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Development and evaluation of aboveground small tree biomass models for naturally regenerated and planted species in eastern Maine, U.S.A.

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ABSTRACT

Numerous models are available in northeastern North America to estimate aboveground tree biomass, yet most have focused on trees ≥ 12.5 cm diameter, and these models are often poor predictors of small tree biomass (< 12.5 cm diameter). Additionally, models available to estimate small tree biomass often lack independent evaluation with field data. We developed a new set of additive biomass component (foliage, branch, and bole) models for five naturally regenerated hardwood species, four hybrid poplar (*Populus* sp.) clones and white spruce (*Picea glauca* (Moench.)), from trees in eastern Maine. Biomass measurements were used to evaluate national and regional models for naturally regenerated species, and species specific models for planted stock. Results showed that the regional and national models provided similar fits for total biomass across all species. Moreover, the small tree biomass models currently used to predict woody biomass substantially underestimated biomass from 19.0% to 36.6% for all of the naturally regenerated hardwood species at our site. This substantial underestimation of small tree biomass may have contributed to the recent 34% decrease in estimated sapling woody biomass, and 15% decrease in aboveground biomass of all living trees in Maine, where nearly one-quarter of the 70,000 km² forestlands are dominated by saplings. This problem may exist in other regions of the United States if substantial proportions of forestlands are dominated by small trees. Further model evaluation is warranted to assess the performance of the current models.

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1. Introduction

Numerous models are available to predict aboveground biomass of tree species in northeastern North America [1–4],

yet the majority of these models were developed for medium and large size trees (≥ 12.5 cm diameter at breast height [DBH]). Small tree (seedlings and saplings; 0.1 cm–12.4 cm DBH) biomass estimates in the region are limited to a few set of models, and their predictions have not

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been well compared to independent data. Therefore, biomass predictions may be inaccurate when naturally regenerated understories and juvenile plantations are common. For instance, alternative models were recently found to produce substantially different estimates of tree biomass in north-eastern North America [5], but there is general lack of data to evaluate biomass models and investigate potentially different estimates. Reliable small tree biomass models are especially important in Maine, U.S.A. where nearly 24% of the forested area (17,000 km² out of 70,000 km²) is dominated by sapling-sized (2.5 cm–12.4 cm DBH) stands [6]. Although different models may produce variable sapling biomass estimates in the region, the scope of the problem may extend across the United States, particularly in regions with large proportions of stands dominated by small trees.

Only a few models are currently available to estimate small tree biomass in northeastern North America, including the national Jenkins et al. (Jenkins), Young et al. (Young), and compilation of models in Ter-Mikaelian and Korzukhin (TMK) [3,4,7]. The Jenkins, Young, and TMK models were developed to predict both individual component (foliage, branch, bole, and stump) and total aboveground biomass. The Jenkins models were developed from a large database of published biomass models and condensed into nine models for all tree species across the United States. The Jenkins models apply to a wide range of tree sizes, but were only fit to trees ≥ 2.5 cm diameter at breast height (DBH). The Young models were developed for many tree species in Maine and estimate total aboveground biomass of trees down to 0.1 cm DBH. The Young models have been used to predict aboveground biomass extensively in the northeastern US and were used for regional sapling biomass estimates by the US Forest Service, Forest Inventory and Analysis (FIA) program from 1998 to 2009 [2]. Like the Jenkins models, the TMK models are compiled biomass models of common North American tree species from multiple sources, but their work has received less attention.

In 2009, the FIA program switched to estimating forest biomass with the component ratio method (CRM), a nationally-consistent approach. The CRM estimates woody aboveground biomass as the sum of the branches, bole, and stump biomass, but is only valid for trees ≥ 12.5 cm DBH (minimum merchantability threshold) [8,9]. The CRM is not applicable for saplings since it relies on estimates of merchantable volume, which is considered zero for trees < 12.5 cm DBH. Instead, the FIA aboveground sapling (FAS) models were developed to estimate woody biomass of trees ranging from 2.5 cm to 12.4 cm DBH. The FAS models multiply the Jenkins woody biomass prediction (total aboveground – foliage) by a species-specific adjustment factor to ensure a smooth transition into larger size-class estimates by the CRM [9,10]. Even though the FAS models have not been compared to field data in northeastern North America, they are the only models used by FIA to estimate sapling woody biomass in the region [10]. Without evaluation of the FAS biomass models, it is difficult to determine whether current estimates accurately represent sapling biomass in northeastern North America. For instance, in Maine, McWilliams et al. [6] reported that there were 18.6×10^9 saplings with an estimated woody biomass of 169.6 Tg in 2003 using the FIA regional model approach.

Comparatively, there were 20.9×10^9 saplings with an estimated biomass of 112.1 Tg in 2010 using the FAS models [11]. The result was an 11% increase in the number of saplings but a 34% decrease in sapling woody biomass in Maine over the seven year period.

Inconsistencies in the prediction of small tree total and woody aboveground biomass in northeastern North America and the selection of appropriate models to refine predictions can be addressed by comparing published models with independent data and fitting new models to field measurements. In particular, no biomass models for Northeast tree species were fit with statistical techniques that force additivity of aboveground components, where predictions from component models sum to predictions from total aboveground models. Therefore, the objectives of this study were to: (1) develop a new set of additive aboveground component (foliage, branch, bole [including stump]) and total aboveground biomass models for five naturally regenerated hardwood species (red maple [*Acer rubrum* L.], paper birch [*Betula papyrifera* Marsh.], gray birch [*Betula populifolia* Marsh.], bigtooth aspen [*Populus grandidentata* Michx.] and trembling aspen [*Populus tremuloides* Michx.]), four planted hybrid poplar clones (D51, DN10, DN70 – *Populus deltoides* \times *Populus nigra*, NM6 – *Populus nigra* \times *Populus maximowiczii*), and white spruce [*Picea glauca* (Moench) Voss] in eastern Maine, (2) compare the partitioning of total aboveground biomass to various components of naturally regenerated hardwood species, hybrid poplar, and white spruce early in stand development, (3) compare small tree total aboveground oven-dry biomass estimates of national and regional models for naturally regenerated hardwood species, hybrid poplar clones, and white spruce, and (4) compare sapling aboveground woody oven-dry biomass to the Jenkins and FAS models currently used by the FIA program for the five naturally regenerated species.

2. Methods

2.1. Study design

Five naturally regenerated hardwood species (red maple, paper birch, gray birch, bigtooth aspen, and trembling aspen), four planted hybrid poplar clones (D51, DN10, DN70, - *P. deltoides* \times *P. nigra*, and NM6 – *P. nigra* \times *P. maximowiczii*), and planted white spruce were destructively sampled to estimate aboveground component oven-dry biomass. Trees were part of an experiment established in 2004 on the Penobscot Experimental Forest in eastern Maine (44° 50' 37" N, 68° 37' 38" W). A detailed description of the experiment, including treatments and planting stock are given in Nelson et al. [12,13]. The experiment consisted of a $3 \times 3 + 1$ factorial array of three silvicultural treatments (thinning, thinning plus enrichment planting, and intensively managed plantations) and three species compositional objectives (hardwood, mixedwood, and conifer), plus an untreated control, each replicated four times. The experiment was installed at a 9.2 ha site that was clearcut in 1995. Therefore, trees were destructively sampled sixteen years after harvest and seven years after the experiment was initiated. Natural species composition at the site when the trees were sampled was dominated by a mixture

of young shade intolerant hardwood and shade tolerant conifer species [12].

