

Improved accuracy of aboveground biomass and carbon estimates for live trees in forests of the eastern United States

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Accurate estimation of forest biomass and carbon stocks at regional to national scales is a key requirement in determining terrestrial carbon sources and sinks on United States (US) forest lands. To that end, comprehensive assessment and testing of alternative volume and biomass models were conducted for individual tree models employed in the component ratio method (CRM) currently used in the US' National Greenhouse Gas Inventory. The CRM applies species-specific stem volume equations along with specific gravity conversions and component expansion factors to ensure consistency between predicted stem volumes and weights, and additivity of predicted live tree component weights to match aboveground biomass (AGB). Data from over 76 600 stem volumes and 6600 AGB observations were compiled from individual studies conducted in the past 115 years – what we refer to as legacy data – to perform the assessment. Scenarios formulated to incrementally replace constituent equations in the CRM with models fitted to legacy data were tested using cross-validation methods, and estimates of AGB were scaled using forest inventory data to compare across 33 states in the eastern US. Modifications all indicated that the CRM in its present formulation underestimates AGB in eastern forests, with the range of underestimation ranging from 6.2 to 17 per cent. Cross-validation results indicated the greatest reductions in estimation bias and root-mean squared error could be achieved by scenarios that replaced stem volume, sapling AGB, and component ratio equations in the CRM. A change in the definitions used in apportioning biomass to aboveground components was also shown to increase prediction accuracy. Adopting modifications tested here would increase AGB estimates for the eastern US by 15 per cent, accounting for 1.5 Pg of C currently unaccounted for in live tree aboveground forest C stock assessments. Expansion of the legacy data set currently underway should be useful for further testing, such as whether similar gains in accuracy can be achieved in estimates of regional or national-scale C sequestration rates.

Introduction

Accurate estimates of forest biomass and carbon (C) stocks at regional to national scales are needed in policymaking and research related to the role of forest ecosystems in the global C cycle and related efforts to mitigate greenhouse-gas emissions through increasing forest C sinks. For example, reporting of forest C stocks is an administrative requirement for participants in the United Nations Framework Convention on Climate Change (IPCC, 2006; Tomppo, 2009). In countries where national forest inventories (NFI) are maintained, year-to-year differences in forest biomass and C stocks are used to estimate C flux and sequestration rates on forest lands (Dunger *et al.*, 2012; Fang *et al.*, 2014; U.S. EPA,

2014). To meet this requirement with maximum accuracy, ongoing efforts focus on testing and improving procedures used in estimating forest C stocks and their year-to-year differences for estimating C fluxes (Smith *et al.*, 2013; Westfall *et al.*, 2013; Woodall, 2012).

Forests in the eastern US currently store an estimated 8.5 Pg (1 Pg (petagram) is equivalent to 10¹⁵ g or 1 billion (10⁹) metric tons) of C in the aboveground components of live growing stock (Miles, 2016), roughly 20 per cent of all C stored in living and dead plants and soil organic matter in forests of the conterminous United States (US). Data collected and maintained by the Forest Inventory and Analysis (FIA) program of the US Forest Service provide the basis for C stock estimates across a range of spatial scales (Domke *et al.*, 2014). Forest vegetation surveys

conducted by FIA personnel provide the statistical means for unbiasedly estimating many parameters of forest resource attributes (McRoberts *et al.*, 2010). In addition, allometric models of individual-tree volume and biomass contents are applied to field measurements, especially in the estimation of the aboveground components of live trees. Consequently considerable accuracy is required in the individual-tree volume and biomass models used in national-scale forest biomass and C stock estimation procedures (Domke *et al.*, 2012; Duncanson *et al.*, 2015).

Because many NFIs were designed with the estimation of growing stock volumes as a primary goal, estimates of biomass and C stocks are often obtained using secondary conversion and expansion functions known as biomass conversion and expansion factors (BCEF), or the somewhat simpler biomass expansion factors (BEF) (Soares and Tomé, 2012). The term BEF is used differently in some contexts; however, a widely-adopted convention defines BEF as a unitless number representing the ratio of the biomass contained in the merchantable stems of trees to the same trees' aboveground biomass (AGB) (IPCC, 2006; Skovsgaard and Nord-Larsen, 2012). BEFs may be defined on either per-tree or per-unit-area bases and these bases are sometimes used interchangeably or left unspecified. BCEF is equivalent to BEF times wood density defined on a dry weight to green volume basis; therefore, BCEF can be used to determine AGB directly from stem wood volumes – typically merchantable volumes (IPCC, 2006).

BEFs are a type of component ratio (CR) – quantities that express the biomass contents in one component of a tree, e.g. stem, crown or foliage, in proportion to the tree's total biomass or AGB (Jenkins *et al.*, 2003). CRs, along with wood density or specific gravity (SG; dry weight per unit of green volume, expressed in relation to density of water at 4°C) values, are used in the component ratio method (CRM) to calculate AGB from stem volumes of individual trees using measurements, e.g. stem diameter, collected in the US NFI (Heath *et al.*, 2009; Woodall *et al.*, 2011). The combined use of wood density information and stem wood CRs provides a means to ensure consistency between estimates of wood volume and AGB in NFIs (Domke *et al.*, 2012).

Despite the extensive body of knowledge that contributes to the workings of the CRM, comprehensive evaluation of the method's performance to date has been limited by a paucity of data suitable for such a task (Domke *et al.*, 2012; MacLean *et al.*, 2014; Westfall, 2012; Zhou and Hemstrom, 2009). To address this need, two objectives were pursued here. The first involved assessing accuracy of CRM predictions using a large collection of tree biomass data and related measurements compiled from legacy sources. The second objective was aimed at testing alternative models to reduce uncertainties in CRM-based predictions and examining the alternative models' effects on AGB estimates for eastern US forests. By design the CRM method provides consistent estimates of stem wood volume, tree biomass components, and AGB obtained by summing the AGB components; accordingly, alternative models for each of the constituent equations or their fitted coefficients were examined for their ability to improve AGB prediction accuracy.

Materials and methods

The geographic scope of the study was limited to 33 states in the US that lie completely east of 100° west longitude, excepting Texas and

Oklahoma, which were included in the study despite ranging west of the 100th meridian. These states are grouped into the following four FIA regions where different gross cubic volume models and coefficients are assigned for AGB determination: Central States; Lake States; Northeastern States; and Southern States (Figure 1).

A large collection of 'legacy' tree measurements was compiled for this work from past studies conducted over the past 115 years where various aboveground attributes were observed on standing or felled trees, including volumetric, weight, and basic wood properties measurements (Radtke *et al.*, 2016). Some harmonization of legacy measurements from different studies was necessary, mainly where stump heights and top-diameter measurement limits differed among studies. Details of the data and methods used to harmonize their measurements are arranged into three general categories: (1) data used to determine stem volumes; (2) weight measurements from tree components and AGB; and (3) wood or bark properties used to convert volumetric measurements to stem weights.

Stem volume data

The largest and most extensive collection of data compiled for this work included stem profile or taper measurements – paired height and diameter measurements from base to the tip of individual tree stems – compiled from 63 published and unpublished studies (Supplementary data, Table A1). Taper measurements from legacy trees allowed for the determination of individual tree stem volumes based on a specified stump height and diameter at the top of the usable portion of the stem. The CRM standard 'merchantable' stem volume specification refers to inside-bark (ib) volume from a 0.305 m (1 ft) stump to a 10.2 cm (4 in) outside-bark (ob) top diameter. This standard is widely used for forest inventories and assessments aimed at wood fibre production in the US and was thus adopted by Jenkins *et al.* (2003) in their development of national scale stem biomass equations. The same trees were used in assessing an alternative merchantability standard adopted here that includes the whole stem, i.e. the ib volume from groundline to the tip of the main stem. In order to be useful in this work, any trees included in the volume data collection were required to include measurements of both diameter at breast height (dbh; 1.37 m) and total tree height.

