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ARTICLE

Toward developing a direct relation between gross volume increment and stand density

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Abstract: A general form for expressing gross volume increment in terms of stand density is derived and tested with data from spacing trials in red alder (*Alnus rubra* Bong.), eastern white pine (*Pinus strobus* L.), longleaf pine (*Pinus palustris* Mill.), and loblolly pine (*Pinus taeda* L.). The equation relates the stand sum of individual-tree volume increment per metre height increment to a power function of quadratic mean diameter times tree density. The proposed equation fit the data best when the model included an intercept. Within each species, the fits were unbiased with respect to the independent variables, plantation age, and site height, and with the exception of the youngest ages for red alder and loblolly pine, they were unbiased with respect to the plot sums of individual-tree volume increment divided by individual-tree height increment. Exponents estimated for quadratic mean diameter for each species ranged from 1.58 to 1.80. The resulting equations indicate a linear relationship between the stand sum of individual-tree volume increment per metre height increment and stand density. Scattergrams of gross-volume increment per hectare per year and stand density can be recovered by multiplying the predicted values of the regressions by Lorey's height. The regressions support the hypothesis that each metre of height growth produces consistent changes in stem size, regardless of initial tree size, age, or site quality, and implies that the change in stem size is a predictable power function of stem diameter for an individual tree or quadratic mean diameter for a stand.

Résumé : Une équation générale qui exprime l'accroissement du volume brut en termes de densité du peuplement est dérivée et testée avec des données provenant d'essais d'espacement de l'aulne rouge (*Alnus rubra* Bong.), du pin blanc (*Pinus strobus* L.), du pin des marais (*Pinus palustris* Mill.) et du pin à encens (*Pinus taeda* L.). L'équation relie la somme de l'accroissement en volume par mètre d'accroissement en hauteur de chaque arbre dans le peuplement à une fonction de puissance du diamètre moyen quadratique des arbres multiplié par la densité du peuplement. L'équation proposée s'ajuste le mieux aux données lorsque le modèle comprend l'ordonnée à l'origine. Pour chaque essence, les ajustements étaient sans biais par rapport aux variables indépendantes : l'âge de la plantation et la hauteur moyenne des tiges. À l'exception des plus jeunes peuplements d'aulne rouge et de pin à encens, les ajustements étaient sans biais par rapport à la somme du rapport entre l'accroissement en volume et l'accroissement en hauteur de chaque arbre dans la placette. L'exposant estimé du diamètre moyen quadratique variait de 1,58 à 1,80 selon l'essence. Les équations ainsi obtenues indiquent une relation linéaire entre la somme de l'accroissement en volume par mètre d'accroissement en hauteur de chaque arbre dans le peuplement et la densité du peuplement. Les diagrammes de dispersion de l'accroissement du volume brut par hectare et par an par rapport à la densité de peuplement peuvent être récupérés en multipliant les valeurs prédites des régressions par la hauteur de Lorey. Les régressions appuient l'hypothèse que chaque mètre de croissance en hauteur produit des changements constants dans la taille de la tige, indépendamment de la taille initiale de l'arbre, de son âge ou de la qualité de station. Elles impliquent que le changement dans la taille de la tige peut être prédit par une fonction de puissance du dhp de la tige dans le cas d'un arbre ou du diamètre moyen quadratique dans le cas d'un peuplement. [Traduit par la Rédaction]

Introduction

That gross volume increment is constant and optimum for stands across a wide range of densities for a given species, site quality, and age is a widely accepted principle in forestry. While Langsaeter (1941) is usually credited with formalizing the concept, statements suggesting its recognition by foresters can be found in the English language 13 years earlier (Toumey 1928). Data indicating that stand leaf area is essentially constant across a broad range of densities (Mar:Möller 1947) provided a supporting physiological mechanism for the relationship and widened its acceptance. By the 1950s, standard textbooks such as Hawley and Smith (1954) and Spurr (1952) were presenting the relationship as a universal theoretical construct. The broad acceptance of this paradigm influenced what was considered supporting evidence for it. For example, Gruschow and Evans (1959) considered a second-degree polynomial fit to gross volume increment of slash pine (*Pinus elliottii* var. *elliottii* Engelm.) and percentage of full stocking after thinning (based on Stahelin (1949)) as support for the paradigm, although the data exhibited no plateau, only an optimum. Worthington et al. (1962) found linear relationships between gross periodic annual volume increment of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and post-thinning residual stand volumes but concluded no thinning effect on growth based on the lack of a significant effect of residual density on gross growth, according to one-way analysis of variance (ANOVA). Hiley (1956) and Staebler (1960) cite evidence contrary to Langsaeter's curves, but created thinning schedules based on the paradigm nonetheless. Mar:Möller (1954) is commonly cited as support for the paradigm, but Mar:Möller (1954) noted a contradicting positive correlation between current annual increment and basal area relative to yield table values for oak.

