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DEVELOPMENT AND EVALUATION OF REFINED ANNUALIZED INDIVIDUAL TREE DIAMETER AND HEIGHT INCREMENT EQUATIONS FOR THE ACADIAN VARIANT OF THE FOREST VEGETATION SIMULATOR: IMPLICATION FOR FOREST CARBON ESTIMATES

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Abstract. Tree diameter increment (ΔDBH) and total tree height increment (ΔHT) are key components of a forest growth and yield model. A problem in complex, multi-species forests is that individual tree attributes such as ΔDBH and ΔHT need to be characterized for a large number of distinct woody species of highly varying levels of occurrence. Based on more than 2.5 million ΔDBH observations and over 1 million ΔHT records from up to 60 tree species and genera, respectively, this study aimed to improve existing ΔDBH and ΔHT equations of the Acadian Variant of the Forest Vegetation Simulator (FVS-ACD) using a revised method that utilize tree species as a random effect. Our study clearly highlighted the efficiency and flexibility of this method for predicting ΔDBH and ΔHT. However, results also highlighted shortcomings of this approach, e.g., reversal of plausible parameter signs as a result of combining fixed and random effects parameter estimates after extending the random effect structure by incorporating North American ecoregions. Despite these potential shortcomings, the newly developed ΔDBH and ΔHT equations outperformed the ones currently used in FVS-ACD by reducing prediction bias quantified as mean absolute bias and root mean square error by at least 11% for an independent dataset and up to 41% for the model development dataset. Using the revised ΔDBH and ΔHT estimates, greater prediction accuracy in individual tree aboveground live carbon mass estimation was also found in general but performance varied with dataset and accuracy metric examined. Overall, this analysis highlights the importance and challenges of developing robust ΔDBH and ΔHT equations across broad regions dominated by mixed-species, managed forests.

Keywords: Multi-level mixed effect models; multi species forests; diameter and height increment; forest growth and yield; FVS—Forest Vegetation Simulator.

1 Introduction

As a transition zone between the boreal forest to the north and the temperate northern hardwood forest to the south, the Acadian Forest located across northeastern North America is a comparatively tree species rich forest ecosystem (Braun, 1950; Rowe, 1972). The various tree species occur as different assemblages in numerous often complex, i.e., multi-species and multi-cohort forest types (Eyre, 1980). Forecasting stand development in the Acadian Forest region thus is a challenging task given the heterogenous stand conditions found across the region. To reliably predict growth and yield of the mixed Acadian forests accurate species-specific individual tree growth equations are required. Such equations need to be capable of accounting and reflecting the complex interactions found in mixtures of multiple tree species differing in growth rate, shade tolerance, and competitive ability. This holds especially true for the two most important submodels of an individual tree growth and yield simulator, namely diameter (ΔDBH) and height increment (ΔHT).

Increment equations for multi species forests have commonly been derived on a species-by-species basis (e.g., Weiskittel et al., 2016), which can become rather laborious and inefficient with increasing species diversity. A quantitative strategy that eliminates the need to obtain individual equations for each species or species group, respectively, is to consider each species as a random element. The use of species as random effect has been applied for various tree attributes (e.g., Colmanetti et al., 2018; Lam et al., 2016; Weiskittel et al., 2015). In a recent study, Kuehne et al. (2020) compared various approaches to project individual tree secondary growth and found that species-specific, realized increment models exhibited similar behavior and accuracy compared to models fitted with modeling species as random effect. Kuehne et al. (2020) thus showed the efficiency of this approach to account for varying growth patterns in multi-species stands, including infrequent species. However, Kuehne et al. (2020) did not examine this approach for ΔHT predictions. Kuehne et al. (2020) also did not compare their findings to the existing equations in the Forest Vegetation Simulator-Acadian Variant (FVS-ACD), an individual-tree growth and yield model (system of equations) for the Acadian Forest region that includes sets of model coefficients predicting individual tree attributes (e.g., crown recession and mortality) for over 50 varying tree species or species groups, respectively (Weiskittel et al., 2017).

Consequently, this study made use of the modeling approach that implements species as a random effect to revise and update annualized ΔDBH and ΔHT equations of FVS-ACD. Using a comprehensive dataset from across the Acadian Forest region, we specifically aimed to i) improve individual ΔDBH and ΔHT submodels of FVS-ACD; ii) compare ΔDBH and ΔHT prediction accuracy of the newly derived and currently used equations; iii) examine effects of newly derived ΔDBH and ΔHT equations on individual tree carbon mass estimation accuracy; and iv) provide specific recommendations for revising ΔDBH and ΔHT predictions in FVS-ACD.

2 Methods

2.1 Study Area

The Acadian Forest region forms a transition zone between the softwood-dominant boreal forests to the north and the hardwood-dominated forests to the south (Braun, 1950; Rowe, 1972). The region is located across New Brunswick, Nova Scotia, and Prince Edward Island, southern portions of Québec, and much of the US state of Maine. Across the region, the climate is cool and humid with an estimated mean annual precipitation of 113 cm (87 – 175 cm) and an estimated average of 1,625 growing degree days (726 - 2,292 degree days, Rehfeldt, 2006). Glacial till is the principal soil parent material. Depending on the local topography, soil types range from well-drained loams and sandy loams on glacial till ridges to poorly and very poorly drained loams on flat areas between low-profile ridges.

The Acadian Forest is dominated by naturally regenerated, mixed-species forests of primarily uneven-aged stand structures. Among the over 60 tree species that occur in the region are coniferous evergreen species such as red spruce (*Picea rubens* Sarg.), balsam fir (*Abies balsamea* L.), eastern white pine (*Pinus strobus* L.) and eastern hemlock (*Tsuga canadensis* (L.) Carr.) as well as deciduous hardwood species such as red maple (*Acer rubrum* L.), yellow birch (*Betula alleghaniensis* Britton), sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), paper birch (*Betula papyrifera* Marsh.), and northern red oak (*Quercus rubra* L.). Common forest types are described in Eyre (1980) as well as Gawler and Cutko (2010) while Bose et al. (2016) describe the generally prevailing environmental conditions in more detail.

2.2 Data

Diameter at breast height (DBH) and total height (HT) measurements of individual trees were obtained from a comprehensive database of permanent sample plots (PSPs) compiled from various data sources including US Forest Service (USFS) Forest Inventory and Analysis (FIA) Program (Bechtold and Patterson, 2005), Penobscot Experimental Forest (Kenefic et al., 2015), Cooperative Forestry Research Unit's Commercial Thinning Research Network (Kuehne et al., 2018c, 2016; Wagner and Seymour, 2006), Maine Ecological Reserves (Kuehne et al., 2018a,b). New Brunswick PSP (McGarrigle et al., 2011; Province of New Brunswick, 2005), Québec PSP, and Nova Scotia PSP (further described by Li et al., 2011; Weiskittel et al., 2010). An overview of plot- and stand-level metrics is provided in Table 1 and a more detailed description of each individual dataset is provided in Kuehne et al. (2020).

2.3 Data Preparation

Missing total tree height (HT, m) and height to crown base (HCB, m) values were imputed based on an approach similar to Rijal et al. (2012a; 2012b), while missing crown width values were calculated using species-specific equations from Russell and Weiskittel (2011). Two-sided competition measures including basal area (BA, m^{2}ha^{-1}), stand density index (SDI, trees ha^{-1}) calculated using the summation method, crown compe-

Table 1: Overview of plot-level (N = 16,204) summary statistics from mixed-species stands across the Acadian Forest region of North America.

Attribute	Mean	SD	Min	Max
Plot size (m^2)	253.6	135.9	168.1	810.1
Interval length ($years$)	10.7	7.5	1.0	40.0
Longitude ($degrees$)	-68.78	2.16	-73.25	-59.81
Latitude ($degrees$)	45.80	1.15	43.11	49.22
Elevation (m)	255.9	188.4	0.0	1095.0
Climate site index (m)	13.9	2.4	4.8	31.0
Stem density ($treesha^{-1}$)	2409	2555	10	31851
Relative density	0.44	0.28	0.00	2.53
Basal area (m^2ha^{-1})	22.8	11.6	0.0	81.7
Percent basal area in hardwoods (%)	41.2	36.8	0.0	100.0
Quadratic mean diameter (cm)	14.5	6.6	2.0	76.5
Species richness ($\#plot^{-1}$)	3.79	1.71	1.00	12.00
Shannon diversity index for species	0.89	0.46	0.00	2.11

tition factor ($CCF, \%$), and relative density (RD) defined as ratio of SDI and maximum SDI (SDI_{MAX}) calculated after Weiskittel and Kuehne (2019) were then summarized at the PSP-level (Weiskittel et al., 2011b). The one-sided, tree-specific competition metrics basal area in larger trees $\left(BAL, \mathrm{m^2ha^{-1}}\right)$ and crown competition factor in larger trees ($CCFL, \%$) were also derived from PSP data except for individuals on FIA plots where BAL and $CCFL$ were quantified at the subplot-level. We argue that making use of the FIA cluster plot design leads to a greater differentiation between stand-level (e.g., BA) and local, i.e., neighborhood competition (e.g., BAL), which was also supported by preliminary findings. BAL and $CCFL$ were further separated into softwood (BAL_{SW}) and hardwood (BAL_{HW}) as well as shade-intolerant (BAL_{INTOL}) and shade-tolerant species (BAL_{TOL}) components, respectively. Such a separation allows to account for species-type differences with regard to growth dynamics that depend on species composition and has been shown to work well for multi species forests (Ninifu, 2009). Shade tolerance was defined based on the shade tolerance scale by Niinemets and Valladares (2006) with species-specific values < 3 defined as low and values ≥ 3 classified as high shade tolerance, respectively. Lastly, individual tree crown ratio was calculated as the ratio of crown length ($HT - HCB$) and HT.

Preliminary analysis suggested using all possible measurement combinations resulted in more robust model behavior, particularly with respect to extrapolation. Consequently, diameter $\left(\Delta DBH, \mathrm{cm \cdot yr^{-1}}\right)$ and height increment $\left(\Delta HT, \mathrm{m \cdot yr^{-1}}\right)$ were not just derived from consecutive inventories but all potential combinations (Salas-Eljatib and Weiskittel, 2020). More precisely, growth data were not just derived from consecutive inventories (e.g., $year_1 - -year_2$, $year_2 - -year_3$, $year_3 - -year_4$, and so on), but all potential combinations (i.e., including $year_1 - -year_3$, $year_1 - -year_4$, $year_2 - -year_4$, and so on). Measurement periods indicating harvest activities were excluded from the analysis. This resulted in a total of 2,656,326 ΔDBH observations across 53 woody species, including 15 softwoods (Table 2) and 38 hardwoods (Table 3). Approximately 0.1% or 2,728 of these observations were recorded to the genus level, including *Alnus* spp., *Amelanchier* spp., *Cornus* spp., *Crataegus* spp., *Malus* spp., *Salix* spp., and *Sorbus* spp. (all hardwoods). Likewise, 1,066,426 ΔHT observations were available from 47 species including, 13 softwoods (Table 4) and 34 hardwoods and six genera (all hardwoods, 276 observations) (Table 5).

2.4 Model Development

We accounted for growth variation linked to each individual species by incorporating tree species as a random effect within the ΔDBH or ΔHT equation, respectively (Kuehne et al., 2020; Russell et al., 2014). This approach is theoretically advantageous in that it can predict growth of infrequent species with a limited number of observations. As outlined in Kuehne et al. (2020), potential drawbacks to this approach are the inability to statistically assess significance of specific species or difference across species and possible biological implausible behavior.

In this analysis, we further extended the random effect structure to a nested design, i.e., species nested within ecoregion. To do so, we made use of the Level III ecoregions of North America (Commission for Environmental Cooperation, 2006). Level III ecoregions covered in our dataset included Central Laurentians and Mecatina Plateau (Code: 5.1.3), Algonquin/Southern

Table 2: Softwood species-specific number of observations (N) and statistics for initial diameter at breast (DBH, cm) and mean periodic annual DBH increment $\left(\Delta DBH, \mathrm{cm} \cdot \mathrm{yr}^{-1}\right)$.