The most useful taper measurements for our purposes included both ib and ob diameter measurements at multiple heights up the stem;

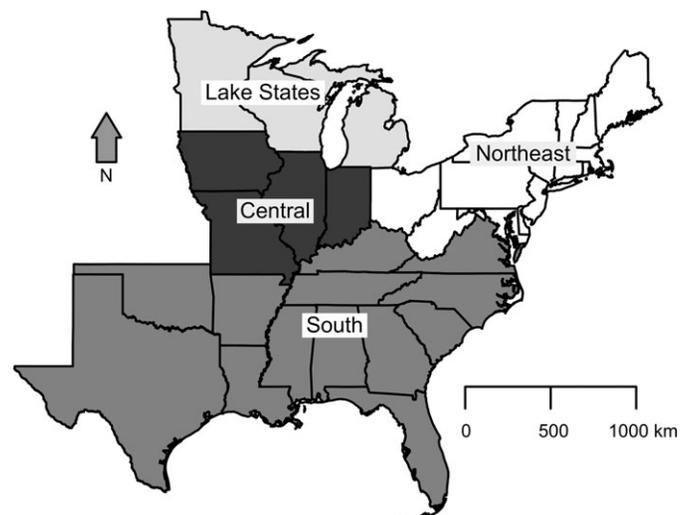


Figure 1 Areas where FIA regional volume equations are adopted for use in the CRM.

however, some legacy data – especially those measured on standing trees using optical dendrometers – only included ob diameters. For data from two such studies (Martin, 1980; Westfall and Scott, 2010) ib diameters were predicted from the ob taper measurements given the availability of suitable bark-thickness models for a number of northeastern US tree species (Hilt *et al.*, 1983; Li and Weiskittel, 2011; Wingerd and Wiant, 1982). In total, 76 610 trees from 80 species or species groups were available for volume and taper determination, with an average of 14 taper measurements per tree from stump to merchantable top (Supplementary data, Table A2; see also, Table A2 for all species names used in this work).

Aboveground biomass data

Data were also compiled from past studies where aboveground component biomass had been observed (Supplementary data, Table A3). Because of the importance of AGB in the CRM framework, the most useful observations came from trees that had been felled and weighed or otherwise measured to obtain estimates of AGB, including stem wood and bark, branches and foliage. Weights of dead branches were excluded where they were separately recorded. Unless otherwise noted, recorded aboveground dry weights were assumed to have included no dead branches. Trees with any recorded hollow or decayed stem sections were omitted. Despite missing one or more aboveground component measurements, trees from a number of studies were usable for evaluating a subset of CRM-related biomass attributes, e.g. stem wood, stem bark, branches or foliage. Depending on how components were defined for any particular study, it was sometimes possible to obtain only a subset of the CRs defined in the CRM. For example, if an author defined the crown as a component, making no distinction between branches – i.e. branch wood and bark – and foliage, the measured AGB and stem wood and bark components were still used in model testing and revision. A total of 6617 trees from 31 species or genera were included in the AGB and component model test data set (Supplementary data, Table A4).

Wood and bark properties

Measurements of wood and bark properties were compiled from subsets of records in the stem volume and biomass data sets described above. Stem bark:wood volume ratios were calculated from ib and ob stem volumes as defined by Miles and Smith (2009). Profile data from 71 907 trees on 76 species groups having ib and ob stem taper measurements were used for this purpose (Supplementary data, Table A5). Bark and wood basic SG were calculated from legacy tree records having both dry weight and green volume measurements of wood and bark. These were generally available only on the subset of legacy records on 33 species groups that had cross-sectional disks cut, measured for volume, and dried before weighing (see supplementary data, Table A6). The numbers of observations available for wood and bark SG determination – 10 672 and 7228, respectively – were greater than AGB sample sizes because they included data from a number of studies focused on stem weights but not AGB.

Component ratio method

Baseline predictions of AGB were generated using the CRM method adopted in the US forest inventory, which is briefly described here and diagrammed in Figure 2, with the steps described here each referring to steps numbered in the diagram (Figure 2). In step 1 merchantable stem wood volumes (V_{merch} , m^3) were predicted for those trees having $dbh \geq 12.7$ cm (5 in) using species-specific regional volume equations (Hahn, 1984; Hahn and Hansen, 1991; Oswald and Conner, 2011; Scott, 1981). Merchantable stem bark volumes were subsequently predicted (step 2) using species-specific tree-level average bark volumes, expressed as ratios

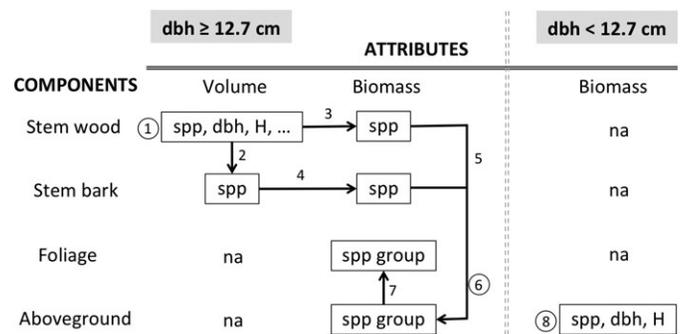


Figure 2 Overview of component ratio method (CRM) applied to individual trees in the US national forest inventory for volume and biomass estimation. Unshaded boxes list variables used to estimate volume and biomass attributes by component. Circled numerals 1, 6, and 8 indicate attributes predicted from regression equations. Noncircled numerals and arrows indicate the sequence and dependencies of calculations: (1) regional volume equations; (2) bark:wood volume ratio; (3 and 4) wood and bark specific gravity coefficients; (5) add wood + bark biomass; (6) division by stem:aboveground component ratio ($CR_{wd} + CR_{bk}$); (7) multiplication by foliage:aboveground component ratio (CR_{fol}); (8) species or species-group specific biomass equations. Note that only the aboveground component biomass attribute is estimated for saplings, i.e. trees with $dbh < 12.7$ cm.

of stem bark : wood volumes (Miles and Smith, 2009). Species-level averages for wood and bark SG from Miles and Smith (2009) were applied in steps 3 and 4 to convert predicted merchantable stem wood and bark volumes to dry weights. Stem wood and bark dry weights were summed in step 5. Next, the CR regression model [1] from Jenkins *et al.* (2003) was used to predict the fraction of each tree's AGB allocated to stem wood (CR_{wd}) and bark (CR_{bk}) components. The summed merchantable stem wood and bark dry weights were divided by the sum ($CR_{wd} + CR_{bk}$) in step 6 to arrive at CRM predictions of AGB (Woodall *et al.*, 2011). Other biomass components were predicted by multiplying AGB by the corresponding CR; for example, foliage biomass was calculated by multiplying AGB x CR_{fol} (step 7). Finally, AGB for sapling-sized trees ($dbh < 12.7$ cm) was predicted directly from a generalized allometric model multiplied by a species-specific sapling adjustment factor (SAP_{adj}) to ensure a smooth transition at the 12.7 cm dbh merchantability threshold (step 8; Heath *et al.*, 2009; Jenkins *et al.*, 2003).

$$\ln(CR) = \beta_0 + \beta_1 \left(\frac{1}{D} \right) \quad (1)$$

where, CR = component:aboveground dry-weight ratio; D = dbh , cm; β_0 and β_1 are the model coefficients.

Two adjustments to calculated AGB were made in accord with the CRM, one that subtracts the foliage component biomass from AGB and another that adjusts stump biomass to ensure consistency with the predicted volume and dry weight contents of the merchantable stem wood and bark.

Alternative model formulations

Seven alternative scenarios were formulated for evaluating the effects that adopting alternative constituent models in the CRM would have on FIA state and regional estimates of live tree AGB in the eastern US. The existing CRM was denoted as the baseline scenario, or scenario 0. In scenarios 1–7 the definitions of CR_{wd} and CR_{bk} were modified to reflect ratios of total stem wood and bark to AGB rather than the merchantable stem wood and bark ratios defined in the baseline scenario. This

modification was based on the work of DeYoung (2014), who noted a somewhat extreme nonlinear pattern in stem CRs for trees close in size to the 12.7 cm dbh threshold that FIA uses to distinguish between saplings and trees. The foliage component definition was left unchanged; however, the branch component ratio (CR_{br}) was redefined in scenarios 1–7 to exclude any part of the main stem, i.e. topwood or stump, thus ensuring that stem, branch, and foliage CRs sum to one. In the approach proposed by Jenkins et al. (2003) CRs were assured to sum to one by fitting Eq. (1) separately to CR_{wd} , CR_{bk} , and the foliage component ratio (CR_{fol}), then calculating CR_{br} by subtraction from one, i.e. $CR_{br} = 1 - (CR_{wd} + CR_{bk} + CR_{fol})$.

The comparatively flexible nonlinear Chapman-Richards functional form [2] was proposed as a potential improvement over Eq. (1) for predicting biomass CRs.

$$CR = a(1 - e^{-bD})^c \quad (2)$$

where, e = the base of the natural logarithm; a , b and c are the model coefficients.

To ensure that aboveground components summed to one Eq. (2) was first fitted separately to data from all four aboveground CRs, then adjusted by dividing each fitted equation by the sum of all four components. For example, the adjusted foliage component (CR_{fol1}) was calculated as $CR_{fol1} = CR_{fol} / (CR_{wd} + CR_{bk} + CR_{br} + CR_{fol})$. Newly fitted component-ratio regression models based on the modified CR definitions and the Eq. (2) were implemented in scenario 1. To maintain a smooth transition for trees near the sapling size dbh = 12.7 cm threshold, SAP_{adj} was recalculated for each species as the national average ratio of the CRM-calculated AGB divided by AGB predicted from the Jenkins et al. (2003) biomass equation for all 5-in trees, as described by Heath et al. (2009). Other than the new CR model and sapling adjustment factors, scenario 1 was equivalent to the baseline CRM (Table 1).