2.2. Measurements

Trees were cut at the root collar in the summer of 2011 during peak foliage display (late June to early August) to ensure accurate estimates of hardwood foliage biomass. For each species, trees were sampled from five DBH classes estimated from observed DBH distributions of the 2010 inventory. For the naturally regenerated hardwood species, between 12 and 17 individuals (3–6 in each DBH class) were sampled per species. Five individuals per hybrid poplar clone were sampled from plantations for a total of 20 trees. Ten planted white spruce were sampled (5 from plantations and 5 from naturally-regenerated treatments with enrichment planting). A total of 102 trees (72 naturally-regenerated and 30 planted; Appendix A) were sampled. Tree size sampled ranged from 0.3 cm DBH for red maple and white spruce to 13.7 cm for the NM6 hybrid poplar clone (Table 1).

DBH, height, and length of live crown were measured for all sample trees. Foliage and branch components were separated from boles in the field and dried in the lab. Foliage and branches were dried at 65 °C for a minimum of two weeks. Boles were cut into approximately 25 cm segments and dried at 65 °C for a minimum of six weeks. While drying, weight was checked periodically to ensure samples dried to constant weight. After drying, foliage and branch components were separated and weighed to the nearest 10 mg. Bole dry weight was measured to the nearest 10 g.

2.3. Analytical approach

2.3.1. Additive biomass models

Since trees were sampled from different silvicultural treatments, we investigated whether accounting for treatment effects in the models influenced the fit of the component biomass equations. Biomass models by species and component were fit as nonlinear mixed-effects models with treatment as a random effect and compared to models fit without random effects using likelihood ratio tests. If the likelihood ratio tests were significant at $\alpha = 0.05$, the mixed-effects model

had a superior fit to the fixed-effects model [14], and accounting for silvicultural treatment was justified. Natural hardwood species were tested across three silvicultural treatments (untreated control, thinning, thinning plus enrichment planting), planted white spruce across two treatments (thinning plus enrichment planting and plantations), and hybrid poplar models were tested for differences among the four clones.

When additivity of component biomass models is not forced, component biomass estimates may not sum to estimated total biomass [15]. Therefore, a system of component and total aboveground biomass models were fit by species using nonlinear seemingly-unrelated regression (NSUR; Table 2) [15,16]. Compared to other additive approaches, such as weighted least squares regression, which assume independence among observations, NSUR is preferred since it accounts for autocorrelation among components of the same tree [17]. Additive biomass models were fit using the MODEL procedure in SAS software version 9.2 [18].

Multiple model forms, including various combinations of DBH, height, and length of live crown were explored, but did not improve predictions compared to a two-parameter power function with DBH as the sole independent variable ($\text{Biomass} = \beta_0 \text{DBH}^{\beta_1}$). Although numerous equation forms can represent exponential relationships common to sapling diameter and biomass, the power function is common because the scaling parameter (β_1) has biological interpretation [19] and estimated biomass is restricted to positive values.

2.3.2. Published models

Several different sets of published model forms and parameters were compared to the field data (Table 2). For the naturally regenerated hardwoods, the Jenkins, Young, and TMK models were evaluated. The Jenkins models were not developed from field measurements; instead parameters were estimated using a generalized regression approach [20], where biomass was predicted with many individual models and then generalized parameters were estimated from the pseudo-data. Comparatively, the Young and TMK models were fit with field measurements. The Young models do not include weight of a 15.2 cm stump length for trees ≥ 2.5 cm DBH. Therefore, the weight of the 15 cm stump of the sampled trees was subtracted from the observed total aboveground biomass for

Table 1 – Descriptive statistics of destructively sampled trees used to fit the additive aboveground biomass equations and evaluate published equations. The number of individuals per species (n), median values and ranges of DBH (cm), foliage biomass (kg), branch biomass (kg) and bole biomass (kg) are shown.

Species	n	DBH median (cm)	DBH range (cm)	Foliage median (kg)	Foliage range (kg)	Branch median (kg)	Branch range (kg)	Bole median (kg)	Bole range (kg)
Red maple	12	2.4	0.3–6.0	0.12	0.01–0.92	0.27	0.01–0.99	0.73	0.01–7.11
Paper birch	13	1.2	0.5–9	0.05	0.01–0.32	0.04	0.01–0.42	0.17	0.02–2.38
Gray birch	15	1.2	0.5–6.9	0.04	0.01–0.54	0.05	0.01–1.50	0.14	0.04–10.02
Bigtooth aspen	17	5.6	1.1–13.1	0.41	0.01–4.08	1.06	0.02–9.46	5.77	0.13–32.33
Trembling aspen	15	5.2	2.6–12	0.38	0.04–7.39	0.76	0.07–18.62	4.03	0.78–29.63
Hybrid poplar (D51)	5	4.3	1.4–7.5	0.56	0.06–1.46	0.72	0.11–2.39	2.52	0.33–7.98
Hybrid poplar (DN10)	5	4.6	2.3–10.9	0.45	0.11–2.67	0.77	0.16–4.70	3.08	0.70–14.94
Hybrid poplar (DN70)	5	4.1	0.7–8.7	0.66	0.02–1.53	1.45	0.04–2.67	2.51	0.10–9.69
Hybrid poplar (NM6)	5	6.8	3–13.7	1.32	0.30–4.12	2.48	0.52–14.99	7.06	1.01–27.89
White spruce	10	1.6	0.3–5.1	0.78	0.20–2.74	0.44	0.12–1.70	0.43	0.13–2.22

Table 2 – Equations forms of the seven equations used for evaluation with data from eastern Maine. M is oven-dry biomass (kg) for foliage, branch, and bole components, and total aboveground biomass. DBH is diameter at breast height in cm. A_s is the species specific sapling adjustment factor that is multiplied by woody biomass for the FIA aboveground sapling (FAS) equations. β_i 's are species or group specific parameters of the models.