Scientific name	N	DBH				ΔDBH			
		Mean	SD	Min	Max	Mean	SD	Min	Max
Abies balsamea	853193	12.4	5.9	1.0	48.2	0.26	0.20	0.01	2.72
Chamaecyparis thyoides	10	21.1	5.8	12.7	30.5	0.29	0.10	0.16	0.52
Larix laricina	18969	15.8	6.3	1.0	65.0	0.21	0.16	0.01	1.47
Picea abies	68	16.1	10.1	4.4	46.0	0.58	0.29	0.03	1.21
Picea glauca	97353	17.1	7.5	1.0	68.9	0.25	0.19	0.01	2.04
Picea mariana	224742	12.4	5.7	1.0	70.0	0.13	0.10	0.01	1.83
Picea rubens	482116	15.6	7.2	1.0	65.2	0.17	0.14	0.01	1.58
Pinus banksiana	11651	17.5	5.3	3.2	38.0	0.14	0.11	0.01	1.03
Pinus pungens	2	5.3	0.0	5.3	5.3	0.06	-	-	-
Pinus resinosa	3804	22.4	10.5	2.5	70.9	0.32	0.23	0.01	1.57
Pinus rigida	185	24.4	7.7	13.0	56.4	0.28	0.22	0.01	0.85
Pinus strobus	54476	22.1	12.6	1.3	105.0	0.26	0.20	0.01	1.90
Pinus sylvestris	30	12.1	2.2	9.1	16.0	0.39	0.19	0.06	0.93
Thuja occidentalis	73830	17.6	8.5	1.0	98.7	0.17	0.12	0.01	1.78
Tsuga canadensis	62597	18.5	11.1	1.1	88.6	0.28	0.19	0.01	1.88

Laurentians (5.2.3), and Northern Appalachian and Atlantic Maritime Highlands (5.3.1) of the Northern Forest Level I ecoregion as well as Eastern Great Lakes and Hudson Lowlands (8.1.1), Northeastern Coastal Zone (8.1.7), Maine/New Brunswick Plains and Hills (8.1.8), and Maritime Lowlands (8.1.9) of the Eastern Temperate Forests Level I ecoregion. ΔHT data, however, was only available from four of these Level III ecoregions, namely Appalachian and Atlantic Maritime Highlands (5.3.1), Northeastern Coastal Zone (8.1.7), Maine/New Brunswick Plains and Hills (8.1.8), and Maritime Lowlands (8.1.9).

Using all observations irrespective of species, the following general model form was used to derive ΔDBH and ΔHT equations, respectively:

$$Y = \exp\left(X\beta\right) \tag{1}$$

where Y is the response variable (ΔDBH or ΔHT), $X\beta$ is the model-specific explanatory variable design matrix (linear predictor, Zuur et al., 2009) with the associated estimated fixed ($\beta_{i,j}$) and random parameters for ecoregion (ER, $b_{i,j,\mathrm{ER}}$) and species (SP) (SP, $b_{i,j,\mathrm{SP}}$) for equation i and explanatory variable j estimated with the *nlme* function found in the nlme package (Pinheiro et al., 2012) of the programming software R (R Development Core Team, 2019). Random effects and residuals of the derived models were assumed to be normally distributed. Explanatory variables of $X\beta$ comprised DBH or HT, respectively, crown ratio (CR, ratio of crown length (HT–HCB) and HT), the climate-derived site index (CSI, m) as an estimate of site productivity (Weiskittel et al., 2011a,b), and varying combinations of one- and two-sided competition metrics previously described. Parameters to vary randomly were optimized based on preliminary analyses by i) testing various combinations of random effects with the best approach selected based on Akaike's information criterion (AIC) and ii) evaluating the overall species-specific effect for explanatory variable parameters allowed to vary randomly after combining fixed and random parameters similar to the methods of Kuehne et al. (2020).

To overcome problems of varying measurement intervals (1-40 years) observed in the data and to provide a finer resolution of tree and stand dynamics, parameters were annualized using an iterative mixed-effects technique of Weiskittel et al. (2007). Based on Cao (2000) the right side of the equation was a function that summed the annual ΔDBH or ΔHT estimates, respectively, over the number of growing seasons during the observed growth period using the updated parameter estimates from the optimization algorithms. For each growing season during the growth period, DBH or HT was subsequently updated using the annual ΔDBH or ΔHT estimates, while all other explanatory variables were linearly interpolated between their beginning values and ending values, except CSI which was assumed to be constant over time. Although the assumption of linear change is likely too simplified for highly irregular and longer remeasurement intervals ($>$ 10 years), the iterative approach used in this analysis does produce model behavior similar to a more sophisticated optimization approach and is more effective than using the remeasurement interval as a covariate (e.g., Juma et al., 2014).

Table 3: Hardwood species-specific number of observations (N) and statistics for initial diameter at breast (DBH, cm) and mean periodic annual DBH increment (ΔDBH, cm/yr).

Scientific name	N	DBH				ΔDBH			
		Mean	SD	Min	Max	Mean	SD	Min	Max
Acer negundo	7	14.6	4.4	10.4	22.1	1.08	0.12	0.86	1.22
Acer pensylvanicum	9116	6.9	4.1	1.0	25.8	0.17	0.13	0.01	1.29
Acer platanoides	7	6.4	5.0	3.8	17.5	0.38	0.33	0.20	1.12
Acer rubrum	295416	14.6	7.5	1.0	78.0	0.18	0.14	0.01	2.48
Acer saccharinum	211	17.9	9.8	9.1	63.3	0.42	0.25	0.01	1.10
Acer saccharum	85794	17.1	9.7	1.0	85.9	0.19	0.15	0.01	2.48
Acer spicatum	1964	5.4	2.1	1.6	20.3	0.10	0.10	0.01	0.80
Ailanthus altissima	1	3.6	-	-	-	0.2	-	-	-
Alnus spp.	304	6.3	1.2	5.1	11.3	0.07	0.06	0.01	0.30
Amelanchier spp.	303	9.3	4.6	1.3	22.4	0.10	0.08	0.01	0.41
Betula alleghaniensis	70959	18.6	10.7	1.0	82.0	0.22	0.17	0.01	2.34
Betula lenta	138	19.6	7.5	5.1	42.2	0.19	0.14	0.01	0.71
Betula papyrifera	142947	13.2	6.7	1.0	64.5	0.14	0.12	0.01	2.54
Betula populifolia	14356	8.2	4.5	1.3	32.5	0.15	0.14	0.01	2.54
Carpinus caroliniana	89	6.0	5.2	2.5	48.5	0.09	0.08	0.01	0.41
Carya cordiformis	7	17.2	4.1	13.5	24.8	0.30	0.10	0.17	0.42
Carya ovata	13	14.2	5.1	5.3	18.8	0.10	0.06	0.01	0.20
Cornus spp.	3	2.3	0.4	2.0	2.8	0.07	0.06	0.01	0.13
Crataegus spp.	37	5.7	2.6	2.5	14.0	0.16	0.16	0.01	0.66
Fagus grandifolia	43726	14.6	8.2	1.3	63.6	0.19	0.15	0.01	1.47
Fraxinus americana	11004	16.5	8.5	1.5	93.0	0.24	0.19	0.01	1.78
Fraxinus nigra	3842	12.2	7.1	1.0	52.0	0.15	0.12	0.01	1.83
Fraxinus pennsylvanica	298	15.5	9.2	2.5	45.2	0.15	0.14	0.01	1.12
Juglans cinerea	18	22.5	8.7	9.4	44.4	0.66	0.39	0.14	1.32
Liriodendron tulipifera	2	16.8	0.0	16.8	16.8	0.27	0.09	0.20	0.33
Malus spp.	203	15.4	7.0	3.3	42.4	0.17	0.16	0.01	0.76
Ostrya virginiana	3629	11.5	6.0	1.3	35.2	0.11	0.01	0.01	0.97
Platanus occidentalis	1	14.0	-	-	-	0.5	-	-	-
Populus balsamifera	2675	16.8	10.4	1.3	63.8	0.26	0.20	0.01	1.73
Populus deltoides	15	9.0	9.2	2.8	32.0	0.56	0.72	0.01	2.47
Populus grandidentata	10675	17.7	8.7	1.8	69.6	0.33	0.21	0.01	1.83
Populus tremuloides	51631	17.1	8.6	1.3	64.0	0.29	0.20	0.01	2.79
Prunus pensylvanica	3994	9.6	4.5	1.3	34.5	0.17	0.15	0.01	1.06
Prunus serotina	1724	14.6	6.8	2.5	42.4	0.20	0.19	0.01	1.17
Prunus virginiana	90	4.9	6.3	2.5	44.2	0.12	0.12	0.01	0.56
Quercus alba	349	18.1	7.3	2.5	39.6	0.19	0.14	0.01	0.61
Quercus bicolor	4	31.1	0.5	30.7	31.8	0.28	0.15	0.20	0.51
Quercus coccinea	3	15.0	0.0	15.0	15.0	0.53	0.07	0.46	0.58
Quercus macrocarpa	1	12.7	-	-	-	0.3	-	-	-
Quercus rubra	14586	18.7	8.6	1.0	84.1	0.25	0.19	0.01	1.42
Quercus velutina	251	23.7	8.2	5.1	46.0	0.42	0.22	0.01	1.12
Salix spp.	374	11.9	4.9	3.1	74.0	0.15	0.13	0.01	0.76
Sorbus spp.	1504	11.2	5.2	1.1	49.1	0.18	0.16	0.01	1.33
Tilia americana	340	18.8	7.6	1.3	48.3	0.24	0.19	0.01	0.89
Ulmus americana	689	15.0	7.2	2.5	54.9	0.37	0.26	0.01	1.32

Table 4: Softwood species-specific total number of observations (N) and statistics for initial total height (HT, m) and mean annual HT increment $\left(\Delta HT, \mathrm{m} \cdot \mathrm{yr}^{-1}\right)$.

Scientific name	N	HT				ΔHT			
		Mean	SD	Min	Max	Mean	SD	Min	Max
Abies balsamea	293533	9.7	3.1	1.3	24.4	0.21	0.18	0.01	2.32
Larix laricina	14713	10.8	3.7	3.0	26.8	0.13	0.1	0.01	1.40
Picea abies	1	4.5	-	-	-	0.0	-	-	-
Picea glauca	55804	10.1	3.5	2.0	31.4	0.20	0.15	0.01	1.43
Picea mariana	65484	9.2	2.7	1.8	22.9	0.11	0.10	0.01	1.04
Picea rubens	195567	10.9	3.4	1.5	31.1	0.17	0.14	0.01	1.58
Pinus banksiana	1433	10.7	3.6	3.0	22.0	0.18	0.14	0.01	0.70
Pinus pungens	1	3.7	-	-	-	0.1	-	-	-
Pinus resinosa	3321	11.5	4.2	3.5	25.9	0.25	017	0.01	1.04
Pinus rigida	89	14.4	2.9	7.9	22.6	0.28	0.22	0.01	0.85
Pinus strobus	32600	13.4	4.9	2.4	34.4	0.26	0.20	0.01	1.90
Thuja occidentalis	19843	10.9	2.6	2.1	23.8	0.19	0.18	0.01	0.98
Tsuga canadensis	26726	11.9	3.8	2.4	27.5	0.19	0.17	0.01	1.49

2.5 Model Evaluation

We calculated mean bias (MB), relative MB ($MB\%$), mean absolute bias (MAB), relative MAB ($MAB\%$), and root mean square error ($RMSE$) to evaluate and compare model prediction accuracy:

$$MB = \frac{\sum_{i=1}^{n}\left(Y_i - \widehat{Y}_i\right)}{n} \tag{2}$$

$$MB\% = \frac{\sum_{i=1}^{n}\left(100\frac{Y_i-\widehat{Y}_i}{Y_i}\right)}{n} \tag{3}$$

$$MAB = \frac{\sum_{i=1}^{n}\left|Y_i - \widehat{Y}_i\right|}{n} \tag{4}$$

$$MAB\% = \frac{\sum_{i=1}^{n}\left(100\frac{\left|Y_i-\widehat{Y}_i\right|}{Y_i}\right)}{n} \tag{5}$$

$$RMSE = \sqrt{\frac{\sum_{i=1}^{n}\left(Y_i - \widehat{Y}_i\right)^2}{n}} \tag{6}$$

where Y_i is the observed DBH or HT, respectively, $\widehat{Y}_i$ is the predicted DBH or HT, respectively, and n is the number of observations (c.f., Kuehne et al., 2020). Predicted DBH and HT were derived by applying the newly developed annualized ΔDBH or ΔHT equations. Using a stepwise approach, all explanatory variables including DBH (ΔDBH) or HT (ΔHT), respectively, were thus updated during the prediction procedure on an annual basis to better represent change in tree attributes and stand-level metrics.

The outlined prediction accuracy measures were calculated i) to compare the various new ΔDBH and ΔHT equations differing in the number and kind of explanatory variables incorporated to ultimately select the best performing model among each set of derived equations and ii) to compare prediction accuracy of the selected, best performing new equations with existing functions including the basal area increment (ΔBA) function published in Weiskittel et al. (2013), the ΔHT equation of Russell et al. (2014) as well as ΔDBH and ΔHT equations currently used in FVS-ACD (unpublished, Table S1). Prediction accuracy measures were derived from the ΔDBH and ΔHT datasets used to develop the new equations and from an additional independent dataset. The independent dataset comprised FIA data from 2003 and 2018 as well as 2004 and 2019 (15 year measurement intervals) not used for model development (Table S4).