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More recently, researchers have begun to challenge the paradigm. Leak (1981) questioned the existence of a plateau in the relationship between gross volume increment and residual density based on positive correlations between gross-volume increment and basal area at the start of the growth interval for eastern white pine. Curtis et al. (1997) summarized the results of a comprehensive study installed in coastal Douglas-fir to explicitly test Langsaeter's curve and found that gross-volume increment consistently rose with residual stand density up to a maximum value measured on the unthinned plots. Dean and Jokela (1992), working with data from young slash pine plantations, and Dean and Baldwin (1996), working with data from a loblolly pine spacing trial in southwestern Louisiana, both reported positive relationships between gross-volume increment and stand density.

The assumed form of the relationship between stand growth and stand density affects decisions concerning planting density thinning schedules and, ultimately, rotation age by influencing the point where marginal benefits intersect marginal costs. The assumed form of the relationship also influences the ecological understanding of site occupancy in terms of resource use and stand density. For example, Miller (1995) argues that growth and belowground resource use are directly related. An asymptotic relationship between growth and stand density will lead to different explanations of site occupancy than a monotonically increasing relationship between gross growth and stand density.

The objective of this study is to test a new formulation for the relationship between gross-volume increment and stand density that is based on the assumption that tree dimensions are constrained by a common intrinsic morphological framework. The new equation form is created by summing the volume increment of each tree divided by its height increment and relating that sum to a power of quadratic mean diameter (Dq) times the number of trees per hectare. The equation is tested by evaluating how well it fits data from four diverse species.

The ratio between tree volume increment and height increment that we propose is derived from Assmann's (1970) equation relating volume increment of an individual tree (i_V) to the basal area added to exterior of the stem and the volume added to the top of the stem. By treating the stem as a cylinder, he related these components with the simple equation

(1) $\qquad i_V = (i_g \times \text{fh}) + (i_\text{fh} \times g)$

where i_g and i_fh are the periodic increments in basal area and form height (fh), respectively, and g is the basal area at the start of the period. Form height is the height of a cylinder with the same volume and diameter as the individual tree. The implicit driving variable in eq. (1) is height growth. If, instead of time, volume increment were measured over a fixed interval of height increment, age, and site quality effects are minimized, transforming volume increment from a rate variable to a structural variable. The amount of volume added with a metre of height growth will depend on the change in crown size associated with the change in height, which should depend on the developmental history of the tree. Within a given stand, stem diameter is a good surrogate for a tree's developmental history (Larson 1963). We postulate, therefore, that the ratio $\dfrac{i_V}{i_H}$ for an individual tree where i_H = height increment, is a simple power function of its initial stem diameter at breast height (D, 1.37 m)

(2) $\qquad \dfrac{i_V}{i_H} = a \times D^x$

where a and x are constants. Summed over N trees in the stand, eq. (2) becomes

(3) $\qquad \displaystyle\sum_{n=1}^{N} \dfrac{i_{V_n}}{i_{H_n}} = a \sum_{n=1}^{N} D_n^x$

where i_{V_n} and i_{H_n} are the volume and height increments of tree n, respectively, and D_n is the initial stem diameter of the nth tree in the stand.

If x were equal to 1.6, the right-hand side of eq. (3) would be the summation form of Reineke's stand density index (SDI) introduced by Long and Daniel (1990) for uneven-aged stands, $\text{SDI} = b \sum_{n=1}^{N} \left(D_n^{1.6}\right)$, where $b = 25^{-1.6}$. The stand-level formula is $\text{SDI} = b(Dq^{1.6}N)$, where Dq is the quadratic mean diameter (Reineke 1933). The two expressions are nearly equivalent in even-aged stands with normally distributed diameter distributions (Ducey and Larson 2003; Ducey 2009). Allowing the exponent x to vary, we hypothesize that Dq^xN substitutes for $\sum_{n=1}^{N} D_n^x$ in eq. (3), producing a general formula relating gross volume increment to stand density in even-aged stands

(4) $\qquad \displaystyle\sum_{n=1}^{N} \dfrac{i_{V_n}}{i_{H_n}} = c(Dq^xN)$

where c is a constant. This equation states that the stand summation of tree-volume increment per metre of height growth for an even-aged monoculture is a linear function of stand density with slope c and a zero intercept.