Equation	Form	Species	Citation
Additive	$M_{\text{foliage}} = \beta_{10} \text{DBH}^{\beta_{11}}$ $M_{\text{branch}} = \beta_{20} \text{DBH}^{\beta_{21}}$ $M_{\text{bole}} = \beta_{30} \text{DBH}^{\beta_{31}}$ $M_{\text{total}} = \sum_{i=1}^3 \beta_{i0} \text{DBH}^{\beta_{i1}}$	ALL	This investigation
Jenkins	$M_{\text{total}} = e^{(\beta_0 + \beta_1 \times \ln(\text{DBH}))}$	ALL	[3]
FAS	$M_{\text{total}} = e^{(\beta_0 + \beta_1 \times \ln(\text{DBH}))}$ $M_{\text{foliage}} = M_{\text{total}} [e^{(\beta_0 + (\beta_1 / \text{DBH}))}]$ $M_{\text{FAS}} = (M_{\text{total}} - M_{\text{foliage}}) \times A_s$	Natural hardwood species	[8]
Young	$M_{\text{total}} = e^{(\beta_0 + \beta_1 \times \ln(\text{DBH}))}$	ALL	[4]
TMK	$M_{\text{total}} = \beta_0 \text{DBH}^{\beta_1}$	Natural hardwood species	[7]
Netzer	$M_{\text{total}} = \beta_0 + \beta_1 \text{DBH} + \beta_2 \text{DBH}^2$	Hybrid poplar clones	[25]
Pitt	$M_{\text{total}} = \beta_0 + \beta_1 \text{DBH}^{\beta_2}$	White spruce	[24]

trees ≥ 2.5 cm DBH to evaluate the Young models. Ter-Mikaelian and Korzukhin [7] present many models for each species, but we selected the models that were fit with data proximate to our study site, namely New Brunswick and Nova Scotia, Canada (Freedman et al. [21] for bigtooth aspen; Ker [22] for gray birch; and Ker [23] for red maple, paper birch, and trembling aspen), and encompassed the range of DBH in the current investigation.

White spruce total aboveground biomass was compared to the Jenkins, Young, and Pitt and Bell [24] (Pitt) models (Table 2). The Pitt model was developed for juvenile plantation white spruce in Ontario, Canada ranging from 0.6 cm to 7.1 cm DBH. Hybrid poplar total aboveground biomass was compared to the Jenkins, Young, and Netzer et al. [25] (Netzer) models. The Jenkins and Young models for aspen species were used, since specific hybrid poplar parameters were not available. The Netzer model was developed from 152 plantation-grown trees in the north central United States. The majority of trees used for the Netzer model were crosses of *P. deltoides* \times *P. nigra*, ranging in age from 3 to 10 years old and 1.6 cm–22.2 cm DBH. All of the aforementioned equations were selected because they used DBH as the only predictor variable, but model form differed by equation (Table 2). For consistency and to evaluate extrapolation potential of the models, total biomass was predicted for all observed data, even if the measured DBH was below the lower limit of the DBH range used to develop the model.

Woody aboveground biomass estimates of the FAS [8] and Jenkins [3] models were evaluated with the sapling-sized sample trees (2.5 cm–12.4 cm DBH). Woody aboveground woody biomass was estimated by the FAS and Jenkins models by subtracting foliage biomass from total aboveground biomass. A species-specific adjustment factor was then multiplied by estimated woody biomass for the FAS models. The FAS adjustment factor varied by species (0.7–0.8) and was the ratio of the average CRM and Jenkins woody biomass estimates for all 12.5 cm DBH trees in the FIA database [8].

2.3.3. Model evaluation

This investigation comprised three phases of model evaluation: (1) total aboveground biomass of all naturally

regenerated hardwood trees for the Jenkins, Young, TMK, and additive models; (2) total aboveground biomass of hybrid poplar clones and white spruce for the Jenkins, Young, Netzer, Pitt, and additive models; and (3) sapling woody aboveground biomass for the naturally regenerated species using the FAS, Jenkins, and additive models. Predictions were evaluated with root mean square error (RMSE) to assess model accuracy, and mean bias (MBIAS) and mean absolute bias (ABIAS) to assess model precision [26,27]. RMSE was calculated as:

$$\text{RMSE} = \sqrt{\frac{\sum_{i=1}^n (y_i - \hat{y}_i)^2}{n}}$$

where y_i are the observed values, \hat{y}_i are the predicted values, and n is the number of observations. MBIAS was calculated as:

$$\text{MBIAS} = \frac{\sum_{i=1}^n y_i - \hat{y}_i}{n}$$

and ABIAS was calculated as:

$$\text{ABIAS} = \frac{\sum_{i=1}^n |y_i - \hat{y}_i|}{n}$$

The minimum detectable negligible difference (MDND) statistic proposed by Parkhurst [28] and used for model evaluation by Radtke and Robinson [29] was used to further assess prediction accuracy. The null hypothesis was the observed and predicted values were not equal [30]. MDND was calculated as:

$$P\left(t \leq \frac{(\mu_{\text{obs}} - \mu_{\text{pred}}) - \text{MDND}}{\sigma_{\mu_{\text{obs}} - \mu_{\text{pred}}}}\right) = \alpha$$

where t is the critical t-value for the respective degrees of freedom and significance level ($\alpha = 0.05$ for this investigation), μ_{obs} and μ_{pred} were the observed and predicted mean biomass, and $\sigma_{\mu_{\text{obs}} - \mu_{\text{pred}}}$ was the standard deviation of the difference between the observed and predicted values. If the mean prediction relative to the observed (PRO) value (i.e. negative or positive percent deviation of predictions from the observed

values) was within the bounds of $\mu_{\text{obs}} \pm \text{MDND}$, the null hypothesis was rejected and the predicted values were considered similar to the observed values.

The MDND was used to define the upper and lower limits of the equivalence region, as the value can vary among models due to absolute differences between observed and predicted values [29]. The MDND can also be used to infer the range of mean predictions where equivalence is assumed between the observed and predicted values. Since a small sample of trees was used for this investigation, a slight difference between the observed and predicted mean biomass can result in an inflated estimate of the percent MDND. Therefore, absolute MDND estimate (kg) was also calculated. Model evaluation was performed in R version 3.0.0 [31].

3. Results

3.1. Silvicultural effects on biomass estimation

Likelihood ratio tests were not significant for 17 of the 21 models examined. Significant results were found for the bole models of red maple ($p = 0.001$) and bigtooth aspen ($p = 0.007$), as well as the branch model of gray birch ($p < 0.001$) and the foliage model of paper birch ($p = 0.015$) (Table 3). Given that the majority of the component models were not influenced by silviculture or clone, and due to the logical and statistical constraints of having only one model with random effects in a system of models, all additive component biomass models were fit with NSUR assuming no difference among treatment or clone.

Table 3 – Likelihood ratios and associated p -values for the likelihood ratio tests comparing the fit of component equations with and without silvicultural treatment or hybrid poplar clone as a random effect. P -values < 0.05 were considered significant and indicate the inclusion of treatment or clone as a random effect significantly improved the fit of the models.