Scenario 2 differed from Scenario 1 in that the newly fitted component-ratio regression model [2] used a predictor consisting of the product of dbh-squared (D^2) and total height (H , m) instead of using dbh alone (Table 1). As in scenario 1 and all subsequent scenarios, new sets of sapling adjustment factors were calculated to maintain a smooth transition between saplings and larger sized trees.

Scenario 3 included a further modification, the replacement of the allometric AGB models from Jenkins et al. (2003) with species and species-group-specific segmented regression models as in Eq. (3) following Clark et al. (1985) fitted to legacy tree AGB observations.

$$AGB = \begin{cases} a(D^2H)^b; & D < D_j \\ a(D_j^2)^{b-c}(D^2)^cH^b; & D \geq D_j \end{cases} \quad (3)$$

where, D = dbh, cm; H = total height, m; D_j = segment joint point 12.7 cm; a , b and c are the model coefficients (Coefficient symbols a , b , c , etc., not intended to signify equivalence in differently numbered equations).

Two possible improvements were sought in this modification. First, including both dbh and height in the AGB model was seen as a way to improve prediction accuracy compared with using dbh as the only predictor. Second, residual plots of $\log(AGB)$ vs either $\log(dbh)$ or $\log(dbh^2 \times H)$ regression models (not shown here) showed some systematic over- or underprediction of AGB across the range of tree sizes, with biases being most evident in small trees. Model fits were assessed using the pseudo R^2 fit index described by Parresol (1999) and a relative root-mean squared error (RMSE) based on per cent errors calculated from observed (obs) and predicted ($pred$) AGB as in Eq. (3) (Supplementary file Eq_3_AGB_Coeffs_SI.csv).

$$RMSE_Percent_Error = \sqrt{\frac{\{(obs - pred)/obs\}^2}{(n - p)}} \quad (4)$$

where, n = number of trees fitted to regression model; and p = number of regression parameters.

While models relying on both dbh and height as predictors were fitted for this purpose, a supplementary model for sapling-sized trees was also fitted that relied only on dbh (Supplementary file Eq_3_Sapling_AGB_D_Coeffs_SI.csv). This was needed to make predictions for roughly 50 per cent of saplings in the FIA database that have no recorded total heights.

Scenario 4 included a further modification, replacing the regional V_{merch} prediction equations with an alternative regression model fitted to volume data from legacy tree measurements. A segmented V_{merch} regression Eq. (5) following Clark et al. (1985) was adopted with dbh joint points $D_j = 22.9$ cm (9 in) for softwoods and $D_j = 27.9$ cm (11 in) for hardwoods. No distinction was made for trees observed in different regions, meaning only one model was fitted for a given species or species group regardless of the geographic distribution of the species and the data representing it in the legacy database.

$$V_{merch} = \begin{cases} a(D^2H)^b; & D < D_j \\ a(D_j^2)^{b-c}(D^2)^cH^b; & D \geq D_j \end{cases} \quad (5)$$

Table 1 Scenarios tested for implementing alternative CRM model formulations in FIA statewide aboveground biomass (AGB) estimates. A sequence of modifications was adopted in steps, including how the stem component was defined, what CR model and predictor were used, the choice of AGB and merchantable volume (V_{merch}) equations, sources of wood and bark specific gravity (SG) averages, and the source and choice of model used to estimate stem bark:wood volume

ID	Description	Stem component	CR	AGB model	V_{merch}	Wood, Bark SG	Bark:wood vol.
0	Baseline CRM	Merchantable stem	dbh ¹	Jenkins	FIA regional	Miles and Smith	Miles and Smith
1	New CR (dbh)	Whole stem	dbh	"	"	"	"
2	New CR (D^2H)	"	D^2H	"	"	"	"
3	New CR (D^2H); AGB	"	"	Eq. (3)	"	"	"
4	New CR (D^2H); AGB; V_{merch}	"	"	"	Eq. (5)	"	"
5	New CR (D^2H); AGB; V_{merch} ; wood/bark SG means	"	"	"	"	Observed data means	Obs. data means
6	New CR (D^2H); AGB; V_{merch} ; wood/bark SG means; new bark:wood model	"	"	"	"	"	Eq. (7)
7	AGB only	na	na	Eq. (3)	na	na	na

¹Baseline scenario used CR regression models from Jenkins et al. (2003). All others used Eq. (2) (Chapman Richards).

where, D = dbh, cm; H = total height, m; D_j = segment joint point, 22.9 cm for softwoods, 27.9 cm for hardwoods; a , b and c are the model coefficients.

In scenario 4 and all other scenarios 1–6, \hat{V}_{merch} predictions from either the regional FIA volume equations or the newly developed models based on Eq. (5) were subsequently adjusted using species-specific regional taper equations to expand \hat{V}_{merch} to the corresponding total stem volume (\hat{V}_{tot}) before converting volumes to dry weights and AGB (Clark et al., 1991; Li et al., 2012; Westfall and Scott, 2010). This adjustment was needed to match the redefinitions of stem components that affected CR_{wd} , CR_{bk} and CR_{br} .

$$\hat{V}_{tot} = \hat{V}_{merch} \times \frac{Vol(0, H | D, H)}{Vol(0.305, H_{10.2} | D, H)} \quad (6)$$

where, \hat{V}_{tot} = predicted total stem ib volume; \hat{V}_{merch} = predicted merchantable stem ib volume; $Vol(h_1, h_2 | dbh, H)$ = stem ib volume between heights h_1 and h_2 ($h_1 < h_2$, m), calculated from the integral form of a suitable taper model; $H_{10.2}$ is the height (m) of the stem to a 10.2-cm db diameter.

We assumed that SG and bark:wood volume values presented by Miles and Smith (2009) were suitable for either merchantable or total stem contents. As such, converting ib volumes from either \hat{V}_{merch} or \hat{V}_{tot} to stem wood and bark biomass could be accomplished using the same SG and bark:wood volume coefficients regardless of how the stem CR was defined.

Scenario 5 replaced published values of wood and bark SG and the average bark:wood volume percentages from Miles and Smith (2009) with values observed from legacy data. A further refinement adopted in scenario 6 was the replacement of species averages for stem bark:wood volume percentages with values predicted from species-specific regression equations based on the Weibull cumulative distribution function fitted to legacy data (Table 1).

$$\text{stem bark : wood volume (\%)} = 100\% \times (1 - e^{-ab^b}) \quad (7)$$

For emphasis we restate here that the reformulation of CRs to represent whole stem biomass contents in scenarios 1–6 did not eliminate the initial step of predicting tree V_{merch} , either with FIA regional volume equations (scenarios 1–3) or from Eq. (5) fitted to legacy tree volumes (scenarios 4–6; Table 1). It did, however, require the use of suitable taper functions for calculating stem ib volumes from $Vol(h_1, h_2 | dbh, H)$ in Eq. (6). Because we considered the development of a comprehensive set of taper models for eastern US tree species to be outside the scope of this work, and because a number of regional taper models were already available for use here, we relied on published taper equations to perform taper-based volume adjustments in Eq. (6) (Clark et al., 1991; Li et al., 2012; Westfall and Scott, 2010).

In scenario 7 AGB was predicted using only species-specific allometric Eq. (3) fitted to legacy biomass tree data. No stem wood or volume predictions, conversions from volume to biomass using SG, or expansion of stem biomass to AGB using CRs were employed. Because of its relative simplicity and direct modelling of AGB, scenario 7 was expected to achieve the highest accuracy of any scenarios tested. As such it would serve as a benchmark for evaluating the accuracy of the other scenarios that included steps needed to ensure consistency between volume and AGB estimates.

Model evaluation

Legacy tree and component observations were used to evaluate the accuracy of tree-level predictions of volumes, wood and bark properties, CRs and AGB. With this suite of variables, up to nine intermediate predicted attributes used in the CRM could be compared with observed values for any particular tree; however, most trees in the legacy database had only a subset of the variables of interest observed on them. The primary variable of interest here was AGB; however, CRM predictions for intermediate attributes were compared with observed data to

identify possible ways to increase their accuracy while maintaining optimal accuracy of AGB.

Given the large number of volume and biomass models employed in the CRM, it seemed likely that some models were originally developed using data being treated here as legacy observations. No effort was made to avoid reusing any legacy observations that had previously been involved in development of regional volume equations or other models that are part of the baseline CRM (Jenkins et al., 2003; Miles and Smith, 2009). In newly developed alternative models, however, legacy data formed the basis for evaluating prediction accuracy. Both bootstrap and tenfold cross-validation procedures were employed, selecting some legacy observations for model fitting and others for model testing (Efron, 1983; Kuhn and Johnson, 2013, pp. 72–73). This ensured some degree of independence between data used for developing new models and those used for model validation. In addition to graphical diagnostics, e.g. inspection of bootstrap prediction errors, two accuracy statistics – mean bias and RMSE – were calculated from bootstrap prediction errors. Accuracy statistics were tabulated and examined at various levels of aggregation including species, region, tree size and overall to gauge whether improvements at one level may have reduced accuracies in some of the subgroups formed at finer levels of aggregation.