The relevance of the ratio between i_V and i_H to stand production can be traced to Eichorn (1904, as cited by Skovsgaard and Vanclay 2008) who presented data for lightly thinned European silver fir (*Abies alba* Mill.) suggesting that total stem volume for a given stand height was constant and independent of age and site quality. Stand height as used by Skovsgaard and Vanclay (2008) is synonymous with site or top height. Gerhardt (1909, as cited by Skovsgaard and Vanclay 2008) found the relationship to apply to other species as well as to total accumulated volume (standing volume plus thinning yields), leading to the relationship being named Eichorn's rule. A corollary to the rule is that for a given segment of the curve, the ratio between volume increment and height increment will also be constant and independent of age and site quality.

Eichorn's rule and its corollary only applies to lightly thinned or normally dense stands because high stand density imparts similar characteristics across stands such as average stem taper and total basal area. Eichorn's rule is not expected to hold across a range of stand densities, however, because stem form changes with density. Curtis and Marshall (1986) evaluated Eichorn's rule by growing Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) at a range of basal areas and found that accumulated volume systematically declined with decreasing basal area and, in this study, a given site height. Viewed in light of Eichorn's corollary, these data would also indicate that for a given interval of height, the change in volume over that interval would also systematically decline with decreasing basal area.

While the ratio between stand-level values of volume increment and top-height increment is useful for minimizing the effects of age and site quality in relating stand growth and stand density with regression analysis, the ratio has no clear biological interpretation as top-height increment pertains only to a subset of trees in the stand. Standardizing gross-volume increment by summing the ratio of individual-tree volume increments by their height increments during a measurement cycle not only retains the ability of consolidating growth data across sites and ages, but it also maintains a biological definition, i.e., the cumulative volume growth of the stand when all the trees grow a metre in height.

Table 1. Minimum and maximum values for various plot characteristics for the spacing trials used in this study.

Species	Age (years)		Dq* (cm)		Trees/ha		Height (m)		Volume (m³/ha)		MAI (m³·ha⁻¹·year⁻¹)†	
	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.
Alder	4	18	0.8	27.4	155	3737	1.8	18.1	<0.1	190.2	<0.1	13.4
Loblolly pine												
Hawaii	4	26	8.9	37.5	489	3086	2.0	23.8	4.1	1285.8	1.0	56.9
Mississippi	5	21	5.2	27.2	647	4174	4.0	24.0	1.7	546.3	0.4	29.8
Longleaf pine	4	63	2.6	48.2	49	3829	2.7	27.8	0.3	676.7	0.7	18.8
Eastern white pine	43	62	12.3	35.9	150	3600	12.8	21.3	75.0	584.2	1.7	10.2

*Quadratic mean diameter.

†Mean annual increment.

Methods

Data

Our hypothesis was tested with data representing two northern US species (eastern white pine (*Pinus strobus* L.) and red alder (*Alnus rubra* Bong.)) and two southern US species (longleaf pine (*Pinus palustris* Mill.) and loblolly pine (*Pinus taeda* L.)). The loblolly pine data were collected from studies in east-central Mississippi and in Hawaii. Ages represented in the various data sets ranged from 4 to 63 years old (Table 1), but the majority of the data are from plots with trees less than 35 years old. Since these data were collected in spacing trials, values of both *Dq* and *N* vary widely, ranging from 0.8 to 48.2 cm and from 49 to 4572 trees/ha. Average heights were similar across the various species and locations within species. Standing volumes for the loblolly pine in Hawaii were over twice as high as the respective values for the loblolly pine in the southern US, longleaf pine, and eastern white pine. However, the average tree sizes of the loblolly pine trees in Hawaii were not extraordinary in relation to loblolly pine in its native range. The two northern species had the lowest values of mean annual increment. Loblolly pine growing in Hawaii had the highest values of mean annual increment of all the species and locations included in this study.

The data used in this study were collected for other studies pursuing other objectives. Methods for collecting these data are summarized as follows.