Species	Component	Likelihood ratio	p -value
Red maple	Foliage	<0.001	0.998
	Branch	0.101	0.751
	Bole	9.768	0.001
Paper birch	Foliage	5.921	0.015
	Branch	<0.001	0.994
	Bole	0.765	0.382
Gray birch	Foliage	0.760	0.383
	Branch	15.264	<0.001
	Bole	<0.001	0.994
Bigtooth aspen	Foliage	<0.001	0.999
	Branch	<0.001	0.998
	Bole	7.365	0.007
Trembling aspen	Foliage	<0.001	0.999
	Branch	<0.001	0.999
	Bole	<0.001	0.999
White spruce	Foliage	0.231	0.631
	Branch	<0.001	0.999
	Bole	<0.001	0.998
Hybrid poplar	Foliage	<0.001	0.999
	Branch	<0.001	0.978
	Bole	2.337	0.126

3.2. Additive component biomass models

A strong relationships between DBH and total aboveground dry weights was found for the majority of the five naturally regenerated hardwood species (Table 4), with the exception of red maple foliage ($R^2 = 0.466$). Scaling exponents (β_1) were similar among the paper birch component models, ranging from 1.519 ± 0.175 (estimate \pm SE; foliage) to 2.323 ± 0.044 (bole). Comparatively, the scaling exponents were more variable among the trembling aspen component models, with estimates of 5.126 ± 0.257 and 2.272 ± 0.107 for foliage and bole biomass, respectively. Constant parameters (β_0) were greater for bole biomass than foliage or branch biomass for paper birch, bigtooth aspen, and trembling aspen, but the difference was most pronounced for the aspen species, where β_0 for bole models were 0.116 ± 0.018 and 0.107 ± 0.026 for bigtooth aspen and trembling aspen, respectively.

A strong relationship between DBH and total aboveground dry weights was also found for hybrid poplar additive component models ($R^2 \geq 0.941$; Table 5). Component scaling exponents ranged from 1.829 ± 0.077 for foliage to 3.272 ± 0.241 for branch biomass, while the constant parameters ranged from 0.003 ± 0.002 for branch biomass to 0.112 ± 0.038 for bole biomass. White spruce component models had R^2 values ranging from 0.733 to 0.940 for foliage and bole biomass, respectively. The scaling exponents for white spruce ranged from 1.289 ± 0.202 to 1.596 ± 0.128 for branch and bole biomass, respectively.

For DBH < 4 cm, the models predicted white spruce, gray birch, paper birch, red maple, and hybrid poplar were respectively the four species with the greatest proportion of total aboveground biomass in foliage; gray birch and white spruce had the greatest proportion of biomass in branch material; and bigtooth aspen, trembling aspen, hybrid poplar, and red maple had the greatest proportion of biomass in the bole (Fig. 1). Across the range of DBH sampled, the proportion of foliage biomass increased for the aspen species, but decreased for all the other species. Conversely, the proportion of bole biomass decreased with greater DBH for the aspen species and hybrid poplar but increased for the other species.

3.3. Evaluation of total aboveground biomass models

The four biomass models exhibited different trends in small tree (0.3 cm–13.1 cm DBH) total biomass with increasing DBH for the naturally-regenerated hardwood species, especially above 2 cm DBH (Fig. 2). For red maple, RMSE and ABIAS of the Young model were 44% and 43% lower than the TMK model (Table 6). The Young and Jenkins models predicted similar total biomass estimates for both aspen species, overestimating bigtooth aspen mean total aboveground biomass (PRO) by 12.3% and 13.3%, respectively, and underestimated trembling aspen biomass by 11.3% and 8.0%, respectively (Table 6). The RMSE and ABIAS of the TMK bigtooth model were 0.98 kg and 0.60 kg, respectively, while the RMSE and ABIAS of the Jenkins models were 2.15 kg and 1.39 kg, respectively. The null hypothesis of the equivalence test was not rejected for the TMK models for red maple, paper birch, gray birch, and trembling aspen, while the null hypothesis of the Young models was only not rejected for trembling aspen.

Table 4 – Naturally regenerated hardwood species oven-dry biomass (kg) model parameter estimates (Est.), standard errors (SE), *p*-values, and fit statistics (mean square error (MSE) and *R*²). Component biomass models were fit with nonlinear seemingly-unrelated regression to restrict the sum of component biomass to total aboveground biomass.

Species	Component	β_0			β_1			Fit statistics	
		Est.	SE	<i>p</i> -value	Est.	SE	<i>p</i> -value	MSE	<i>R</i> ²
Red maple	Foliage	0.135	0.069	0.079	0.811	0.366	0.051	0.045	0.466
	Branch	0.132	0.040	0.008	1.148	0.200	<0.001	0.023	0.830
	Bole	0.091	0.022	0.002	2.421	0.140	<0.001	0.079	0.981
	Total							0.169	0.979
Paper birch	Foliage	0.042	0.009	<0.001	1.519	0.175	<0.001	0.001	0.906
	Branch	0.039	0.014	0.015	1.742	0.287	<0.001	0.003	0.844
	Bole	0.100	0.006	<0.001	2.323	0.044	<0.001	<0.001	0.999
	Total							0.008	0.990
Gray birch	Foliage	0.101	0.019	<0.001	0.913	0.122	<0.001	0.008	0.792
	Branch	0.109	0.029	0.002	1.418	0.149	<0.001	0.017	0.933
	Bole	0.088	0.003	<0.001	2.449	0.017	<0.001	0.001	0.999
	Total							0.039	0.997
Bigtooth aspen	Foliage	0.001	0.001	0.055	3.264	0.194	<0.001	0.032	0.966
	Branch	0.001	0.001	0.095	3.612	0.225	<0.001	0.167	0.996
	Bole	0.116	0.018	<0.001	2.191	0.064	<0.001	0.643	0.991
	Total							0.985	0.993
Trembling aspen	Foliage	0.001	0.001	0.137	5.126	0.257	<0.001	0.044	0.987
	Branch	0.001	0.001	0.132	4.848	0.254	<0.001	0.356	0.984
	Bole	0.107	0.026	0.001	2.272	0.107	<0.001	1.567	0.976
	Total							1.580	0.992

The Young and Jenkins aspen models produced similar total aboveground biomass estimates for hybrid poplar (Fig. 3), overestimating mean observed biomass (PRO) by 10.6% and 11.4%, respectively (Table 7). The null hypothesis of the equivalence test was not rejected for the Netzer model where biomass was underestimated by 9.4%. White spruce total aboveground biomass was underestimated by 52.4%, 12.8%, and 2.1% by the Jenkins, Additive, and Young models, and overestimated by 15.0% by the Pitt equation (Table 7). The null hypothesis for the white spruce equivalence test was not rejected for the Additive and Jenkins models.