Given its importance and current wide application, we further examined how changes in prediction accuracy in ΔDBH and ΔHT affected accuracy of individual tree aboveground live carbon mass (kg C) estimation. Using the two available ΔHT datasets of this study as well as scenario 6 of Radtke et al. (2017) to calculate total aboveground live biomass we then applied carbon content estimators (Lamlon and Savidge, 2003; Martin et al., 2015; Thomas and Martin, 2012) to convert individual tree biomass to carbon mass. Observed tree car-

Table 5: Hardwood species-specific total number of observations (N) and statistics for initial total height (HT, m) and mean annual HT increment $\left(\Delta HT, \mathrm{m} \cdot \mathrm{yr}^{-1}\right)$.

Scientific name	N	HT				ΔHT			
		Mean	SD	Min	Max	Mean	SD	Min	Max
Acer negundo	3	11.6	1.1	10.4	12.2	0.76	0.30	0.52	1.10
Acer pensylvanicum	487	9.5	2.8	2.4	18.0	0.23	0.19	0.01	0.91
Acer platanoides	1	11.6	-	-	-	0.1	-	-	-
Acer rubrum	160488	12.0	3.2	1.3	26.5	0.14	0.14	0.01	3.44
Acer saccharinum	28	12.5	4.6	7.9	25.9	0.24	0.22	0.01	0.73
Acer saccharum	37943	13.4	3.5	2.7	30.5	0.16	0.15	0.01	1.4
Acer spicatum	36	5.2	2.8	1.8	15.9	0.22	0.21	0.01	0.98
Alnus spp.	9	6.2	0.8	4.5	7.0	0.02	0.07	0.01	0.20
Amelanchier spp.	81	11.4	2.2	7.9	17.1	0.22	0.18	0.01	0.80
Betula alleghaniensis	39604	12.2	3.2	3.0	25.9	0.15	0.16	0.01	1.40
Betula lenta	74	16.8	2.9	9.1	24.1	0.28	0.26	0.01	1.04
Betula papyrifera	50372	11.7	3.1	1.6	24.6	0.14	0.15	0.01	1.49
Betula populifolia	4453	10.6	2.1	2.7	21.3	0.15	0.17	0.01	2.87
Carpinus caroliniana	10	5.9	2.0	3.4	8.5	0.13	0.12	0.01	0.30
Carya ovata	4	16.2	2.4	13.7	18.6	0.27	0.16	0.09	0.43
Crataegus spp.	3	4.2	0.4	4.0	4.6	0.12	-	0.12	0.12
Fagus grandifolia	18674	10.6	3.3	1.5	24.1	0.15	0.17	0.01	1.46
Fraxinus americana	6309	14.7	3.7	2.7	29.9	0.19	0.20	0.01	1.34
Fraxinus nigra	972	12.2	2.9	3.5	24.4	0.22	0.20	0.01	0.98
Fraxinus pennsylvanica	154	12.9	4.2	4.3	26.2	0.27	0.22	0.01	0.98
Juglans cinereal	9	12.6	1.7	9.8	14.0	0.48	0.34	0.01	1.04
Liriodendron tulipifera	2	7.3	0.0	7.3	7.3	0.18	0.09	0.12	0.24
Malus spp.	80	7.8	1.6	4.6	11.9	0.17	0.18	0.01	0.67
Ostrya virginiana	1093	11.4	2.2	3.7	17.7	0.17	0.18	0.01	0.8
Populus balsamifera	538	14.1	3.1	3.7	25.6	0.33	0.23	0.01	1.16
Populus deltoides	1	15.5	-	-	-	0.5	-	-	-
Populus grandidentata	7035	13.7	4.1	4.5	30.5	0.21	0.19	0.01	1.46
Populus tremuloides	14562	13.9	3.5	3.1	29.6	0.22	0.20	0.01	3.02
Prunus pensylvanica	260	10.3	2.9	2.7	18.3	0.28	0.24	0.01	0.98
Prunus serotine	960	10.0	3.4	3.7	21.3	0.16	0.20	0.01	1.46
Prunus virginiana	5	8.1	2.5	5.4	11.2	0.14	0.13	0.01	0.26
Quercus alba	226	13.9	3.0	8.2	25.0	0.27	0.19	0.01	0.98
Quercus coccinea	3	11.3	0.0	11.3	11.3	0.45	0.04	0.43	0.49
Quercus macrocarpa	1	7.6	-	-	-	0.3	-	-	-
Quercus rubra	12006	12.7	4.2	2.7	27.7	0.18	0.19	0.01	1.46
Quercus velutina	208	16.3	4.1	6.7	30.2	0.38	0.27	0.01	1.22
Salix spp.	6	15.1	4.6	7.3	18.6	0.24	0.20	0.01	0.55
Sorbus spp.	97	9.7	2.2	3.4	14.3	0.23	0.24	0.01	0.91
Tilia americana	173	13.7	2.4	8.2	19.5	0.28	0.23	0.01	1.34
Ulmus americana	341	12.0	2.4	4.0	19.8	0.29	0.26	0.01	1.29

bon stocks quantified from observed DBH and HT measurements at the end of an inventory period were compared to estimations using DBH and HT predictions derived from i) ΔDBH and ΔHT equations currently used in FVS-ACD as well as ii) equations developed in this study, respectively. Prediction accuracy was quantified using the same evaluation measures as described previously (Eqs. 2 - 6).

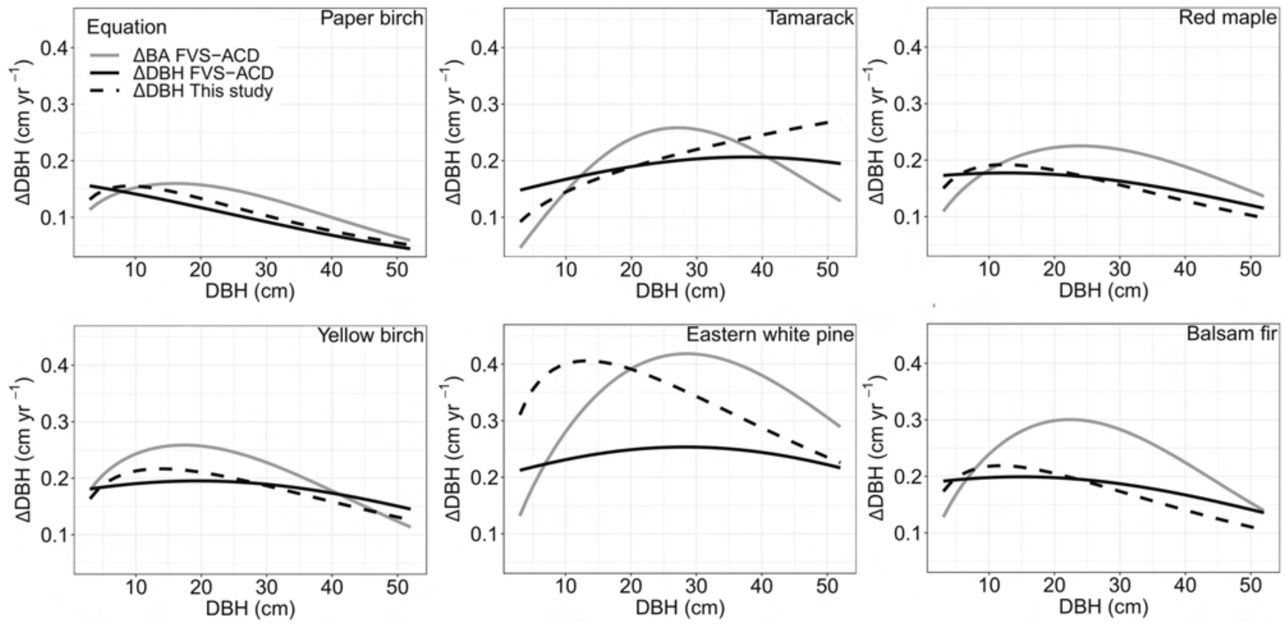

Figure 1: Annual diameter increment ($\Delta DBH, \mathrm{cm yr}^{-1}$) versus tree diameter at breast height (DBH, cm) for six tree species of varying shade tolerances common to the Acadian Forest region. Curves represent equations currently used in the Acadian Variant of the Forest Vegetation Simulator (FVS-ACD) as well as the equations developed in this study and were derived for average tree and stand conditions.

3 Results

3.1 Diameter Increment (ΔDBH)

Besides tree DBH, the final ΔDBH model also included CR, BAL_{SW}, BAL_{HW}, and CSI as explanatory variables with species-specific random effects ($b_{i,j,\mathrm{SP}}$) incorporated for DBH, $\ln(CR)$ and $\ln(BAL_{\mathrm{SW}} + 0.1)$ as well as the intercept (β_{10}) of the linear predictor (Tables 6, S2, and S5; Fig. 1):

$$\begin{aligned}\Delta DBH = \exp\Big(&\beta_{10} + b_{10,\mathrm{SP}} + \beta_{11}\ln(DBH)\\ &+ (\beta_{12} + b_{12,\mathrm{SP}})DBH + (\beta_{13} + b_{13,\mathrm{SP}})\ln(C)\\ &+ (\beta_{14} + b_{14,\mathrm{SP}})\ln(BAL_{SW} + .01) + \beta_{15}BAL_{HW}\\ &+ \beta_{16}\ln(CSI)\Big)\end{aligned} \tag{7}$$

Extending the random effect structure to species within ecoregion improved model performance only slightly but often resulted in implausible parameter estimates when considering the combined species-specific total of fixed and random effects. Compared to the existing FVS-ACD ΔBA and ΔDBH submodels, prediction accuracy of the newly developed ΔDBH equation improved in terms of both MAB and $RMSE$, decreasing between 11 to 13% and 11 to 14% for the model development and the independent dataset, respectively (Table 7, Fig. 2a). Differences in prediction accuracy of the newly developed ΔDBH equation were comparatively small across species and various groupings of species. The rare species tended to exhibit lower prediction accuracy compared to more frequent species (i.e., species with a high number of observations; Tables S3 and S7).

3.2 Tree height increment (ΔHT)

Besides HT, the final ΔHT model also included CR, $CCFL$ and CSI as explanatory variables with species-specific random effects incorporated for HT and the intercept (β_{20}) of the linear predictor (Tables 8, S6 and S8; Fig. 3):

$$\begin{aligned}\Delta HT = \exp\Big(&\beta_{20} + b_{20,sp} + \beta_{21}\ln(HT)\\ &+ (\beta_{22} + b_{22.sp})HT + \beta_{23}CR + \beta_{24}CCFL/100\\ &+ \beta_{25}CSI^2\Big)\end{aligned} \tag{8}$$

Similar to the ΔDBH analysis, extending the random effect structure to species within ecoregion improved model performance only slightly, but often resulted in implausible parameter estimates when considering the combined species-specific total of fixed and random effects. Compared to the existing ΔHT submodels, prediction accuracy of the newly developed ΔHT equation improved substantially with MAB and $RMSE$ decreasing between 41 to 74% and 12 to 68% for the model development and the independent dataset, respectively (Table 9, Fig. 2b). Minor differences in prediction accuracy were found for the newly developed ΔHT equa-

Table 6: Fixed effects parameter (β_{ij}) estimates and statistics of the final tree breast height diameter increment $\left(\Delta DBH, \mathrm{cm} \cdot \mathrm{yr}^{-1}\right)$ mixed effects model. See Table S3 for the corresponding species-specific random effects parameter estimates.