Red alder

The characteristics of the experimental alder plantations and the measurement protocols are described in detail by Weiskittel et al. (2009). Plantations representing four initial spacings were established by Oregon State University's Hardwood Silviculture Cooperative in western Oregon, western Washington, and southwestern British Columbia. Permanent measurement plots were established at each installation ranging in size from 0.13 to 0.20 ha, excluding buffers. Beginning at age 3 years and every 3–5 years thereafter, diameter at breast height, *D*, was measured on all trees and height and height to the base of the live crown was measured on a subsample of 40 trees spatially distributed across the plots: 10 of the smallest diameter trees, 10 of the largest diameter trees, and 20 mid-diameter trees. Heights of unmeasured trees were calculated with an overall regression equation developed by the cooperative (Table 2). Inside-bark tree volume was calculated with a taper equation developed from 204 destructively measured trees from the various installations (Hibbs et al. 2007).

Eastern white pine

The description of the site in Maine where the white pine data were collected and the methodology of collecting these data are described by Seymour (2007). The data used in this analysis were from both thinned and unthinned plots of an unreplicated thinning trial that was 42 years old at the time of installation. Data were collected four times over the course of 20 years.

Diameter at breast height, total height, and height to the base of the live crown were measured for all trees with the exception of the 1992 measurement. In that year, heights were measured on a subsample of trees in the unthinned plots; missing heights were calculated with plot-specific regression equations of the form $b_0 + b_1 \log D$ that explained from 38% to 99% of the variation in the height of four to nine trees for the eight plots (Table 2). Individual-tree volumes were calculated using Honer's (1967) equation for total stem volume.

Longleaf pine

Data for longleaf pine were compiled from five studies established by the USDA Forest Service Southern Research Station at locations in Texas, Louisiana, Mississippi, Alabama, and Florida. Depending on the location, treatments included initial spacing, thinning, pruning, and fertilization. Only unthinned, unpruned, and unfertilized plots were used in this analysis. Up to 10 measurement periods were included in the data set, with ages ranging from 4 to 63 years.

Diameter at breast height was measured on all trees at each measurement period. Height and height to base of the live crown were measured on a subsample of trees at each measurement period. Missing heights were calculated with plot-specific regression models based on *D* (Table 2). Individual tree volumes were calculated with several equations depending on whether height to the base of the live crown and total tree height were recorded. For trees with measurements of both total height and height to the base of the live crown, individual tree volume was calculated with an equation developed by Farrar (1984). For trees without measurements of height to the base of the live crown, volume was calculated with an equation developed by Baldwin and Saucier (1983).

Loblolly pine

Loblolly pine data from two unrelated studies were used in this analysis. One study was located in east-central Mississippi and the other study was located in Olinda, Hawaii. Land et al. (1991) described the east-central Mississippi study (eight replications of three spacings of mixed-family plantings measured five times between age 5 and 21 years), and Whitesell (1970) described the study in Olinda, Hawaii (four replications of four spacings measured five times between age 4 and 26 years).

In both studies, *D* was measured on all trees at each measurement interval. Total tree height was measured on all trees at the east-central Mississippi study, but at the Hawaii site, tree height was measured on a subsample of trees. Missing tree heights were calculated with spacing-specific regression models based on *D* (Table 2). Outside-bark stem volume for trees at all these locations was calculated with a volume equation developed by Dean and Roberts (unpublished data).

Table 2. Regression and residual statistics for models predicting total height from diameter at breast height (D) for studies that measured height on a subsample of trees.

Species	Equation	b_0	b_1	b_2	n	MD*	MAD†	Fit index‡
Red alder	$4.5 + \exp(b_0 + 1 \times D_2^{b})$	6.768	−4.637	−0.231	157232	−0.42	2.65	90.7
Eastern white pine	$b_0 + b_1 \log(D)$	16.135 (9.106, 37.121)§	24.427 (4.123, 35.626)		6 (4, 9)			73.7 (37.9, 99.2)
Longleaf pine	$4.5 + b_0[1 − \exp(b_1 \times D)]$	137.435 (42.444, 238.463)	−0.106 (−0.308, −0.026)		93 (14, 226)	−0.084 (−0.68, 0.42)	5.141 (1.202, 9.936)	78.9 (24.8, 97.4)
Loblolly pine (Hawaii)	$4.5 + \exp(b_0 − b_1/D)$	3.881	20.574		815	0.044	2.859	67.3

Note: Residual statistics for red alder determined from values calculated with the equation developed by the Oregon State University Hardwood Silviculture Cooperative for the data set provided by the cooperative.
*Mean deviation = $\sum(y − \hat{y})$, where $\hat{y}$ is the predicted value of y in feet (1 ft = 0.3048 m).
†Mean absolute deviation = $\sum|y − \hat{y}|$ in feet.
‡$100 \cdot \left[1 − \sum(y − \hat{y})^2/\sum(y − \bar{y})^2\right]$, where $\bar{y}$ is the mean value of y.
§Values in parentheses show the range in values where the model was fit to individual plots.