3.4. Aboveground woody biomass evaluation

Fewer trees were used to evaluate woody biomass than total biomass because the DBH of some trees was below the lower

cutoff used by the FAS models (≥ 2.5 cm– < 12.5 cm DBH). Paper birch and gray birch were combined for evaluation of the woody biomass models because of the small sample size for both species within the FAS range of DBH, and both species use the same Jenkins equation and FAS adjustment factors. The FAS models substantially underestimated mean aboveground woody biomass (PRO) relative to the observed data for all four naturally regenerated hardwood species/species groups (Fig. 4), from 36.6% for trembling aspen to 19.0% for the birch species (Table 8). Similarly, the equivalence test of the FAS model was not rejected for any of the groups. Comparatively, the Jenkins models overestimated woody biomass by 8.4%, 11.3%, and 17.0% for birch species, red maple, and bigtooth aspen, respectively, and underestimated trembling aspen woody biomass by 3.4%. The Jenkins model equivalence test was rejected for all species.

Table 5 – Hybrid poplar and white spruce additive oven-dry biomass (kg) model parameter estimates (Est.), standard errors (SE), *p*-values, and fit statistics (mean square error (MSE) and *R*²). The four hybrid poplar clones were combined for a single model. Component biomass models were fit with nonlinear seemingly-unrelated regression to restrict the sum of component biomass to total aboveground biomass.

Species	Component	β_0			β_1			Fit statistics	
		Est.	SE	<i>p</i> -value	Est.	SE	<i>p</i> -value	MSE	<i>R</i> ²
Hybrid poplar	Foliage	0.034	0.006	<0.001	1.829	0.077	<0.001	0.026	0.975
	Branch	0.003	0.002	0.118	3.272	0.241	<0.001	0.642	0.941
	Bole	0.112	0.038	0.009	2.112	0.141	<0.001	2.682	0.944
	Total							5.415	0.960
White spruce	Foliage	0.299	0.090	0.010	1.346	0.209	<0.001	0.133	0.733
	Branch	0.211	0.060	0.008	1.289	0.202	0.001	0.046	0.801
	Bole	0.163	0.031	0.001	1.596	0.128	<0.001	0.022	0.940
	Total							0.612	0.847

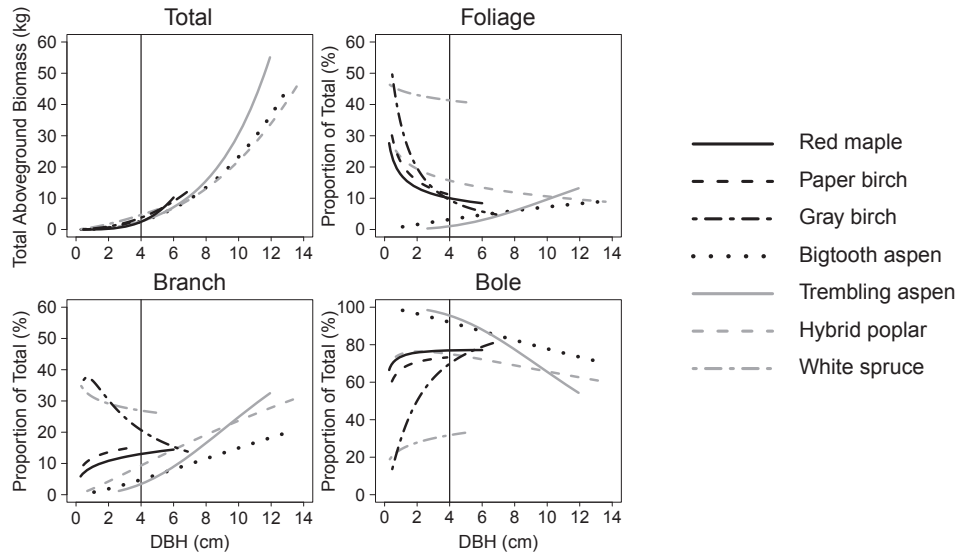


Fig. 1 – Total aboveground biomass (kg) and the proportion of total biomass (%) by component (foliage, branch, and bole) predicted from the additive models for red maple, paper birch, gray birch, bigtooth aspen, trembling aspen, hybrid poplar, and white spruce.

4. Discussion

4.1. Additive component models

A total of 21 component models were fit as nonlinear mixed-effects models, where silvicultural treatment or hybrid poplar clone were included as random effects, but only 4 of the mixed-effects models were significantly improved compared to models without random effects. This suggests that silvicultural treatment or hybrid poplar clone were not important

factors to account for in the additive component biomass models and DBH alone was sufficient to account for their influence. The juvenile age of the trees is one possible reason for insignificant likelihood ratio tests, since the trees had yet to differentiate within the stands. Other biomass studies have also found that including treatment characteristics, such as density, basal area, and pruning effects did not increase the fit of aboveground biomass models [24,32–35]. Comparatively, treatment effects may be significant in some biomass models [36]. The strong allometric relationships between tree dimensions and biomass components [19] are another reason

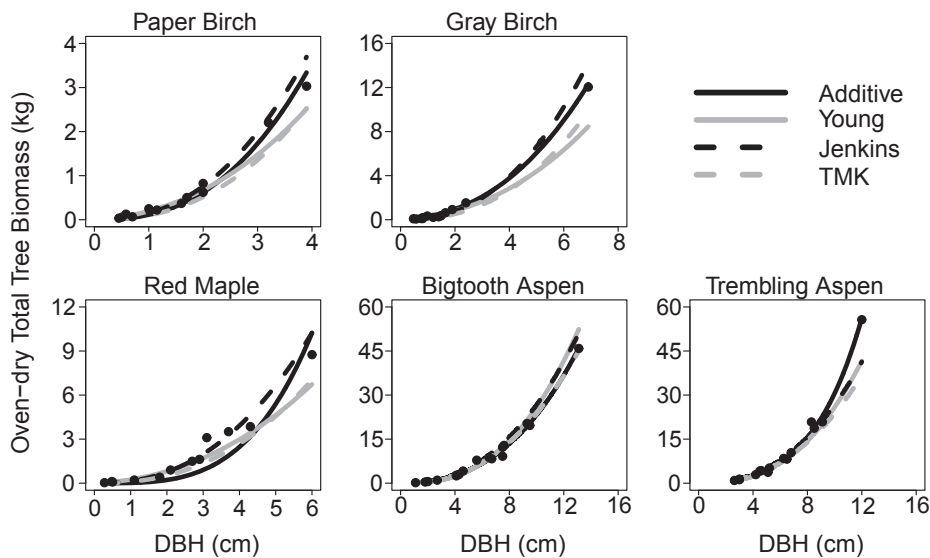


Fig. 2 – Small tree (0.3 cm–13.1 cm DBH) total aboveground oven-dry biomass (kg) versus DBH (cm) for the five naturally regenerated hardwood species. Observed data are shown as solid circles, while each of the four lines represents a different biomass model. The models were: Additive – this investigation, Young [4], Jenkins [3] and Ter-Mikaelian [7]. Note the difference in the X- and Y-axis values.