Since each scenario relied on different sets of calculations to obtain CRM-based and allometric-model-based AGB predictions, a different set of SAP_{Adj} factors was calculated for application in each scenario (Supplementary data, Table A7).

Results

Stem wood and bark volume

The accuracy of V_{merch} equations used in the CRM varied considerably by FIA region when compared with legacy tree volume measurements across all species (Table 2). Southern States FIA

Table 2 Merchantable volume prediction errors = 100%(predicted – observed)/observed for legacy tree observations compared with predictions from regional volume equations and newly developed Eq. (5)

Region	Model	N	Prediction error (%)	
			Mean	Std. dev.
Central States	FIA	1735	–19.2	20.9
	Clark R9		6.7	13.3
	Burk and Ek		2.1	14.2
	[5] ¹		–7.3	12.1
Lake States	FIA	7444	–15.0	10.6
	Clark R9		8.8	12.4
	Hahn (1984)		–12.8	19.6
	Stone		–12.7	10.4
	Burk and Ek		1.2	16.8
Northeastern States	[5] ¹	9910	1.6	16.6
	FIA		–6.0	14.5
	Clark R9		2.4	12.0
	Burk and Ek		–2.7	14.2
Southern States	[5] ¹	59 151	–2.8	13.9
	FIA		–0.7	17.7
	Clark et al.		–2.3	13.3
	[5] ¹		0.9	18.2

¹Prediction errors for Eq. (5) calculated from bootstrap out-of-bag observations.

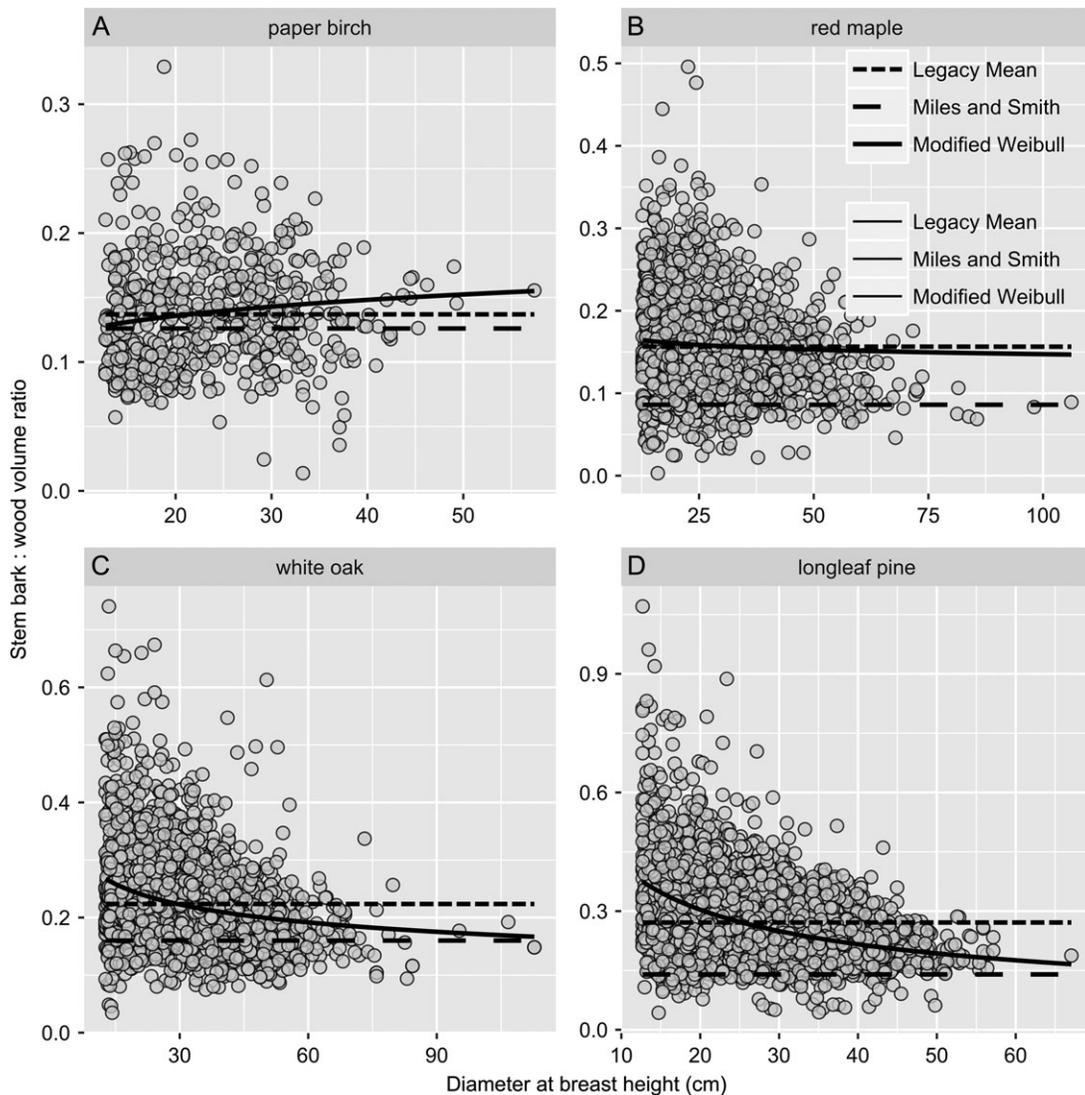


Figure 3 (A, B) Stem bark:wood volume ratios from paper birch and red maple showed nearly constant relationships across a range of tree sizes. (C, D) Decreasing trends were evident for several thick-barked species including white oak and longleaf pine. Dashed lines represent species-specific average bark ratios from published values (Miles and Smith, 2009) and the means of the legacy data shown.

volume equations resulted in smaller prediction biases than other regional FIA equations, especially those used in Central States and Lake States regions, which underpredicted by 15 per cent or more on average. The Northeastern region FIA volume equation was intermediate in prediction bias compared with the other regions' equations. Comparison to alternative models showed the possibility of improving accuracy in predicting merchantable volumes in all FIA regions, with the possible exception of the Southern States. No single model tested here proved to be most accurate in every region.

The profile-based model of Clark *et al.* (1991), including a variant used by the US Forest Service (2011) for species in its Eastern Region (R9, Table 2) showed relatively high precision as measured by prediction error standard deviation. However, considerable biases in the R9 variant for Central and Lake States regions indicated some need for additional testing or development before implementing it widely across those regions. The

approximation of Gevortantz and Olsen's (1955) volume and taper tables implemented by Burk and Ek (1999) was most accurate of any existing merchantable volume models for Central and Lake States regions. In contrast, the models of Hahn (1984) and Stone (cf. Hahn, 1973; Hahn, 1984) were among the most heavily-biased of any models tested.

The V_{merch} model of Eq. (5) fitted to legacy tree taper data (Supplementary file Eq_5_Merch_Vol_Coefs_SI.csv) represented improvements over Central, Northeastern, and Lake States regional FIA volume models; however, it did not consistently result in smallest prediction biases nor variance when compared with other models evaluated (Table 2). Detailed analysis of model prediction accuracy among regions for various species and species groups showed a range of results (Supplementary file Error_Vol_Species.csv). Among them, we noted potentially useful relationships between model prediction variance and sample sizes that could help to inform future efforts to balance

costs with accuracy requirements in volume prediction applications (Duncanson *et al.*, 2015).

Observed bark:wood volume ratios showed varying relationships with stem dbh. Some species with thin, smooth bark, e.g. American beech, paper birch and quaking aspen (cf. Borger, 1973), showed nearly constant bark ratios across a range of tree sizes (Figure 3A). Thin, scale-barked species like balsam fir, red maple, and red, white and black spruces exhibited weak correlations and slightly decreasing bark volume ratios with tree size (Figure 3B). Thick, scale- and furrowed-bark species including many pines and hardwoods showed more-pronounced decreases in bark volume ratios with increasing stem dbh, despite there being considerable variability in the data (Figure 3C,D).

Observed bark:wood volume means were nearly all larger than published values, with largest discrepancies in several southern yellow pine and gum species (*Nyssa sylvatica*, *N.*

biflora, *Liquidambar styraciflua*). The same species were generally the ones with the highest observed mean bark volume ratios (Table 3). Reduction in RMSE using species-specific non-linear regression models showed the potential for predicting bark volume ratios more accurately using dbh as a predictor, as compared with simply using species means (Table 3). Southern yellow pines, oaks and hickory showed the greatest gains when modelling bark volume ratios from dbh, but sweetgum and white spruce also showed reductions in RMSE of up to 10 per cent compared with using species means (Table 3).