Variable	Parameter	Estimate	SE	t-value	p-value
Intercept	$\Delta\beta_{10}$	-1.64234	0.098882	-16.61	<0.0001
ln(DBH)	$\Delta\beta_{11}$	0.376978	0.002051	183.78	<0.0001
DBH	$\Delta\beta_{12}$	-0.02568	0.002751	-9.33	<0.0001
ln(CR)	$\Delta\beta_{13}$	0.713456	0.064804	11.01	<0.0001
ln($BALSW$+0.1)	$\Delta\beta_{14}$	-0.06575	0.008251	-7.97	<0.0001
$BALHW$	$\Delta\beta_{15}$	-0.01774	0.000077	-231.23	<0.0001
ln(CSI)	$\Delta\beta_{16}$	0.135377	0.002403	56.34	<0.0001

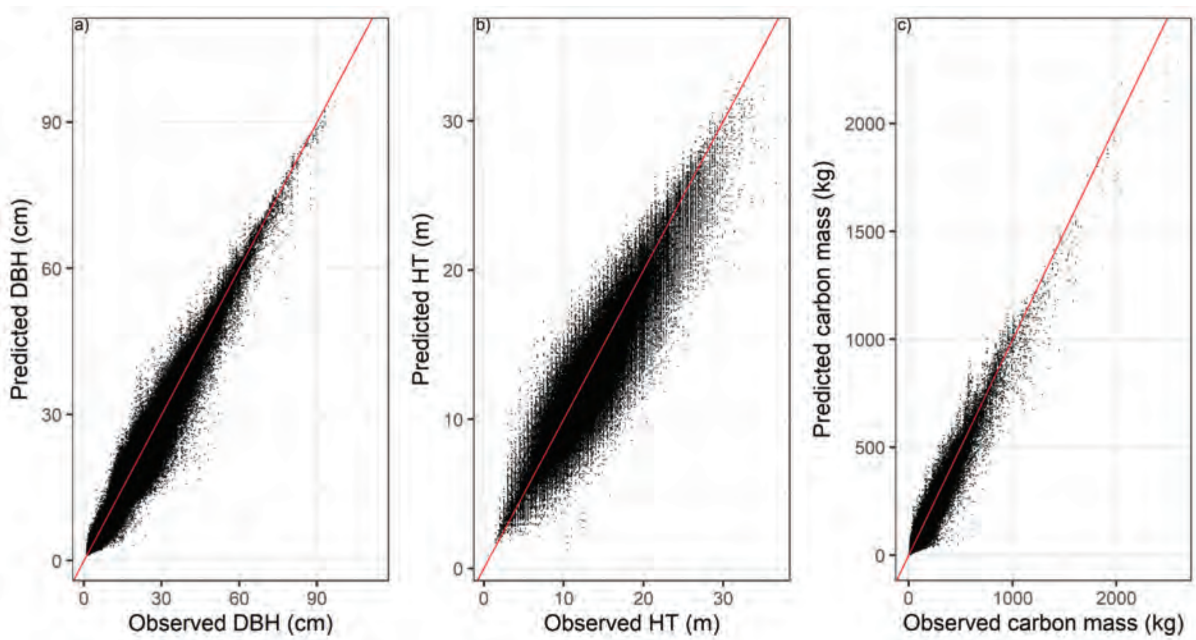

Figure 2: Observed versus predicted values for a) diameter at breast height (DBH, cm), b) total tree height (HT, m), and c) individual tree live aboveground carbon mass (kg). Residuals are based on predictions using the newly developed increment equations of this study and in the case of carbon mass include DBH and HT predictions.

tion across species and varying groupings of species (Tables S7 and S8).

3.3 Carbon mass estimation

Comparing observed individual tree aboveground live carbon mass derived from observed DBH and observed HT with carbon mass estimations calculated based on DBH and HT predictions derived from ΔDBH and ΔHT equations currently used in FVS-ACD as well as the ones developed in this study revealed substantial improvement in prediction accuracy for the development data set with MAB and $RMSE$ decreasing by approximately 32% (Table 10, Fig. 2c). However, improvement in prediction accuracy was less pronounced for the independent dataset with MB and $RMSE$ indicating lower prediction accuracy for the newly developed models (Table 8). Differences in carbon mass prediction accuracy across various tree and species groupings were mostly marginal for both examined datasets (Table 10).

4 Discussion

Individual tree stem diameter increment (ΔDBH) and total tree height increment (ΔHT) equations are key components of individual tree forest growth and yield simulators. Robust predictions of both ΔDBH and ΔHT are needed since they are often used by other submodels. This can create error compounding and greater prediction uncertainty when the resulting tree-level predictions are scaled up to represent stand-level

Table 7: Prediction accuracy metrics for the current FVS-ACD basal area increment (ΔBA, Weiskittel et al. 2013) and the current FVS-ACD diameter increment submodels (ΔDBH, unpublished) as well as for the ΔDBH equation presented in this study. Using DBH at the end of the measurement period, metrics were calculated from this study's model development dataset (N = 2,656,326) and an independent US Forest Service Forest Inventory and Analysis (FIA) dataset (N = 18,775).

Data Source	Error Statistic				
Model	MB	MB%	MAB	MAB%	RMSE
Model development dataset					
FVS-ACD ΔBA	-0.2021	-2.2327	1.0592	7.6987	1.5974
FVS-ACD ΔDBH	-0.1516	-2.2804	1.0265	7.395	1.6145
This study ΔDBH	0.0509	-1.0622	0.9161	6.5964	1.4208
Independent FIA dataset					
FVS-ACD ΔBA	0.1245	-2.2285	1.7823	12.8202	2.3917
FVS-ACD ΔDBH	0.2234	-2.3367	1.7434	12.4132	2.3784
This study ΔDBH	0.4145	-1.1659	1.526	10.7656	2.1272

Table 8: Fixed effect parameter (β_{ij}) estimates and statistics of the final total tree height increment ($\Delta HT, m \cdot yr^{-1}$) mixed effects model. See Table S5 for the corresponding species-specific random effect parameter estimates.

Variable	Parameter	Estimate	SE	t-value	p-value
Intercept	β_{20}	-2.19445	0.140713	-15.6	<0.0001
$\ln(HT)$	β_{21}	0.426404	0.014355	29.7	<0.0001
HT	β_{22}	-0.06471	0.008082	-8.01	<0.0001
CR	β_{23}	0.394837	0.005498	71.81	<0.0001
$CCFL/100$	β_{24}	-0.01143	0.000533	-21.46	<0.0001
CSI^2	β_{25}	0.000294	0.000014	20.84	<0.0001

Table 9: Prediction accuracy metrics for the tree height increment ($\Delta HT, \mathrm{m} \cdot \mathrm{yr}^{-1}$) submodel of Russell et al. (2014), the current FVS-ACD ΔHT submodel (unpublished) and for the ΔHT equation presented in this study. Using total tree height at the end of the measurement period, metrics were calculated from this study's model development dataset (N = 1,066,426) and an independent US Forest Service Forest Inventory and Analysis (FIA) dataset (N = 9,948).

Data Source	Error Statistic				
Model	MB	MB%	MAB	MAB%	RMSE
Model development dataset					
Russell et al. (2014)	-3.6497	-33.6108	3.7004	33.9196	4.6652
FVS-ACD	-1.2583	-12.4942	1.6162	14.9483	2.1889
This study	0.1510	0.0573	0.9564	8.0271	1.2945
Independent FIA dataset					
Russell et al. (2014)	-4.8368	-35.9542	4.8698	36.0987	5.3177
FVS-ACD	-1.3869	-11.4041	1.9466	14.4343	2.3308
This study	0.7030	3.3108	1.5541	10.2485	2.0432

metrics such as total volume (e.g., Wilson et al., 2019). Using a fairly novel approach by making species as random effect previously verified for ΔDBH by Kuehne et al. (2020), this study was able to derive new ΔDBH and ΔHT equations that exhibit higher prediction accuracy than the models currently used as part of the growth and yield simulator FVS-ACD for the Acadian Forest region of North America (Weiskittel et al., 2017). Theoretically, this should result in more accurate predictions of stand-level basal area, volume, and biomass/carbon given the importance of both DBH and HT on those estimates. Mixed prediction accuracy for carbon mass

Table 10: Prediction accuracy metrics for individual-tree aboveground live carbon mass estimates (kg C) derived by comparing observed tree carbon stocks quantified from observed diameter at breast height (DBH) and total tree height (HT) measurements at the end of an inventory period with estimations calculated based on DBH and HT predictions derived from i) ΔDBH and ΔHT equations currently used in FVS-ACD as well as ii) equations developed in this study, respectively. Evaluation metrics were calculated from this study's model development dataset (N = 1,066,426) and an independent US Forest Service Forest Inventory and Analysis (FIA) dataset (N = 9,948).

Data Source	Error Statistic				
Model	MB	MB%	MAB	MAB%	RMSE
Model development dataset					
FVS-ACD	-7.6573	-17.9825	13.2011	24.6731	25.9968
This study	1.7955	-1.3842	9.0731	14.7959	17.6408
Independent FIA dataset					
FVS-ACD	-2.8749	-9.1378	21.2474	22.8549	34.2632
This study	13.0800	6.5701	19.8077	17.9258	35.2287

observed for the independent dataset of this study might be at least in part result from a smaller number of observations or the potential independence of improving ΔDBH and ΔHT, which is further discussed below. However, performance of the newly derived equations was relatively robust across species and the broader study region, while the use of ecological regions as an additional predictor did not improve robustness and actually created more illogical behavior.

In general, the higher prediction accuracy of the newly derived equations was in part a result of the greater number of observations available for each of the modeled individual tree attributes and recorded all across the Acadian region as well as over a time period of several decades. Russell et al. (2014) for example, derived their ΔHT equations for the study region from only a fraction of observations compared to this work (88,956 vs. 1,066,426). In combination with the modeling approach applied, the higher number of available observations for this study also resulted in a much larger number of species ΔHT increment equations could be derived for. Consequently, this study developed ΔHT

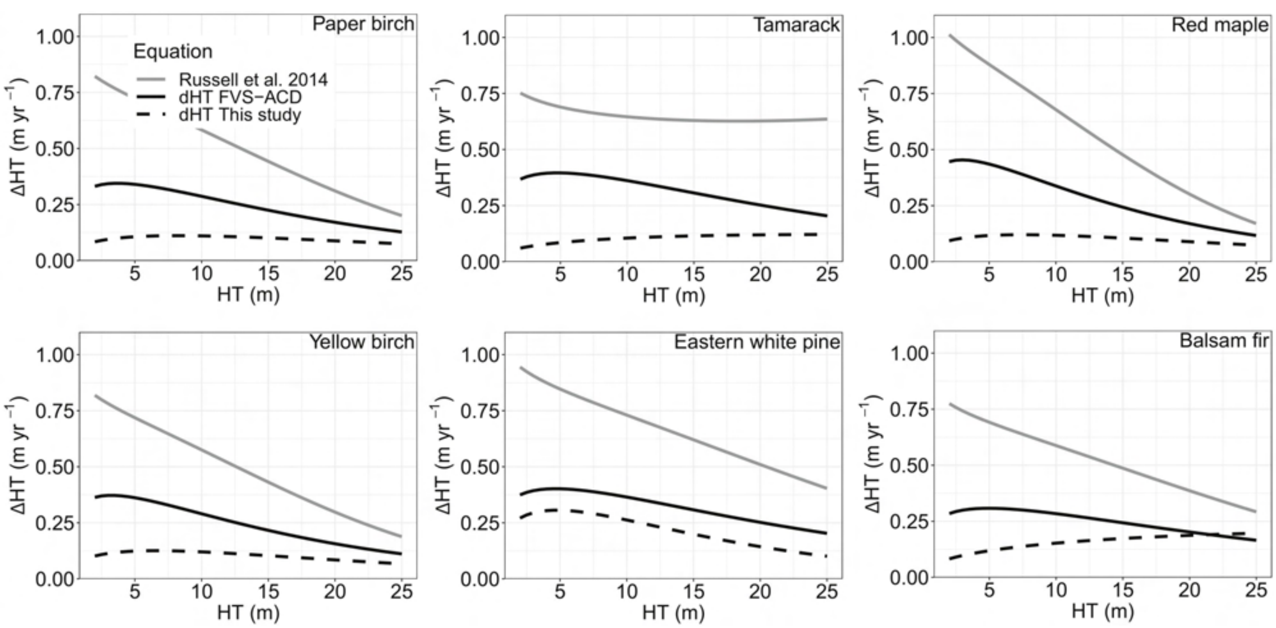

Figure 3: Annual height increment predictions (ΔHT, $\mathrm{m \cdot yr^{-1}}$) for six common Acadian tree species of varying shade tolerance over total tree height (HT, m) for the average tree and stand conditions. Curves represent equations currently used in the Acadian Variant of the Forest Vegetation Simulator (FVS-ACD) as well as the equation developed in this study.

equations for 47 species and six genera whereas Russell et al. (2014) reported 25 species-specific equations. Further, this study derived ΔDBH equations for 53 species and seven genera as part of the overall ΔDBH submodel, while Weiskittel et al. (2013) developed ΔBA equations for 58 species or species groups, respectively. The comparable number of currently used and newly developed species-specific ΔDBH equations is likely the reason why improvements in prediction accuracy were less prevalent in ΔDBH when compared to ΔHT.

Further improvement in prediction accuracy for both studied tree attributes was hampered twofold. First, the inclusion of an additional two-sided competition metric resulted in biologically implausible fixed effect parameter estimates for both ΔDBH and ΔHT despite evaluating several alternative metrics. This suggests that competition is highly dynamic and might depend on alternative factors like past management or species composition that are not fully captured in our available data. Second, additional species-specific random effects also often resulted in biologically implausible behavior of important explanatory variables (e.g., CSI) for a varying number of tree species and genera when examining the total parameter estimate, i.e., the sum of the species-specific random and the general fixed effect. As highlighted by Kuehne et al. (2020), making species as random effect can significantly modify predictor variable effects, i.e., leading to a reversal of plausible parameter signs after summing fixed and random effects parameter estimates. In species-specific models, such outcomes can be avoided by excluding the specific explanatory variable from the equation, while it can remain in equations for other species as part of the general model structure derived from biological theory. Since the fixed parameter estimate for CSI (as well as other additional explanatory variables) suggested a plausible, here significantly positive effect on ΔDBH and ΔHT in this study, the predictor variable was retained in both models, but not allowed to vary randomly. Depending on the studied submodel considered, other explanatory variables exhibit the same behavior and thus were also excluded to vary randomly within the model framework.