Table 6 – Evaluation statistics of the Additive and published models for natural hardwood (0.3 cm–13.1 cm DBH) total aboveground oven-dry biomass. Root mean square error (RMSE), mean bias (MBIAS), mean absolute bias (ABIAS) and minimum detectable negligible difference (MDND) were used to compare models to observed data. The number of observations (n), observed and predicted means, predicted mean relative to observed (PRO), MDND expressed as a percent and in absolute values, and the results of the equivalence test are shown. The Additive models were developed from the field data, while the other models were: Young–Young et al. [4], Jenkins–Jenkins et al. [3], and TMK - Ter-Mikaelian and Korzukhin [7]. Data used to evaluate the Young models excluded the 15 cm stump weight for trees ≥ 2.5 cm DBH.

Species	n	RMSE (kg)	MBIAS (kg)	ABIAS (kg)	Observed mean (kg)	Predicted mean (kg)	PRO (%)	MDND (%)	MDND (kg)	Null hypothesis
Red maple										
Additive	12	0.37	-0.05	0.28	2.01	2.06	2.7	14.5	0.29	Reject
Young	12	0.48	-0.02	0.32	1.92	1.94	1.0	17.1	0.33	Reject
Jenkins	12	0.59	-0.11	0.35	2.01	2.11	5.3	24.0	0.48	Reject
TMK	12	0.86	0.56	0.56	2.01	1.45	-27.8	7.6	0.15	Not reject
Paper birch										
Additive	13	0.08	0.01	0.06	0.65	0.65	-0.1	7.6	0.05	Reject
Young	13	0.32	-0.03	0.23	0.63	0.66	4.9	35.8	0.23	Reject
Jenkins	13	0.20	-0.05	0.10	0.65	0.70	7.7	26.2	0.17	Reject
TMK	13	0.26	0.17	0.17	0.65	0.48	-26.6	8.8	0.06	Not reject
Gray birch										
Additive	15	0.18	-0.04	0.14	1.60	1.64	2.8	9.0	0.14	Reject
Young	15	0.65	-0.28	0.36	1.53	1.82	18.3	39.4	0.61	Reject
Jenkins	15	0.61	-0.09	0.25	1.60	1.69	5.6	26.5	0.42	Reject
TMK	15	0.85	0.44	0.44	1.60	1.16	-27.4	2.6	0.04	Not reject
Bigtooth aspen										
Additive	17	0.93	0.09	0.59	9.39	9.30	-1.0	4.1	0.39	Reject
Young	17	2.53	-1.09	1.37	8.92	10.02	12.3	25.3	2.26	Reject
Jenkins	17	2.15	-1.25	1.39	9.39	10.64	13.3	22.8	2.14	Reject
TMK	17	0.98	-0.06	0.60	9.39	9.45	0.6	6.0	0.56	Reject
Trembling aspen										
Additive	15	1.17	0.12	0.70	11.12	11.00	-1.1	4.7	0.53	Reject
Young	15	3.61	1.20	1.49	10.65	9.45	-11.3	6.5	0.69	Not reject
Jenkins	15	4.01	0.89	1.63	11.12	10.23	-8.0	11.6	1.29	Reject
TMK	15	5.40	2.03	2.26	11.12	9.10	-18.2	6.7	0.75	Not reject

for the lack of model improvement when accounting for silvicultural treatment. This was demonstrated by the additive biomass models in this investigation with DBH as the sole predictor, where R^2 values were greater than 0.900 except for five of the component models (red maple foliage and branch, paper birch branch, gray birch foliage, and white spruce foliage).

The additive aboveground component biomass models (foliage, branch, and bole) were fit using NSUR, which restricted the sum of the components to total biomass. Additivity of component biomass estimates is desirable since it is logical to assume component biomass sums to total biomass, and that there is inherent correlation among components on the same tree [37]. When component biomass

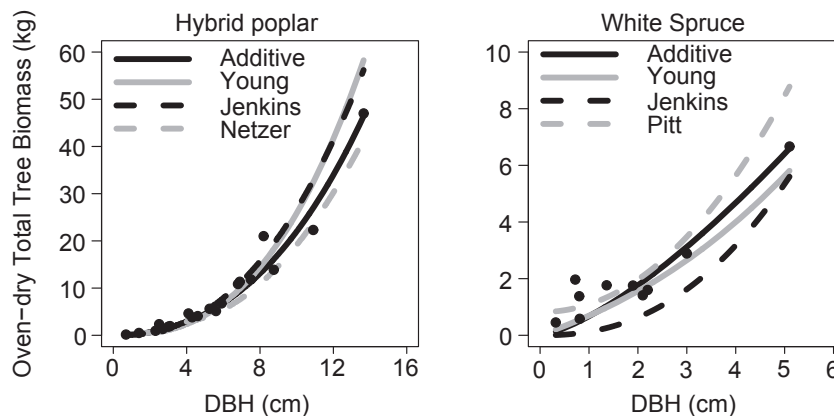


Fig. 3 – Small tree (0.3 cm–13.7 cm) total aboveground oven-dry biomass (kg) versus DBH (cm) for hybrid poplar and white spruce. The observed data are shown as solid circles, while each of the four lines represents a different biomass model. The models were: Additive – this investigation, Young [4], Jenkins [3], Netzer [25], and Pitt [24]. Note the difference in the X- and Y-axis values.

Table 7 – Evaluation statistics of the Additive and published models for hybrid poplar and white spruce (0.3 cm–13.7 cm DBH) total aboveground oven-dry biomass. Root mean square error (RMSE), mean bias (MBIAS), mean absolute bias (ABIAS) and minimum detectable negligible difference (MDND) were used to compare models to observed data. The number of observations (n), observed and predicted means, predicted mean relative to observed (PRO), MDND expressed as a percent and in absolute values, and the result of the equivalence tests are shown. The Additive models were developed from the field data, while the other models were: Young–Young et al. [4], Jenkins–enkins et al. [3], and Netzer–etzer et al. [25], and Pitt–Pitt and Bell [24].

Species	n	RMSE (kg)	MBIAS (kg)	ABIAS (kg)	Observed mean (kg)	Predicted mean (kg)	PRO (%)	MDND (%)	MDND (kg)	Null hypothesis
Hybrid poplar										
Additive	20	1.35	−0.17	0.97	8.87	9.04	1.9	9.0	0.80	Reject
Young	20	4.31	−0.90	2.26	8.45	9.35	10.6	34.0	2.88	Reject
Jenkins	20	3.67	−1.01	1.94	8.87	9.88	11.4	30.1	2.67	Reject
Netzer	20	3.25	0.84	2.29	8.87	8.03	−9.4	7.2	0.64	Not reject
White spruce										
Additive	10	0.69	0.26	0.49	2.05	1.79	−12.8	9.8	0.20	Not reject
Young	10	0.94	0.04	0.75	2.01	1.96	−2.1	31.9	0.64	Reject
Jenkins	10	1.22	1.07	1.07	2.05	0.98	−52.4	35.9	0.74	Not reject
Pitt	10	0.90	−0.31	0.67	2.05	2.36	15.0	45.1	0.92	Reject

models are not fit simultaneously, there is often disagreement between the total biomass estimates from summing component predictions and predictions from a total biomass model [38]. For instance, sapling (2.5 cm–12.4 cm DBH) total biomass estimated with the Young total biomass models was between 3.2% and 10.1% greater than estimated total biomass by summing component predictions for the five naturally regenerated species (Appendix A). Fitting additive component biomass models is becoming more common due to available statistical software and the recognition of the greater statistical efficiency [15]. For instance, the technique has been used to fit additive biomass models in Canada [39], Portugal [33], and the southern hemisphere [38,40].