Specific gravity

Observed species averages for whole-stem wood SG were strongly correlated ($\rho = 0.945$) with published values from Miles

Table 3 Stem bark-to-wood volumes and root mean-squared errors (RMSE) of observed (Obs.) vs predicted values for 35 species, calculated by bootstrap cross-validation. Species shown comprise 80% of aboveground estimated live-tree biomass in the Eastern US

Species	Mean bark:wood volume (%)			RMSE (%)		
	N	Obs.	Miles and Smith	Obs. mean	Miles and Smith	Weibull
Balsam fir	788	12.6	12	3.5	3.6	3.5
White spruce	919	11.1	13	3.1	3.9	3.0
Black spruce	901	12.8	13	3.2	2.9	3.1
Jack pine	1591	11.6	14	4.2	4.3	4.1
Sand pine	468	13.5	15	5.3	5.8	5.3
Shortleaf pine	4559	27.1	16	11.3	15.8	9.6
Slash pine	6273	37.0	18	13.2	23.5	11.5
Longleaf pine	4290	27.1	14	9.5	16.7	8.6
Red pine	1456	13.1	16	4.5	5.3	4.5
Pitch pine	451	30.3	13.4	9.2	19.9	8.2
Pond pine	1000	35.9	13.4	12.7	27.2	11.3
Eastern white pine	1798	16.9	16	6.6	6.1	6.6
Loblolly pine	12 209	27.0	16.6	10.1	14.4	8.9
Virginia pine	1805	16.7	13.4	8.5	9.4	8.2
Pondcypress	436	27.1	20	10.7	13.4	10.3
Red maple	1928	15.7	8.6	5.9	9.7	5.8
Sugar maple	574	15.7	15.6	6.2	5.0	6.1
Yellow birch	508	13.1	9.8	4.2	4.7	4.2
Paper birch	588	13.7	12.6	4.5	3.8	4.6
Hickory spp.	1809	26.7	16	8.3	14.6	7.8
American beech	597	10.1	6	4.4	5.7	4.5
Sweetgum	2569	24.5	15	9.7	13.9	8.7
Yellow-poplar	2522	25.2	18	7.7	9.7	7.4
Blackgum	514	28.7	14	7.9	16.7	7.8
Swamp tupelo	983	26.2	14	8.2	15.1	8.1
Quaking aspen	439	15.6	14.4	6.2	5.9	6.2
White oak	2933	22.3	16	7.4	9.8	7.1
Scarlet oak	1182	22.3	22	7.3	6.8	6.4
Southern red oak	900	25.8	22	7.3	7.4	6.8
Laurel oak	502	17.7	16	6.2	6.4	6.0
Water oak	795	17.1	16	5.3	5.1	5.1
Chestnut oak	1549	30.1	23	9.4	13.4	8.6
Northern red oak	1277	20.2	20	5.9	5.8	5.5
Post oak	651	25.7	22	7.8	7.7	7.1
Black oak	1184	27.2	18.5	8.1	11.4	7.3

and Smith (2009). For 33 species having at least $n = 50$ trees in the legacy data set, observed wood SG means by species averaged just 2 per cent greater than published values. The largest difference was noted in quaking aspen with an observed mean-tree wood $SG_{obs} = 0.44$ ($n = 88$) compared with the published value $SG_{pub} = 0.35$. Other notable differences were observed for southern red oak ($SG_{obs} = 0.59$; $SG_{pub} = 0.52$; $n = 81$), elm ($SG_{obs} = 0.595$; $SG_{pub} = 0.54$; $n = 55$), chestnut oak ($SG_{obs} = 0.62$; $SG_{pub} = 0.57$; $n = 100$) and water tupelo ($SG_{obs} = 0.41$; $SG_{pub} = 0.46$; $n = 150$).

Compared with wood SG, bark SG values observed here were less strongly correlated ($\rho = 0.846$) with values reported by Miles and Smith (2009). For 27 species having at least $n = 50$ trees in the data set, observed bark SG was lower than published values by about 14 per cent (Table 4). Only shortleaf pine had an observed mean bark SG larger than the species' published value. Observed variation in bark SG among trees of a given species was generally low, with coefficients of variation (CV) between 5 and 20 per cent in all but two species studied, longleaf and loblolly pines (Table 4). Scatterplots (not shown) generally showed no relationship between bark SG and tree dbh; however, weak correlations – either positive or negative – were noted in some hardwoods including sweetgum, yellow poplar, and several oak species.

Component ratios

In baseline analyses stem CR_{wd} and CR_{bk} both showed steep drops toward zero as tree dbh values decreased toward the CRM-specified merchantable top diameter (Figure 4A,B). This pattern matched the CRM merchantability limits; namely, any tree having a stump diameter equal to the CRM-specified top diameter would, by definition, contain no stem wood or bark biomass (Heath et al., 2009). A contrasting pattern – owing to the additivity of merchantable stem and branch components – was observed in CR_{br} , which increased sharply toward 1.0 where dbh approached the merchantable top diameter limit (Figure 4C). Similar trends were noted in both hardwoods and conifers, with only data from conifers shown in Figure 4.

Considerable changes in CR trends with dbh were noted after reformulating them so stem wood and bark components were based on total rather than merchantable stem biomass (Figure 4D–F). The decreasing pattern of the CR_{wd} with dbh became less steep, with minimum values of wood biomass generally not falling below 20 per cent of AGB, even in trees as small as 3 cm dbh (Figure 4D). Total stem bark comprised a larger share of AGB in small-diameter softwoods than in larger trees, a trend opposite of that observed in merchantable stem bark (Figure 4B,E). Branch biomass component relationships to dbh also changed markedly following the whole stem component reformulation. In contrast to the existing CRM branch CRs, which approached 100 per cent of AGB in small trees, branch biomass under the new formulation did not exceed 50 per cent of AGB in any of the eastern conifers observed here (Figure 4F). Reformulated CR_{br} often appeared flat over a wide range of tree sizes in conifers (Figure 4F); however, gradual increases in branch biomass ratios with dbh were noted in relatively large trees of some species – both hardwoods and conifers (some plots not shown).

Table 4 Bark specific gravity summary statistics from species having $n > 50$ trees in the legacy data set

Common name	n	Miles and Smith	Observed mean	Observed CV (%)
Sand pine	138	0.45	0.42	9
Shortleaf pine	361	0.35	0.36	17
Slash pine	831	0.35	0.35	14
Spruce pine	75	0.45	0.37	12
Longleaf pine	625	0.45	0.38	25
Pond pine	100	0.33	0.28	11
Eastern white pine	76	0.47	0.35	17
Loblolly pine	1808	0.33	0.32	33
Virginia pine	110	0.54	0.38	10
Pondcypress	63	0.5	0.35	15
Red maple	193	0.6	0.52	10
Hickory spp.	160	0.62	0.53	10
Flowering dogwood	56	0.58	0.37	8
Ash spp.	271	0.46	0.41	8
Sweetgum	732	0.42	0.37	19
Yellow-poplar	228	0.38	0.38	11
Water tupelo	150	0.58	0.36	7
Swamp tupelo	142	0.51	0.41	18
Poplar spp.	112	0.46	0.32	11
White oak	282	0.56	0.53	14
Scarlet oak	99	0.71	0.63	6
Southern red oak	81	0.68	0.65	8
Water oak	202	0.62	0.59	15
Chestnut oak	100	0.54	0.52	8
Northern red oak	95	0.68	0.63	5
Black oak	83	0.6	0.57	8
Elm spp.	55	0.43	0.35	16

Examination of biomass CRs vs the combined variable $dbh^2 \times \text{total height}$ (D^2H) indicated some potential for improving predictions using both dbh and height as predictors, as compared with dbh alone (Figure 5). Replacing dbh with D^2H in Eq. (2) reduced RMSEs by 6 per cent on average over 32 species having observations from $n \geq 50$ trees (Table 5). The gains in models of stem CR_{wd} were comparatively modest at under 2 per cent reduction of RMSE. The accuracy of fitted CR_{bk} and CR_{br} models were improved only slightly by adding height as a predictor. Their RMSE reductions averaged < 1 per cent across all species; nonetheless, some species' RMSE were reduced as much as 8 and 14 per cent for bark and branch CRs, respectively (Table 5).