Similarly to the aforementioned challenges, extending the random effect structure by including an additional level of spatial scale, in this case the ecoregions of North America, also often led to the reversal of parameter signs for a subset of species and genera depending on the explanatory variable and submodel examined. This finding was a bit surprising given the successful use of ecoregions in prior studies in this region (e.g., Bose et al., 2017) and the utilization of habitat type in other ΔDBH equations (e.g., Pokharel and Dech, 2012). This finding may highlight a potential limitation of the comprehensive and overarching modeling approach applied here when compared to the more conventional way of developing individual equations for each species of interest. Alternatively, ecoregions may not represent the fine-scale variability in site conditions potentially better reflected by CSI, which is based on down-scaled climate data with a 1 km resolution. Likely, continual refinement of site productivity measures like BGI (e.g., Rahimzadeh-Bajgiran et al., 2020) and their inclusion in increment equations is an important area of future research and model refinement.

In addition to the improved and more robust predictions of the equations developed in this analysis, the findings do have broader implications for future increment equations. First, the prediction of diameter and not basal area increment proved superior as highlighted in prior analyses despite often having lower model fit statistics (e.g., Kuehne et al., 2020; Russell et al., 2011). Second, even at very broad spatial scales and across complex stand structures as well as species mixtures, tree-size attributes, particularly crown-based metrics like CR, can be highly effective integrators of various factors on tree increment. This is even true when metrics like CR are primarily imputed, but this likely depends on the accuracy of the imputation and may not always be the case (e.g., Leites et al., 2009). Although CR was found to be effective in ΔDBH and ΔHT, accurate predictions of ΔHT and ΔHCB are now needed to ensure robust behavior in simulations (e.g., Russell et al. 2014). Likewise, this analysis found that even complex competition metrics BAL adjusted for relative spacing (e.g., Schröder and von Gadow, 1999) and relative density (e.g., Weiskittel and Kuehne, 2019), respectively, were no more effective than rather simple measures of competition despite the wide range of conditions in this analysis. This aligns with the recent findings of Kuehne et al. (2019) who indicated no general superiority of highly sophisticated 2D and 3D crown-based, distance-dependent competition metrics over much more simplistic distance-independent counterparts for predicting either tree ΔDBH or survival. This finding would support the broad-scale use of these specific competition metrics as currently implemented in a variety of existing Forest Vegetation Simulator variants (Crookston and Dixon, 2005 (@).

Third, the use of all remeasurement intervals during the fitting process for both ΔDBH and ΔHT greatly increased the available data yet did not substantially alter equation predictive performance (Tables S9 and S10). Although models fit with measurement intervals equal or less than 10 years often performed the best in this analysis, the ΔDBH fit to all possible intervals performed the best when projections were greater than or equal to 20 years. This is important given that most operational growth model projections are 30-50 years in length and even over 100 years (Weiskittel et al., 2011c). Finally, although ΔDBH and ΔHT are often significantly correlated, the degree of correlation varies considerably and can even be non-significant for some species (Table S11). This would suggest that potential gains from a simultaneous regression approach (e.g., Hasenauer et al., 1998) for ΔDBH and ΔHT might vary by species but will limit the number of observations available for model development. Consequently, fitting the increment equation separately as in this analysis is likely justified, but future analyses may consider using a simultaneous mixed-effects approach as outlined in Affleck and Diéguez-Aranda (2016). This variable correlation between ΔDBH and ΔHT might also explain the significant yet limited improvement in forest carbon estimates, which was likely driven more by improvements ΔDBH than ΔHT. A similar influence of ΔDBH and ΔHT was observed by Hann and Weiskittel (2010) for predicting tree-level volume increment.

5 Conclusions

This study strongly suggests that using species as random effects is an effective and accurate approach for predicting ΔDBH and ΔHT at the species level. Despite shortcomings regarding the potential model complexity and lack of more sophisticated measures of site productivity or competition, the derived equations exhibit greater prediction accuracy compared to submodels currently used as part of FVS-ACD. Our findings are thus in agreement with findings from similar previous modeling efforts demonstrating the general applicability and suitability of the modeling approach used here (e.g., Kuehne et al., 2020). As indicated in our findings for rare species, however, the distribution of observations across species appears to affect the overall performance of the approach, which deserves further evaluation. As demonstrated in this analysis, accurate and robust predictions of both ΔDBH and ΔHT are critical, particularly when they are combined to estimate various tree- or stand-level attributes like forest carbon.

Overall, the analysis highlights a potential approach for developing refined ΔDBH and ΔHT across numerous species as well as broad spatial scales. However, continual model refinement and evaluation is needed given shifting environmental conditions and forest management practices, especially in the Acadian Forest Region (e.g., Hennigar and Weiskittel, 2018). This suggests the need to better refine measures of both site productivity and competition, particularly given the findings of this analysis. Consequently, regional continuous forest inventory networks and their measurement as used in this analysis will remain vital in the years to come despite significant advances in remote sensing technologies.

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References

Affleck, D.L.; U. Diéguez-Aranda. 2016. Additive nonlinear biomass equations: a likelihood-based approach. For. Sci. 62(2): 129–140. doi: https://doi.org/10.5849/forsci.15-126

Bechtold, W.A.; P.L. Patterson (Eds). 2005. Forest Inventory and Analysis national sample design and estimation procedures. USDA For Serv Gen. Tech. Rep. SRS-GTR-80. Available online at: https://www.fs.usda.gov/treesearch/pubs/20371. Last accessed Aug. 31, 2022

Bose, A.K.; A.R. Weiskittel; R.G. Wagner; C. Kuehne. 2016. Assessing the factors influencing natural regeneration patterns in the diverse, multi-cohort, and managed forests of Maine, USA. J. Veg. Sci. 27(6): 1140–1150. doi: https://doi.org/10.1111/jvs.12433

Bose, A.K., A. Weiskittel; R.G. Wagner. 2017. A three decade assessment of climate-associated changes in forest composition across the north-eastern USA. J. Appl. Ecol. 54: 1592–1604. doi: https://doi.org/10.1111/1365-2664.12917

Braun, E.L. 1950. Deciduous forests of eastern North America. Hafner, New York, NY. 596 pp.

Cao, Q.V. 2000. Prediction of annual diameter growth and survival for individual trees from periodic measurements. For. Sci. 46(1): 127–131. doi: https://doi.org/10.1093/forestscience/46.1.127

Colmanetti, M.A.A.; A. Weiskittel; L.M. Barbosa; R.T. Shirasuna; F.C. de Lima; P.R.T. Ortiz; E.L.M. Catharino; T.C. Barbosa; H.T.Z. do Couto. 2018. Aboveground biomass and carbon of the highly diverse Atlantic Forest in Brazil: comparison of alternative individual tree modeling and prediction strategies. Carbon Manage. 9(4): 383–397. doi: https://doi.org/10.1080/17583004.2018.1503040

Commission for Environmental Cooperation. 2006. Ecological regions of North America – Levels I, II, and III: Montreal, Quebec, Canada, Commission for Environmental Cooperation, scale 1:10,000,000, Available online at: https://www.epa.gov/eco-research/ecoregions-north-america. Last accessed Aug. 31, 2022

Crookston, N.L.; G.E. Dixon. 2005. The forest vegetation simulator: a review of its structure, content, and applications. Comput. Electron. Agr. 49(1): 60–80. doi: https://doi.org/10.1016/j.compag.2005.02.003

Dixon, G.E.; C.E. Keyser. 2018. Northeast (NE) variant overview-Forest Vegetation Simulator (revised March 16, 2018). Internal Rep Fort Collins, CO. USDA For. Serv. For. Manage. Serv. Cen. Fort Collins, CO. 40 p.

Eyre, F.H.. 1980. Forest cover types of the United States and Canada. Society of American Foresters. Washington DC.

Gawler, S.C.; A. Cutko. 2010. Natural landscapes of Maine: A guide to natural communities and ecosystems. Maine Natural Areas Program. Department of Conservation, Augusta, ME.

Hann, D.W.; A.R. Weiskittel. 2010. Evaluation of alternative approaches for predicting individual tree volume growth rate. West. J. Appl. For. 25: 120–126. doi: https://doi.org/10.1093/wjaf/25.3.120

Hasenauer, H.; R.A. Monserud; T.G. Gregoire. 1998. Using simultaneous regression techniques with individual-tree growth models. For. Sci. 44(1): 87–95. doi: https://doi.org/10.1093/forestscience/44.1.87

Hennigar, C.; A. Weiskittel. 2018. Stand development prediction accuracy of two individual-tree growth models for the Acadian Forest Region: FVS-ACD & OSM-ACD. NEFIS Publication 14715, Center for Research on Sustainable Forests. University of Maine, Orono, ME. Available online at: https://nefismembers.org/documents/stand-development-prediction-accuracy-of-two-individual-tree-statistical-growth-models-for-the-acadian-forest-region-fvs-acd-and-osm-acd/. Last accessed Aug. 31, 2022..

Juma, R.; T. Pukkala; S. de–Miguel; M. Muchiri. 2014. Evaluation of different approaches to individual tree growth and survival modelling using data collected at irregular intervals — a case study for Pinus patula in Kenya. For. Ecosyst. 1: 14. doi: https://doi.org/10.1186/s40663-014-0014-3

Kenefic, L.S.; N. Rogers; J.J. Puhlick; J.D. Waskiewicz; J.C. Brissette. 2015. Overstory tree and regeneration data from the "Silvicultural Effects on Composition, Structure, and Growth" study at Penobscot Experimental Forest. 2nd Edition. Fort Collins, CO: Forest Service Research Data Archive. Available online at: https://doi.org/10.2737/RDS-2012-0008-2. Last accessed Aug. 31, 2022..

Kuehne, C; JJ Puhlick; AR Weiskittel. 2018a. Ecological Reserves in Maine: Initial results of long-term monitoring. University of Maine. Center for Research on Sustainable Forests. Available online at: http://www.nefismembers.org/documents/ecological-reserves-in-maine-initial-results-of-long-term-monitoring. Last accessed Aug. 31, 2022..

Kuehne, C.; J. Puhlick; A. Weiskittel; A. Cutko; D. Cameron; N. Sferra; J. Schlawin. 2018b. Metrics for comparing stand structure and dynamics between Ecological Reserves and managed forest of Maine, USA. Ecology 99(12): 2876. doi: https://doi.org/10.1002/ecy.2500

Kuehne, C.; A. Weiskittel; A. Pommerening; R.G. Wagner. 2018c. Evaluation of 10-year temporal and spatial variability in structure and growth across contrasting commercial thinning treatments in spruce-fir forests of northern Maine, USA. Ann. For. Sci. 75: 20. doi: https://doi.org/10.1007/s13595-018-0697-7

Kuehne, C.; A.R. Weiskittel; R.G. Wagner; B.E. Roth. 2016. Development and evaluation of individual tree- and stand-level approaches for predicting spruce-fir response to commercial thinning in Maine, USA. For. Ecol. Manage. 376: 84–95. doi: https://doi.org/10.1016/j.foreco.2016.06.013

Kuehne, C.; A.R. Weiskittel; J. Waskiewicz. 2019. Comparing performance of contrasting distance-independent and distance-dependent competition metrics in predicting individual tree diameter increment and survival within structurally-heterogeneous, mixed-species forests of Northeastern United States. For. Eco. Manage. 433: 205–216. doi: https://doi.org/10.1016/j.foreco.2018.11.002

Kuehne, C.; M.B. Russell; A.R. Weiskittel; J.A. Kershaw Jr.. 2020. Comparing strategies for representing individual-tree secondary growth in mixed-species stands in the Acadian Forest region. For. Ecol. Manage. 459: 117823. doi: https://doi.org/10.1016/j.foreco.2019.117823

Lam, T.Y.; J.A. Kershaw Jr.; Z.S.N. Hajar; K.A. Rahman; A.R. Weiskittel; M.D. Potts. 2016. Evaluating and modelling genus and species variation in height-to-diameter relationships for Tropical Hill Forests in Peninsular Malaysia. Forestry 90(2): 268-278. doi: https://doi.org/10.1093/forestry/cpw051

Lamlom, S.; R. Savidge. 2003. A reassessment of carbon content in wood: variation within and between 41 North American species. Biomass Bioenergy 25: 381–388. doi: https://doi.org/10.1016/S0961-9534(03)00033-3

Leites, L.P.; A.P. Robinson; N.L. Crookston. 2009. Accuracy and equivalence testing of crown ratio models and assessment of their impact on diameter growth and basal area increment predictions of two variants of the Forest Vegetation Simulator. Can. J. For. Res. 39: 655–665. doi: https://doi.org/10.1139/X08-205

Li, R.; A.R. Weiskittel; J.A. Kershaw Jr.. 2011. Modeling annualized occurrence, frequency, and composition of ingrowth using mixed-effects zero-inflated models and permanent plots in the Acadian Forest region of North America. Can. J. For. Res. 41: 2077–2089. doi: https://doi.org/10.1139/x11-117

Martin, A.R.; S. Gezahegn; S.C. Thomas. 2015. Variation in carbon and nitrogen concentration among major woody tissue types in temperate trees. Can. J. For. Res. 45: 744–757. doi: https://doi.org/10.1139/cjfr-2015-0024

McGarrigle, E.; J.A. Kershaw Jr.; M.B. Lavigne; A.R. Weiskittel; M. Ducey. 2011. Predicting the number of trees in small diameter classes using predictions from a two-parameter Weibull distribution. Forestry 84(4): 431–439. doi: https://doi.org/10.1093/forestry/cpr033

Niinemets, Ü.; F. Valladares. 2006 Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. Ecol. Monogr. 76: 521–547. doi: https://doi.org/10.1890/0012-9615(2006)076[0521:TTSDAW]2.0.CO;2

Nunifu, T.K. 2009 Compatible diameter and height increment models for lodgepole pine, trembling aspen, and white spruce. Can. J. For. Res. 39(1): 180–192. doi: https://doi.org/10.1139/X08-168

Pinheiro, J.; D. Bates; S. DebRoy; D. Sarkar. 2012 nlme: Linear and nonlinear mixed effects models. R package version 3.1-103. Available online at: http://www.r-project.org. Last accessed Aug. 31, 2022.