Even though other covariates and model forms were investigated, a two-parameter power function was found to provide a good fit to the observed exponential relationship between DBH and component biomass for all of the species. Sometimes, height is included as a covariate in biomass models when models are fit to trees from multiple sites [39], as height growth tends to be more sensitive to site conditions than diameter. Height was likely not a significant variable in the additive models since all of the trees were sampled from the same site.

Although total aboveground biomass at a given diameter may be similar among species, partitioning of the various aboveground components varied substantially among the

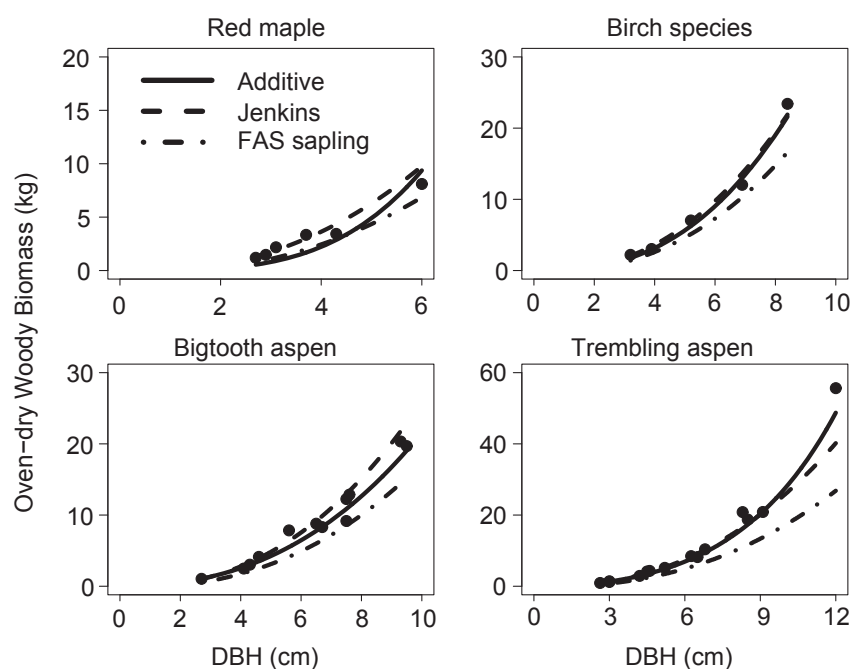


Fig. 4 – Sapling (2.5 cm–12.4 cm DBH) woody aboveground oven-dry biomass (kg) versus DBH (cm) for the five naturally regenerated hardwood species (paper birch and gray birch combined). The observed data are shown as solid circles, while the three lines represent predictions of the different models. The models were: Additive – this investigation, Jenkins [3] and FIA aboveground sapling [8]. Note the difference in the X- and Y-axis values.

Table 8 – Evaluation statistics of the Additive and published models for aboveground woody biomass of natural hardwood saplings (2.5–12.4 cm DBH). Root mean square error (RMSE), mean bias (MBIAS), mean absolute bias (ABIAS) and minimum detectable negligible difference (MDND) were used to compare models to observed data. The models were: Additive – this investigation, Jenkins – Jenkins et al. [3], and FAS–FIA aboveground sapling [8]. The number of observations (*n*), observed and predicted means, predicted mean relative to observed (PRO), MDND expressed as a percent and in absolute values, and the result of the equivalence tests are shown. Paper birch and gray birch were combined (birch species) due to low sample sizes.

	<i>n</i>	RMSE (kg)	MBIAS (kg)	ABIAS (kg)	Observed mean (kg)	Predicted mean (kg)	PRO (%)	MDND (%)	MDND (kg)	Null hypothesis
Red maple										
Additive	6	0.362	0.012	0.289	3.28	3.27	–0.4	12.1	0.40	Reject
Jenkins	6	0.876	–0.371	0.575	3.28	3.65	11.3	38.1	1.25	Reject
FAS	6	0.997	0.825	0.825	3.28	2.46	–25.1	10.6	0.35	Not reject
Birch species										
Additive	5	3.010	1.242	1.336	8.85	7.61	–14.0	28.9	2.55	Reject
Jenkins	5	1.162	–0.743	0.743	8.85	9.59	8.4	21.5	1.90	Reject
FAS	5	2.686	1.681	1.681	8.85	7.17	–19.0	11.9	1.05	Not reject
Bigtooth aspen										
Additive	13	0.947	0.070	0.742	8.12	8.05	–0.9	6.2	0.51	Reject
Jenkins	13	2.152	–1.382	1.508	8.12	9.51	17.0	29.0	2.36	Reject
FAS	13	2.427	1.889	1.889	8.12	6.23	–23.3	12.6	1.02	Not reject
Trembling aspen										
Additive	15	1.097	0.045	0.655	10.18	10.13	–0.4	5.6	0.57	Reject
Jenkins	15	2.413	0.347	1.208	10.18	9.83	–3.4	9.7	0.98	Reject
FAS	15	6.711	3.722	3.722	10.18	6.45	–36.6	6.4	0.66	Not reject

species-specific models. For instance, at the median DBH of 3 cm across all species (Appendix A), planted white spruce had the greatest proportion of biomass partitioned to foliage (42%), followed by hybrid poplar (17%), gray birch (13%), paper birch (13%), red maple (11%), bigtooth aspen (2%), and trembling aspen (0.5%). A similar pattern was found for branch biomass indicating the proportion of crown biomass (foliage + branch) tended to be lower for the aspen species than red maple and the birch species. In contrast, trembling aspen had the greatest proportion of biomass partitioned to the bole (98%), followed by bigtooth aspen (94%), red maple (77%), hybrid poplar (76%), paper birch (72%), gray birch (62%), and white spruce (30%) at the median DBH. It was expected that the majority of biomass of shade intolerant aspen species was partitioned to the bole due to fast early growth rates and dominance in the overstory [41,42], and greater partitioning to crown biomass for mid-tolerant red maple and white spruce that commonly occupy mid- and understories in natural stands where there is often high competition for light. Therefore, greater crown biomass may facilitate increased light interception in low light conditions [43].