Aboveground biomass

Examination of legacy tree data indicated some potential for improving the accuracy of AGB models over those developed by Jenkins et al. (2003) and Chojnacky et al. (2014). The most

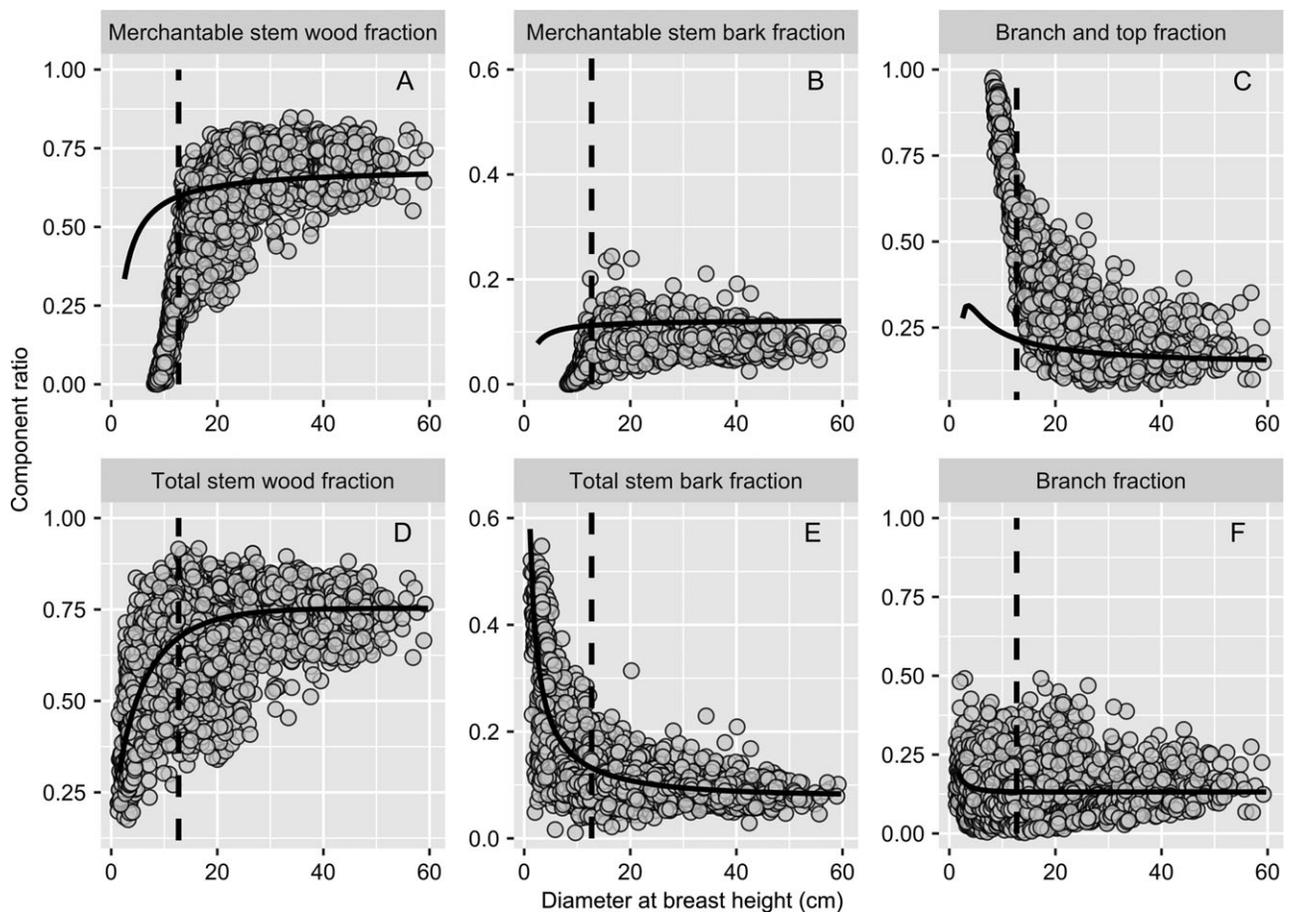


Figure 4 Softwood stem wood CRs exhibit discontinuities in trees having dbh close to the merchantable top diameter (vertical dashed lines; upper panels, A–C) adopted in the CRM. The Jenkins *et al.* (2003) model form (Eq. (1); curves in (A–C)) was not sufficiently flexible to reproduce the non-linearity. Reformulating the ratio as total stem wood:aboveground biomass reduced the degree of discontinuity in small trees, facilitating accurate modelling of CRs (lower panels, D–F).

notable discrepancies between observed and predicted AGB were in pines (Figure 6A). Smaller differences were noted between observed data and published model predictions in hardwood species groups (Figure 6B,C). The fir and hemlock model, which agreed well with observed data showed little need for improvement (Figure 6D). Allometric models of AGB fitted here all predicted higher biomass than the models of Jenkins *et al.* (2003) currently used in the CRM.

AGB estimation scenarios

All seven alternatives tested as potential modifications to the CRM produced AGB estimates higher than the baseline (scenario 0) estimate of 17.1 Pg. The magnitudes of increases over scenario 0 ranged from 6.6 to 20.1 per cent, corresponding to between 1.1 and 3.4 Pg of additional live-tree biomass (Figure 7). Cross-validation prediction errors from $n = 6480$ trees indicated that RMSE could be reduced from the baseline value of 39.5 per cent by any of the scenarios tested. Scenario 7 netted the greatest reduction in RMSE by replacing the CRM approach with predictions from species-specific AGB allometric

Eq. (3) (Figure 7). Scenarios 1–6, all of which functioned within the existing CRM framework were able to improve prediction accuracy, with the greatest overall improvement achieved by adopting scenario 5, which resulted in RMSE for AGB predictions of 28.8 per cent.

The baseline scenario exhibited an average bias of 12.2 per cent, meaning CRM predictions underestimated legacy tree AGB by this amount (Figure 7). Alternative scenarios also exhibited some underprediction bias, but none as large as scenario 0. Several scenarios resulted in underprediction biases smaller than 5 per cent, including scenario 5, which, at 2.5 per cent, exhibited the smallest bias of any scenario tested (Figure 7).

Despite its having the smallest per cent bias and second-smallest per cent RMSE of any scenarios tested, scenario 5 was not particularly accurate in predicting biomass for sapling-sized trees (Table 6). Biomass predictions for saplings were generally less accurate as measured by RMSE compared with merchantable sized trees (Table 6). Detailed breakdowns of cross-validation accuracy statistics by species and size classes (not shown) indicated that a relatively small number of species contributed to the high variance and bias noted for saplings. Included in this group were species: red spruce (*Picea rubens*

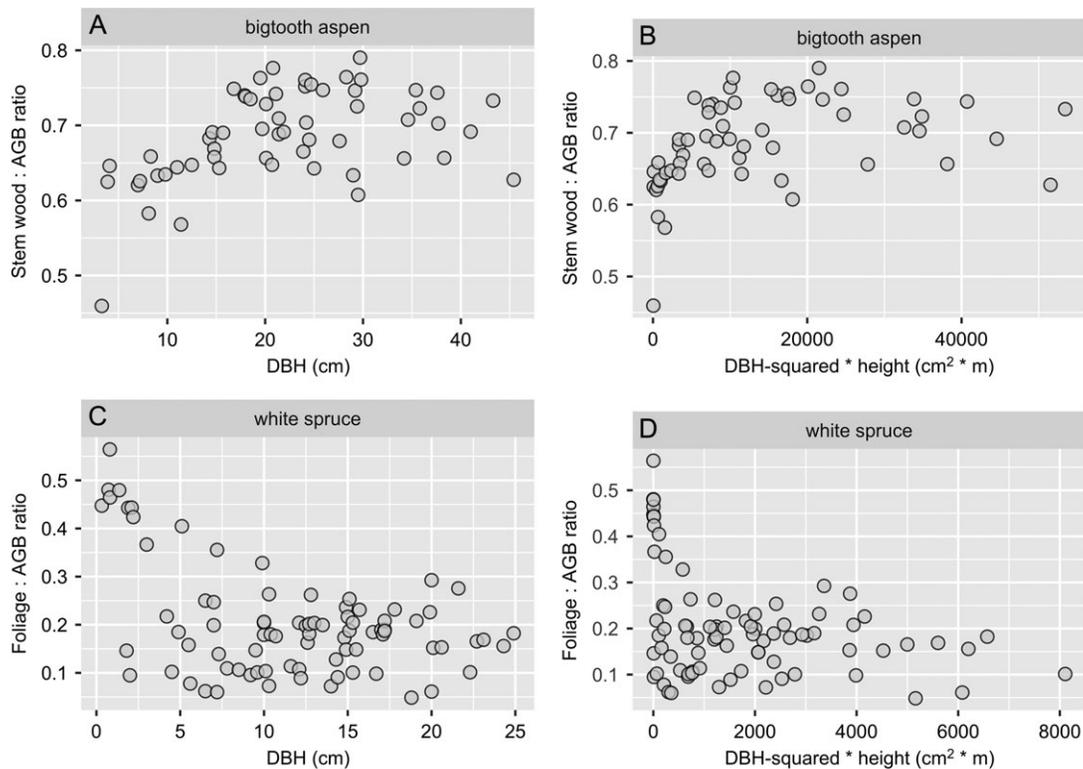


Figure 5 Prediction models for CRs were less precise when fitted to dbh alone (A, C) than when fitted to a variable combining dbh and total height (B, D).