Pokharel, B.; J.P. Dech. 2012. Mixed-effects basal area increment models for tree species in the boreal forest of Ontario, Canada using an ecological land classification approach to incorporate site effects. Forestry 85: 255–270. doi: https://doi.org/10.1093/forestry/cpr070

Province of New Brunswick. 2005. Partial harvest permanent sample plot establishment manual. Internal report. 27 pp.

R Development Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available online at: http://www.r-project.org. Last accessed Aug. 31, 2022.

Radtke, P.; D. Walker; J. Frank; A. Weiskittel; C. DeYoung; D. MacFarlane; G. Domke; C. Woodall; J. Coulston; J. Westfall. 2017. Improved accuracy of aboveground biomass and carbon estimates for live trees in forests of the eastern United States. Forestry 90: 32–46. doi: https://doi.org/10.1093/forestry/cpw047

Rahimzadeh-Bajgiran, P.; C. Hennigar; A. Weiskittel; S. Lamb. 2020. Forest potential productivity mapping by linking remote-sensing derived metrics to site variables. Remote Sens. 12: 2056. doi: https://doi.org/10.3390/rs12122056.

Rehfeldt, G.E. 2006. A spline model of climate for the western United States. USDA For. Serv. Gen. Tech. Rep. RMRS-165.

Rijal, B; AR Weiskittel; JA Jr Kershaw. 2012a. Development of height to crown base models for thirteen tree species of the North American Acadian Region. For. Chron. 88(1): 60–73. doi: https://doi.org/10.5558/tfc2012-011

Rijal, B.; A.R. Weiskittel; J.A. Kershaw Jr.. 2012b. Development of regional height to diameter equations for 15 tree species in the North American Acadian Region. Forestry 85(3): 379–390. doi: https://doi.org/10.1093/forestry/cps036

Rowe, J.S. 1972. Forest regions of Canada. Publ 1300. Dept. Env. Can. For. Serv. 251 Ottawa. 172 pp.

Russell, M.B.; A.R. Weiskittel. 2011. Maximum and largest crown width equations for fifteen tree species in Maine. Nor. J. Appl. For. 28: 84–91. doi: https://doi.org/10.1093/njaf/28.2.84

Russell, M.B.; A.R. Weiskittel; J.A. Kershaw Jr. 2011. Assessing model performance in forecasting long-term individual tree diameter versus basal area increment for the primary Acadian tree species. Can. J. For. Res. 41: 2267–2275. doi: https://doi.org/10.1139/x11-139

Russell, M.B.; A.R. Weiskittel; J.A. Kershaw Jr. 2014. Comparing strategies for modeling individual-tree height and height-to-crown base increment in mixed-species Acadian Forests of northeastern North America. Eur. J. For. Res. 133: 1121–1135. doi: https://doi.org/10.1007/s10342-014-0827-1

Salas-Eljatib, C.; A. Weiskittel. 2020. On studying the patterns of individual-based tree mortality in natural forests: a modelling analysis. For. Ecol. Manage. 475: 118369. doi: https://doi.org/10.1016/j.foreco.2020.118369

Schröder, J.; K. von Gadow. 1999. Testing a new competition index for Maritime pine in northwestern Spain. Can. J. For. Res. 29: 280–283. doi: https://doi.org/10.1139/x98-199

Thomas, S.C.; A.R. Martin. 2012. Carbon content of tree tissues: a synthesis. Forests 3: 332–352. doi: https://doi.org/10.3390/f3020332

Wagner, R.G.; R.S. Seymour. 2006. Commercial Thinning Research Network. In: 2004-2005 Cooperative Forestry Research Unit Annual Report. University of Maine, Orono, ME. pp. 34–41.

Weiskittel, A.R.; N.L. Crookston; P.J. Radtke. 2011a. Linking climate, gross primary productivity, and site index across forests of the western United States. Can. J. For. Res. 41: 1710–1721. doi: https://doi.org/10.1139/x11-086

Weiskittel, A.R.; S.M. Garber; G.P. Johnson; D.A. Maguire; R.A. Monserud. 2007. Annualized diameter and height growth equations for Pacific Northwest plantation-grown Douglas-fir, western hemlock, and red alder. For. Ecol. Manage. 250(3): 266–278. doi: https://doi.org/10.1016/j.foreco.2007.05.026

Weiskittel, A.R.; J.A. Kershaw Jr.; N.L. Crookston; C.R. Hennigar. 2017. The Acadian Variant of the Forest Vegetation Simulator: Continued development and evaluation. In: Keyser, C.E.; T.L. Keyser (Eds). Proceedings of the 2017 Forest Vegetation Simulator (FVS) e-Conference. e-Gen Tech Rep SRS-224. Asheville, NC: USDA For. Ser., Southern Research Station; p. 10–13.

Weiskittel, A.R.; J.A. Kershaw Jr.; C. Hennigar. 2013. Refinement of the Forest Vegetation Simulator individual-tree growth and yield model for the Acadian Region. In: 2012 Cooperative Forestry Research Unit Annual Report (SR Meyer, Ed). Univ. of Maine, Orono, ME. pp. 67–77.

Weiskittel, A.R.; C. Kuehne. 2019. Evaluating and modeling variation in site-level maximum carrying capacity of mixed-species forest stands in the Acadian Region of northeastern North America. For. Chron. 95(3): 171–182. doi: https://doi.org/10.5558/tfc2019-026

Weiskittel, A.; J. Frank; D. Walker; P. Radtke; D. Macfarlane; J. Westfall. 2015. Advancing individual tree biomass prediction: assessment and alternatives to the component ratio method. In: Stanton, S.M.; G.A. Christensen (Comps). Pushing boundaries: new directions in inventory techniques and applications: Forest Inventory and Analysis 2015 symposium. Gen. Tech. Rep. PNW-GTR-931: 125–132.

Weiskittel, A.; C. Kuehne; J.P. McTague; M. Oppenheimer. 2016. Development and evaluation of an individual tree growth and yield model for the mixed species forest of the Adirondacks Region of New York, USA. For. Ecosyst. 3(1): 26. doi: https://doi.org/10.1186/s40663-016-0086-3

Weiskittel, A.R.; R.G. Wagner; R.S. Seymour. 2010. Refinement of the Forest Vegetation Simulator, northeastern variant growth and yield model: Phase 1. In: 2009 Cooperative Forestry Research Unit Annual Report (S.R. Meyer, Ed). Univ. Maine, Orono, ME. pp. 44–48.

Weiskittel, A.R.; R.G. Wagner; R.S. Seymour. 2011b. Refinement of the forest vegetation simulator, northeastern variant growth and yield model: Phase 2. In: Mercier, W.J.; A.S. Nelson (Eds). Cooperative Forestry Research Unit. 2010 Annual Report. Univ. Maine. Orono, ME., 23–30.

Weiskittel, A.R.; D.W. Hann; J.A. Kershaw Jr.; J. Vanclay. 2011c. Forest growth and yield: Concepts and applications. Wiley-Blackwell, New York. 430p.

Wilson, D.; V. Monleon; A. Weiskittel. 2019. Quantification and incorporation of uncertainty in forest growth and yield projections using a Bayesian probabilistic framework: A demonstration for plantation coastal Douglas-fir in the Pacific Northwest, USA. Math. Comput. For. Nat. Res. Sci. 11: 264–285. Available online: http://mcfns.net/index.php/Journal/article/view/11.3

Zuur, A.F.; E.N. Leno; N.J. Walker; A.A. Saveliev; G.M. Smith. 2009. Mixed effects models and extensions in ecology with R. New York, NY. Springer. p 574.

A Supplementary materials

Table S1. Overview of the diameter at breast height (DBH) increment (ΔDBH) and total height (HT) increment (ΔHT) equations currently used in FVS-ACD. See corresponding paper for definition and explanation of variables and parameters. Parameter estimates are available from the authors upon request.

Attribute	Formula[1]
ΔDBH	$exp\left(\begin{array}{l}\beta_{30}+b_{30,SP}+(\beta_{31}+b_{31,SP})\times DBH+\beta_{32}\times DBH^2+\beta_{33}\times ln\,(CR)+\beta_{35}\times ln\,(CSI)\\ +(\beta_{34}+b_{34,SP})\times ln\,(BAL_{MOD}+0.1)+b_{37}\times\sqrt{pBAL_{SW}+0.0001}\\ +(\beta_{36}+b_{36,SP})\times\sqrt{BA\times RD+1}\end{array}\right)$
ΔHT	$exp\left(\begin{array}{l}\beta_{40}+b_{40,SP}+(\beta_{41}+b_{41,SP})\times HT+\beta_{42}\times ln\,(HT)+\beta_{43}\times CR+\beta_{45}\times ln\,(CSI)\\ +(\beta_{44}+b_{44,SP})\times ln\,(BAL_{MOD}+1)+(\beta_{47}+b_{47,SP})\times\sqrt{pBAL_{SW}}\\ +(\beta_{46}+b_{46,SP})\times ln\,(BA\times RD+1)+\beta_{48}\times(BA\times RD)\end{array}\right)$

[1]BAL_{MOD} = (1-pBA)/RS with pBA = 1-((BAL+0.001)/BA) and RS = ($\sqrt{10000/TPH}$)/TopHT with TPH is number of tree per hectare and TopHT is dominant height, i.e., average height of the 100 thickest trees per hectare; RD = SDI/maximum SDI with SDI is stand density index and maximum SDI calculated based on

Table S2. Estimated variances, standard deviations, and correlations between the random-effects terms in the nonlinear mixed-effects tree diameter increment (ΔDBH, cm×yr^{-1}) model.

Parameter	Variance	SD	Correlation					
			b10	b11	b12	b13	b14	b15
b10	0.8050	0.8972	-	-	-	-	-	-
b11	0.1885	0.4342	-0.4960	-	-	-	-	-
b12	0.0014	0.0369	0.2190	-0.7640	-	-	-	-
b13	0.4552	0.6747	0.5260	0.2740	-0.4280	-	-	-
b14	0.0049	0.0703	-0.0520	0.1440	0.1110	-0.0640	-	-
b15	0.0075	0.0866	0.0190	-0.1810	0.5410	-0.1040	-0.2740	-
b16	0.0008	0.0289	-0.0050	-0.0710	-0.4070	0.2270	-0.6270	-0.3690
Residual	0.6856	0.8280	-	-	-	-	-	-

Table S3. Relative mean absolute bias (MAB%) summary statistics for the ΔDBH and ΔHT equations developed in this study and calculated for various tree and species groupings including frequent (number of observations ≥ 5,000) and infrequent species/genera (number of observations < 5,000). Using diameter at breast height (DBH) and total tree height (HT), respectively, at the end of the measurement period, mean and standard deviation (SD) of MAB% were calculated from this study's model development dataset.

Grouping	ΔDBH			ΔHT		
	N	Mean	SD	N	Mean	SD
DBH < 12.7 cm	888487	9.258	10.26	179,217	8.377	7.853
DBH ≥ 12.7 cm	1767839	5.259	5.747	887,209	7.957	7.629
Hardwood	773300	7.132	7.936	357,311	7.377	6.566
Softwood	1883026	6.376	7.723	709,115	8.355	8.148
Shade tolerant	2360613	6.539	7.744	948,592	8.076	7.757
Shade intolerant	295713	7.051	8.16	117,834	7.636	6.905
Frequent	2629137	6.594	7.798	1,051,263	8.029	7.674
Infrequent	27189	6.795	7.362	15,163	7.907	7.277

Table S4. Species-specific number of observations (N) and statistics for initial diameter at breast height (DBH, cm) and initial total height (HT, m) of the US Forest Service Forest Inventory and Analysis Program (FIA) independent data set.

