression coefficients such as those in the stem volume, total biomass, and component biomass models these were normal priors with a mean of zero and a scale equivalent to several standard deviations (i.e. $\beta \sim N(0, 25)$), although precise specifications varied depending on the scale and units of the data. Scale parameters, including both data-level variances and variance of regression coefficients were specified with weakly informative half-Cauchy priors (i.e. $\tau \sim \text{Cauchy}(0, 5)$). Once sub-models were specified, the 1 000 posterior simulations were drawn from 4 MCMC chains following a ‘warm up’ period to allow for model convergence (2 000 total iterations). Posterior predictive draws were taken for each tree in the fitting data simultaneously and saved as $n \times 2\,000$ matrices of predicted attributes where $n = 1, \dots, N$ observations in the validation datasets. In the proceeding section the computation of total biomass is described for one point estimate, but it should be understood that in our procedure these calculations were done using every row of these matrices of posterior predictions, thus generating 2 000 posterior estimates of AGB.

Computing AGB via the n-CRM

Our algorithm for converting posterior predictions of the sub-models in Table 2 to posterior estimates of total biomass proceeds as follows:

Step 1: Calculating stem wood, stem bark, and bole biomass

Posterior predictions of stem wood volume (Vol) and bark ratio (BR) are generated by fitting relevant equations in Table 2 to the fitting data. From these stem wood volume arises naturally while bark volume is subsequently estimated as:

$$\text{Vol}_{\text{bk}} = \text{Vol} * \text{BR} \quad (\text{A.1})$$

where all three elements are $n \times 2\,000$ matrices of posterior predictions, and these dimensions should be assumed for all subsequent calculations. Once wood and bark volumes are obtained they are expanded into biomass using posterior predictions of wood specific gravity (WSG) and bark specific gravity (BSG) as:

$$\text{BM}_{\text{wood}} = \text{Vol} * \text{WSG} * k \quad (\text{A.2})$$

$$\text{BM}_{\text{bark}} = \text{Vol}_{\text{bk}} * \text{BSG} * k \quad (\text{A.3})$$

where k is constant that converts biomass estimates to green weight (kg). Once estimates of wood and bark biomass are obtained, total bole biomass is calculated as:

$$\text{BM}_{\text{bole}} = \text{BM}_{\text{wood}} + \text{BM}_{\text{bark}} \quad (\text{A.4})$$

Step 2: Calculating CRM adjustment factors

$$\text{Vol}_{\text{sbk}} = \text{Vol}_{\text{sosb}} - \text{Vol}_{\text{sisb}} \quad (\text{A.6})$$

The approach used by Woodall *et al.* (2011) applies ‘CRM adjustment factors’ to estimates of component biomass obtained via the CRM. The purpose of these adjustments is to correct biomass estimates obtained via an expansion factor approach relative to those obtained using component allometric equations (Jenkins *et al.*, 2003). While it is unclear that these corrections are necessary when performing a data-fitted hybrid approach such as n-CRM, we preserved this step to remain consistent with current USFS procedures. Given the general posterior mean agreement between n-CRM and the allometric model (e.g. Figure 1) the practical impact of these adjustments on our work is small. The adjustment factor is calculated as:

$$\text{CRM}_{\text{adj}} = \frac{\text{BM}_{\text{bole}}}{\text{BM}_{\text{stem}}} \quad (\text{A.5})$$

where BM_{stem} is predictions of stem biomass from the data-fitted stem allometric model described in Table 2.

Step 3: Estimate component (stump, branch, foliage) biomass

As described in the Methods section, the legacy data do not possess measurements of stump biomass or volume, so we use an expansion factor approach that synthesizes our data-estimated posterior distributions of WSG and BSG with empirically calculated estimates of stump volume using the equations of Raile (1982; Table 2). In brief, these models separately estimate stump outside bark volume (Vol_{sosb}) and inside bark volume (Vol_{sisb}) and then obtain stump bark volume as:

Stump wood and bark biomass are then calculated using the same expansions described in (A.2) and (A.3), but substituting stump wood and bark volume for bole wood and bark volume. Stump biomass is then calculated as:

$$\text{BM}_{\text{stump}} = (\text{BM}_{\text{stumpwood}} + \text{BM}_{\text{stumpbark}}) * \text{CRM}_{\text{adj}} \quad (\text{A.7})$$

Top biomass is calculated as the sum of predictions from the branch and foliage allometric models in Table 2, with the CRM adjustment factor applied:

$$\text{BM}_{\text{top}} = (\text{BM}_{\text{branch}} + \text{BM}_{\text{foliage}}) * \text{CRM}_{\text{adj}} \quad (\text{A.8})$$

Step 4: Calculate total aboveground biomass

In the final step, total aboveground biomass is calculated as the sum of the bole, stump, and top components:

$$\text{BM}_{\text{agb}} = \text{BM}_{\text{bole}} + \text{BM}_{\text{stump}} + \text{BM}_{\text{top}}$$