Sarg.); eastern white pine (*Pinus strobus*, L.); water and swamp tupelos (*Nyssa aquatica* L., *N. biflora* Walter); chestnut oak (*Quercus prinus* L.) and northern red oak (*Q. rubra* L.). In this group only water tupelo, with $n = 85$ sapling-sized trees in the legacy database had a sample size ≥ 50 .

Discussion

Several findings of this study demonstrate the potential for improvement of live-tree AGB estimates obtained by linking CRM predictions with field-plot data from the U.S. Forest Service FIA NFI data. In Lake States and Central States regions merchantable volume equations are among the constituent parts of the CRM that can likely be improved without undue effort (Miles and Hill, 2010). The cubic foot volume equation of Stone is a notable candidate for improvement (Hahn, 1984), as it was originally developed from cordwood volumes and adapted for cubic volumes using multiplication by a single conversion factor, 2.24 m^3 (79 ft^3) per cord. Regional volume equations from the Central and Northeastern States relied on tree volumes imputed from volume tables, such as those developed by Gevorkiantz and Olsen (1955) and Bickford (1951), rather than on regression models developed directly from observed stem volumes and associated predictor variables (Barnard et al., 1973; Hahn and Hansen, 1991; Scott, 1981). Where existing models can be validated for accuracy in regional applications, it may be possible to improve CRM accuracy using existing volume estimators (e.g. Burk and Ek, 1999). Where no such models currently exist

improving CRM V_{merch} predictions should be an attainable goal assuming sufficient sample data can be obtained for developing new equations (e.g. Westfall and Scott, 2010).

Defining BEFs according to merchantable stem biomass is a preferred approach in national C assessments conforming to Intergovernmental Panel on Climate Change good practice guidelines (IPCC, 2006). This definition was found to be problematic when applied to individual trees at or near the 12.7 cm sapling DBH threshold (Figure 4). Even after reformulating CR definitions based on whole stem rather than merchantable stem biomass contents, the equation form used by Jenkins et al. (2003) was found to be insufficiently flexible to adequately represent observed CR patterns across a range of tree sizes. Other work has found nonlinearities like those noted here in BEFs computed in forests comprised of small-sized trees (Soares and Tomé, 2012). Sapling adjustment factors likely contribute to biases unresolved by modifications to the CRM examined here (Nelson et al., 2014).

Felled tree studies have often collected stem profile data for both ob and ib diameters, from which accurate models of wood and bark volume can be developed (Li and Weiskittel, 2011). We noted that bark:wood volume ratios from legacy trees (Table 3) agreed with results reported by Gevorkiantz and Olsen (1951) better than those reported by Miles and Smith (2009) for 24 Lake States species. This agreement may be due in part to consistency of definitions, as Gevorkiantz and Olsen (1951) were clear in noting that their bark volumes were calculated using ob diameters, which include airspaces in bark (MacFarlane and Luo, 2009). Laboratory determination of bark volumes is often done

Table 5 Chapman Richards model Eq. (2) root-mean squared errors (RMSE) as percentages of biomass CRs predicted from D^2H , for 32 species comprising 65% of biomass in eastern US Forests

Common name	Stem components			Crown components		
	n	RMSE (%)		n	RMSE (%)	
		Wood	Bark		Branches	Foliage
Balsam fir	97	11.7	7.7	99	7.1	6.5
White spruce	73	9.4	1.5	83	5.9	8.1
Black spruce	69	9.3	1.6	69	6.9	6.1
Red spruce	64	9.6	1.9	49	8.2	4.4
Shortleaf pine	438	5.6	2.8	221	4.2	3.2
Slash pine	473	5.8	3.4	270	4.2	3.5
Longleaf pine	603	6.0	2.9	330	5.1	3.8
Red pine	73	6.0	0.7	73	4.0	3.4
Eastern white pine	116	9.5	3.2	119	8.8	5.7
Loblolly pine	1184	7.4	3.6	867	5.7	5.7
Virginia pine	86	10.4	3.0	90	8.3	6.8
Red maple	283	8.8	2.3	289	7.8	3.1
Sugar maple	130	8.5	2.8	109	6.2	1.8
Paper birch	53	7.6	2.3	67	7.6	3.3
Amer. hornbeam	61	10.0	1.5	61	9.4	2.1
Hickory spp.	133	8.4	4.2	133	7.5	1.9
Flowering dogwood	56	8.7	1.6	56	8.7	2.8
Ash spp.	287	6.8	2.5	287	6.9	1.9
Sweetgum	665	5.8	2.8	665	5.4	2.4
Yellow-poplar	142	5.3	2.9	143	5.6	1.8
Water tupelo	148	3.3	1.5	148	3.3	1.3
Swamp tupelo	142	7.6	3.3	142	6.7	1.1
<i>Populus</i> spp.	111	3.4	2.6	131	6.0	3.3
Bigtooth aspen	58	4.4	2.7	75	4.8	2.0
Quaking aspen	105	4.3	2.6	120	5.3	1.5
White oak	249	6.8	2.5	262	7.1	1.5
Scarlet oak	73	7.2	2.5	73	7.5	1.3
Southern red oak	52	6.8	2.8	52	7.1	1.5
Water oak	193	8.2	2.6	193	8.3	2.6
Chestnut oak	78	7.3	3.6	78	8.4	1.1
Northern red oak	50	6.8	3.7	50	7.1	2.2
Elm spp.	55	7.6	3.0	55	8.3	2.8

using water displacement, which excludes airspaces in the volume measurement (Phillips and Taras, 1987). Any revisions to the bark volume quotients used in the CRM should be developed to ensure consistency of definitions, but also to account for the large number of species for which FIA requires accurate bark volume quotient information.

Our observations showed somewhat distinct patterns in how bark:wood volume ratios varied in trees of differing sizes and species (Figure 2). Smooth-barked species such as paper birch and quaking aspen tended to maintain a relatively constant bark:wood volume ratio over a range of tree dbh, while furrowed and scale type barks such as oaks and pines tended to show decreasing bark:wood volumes with increasing dbh. These patterns are consistent with shedding characteristics of various bark types; while smooth barked species shed little material

over time under ideal growing conditions, shedding is continual and typical in other bark types (Borger, 1973; Kaufert, 1937). These details notwithstanding, direct accounting of bark:wood volume ratio relationships to dbh in scenario 6 did not lead to appreciable improvement in overall accuracy of AGB predictions in the CRM framework compared with using species averages (Table 1, Figure 7).

Published SG values for North American tree species date at least as far back as Fernow (1897), with numerous studies having been conducted in past century (Antony et al., 2015; Newlin and Wilson, 1917; Wahlgren et al., 1966). One challenge in working with published SG summaries is that the variability in sample data is not always well characterized, whether it be in terms of variation among specimens collected from a single tree, variation among trees from a particular study site or region, or variation across species' geographic ranges. Another challenge is that many wood properties surveys were limited to clear wood specimens, so the suitability of using their SG measurements as standing-tree BEFs should be tested (Markwardt, 1930). Also, since bark SG relies on laboratory measurements of green volume, the method of bark volume determination – either including airspaces or not – directly affects results. Bark SG determined using water displacement for green volume determination will necessarily overestimate bark biomass on standing trees unless the standing-tree bark volume measurement is adjusted to exclude airspaces (MacFarlane and Luo, 2009).

Notable improvement in CRM accuracy was achieved by revising bark and wood properties to match observed values from legacy felled-tree studies, including a threefold reduction in prediction bias between scenarios 4 and 5 (Table 1, Figure 7). Wood and bark properties are known to vary with tree size and tissue position in stems, with different silvicultural practices, and across space; however, the quantification of these patterns is not always straightforward because the same relationships that hold for one species may not be present in others (Antony et al., 2015; Tasissa and Burkhart, 1998; Wiemann and Williamson, 2014).

Despite the relatively complex formulation of volume, SG, and CR models used to obtain volume and biomass estimates in the CRM under alternative scenarios 1–6, results showed potential for reducing RMSE and bias to levels comparable with the relatively simple formulation tested in scenario 7. Although scenario 7 achieved greater precision than any of other alternatives tested it has some notable limitations. One is that it relies entirely on species or species-group-specific AGB allometric equations, with no accounting for stem volumes, component relationships, or wood properties in forest trees. Another is that the use of AGB allometric equations alone does not ensure any consistency between estimates of wood volume and AGB. In multiresource inventories like NFIs, such consistency is often needed (Weiskittel et al., 2015). The overall reduction of apparent bias in scenario 5 is also a favourable outcome compared with the other scenarios tested since bias is an overriding concern in estimators that are applied to large data sets in NFI applications (Roxburgh et al., 2015).