Acronym	Scientific name	DBH					HT				
		N	Mean	SD	Min	Max	N	Mean	SD	Min	Max
AB	*Fagus grandifolia*	574	14.76	8.46	2.54	42.42	281	12.95	3.28	4.57	21.34
AE	*Ulmus americana*	20	11.18	6.87	2.54	29.72	11	12.05	2.68	7.32	16.46
AH	*Carpinus caroliniana*	3	5.59	0.25	5.33	5.84					
AP	*Malus spp.*	8	16.00	1.52	12.70	17.78	5	8.72	1.86	6.10	11.28
BA	*Fraxinus nigra*	125	10.74	7.17	2.54	38.35	33	12.97	2.07	9.75	16.46
BC	*Prunus serotina*	37	16.76	8.62	2.79	34.04	25	13.74	3.80	4.88	20.73
BF	*Abies balsamea*	4,114	8.55	6.13	2.54	36.83	1,361	10.22	3.45	2.13	21.34
BO	*Quercus velutina*	5	21.03	9.71	13.72	38.10	4	15.01	5.11	11.28	22.56
BP	*Populus balsamifera*	43	15.48	10.04	2.54	40.64	23	13.57	3.23	8.23	24.99
BS	*Picea mariana*	553	14.74	6.84	2.54	38.61	349	12.74	3.49	2.44	26.21
BT	*Populus grandidentata*	192	21.10	9.17	2.54	54.10	145	18.81	3.91	10.06	28.96
BW	*Tilia americana*	5	16.97	3.66	13.72	22.35	5	13.78	2.04	10.67	15.54
CC	*Prunus virginiana*	1	3.56	-	-	-					
EH	*Tsuga canadensis*	810	20.80	11.01	2.54	70.61	636	12.59	4.12	2.74	24.99
GA	*Fraxinus pennsylvanica*	7	11.58	7.58	5.08	23.11	3	15.44	3.20	12.19	18.59
GB	*Betula populifolia*	108	7.38	4.72	2.79	26.92	20	12.36	3.87	6.10	19.81
HH	*Ostrya virginiana*	39	11.76	6.54	2.54	27.43	20	12.42	2.87	7.62	18.29
JP	*Pinus banksiana*	2	24.13	4.67	20.83	27.43	2	14.48	2.37	12.80	16.15
MA	*Sorbus spp.*	13	14.89	10.65	3.05	35.81	7	10.76	1.89	7.92	12.50
MM	*Acer spicatum*	27	4.40	1.45	2.54	8.89	1	4.27	-	-	-
PB	*Betula papyrifera*	1,161	14.31	7.73	2.54	41.91	481	13.85	2.99	3.05	22.56
PP	*Pinus rigida*	3	26.59	1.30	25.15	27.69	3	13.72	1.10	12.50	14.63
PR	*Prunus pensylvanica*	26	5.74	3.71	2.54	16.26	2	9.60	2.80	7.62	11.58
QA	*Populus tremuloides*	253	16.06	9.51	2.54	44.20	146	16.49	3.02	6.10	23.77
RM	*Acer rubrum*	2,466	16.58	9.05	2.54	66.04	1,408	14.55	3.52	3.66	26.21
RN	*Pinus resinosa*	33	24.55	13.88	3.81	70.10	25	13.92	4.25	7.32	22.56
RO	*Quercus rubra*	253	21.94	10.59	2.79	81.79	195	16.56	3.43	4.57	25.60
RS	*Picea rubens*	2,586	15.57	9.40	2.54	54.86	1,507	12.91	4.07	2.13	28.65
SB	*Betula lenta*	4	21.59	15.56	5.08	40.39	3	18.19	3.76	14.02	21.34
SE	*Amelanchier spp.*	5	3.96	1.03	2.54	5.08					
SM	*Acer saccharum*	714	20.31	11.90	2.54	75.69	412	15.57	3.67	3.96	25.30
ST	*Acer pensylvanicum*	130	4.78	2.91	2.54	19.56	21	7.90	2.29	4.27	13.41
TA	*Larix laricina*	75	17.54	10.25	2.54	48.01	52	14.19	4.67	3.96	24.69
WA	*Fraxinus americana*	204	16.98	8.40	2.54	50.04	132	15.75	3.80	4.57	26.21
WC	*Thuja occidentalis*	2,147	20.22	8.85	2.54	76.45	1,217	10.81	2.65	2.74	22.56
WI	*Salix spp.*	1	28.45	-	-	-					
WO	*Quercus alba*	10	18.36	5.10	8.89	25.40	9	14.77	3.46	8.53	19.51
WP	*Pinus strobus*	810	23.01	13.35	2.54	84.07	673	15.25	5.33	4.27	39.01
WS	*Picea glauca*	333	17.26	8.38	2.54	46.23	256	11.96	4.08	3.66	24.38
YB	*Betula alleghaniensis*	875	18.50	11.69	2.54	67.06	475	13.60	3.05	3.35	22.56
Overall		18,775	15.46	10.04	2.54	84.07	9,948	13.06	4.15	2.13	39.01

Table S5. Parameters for species-specific random effects of the final tree diameter increment (ΔDBH, cm/yr) model.

Acronym	Species	$b10_{SP}$	$b12_{SP}$	$b13_{SP}$	$b14_{SP}$
AB	*Fagus grandifolia*	-0.352293	-0.003203	-0.280947	0.022414
AE	*Ulmus americana*	0.525848	0.013991	0.412199	0.133837
AH	*Carpinus caroliniana*	-0.563197	-0.010771	0.067013	0.041163
AI	*Ailanthus altissima*	0.020656	-0.000134	0.006044	-0.000291
AL	Alnus spp.	-1.395669	-0.000609	-0.358275	0.018989
AP	Malus spp.	0.274306	-0.010207	0.670513	0.037892
AW	*Chamaecyparis thyoides*	0.274057	0.003327	0.111765	-0.002334
BA	*Fraxinus nigra*	-0.438617	-0.002293	-0.226867	0.000647
BC	*Prunus serotina*	-0.279503	-0.016519	-0.448778	0.129219
BE	*Acer negundo*	0.757731	0.001850	-0.145271	-0.079686
BF	*Abies balsamea*	0.218141	-0.006434	-0.026202	-0.064687
BH	*Carya cordiformis*	0.081967	0.000841	0.017040	-0.003825
BN	*Juglans cinerea*	0.058962	0.016877	-0.512635	-0.085604
BO	*Quercus velutina*	0.107936	0.017656	-0.005441	-0.006162
BP	*Populus balsamifera*	0.606189	-0.009772	0.214468	-0.016437
BR	*Quercus macrocarpa*	-0.066423	-0.000131	-0.022130	0.003153
BS	*Picea mariana*	-0.276634	-0.022393	-0.062196	-0.034021
BT	*Populus grandidentata*	-0.350924	0.006776	-0.501316	0.000443
BW	*Tilia americana*	0.852839	-0.007495	0.563427	0.086568
CC	*Prunus virginiana*	-0.646060	0.018564	-0.217333	-0.004688
DW	Cornus spp.	-0.288350	0.002268	-0.072789	0.006209
EC	*Populus deltoides*	1.585344	0.022156	0.990116	-0.031672
EH	*Tsuga canadensis*	0.238328	0.001187	0.119839	-0.064943
GA	*Fraxinus pennsylvanica*	-0.266610	0.014244	-0.157161	0.020105
GB	*Betula populifolia*	0.569984	-0.066477	0.198469	-0.000183
HH	*Ostrya virginiana*	-0.501570	-0.006702	-0.019652	0.090652
HT	Crataegus spp.	-0.061323	-0.000890	0.043003	-0.002790
JP	*Pinus banksiana*	-0.420043	0.004036	-0.187599	-0.038909
MA	Sorbus spp.	0.468084	0.009581	0.678224	0.029581
MM	*Acer spicatum*	0.031721	-0.034040	0.168053	0.008823
NM	*Acer platanoides*	0.547338	0.003690	0.192703	-0.025724
NS	*Picea abies*	0.920842	-0.010530	0.364151	-0.069416
PB	*Betula papyrifera*	-0.385839	-0.015560	-0.308091	-0.018701
PP	*Pinus rigida*	0.225132	0.000349	-0.049214	-0.021454
PR	*Prunus pensylvanica*	0.300351	-0.005188	0.287347	-0.012999
QA	*Populus tremuloides*	-0.150772	0.005397	-0.340233	0.019922
RM	*Acer rubrum*	-0.298279	-0.004982	-0.265475	0.000258
RN	*Pinus resinosa*	0.821040	-0.022264	-0.070509	-0.062075
RO	*Quercus rubra*	-1.201767	0.020835	-0.650193	0.013835
RS	*Picea rubens*	0.061849	0.002025	0.009919	-0.047102
SB	*Betula lenta*	0.180028	0.004077	0.294830	0.045629
SC	*Pinus sylvestris*	0.291684	0.008405	0.103224	-0.037517
SE	Amelanchier spp.	-0.844748	0.019405	-0.185321	0.004814
SH	*Carya ovata*	-0.276496	-0.004078	0.001486	0.010529
SM	*Acer saccharum*	-0.638439	0.010115	-0.449980	0.035974
SO	*Quercus coccinea*	0.576834	0.011811	0.050454	-0.023841
ST	*Acer pensylvanicum*	-0.087304	0.004363	-0.116020	0.004529
SV	*Acer saccharinum*	1.958609	-0.021443	1.324443	-0.010769
SW	*Quercus bicolor*	-0.039336	-0.001347	-0.010139	0.002620
SY	*Platanus occidentalis*	0.118395	0.001106	0.006663	-0.009507
TA	*Larix laricina*	-0.897320	0.025871	-0.196337	0.028969
TM	*Pinus pungens*	-0.108286	0.000105	0.021034	0.001944
WA	*Fraxinus americana*	-0.590367	0.006056	-0.606967	-0.033860
WC	*Thuja occidentalis*	-0.585164	0.012973	0.099730	0.017663
WI	Salix spp.	-0.527848	-0.003957	-0.152094	0.032589
WO	*Quercus alba*	-0.838566	0.030299	-0.102629	0.050289
WP	*Pinus strobus*	0.789109	-0.002763	0.068527	-0.033423
WS	*Picea glauca*	0.237471	-0.008055	-0.043558	-0.062803
YB	*Betula alleghaniensis*	-0.209370	-0.001571	-0.237821	0.004480
YP	*Liriodendron tulipifera*	-0.113658	-0.000426	-0.055511	0.001681

Table S6. Parameter estimates for species-specific random effects of the final tree height increment (ΔHT, m/yr) model.

Acronym	Species	$b20_{SP}$	$b22_{SP}$
AB	*Fagus grandifolia*	-1.02612820	0.03460380
AE	*Ulmus Americana*	1.43819560	-0.09595720
AH	*Carpinus caroliniana*	-0.67306200	0.02309220
AL	*Alnus spp.*	-0.66494400	0.02863710
AP	*Malus spp.*	-0.51307620	0.00891800
BA	*Fraxinus nigra*	-0.37524270	0.03371860
BC	*Prunus serotine*	-1.81264790	0.11668200
BE	*Acer negundo*	1.27871260	-0.03410890
BF	*Abies balsamea*	-0.77616360	0.05558970
BN	*Juglans cinereal*	1.28974290	-0.03345930
BO	*Quercus velutina*	1.12645060	-0.01953680
BP	*Populus balsamifera*	0.69466220	-0.00698750
BR	*Quercus macrocarpa*	0.07550270	-0.00306680
BS	*Picea mariana*	-0.73312190	0.00145780
BT	*Populus grandidentata*	-0.94247830	0.06439440
BW	*Tilia Americana*	0.91146180	-0.03657630
CC	*Prunus virginiana*	-0.12284840	0.00498900
EC	*Populus deltoides*	0.08510040	-0.00053100
EH	*Tsuga canadensis*	-0.42265190	0.01380660
GA	*Fraxinus pennsylvanica*	-0.05927530	0.02333720
GB	*Betula populifolia*	-0.23919610	-0.01157780
HH	*Ostrya virginiana*	0.15092190	-0.04731140
HT	*Crataegus spp.*	-0.23586330	0.01061410
JP	*Pinus banksiana*	-0.97224940	0.08198960
MA	*Sorbus spp.*	0.33943990	-0.03253610
MM	*Acer spicatum*	-0.39199470	0.02280890
NM	*Acer platanoides*	-0.08663730	0.00270420
NS	*Picea abies*	-0.20464490	0.00916750
PB	*Betula papyrifera*	-0.67232510	0.01280720
PP	*Pinus rigida*	1.30938460	-0.06020800
PR	*Prunus pensylvanica*	0.63153660	-0.02445230
QA	*Populus tremuloides*	-0.05290320	0.00999110
RM	*Acer rubrum*	-0.55140980	0.00747420
RN	*Pinus resinosa*	0.96122520	-0.06245060
RO	*Quercus rubra*	-1.40760440	0.07745450
RS	*Picea rubens*	-0.01913860	-0.01238210
SB	*Betula lenta*	0.86484500	-0.02484960
SE	*Amelanchier spp.*	1.01998130	-0.07734720
SH	*Carya ovata*	0.11834260	-0.00302870
SM	*Acer saccharum*	-0.28197470	0.00337390
SO	*Quercus coccinea*	0.98746190	-0.02298130
ST	*Acer pensylvanicum*	0.66782250	-0.04029370
SV	*Acer saccharinum*	0.39617750	-0.02463580
TA	*Larix laricina*	-1.07442970	0.04806780
TM	*Pinus pungens*	-0.09631790	0.00440060
WA	*Fraxinus Americana*	-0.84083500	0.03629290
WC	*Thuja occidentalis*	-0.12878340	-0.01051280
WI	*Salix spp.*	-0.03777930	0.01430550
WO	*Quercus alba*	0.91407590	-0.03959660
WP	*Pinus strobus*	0.57349300	-0.02518620
WS	*Picea glauca*	-0.03431860	-0.00095480
YB	*Betula alleghaniensis*	-0.45683610	-0.00018970
YP	*Liriodendron tulipifera*	-0.01346320	0.00063620

Table S7. Species-specific relative mean absolute bias (MAB%) summary statistics for the ΔDBH and ΔHT equations presented in this study. Using diameter at breast height (DBH) and total tree height (HT), respectively, at the end of the measurement period, mean and standard deviation (SD) of MAB% were calculated from this study's model development dataset.