4.2. Evaluation of total aboveground biomass models

Although the Jenkins, Young, and TMK models were not fit with techniques that force additivity of component models, the Jenkins and Young total aboveground biomass models both had good agreement with the observed data for the naturally regenerated species. The results showed that the Jenkins model produced similar or better estimates than the Young models as RMSE was lower for paper birch, gray birch, and bigtooth aspen. Even though the equivalence tests provided evidence whether the predicted values were similar to the observed values, the test has some limitations. For instance, due to low sample sizes and the skewness of the

data towards small diameter trees, the standard deviation between the observed and predicted values were often large. The MDND statistic requires an estimate of the standard deviation, and if the value is large, the MDND can also be large, resulting in a wide equivalence region to reject the null hypothesis. With greater sample sizes, the standard deviation should be lower, providing a more conservative estimate of the MDND.

The equivalence test null hypothesis of the TMK models was not rejected for all species except bigtooth aspen, suggesting the predicted values were not within an acceptable range to consider them similar to the observed values. In particular, the TMK models underestimated total aboveground biomass by more than 25% for red maple, paper birch, and gray birch. Data used to fit the models in TMK for these species were collected from Nova Scotia and New Brunswick, Canada, and included trees with DBH <1 cm [22,23]. The poor fit of these models were unexpected because of the close geographic proximity, large number of observations (44, 196, and 197 for gray birch, paper birch, and trembling aspen, respectively) and similar DBH ranges to the trees in the current investigation.

The Jenkins models were developed to encompass all tree species across the United States and are currently part of the CRM methods used by the FIA program, yet the models were fit using generalized regression of pseudo-data [20] and have not been well evaluated with actual field data. In this investigation, null hypotheses of the equivalence tests were rejected for the Jenkins total aboveground biomass predictions for all naturally regenerated species and hybrid poplar (using the aspen/birch equation). It was hypothesized that the Jenkins models would provide poor estimates of biomass in this investigation because the models were only developed for trees ≥ 2.5 cm DBH, while we predicted biomass down to a 0.3 cm DBH. Predicting biomass beyond the range of the data

used to fit the models or across sites is typically discouraged since erroneous results can occur [44]. In this investigation, testing the lower extremes of the Jenkins models was important to assess their accuracy in estimating biomass of trees <2.5 cm DBH since a substantial proportion of stands in Maine are dominated by small trees [6]. Although further validation of the Jenkins models is warranted across a wider range of tree size and geographic location, the results from this investigation suggest the Jenkins models provided adequate estimates of total aboveground biomass of the species investigated at this particular site, except for white spruce.

Supplementing commercial forest production with planted stock to increase growth rates in northeastern North America has been proposed to accommodate increasing wood fiber demands [45]. Planting tree species, such as hybrid poplar and white spruce, to enrich naturally regenerated stands is not well studied in the region and without evaluation of biomass models it is difficult to predict potential gains in productivity. We compared the fit of the Jenkins, Young, Netzer, and additive models to 7-year-old plantation hybrid poplar clones and the results showed that predictions of total aboveground biomass were similar to the observed values for all models except the Netzer model, with the additive equation outperforming the Jenkins and Young models. Even though the Netzer model was developed for hybrid poplar the majority of the trees used to develop the model were *P. deltooides* × *P. nigra* clones, and our sample included a *P. nigra* × *P. maximowiczii* clone. This is a possible reason for the substantial underestimation by the model (9.4%). In addition, the hybrid poplar used to fit the Netzer model were grown on better quality sites (post-agriculture) than the site in our investigation where rocky, poorly-drained conditions were prevalent [13]. The Netzer model also cannot predict component biomass, a key feature for hybrid poplar clones grown for wood fiber.

Total aboveground biomass estimates are often expressed at a stand-level as this is the typical management unit in most forestry applications. Alternate biomass models can produce different stand-level estimates of biomass since models often differ in the precision among species and tree sizes, and natural stands often have diverse species composition and stand structure. Total aboveground biomass was predicted for stands in the experiment where trees were destructively sampled. The stands were approaching self-thinning and dominated by the five naturally regenerated species in this investigation. Total aboveground biomass estimates were: Jenkins – $512.0 \pm 118.2 \text{ Mg km}^{-2}$ (mean ± SD), Young – $470.6 \pm 110.4 \text{ Mg km}^{-2}$, TMK – $437.7 \pm 100.1 \text{ Mg km}^{-2}$, and additive – $460.2 \pm 89.3 \text{ Mg km}^{-2}$. The TMK stand estimate was the lowest, which corresponds to the individual-tree model evaluation results.

4.3. Woody aboveground biomass model evaluation

Oven-dry sapling woody biomass was predicted by the FAS, Jenkins, and additive models for the five naturally regenerated hardwood species. The FAS models multiple a sapling adjustment factor by the Jenkins woody biomass estimate. Since the adjustment factors were all less than 1, the FAS estimates were all less than the Jenkins estimates. In addition, the FAS models underestimated mean biomass between

19.0% and 36.6%. Similar to the Jenkins models, the FAS models lack evaluation with field data in northeastern North America. In stands dominated by saplings, such as 24% of the forested area in Maine, our results suggest sapling woody biomass may be substantially underestimated. These results correspond to the 34% reduction in sapling biomass in the state of Maine when FIA switched from regional models to the current methods [6,11]. Since nearly one-quarter of forestlands in Maine are dominated by saplings, the switch to the FAS models may have also influenced reduction in aboveground biomass predictions of all living trees in the state. For instance, aboveground biomass of all living trees >2.5 cm DBH decreased by 15% between 2003 and 2010 [11]. Greater biomass removal, the change to the CRM for estimating biomass of tree >12.5 cm DBH, and the switch to the FAS models for sapling biomass are all contributing factors to biomass declines. Only a small sample of trees was used in the current study, and the FAS models require additional evaluation to refine biomass estimation methods by the FIA program.

5. Conclusion

We investigated the fit of various small tree total (foliage, branches, bole) and sapling woody (total – foliage) aboveground biomass models to data collected from eastern Maine. The results suggested that the national Jenkins and regional Young models predicted biomass within an acceptable range of the observed data, while the TMK and FAS models provided poor fits to the data. Even though many of these models can predict biomass of individual aboveground components, one major limitation is that they were not fit with statistical techniques that force additivity of the component predictions to predictions obtained with a total aboveground equation. Therefore, we developed a new set of additive component models for naturally regenerated hardwood species and planted stock small trees in Maine. These additive models are simple in form and only require DBH as a predictor variable but provided a good fit to the observed data. Additionally, biomass equations and aboveground biomass partitioning of small trees have not received much attention in the literature. There is increasing national interest in accurately estimating forest biomass for carbon accounting and potential bioenergy purposes. The uncertainties of landscape biomass estimation in Maine have been driven partly by the high proportion of small tree-dominated stands in the region and the unknown performance of the small tree biomass models. We propose that the current FAS models may be inadequate for providing reliable sapling biomass estimates in Maine, and that new techniques be developed, such as similar additive models presented in this investigation, using field data spanning various species and across multiple sites to account for heterogeneous growing conditions.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.biombioe.2014.06.015>.

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