It is important to note that RMSE and bias values reported here pertain to legacy data rather than biomass and AGB estimates reported by the US Forest Service FIA program. Errors in regional carbon estimates are subject to many factors including

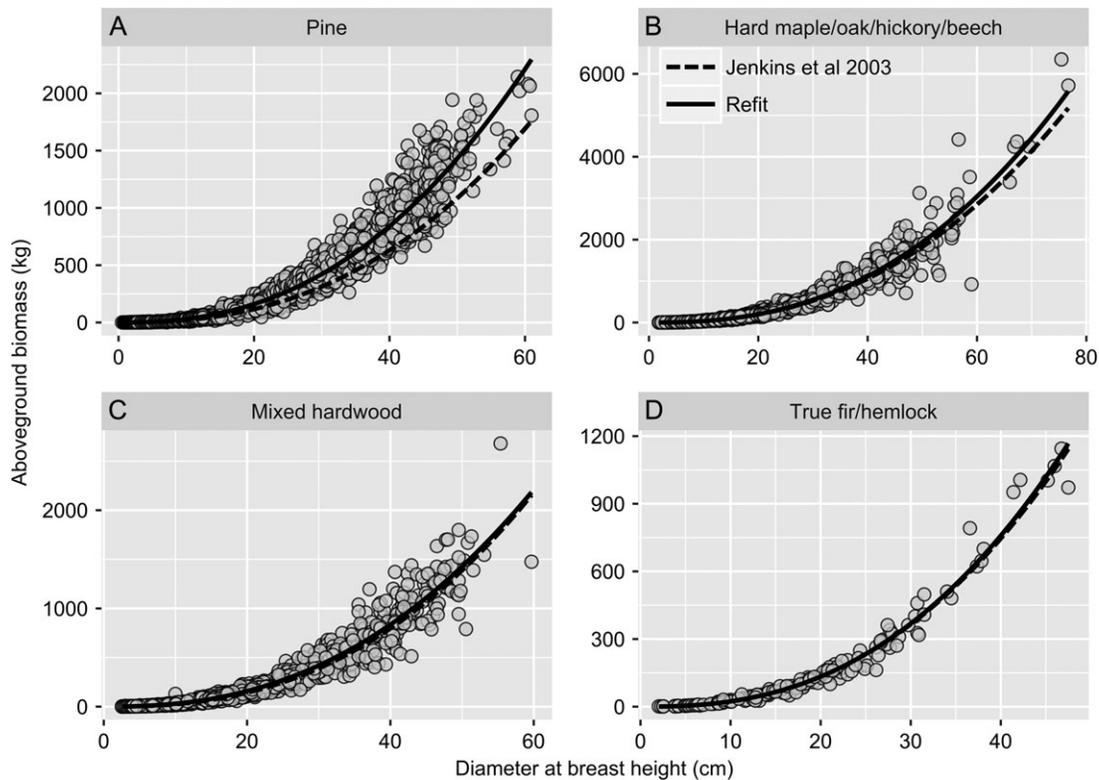


Figure 6 Aboveground biomass data for four eastern US species groups with allometric models of [Jenkins et al. \(2003\)](#) and Eq. (3) fitted to the data shown. (A) Pine, (B) hard maple/oak/hickory/beech, (C) mixed hardwood and (D) true fir/hemlock.

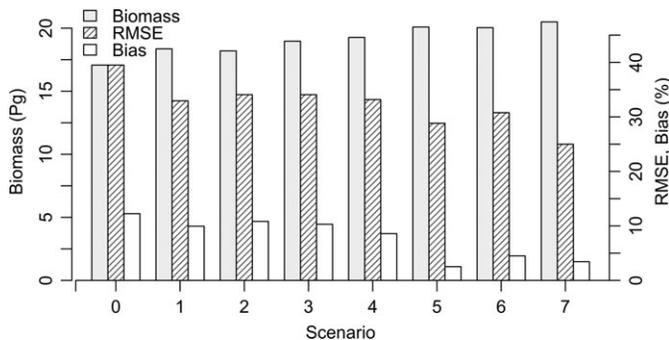


Figure 7 Eastern US live-tree aboveground biomass estimates under alternatives (Table 1) to the current CRM estimator (scenario 0). Per cent RMSE and underestimation Biases were calculated by 10-fold cross-validation of AGB values predicted for $n = 6480$ trees under each scenario.

sampling error and model prediction errors that can be investigated using a number of analytical techniques ([McRoberts and Westfall, 2014](#)), all of which employ certain assumptions that must be considered. A key assumption in the errors reported here is that suitable model forms were chosen for volume, CR, and AGB equations. Another concern is whether data compiled from legacy volume and biomass studies adequately characterize the ranges of tree form, wood and bark properties, component relationships, and AGB that arise in forests of the eastern US. Legacy data undoubtedly include fewer trees of poor form than trees in larger populations due to longstanding recommendations

Table 6 Per cent RMSE and bias from 10-fold cross-validation on legacy trees show relatively poor performance of biomass prediction methods for saplings ($\text{dbh} < 12.7 \text{ cm}$; $n = 2306$) compared with larger merchantable sized trees ($\text{dbh} \geq 12.7 \text{ cm}$; $n = 4174$)

Scenario	$\text{dbh} < 12.7 \text{ cm}$		$\text{dbh} \geq 12.7 \text{ cm}$	
	RMSE	Bias	RMSE	Bias
0	51.5	-30.8	28.4	-11.9
1	46.5	-20.0	25.7	-10.0
2	48.2	-20.0	26.7	-10.9
3	48.2	9.3	26.7	-10.9
4	46.6	22.6	25.7	-9.4
5	40.8	29.8	22.5	-3.9
6	43.7	35.2	24.2	-5.8
7	34.5	0.7	19.1	-3.7

that forked, broken, leaning or scarred trees be excluded from mensurational studies ([Behre et al., 1926](#)). Destructive sampling for volume and biomass is often limited to areas where road access is good to accommodate equipment needs and specimen collection ([Williams et al., 1999](#)). These and other concerns about the data used here apply in most applications of allometric model development.

Notwithstanding the extraordinary collection of legacy biomass equations and wood properties information compiled for

the development of US national-scale biomass and C estimators currently in use (Jenkins *et al.*, 2004; Miles and Smith, 2009), the magnitudes of prediction errors observed here indicated considerable room for improvement. Legacy tree data may serve a vital role in future research, both in testing existing methods and developing new models that may ultimately prove superior in national forest C assessments (MacFarlane, 2015; Ung *et al.*, 2008; Weiskittel *et al.*, 2015). The work carried out here points to a possible reduction in prediction biases of nearly 80 per cent over the baseline CRM, and reduction of overall prediction RMSE of more than 25 per cent (Figure 7). The need for additional research on improving national scale biomass estimators seems clear given the impact such improvements will have on C stock estimates for NFIs in the US and other countries.

Even though AGB can be predicted accurately for many species using conventional allometric modelling, substantial challenges remain in predicting stem volume, AGB, and biomass components simultaneously (Castedo-Dorado *et al.*, 2012; Enes and Fonseca, 2014). Recent work has shown advances in the development of regression equations that maintain additivity in biomass component predictions (Affleck and Diéguez-Aranda, 2016; Dong *et al.*, 2015; Poudel and Temesgen, 2016; Zhao *et al.*, 2015). Past work has also demonstrated positive results in the simultaneous estimation of volume and biomass, although primarily in stem wood and bark (Brooks *et al.*, 2007; Jiang and Brooks, 2008; Parresol and Thomas, 1995). To meet the information needs for both volume and biomass inventories, further work is needed to identify suitable approaches for combining information on both attributes (Weiskittel *et al.*, 2015).

While this work focused on models used to estimate AGB and C stocks in forests of the eastern US, additional work is needed to determine how revisions to CRM biomass estimators might affect regional estimates of C stock change (Magnussen *et al.*, 2014). Stock change is a primary determinant of forest C sequestration or emissions over time, e.g., in tier 2 and 3 methods adopted in the United Nations' Good Practice Guidance for Land Use, Land-Use Change, and Forestry (IPCC, 2006). The US NFI includes remeasured data for all the states studied here, which will facilitate the determination of what effects the alternatives proposed here may have on estimates of C stock change. Despite the findings here that C stocks are presently underestimated in eastern US forests, a similar finding for sequestration rates is not assured (Domke *et al.*, 2012; Woodall, 2012). Aside from land use and land-use changes, forest C sequestration rates are affected by many factors including the mixtures of tree species, ages, and size classes. How these factors interact in forest C sequestration is a subject of ongoing investigation (Coulston *et al.*, 2015; Woodall *et al.*, 2015).

Supplementary data

Supplementary data are available at *Forestry* Online.

Conflict of interest statement

None declared.

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