Acronym	Scientific name	ΔDBH		ΔHT	
		Mean	SD	Mean	SD
AB	*Fagus grandifolia*	6.6979	7.1927	8.2367	7.1890
AE	*Ulmus americana*	9.5569	9.5279	10.5263	9.2758
AH	*Carpinus caroliniana*	7.2586	6.4902	14.6797	8.0361
AI	*Ailanthus altissima*	2.9045	-	10.3772	2.1942
AL	Alnus spp.	3.7995	3.3734	-	-
AP	Malus spp.	4.4352	5.6474	9.8309	6.9461
AW	*Chamaecyparis thyoides*	2.4264	1.7027	-	-
BA	*Fraxinus nigra*	6.2018	6.3366	7.9176	6.3686
BC	*Prunus serotina*	9.2800	9.8264	9.1462	8.0151
BE	*Acer negundo*	5.1403	2.4243	10.9141	7.5383
BF	*Abies balsamea*	7.0658	8.3287	9.1361	8.8908
BH	*Carya cordiformis*	2.5493	1.7828	-	-
BN	*Juglans cinerea*	6.8155	4.1073	11.1916	5.2834
BO	*Quercus velutina*	4.5831	4.5315	8.0930	7.2734
BP	*Populus balsamifera*	6.7896	9.0221	7.2256	6.0916
BR	*Quercus macrocarpa*	1.9699	-	4.2653	-
BS	*Picea mariana*	5.8654	6.8182	7.1019	6.6163
BT	*Populus grandidentata*	7.1801	7.1794	7.6327	6.2709
BW	*Tilia americana*	6.2288	6.3369	7.4350	6.4077
CC	*Prunus virginiana*	10.7328	8.8704	-	-
DW	Cornus spp.	15.7491	12.7202	-	-
EC	*Populus deltoides*	8.6319	5.9809	8.8763	-
EH	*Tsuga canadensis*	7.4496	10.2142	8.0744	7.4805
GA	*Fraxinus pennsylvanica*	7.1465	7.4790	8.9579	8.1450
GB	*Betula populifolia*	10.1371	12.3478	6.8394	5.9588
HH	*Ostrya virginiana*	6.0290	6.3979	7.4141	6.8759
HT	Crataegus spp.	12.2192	7.3825	5.6563	2.5365
JP	*Pinus banksiana*	4.1235	4.6095	10.6288	10.0723
MA	Sorbus spp.	8.0389	7.0793	9.2515	7.5726
MM	*Acer spicatum*	7.5017	6.7952	14.1144	12.9440
NM	*Acer platanoides*	4.1006	2.4576	6.0712	-
NS	*Picea abies*	7.3344	6.8956	21.5357	-
PB	*Betula papyrifera*	6.9327	8.1732	7.2355	6.6801
PP	*Pinus rigida*	4.6678	4.3266	7.2086	5.4720
PR	*Prunus pensylvanica*	7.9458	7.9951	10.1192	8.4401
QA	*Populus tremuloides*	7.4308	8.2541	7.4092	6.5794
RM	*Acer rubrum*	7.2396	7.9323	7.3861	6.5560
RN	*Pinus resinosa*	5.5557	6.3725	7.4713	7.1510
RO	*Quercus rubra*	6.0832	6.0114	7.9111	6.7803
RS	*Picea rubens*	5.3276	6.5400	7.3623	6.9957
SB	*Betula lenta*	3.7083	3.3441	6.2411	4.6998
SC	*Pinus sylvestris*	6.1005	4.2639	-	-
SE	Amelanchier spp.	4.8852	4.6056	6.8600	5.7456
SH	*Carya ovata*	3.5476	4.0912	3.8556	3.1064
SM	*Acer saccharum*	6.4026	6.4978	6.5872	5.6793
SO	*Quercus coccinea*	2.4983	1.4698	4.6137	4.7716
ST	*Acer pensylvanicum*	9.3749	9.7671	8.5926	7.0835
SV	*Acer saccharinum*	7.7719	6.9559	7.9761	5.9646
SW	*Quercus bicolor*	1.8273	1.5067	-	-
SY	*Platanus occidentalis*	5.7501		-	-
TA	*Larix laricina*	7.3287	7.5761	8.9062	7.9705
TM	*Pinus pungens*	15.9938	5.4201	12.8932	-
WA	*Fraxinus americana*	7.0925	7.6389	7.5026	6.6017
WC	*Thuja occidentalis*	4.3672	5.8447	7.4034	6.0071
WI	Salix spp.	5.3208	4.4320	5.9152	4.3686
WO	*Quercus alba*	4.0316	4.4525	6.8603	5.4861
WP	*Pinus strobus*	8.2913	9.7488	8.8821	9.1647
WS	*Picea glauca*	6.5882	6.9418	9.2103	9.1549
YB	*Betula alleghaniensis*	7.3764	8.2428	7.5511	6.7798
YP	*Liriodendron tulipifera*	2.8751	2.4980	4.8802	2.9347
Overall		6.5964	7.7934	8.2367	7.1890

Table S8. Estimated variances, standard deviations, and correlations between the random-effects terms in the nonlinear mixed-effects tree height increment (ΔHT, m$\times$yr^{-1}) model.

Parameter	Variance	SD	Correlation b20
b20	0.6744	0.8212	-
b22	0.0021	0.0458	-0.894
Residual	4.9013	2.2139	-

Table S9. Evaluation of alternative ΔDBH models using the fitting dataset and an independent dataset. Mean bias (MB) was computed using as observed-predicted, while RMSE is root mean square error. For both measurements, the units are cm/yr. The values in bold are the best for each category.

Species/ Method	Fitting dataset (all intervals)		Fitting dataset (intervals $\geq$ 20 years)		Independent dataset (5-year interval)	
	MB	RMSE	MB	RMSE	Bias	RMSE
			Hardwood			
All intervals	0.00787	0.1455	**-0.008**	**0.1141**	0.0507	0.1616
10-year interval	**-0.0049**	**0.1454**	-0.0201	0.121	0.0296	0.1536
5-year interval	-0.0076	0.1462	-0.0236	0.1239	**0.0275**	**0.1519**
			Softwood			
All intervals	0.01703	0.1602	**-0.0059**	**0.1171**	0.0169	0.1323
10-year interval	0.00249	0.1542	-0.0155	0.1271	**0.0044**	0.1278
5-year interval	**0.00119**	**0.1542**	-0.0178	0.1296	0.0056	**0.1272**
			Overall			
All intervals	0.01486	0.1568	**-0.0066**	**0.1161**	0.028	0.1426
10-year interval	0.00073	**0.1522**	-0.0171	0.1251	**0.0127**	0.1368
5-year interval	**-0.0009**	0.1524	-0.0198	0.1277	0.0128	**0.1358**

Table S10. Evaluation of alternative ΔHT models using the fitting dataset and an independent dataset. Mean bias (MB) was computed using as observed-predicted, while RMSE is root mean square error. For both measurements, the units are m/yr. The values in bold are the best for each category.

Species/ Method	Fitting dataset (all intervals)		Fitting dataset (intervals $\geq$ 20 years)		Independent dataset (5-year interval)	
	MB	RMSE	MB	RMSE	MB	RMSE
			Hardwood			
All intervals	-0.018290	0.161840	-0.063010	0.091370	0.065470	0.150790
10-year interval	**-0.000480**	**0.152020**	**-0.038730**	**0.078240**	**-0.001620**	**0.136460**
5-year interval	-0.036290	0.156840	-0.066190	0.098670	-0.047170	0.151010
			Softwood			
All intervals	0.003350	0.165580	-0.049110	0.092150	0.037990	0.129990
10-year interval	**0.000450**	**0.154810**	**-0.032800**	**0.082840**	**-0.005850**	**0.120820**
5-year interval	-0.001520	0.155990	-0.050260	0.093890	-0.040270	0.133960
			Overall			
All intervals	-0.002880	0.164510	-0.054060	0.091870	0.047440	0.137510
10-year interval	**0.001810**	**0.150080**	**-0.034920**	**0.081230**	**-0.004390**	**0.126420**
5-year interval	-0.002130	0.156240	-0.056090	0.095620	-0.042640	0.140060

Table S11. Pearson's correlation coefficient, 95% confidence interval, and associated p-value between ΔDBH and ΔHT by species.

Species	N	Pearon's Coefficient	Confidence interval		P-value
			Low	High	
AB	18674	0.4558	0.4443	0.4671	0.0000
AE	341	0.4792	0.3930	0.5571	0.0000
AH	10	0.7085	0.1423	0.9253	0.0218
AL	9	0.7603	0.1944	0.9465	0.0174
AP	80	0.2318	0.0127	0.4296	0.0386
BA	972	0.3392	0.2823	0.3937	0.0000
BC	960	0.5270	0.4797	0.5712	0.0000
BF	293533	0.6481	0.6460	0.6502	0.0000
BN	9	0.4158	-0.3431	0.8462	0.2657
BO	208	0.4794	0.3673	0.5778	0.0000
BP	538	0.4945	0.4279	0.5558	0.0000
BS	65484	0.6987	0.6948	0.7026	0.0000
BT	7035	0.6472	0.6334	0.6605	0.0000
BW	173	0.4772	0.3531	0.5847	0.0000
CC	5	-0.0547	-0.8938	0.8695	0.9304
EH	26726	0.5420	0.5335	0.5504	0.0000
GA	154	0.2442	0.0895	0.3874	0.0023
GB	4453	0.6142	0.5956	0.6322	0.0000
HH	1093	0.3807	0.3289	0.4303	0.0000
JP	1433	0.8338	0.8173	0.8489	0.0000
MA	97	0.0828	-0.1186	0.2777	0.4198
MM	36	-0.0799	-0.3980	0.2553	0.6432
PB	50372	0.5961	0.5904	0.6017	0.0000
PP	89	0.2815	0.0778	0.4627	0.0075
PR	260	0.4001	0.2927	0.4976	0.0000
QA	14562	0.6866	0.6779	0.6951	0.0000
RM	160488	0.5915	0.5883	0.5947	0.0000
RN	3321	0.6593	0.6396	0.6781	0.0000
RO	12006	0.5313	0.5183	0.5440	0.0000
RS	195567	0.7236	0.7215	0.7257	0.0000
SB	74	0.3752	0.1605	0.5560	0.0010
SE	81	0.5902	0.4269	0.7162	0.0000
SH	4	-0.0269	-0.9631	0.9590	0.9731
SM	37943	0.6194	0.6132	0.6256	0.0000
ST	487	0.5656	0.5020	0.6231	0.0000
SV	28	0.1442	-0.2419	0.4909	0.4641
TA	14713	0.6870	0.6783	0.6954	0.0000
WA	6309	0.5106	0.4921	0.5286	0.0000
WC	19843	0.1874	0.1740	0.2008	0.0000
WI	6	0.5084	-0.5161	0.9344	0.3031
WO	226	0.4991	0.3943	0.5911	0.0000
WP	32600	0.6793	0.6734	0.6851	0.0000
WS	55804	0.7538	0.7502	0.7574	0.0000
YB	39604	0.5532	0.5464	0.5600	0.0000
Average		0.4782	0.3063	0.6101	0.0929