Table 3. Values of Akaike's information criterion (AIC) for variants of the regression model $\sum_{n=1}^{N} \frac{i_{V_n}}{i_{H_n}} = m + u_1 + c\left[Dq^{(x+u_2)}N\right] + \varepsilon$, where i_{V_n} and i_{H_n} are the volume increment and height increment of tree n, respectively; Dq is the quadratic mean diameter, N is the number of trees per hectare; m, c, and x are regression coefficients; u_1 and u_2 are random plot effects normally distributed both with zero mean and variances τ_1^2 and τ_2^2, respectively; and ε is the error also normally distributed with mean zero and variance σ^2 fit to data from three species.

	Red alder		Eastern white pine		Longleaf pine	
Random effect included	m = 0	m ≠ 0	m = 0	m ≠ 0	m = 0	m ≠ 0
None	1604	1516	502	**461**	3756	3756
u_1	—	1527	—	463	—	3617
u_2	1520	**1479**	505	463	3541	**3537**
u_1, u_2	—	1481	—	504	—	nc*

Note: Model variants created by excluding various combinations of m, u_1, and u_2. Values in boldface type are the model variants with the lowest value of AIC for each species.
*No convergence.

Table 4. Values of Akaike's information criterion (AIC) for variants of the regression model $\sum_{n=1}^{N} \frac{i_{V_n}}{i_{H_n}} = m + b_0 + I_H + u_1 + c\left[Dq^{(x+b_1\times I_H+u_2)}N\right] + \varepsilon$, where i_{V_n} and i_{H_n} are the volume increment and height increment of tree n, respectively; Dq is the quadratic mean diameter, N is the number of trees per hectare; m, c, x, b_0, and b_1 are regression coefficients; I_H is the indicator variable ($I_H = 1$ for data from Hawaii, 0 otherwise); u_1 and u_2 are random plot effects normally distributed both with zero mean and variances τ_1^2 and τ_2^2, respectively; and ε is the error also normally distributed with mean zero and variance σ^2 fit to the loblolly pine data from east-central Mississippi and from Hawaii.

	Exponent component			
Intercept component	x	x, I_H	x, u_2	x, I_H, u_2
m = 0	1321	1322	1304	nc*
m ≠ 0	1262	1253	1243	9310
m ≠ 0, I_H	1241	1242	**1232**	9310
m ≠ 0, u_1	1262	1259	1264	8261
m ≠ 0, I_H, u_1	1305	1276	1262	8266

Note: Model variants created by excluding various combinations of the m, u_1, and u_2. Value in boldface type is the model variant with the lowest value of AIC.
*No convergence.

Regression analyses

To test our hypothesis, data for each species were fit to the following model using nonlinear regression for mixed models:

$$(5) \qquad \sum_{n=1}^{N} \frac{i_{V_n}}{i_{H_n}} = m + u_1 + c[Dq^{(x+u_2)}N] + \varepsilon$$

where m, c, and x are unknown fixed effects; u_1 and u_2 are normally distributed random effects of repeatedly measured plots with means of zero and variances of τ_1^2 and τ_2^2, respectively; and ε is the error also normally distributed with a mean of zero and variance of σ^2. The parameter m was added to the model because the value of $\sum\left(\frac{i_V}{i_H}\right)$ is greater than zero when Dq = 0. All combinations of models including or excluding the intercept m and random components u_1 and u_2 were fit to the data, and the best combination of parameters was selected on the basis of the value of Akaike's information criterion (AIC) for each fit. The parameter c

Table 5. Regression and residual statistics for the model variants of eq. (5) identified in Tables 3 and 4 with the best correspondence with data for each of the species according to the value of Akaike's information criterion.

Species	n	$\bar{y}$ (m³·ha⁻¹·m⁻¹)	Fixed effect					Residual statistics	
			m	$c \times 10^{-4}$	x	$\tau_2^2 \times 10^{-3}$	σ^2	MD*	MAD†
Red alder	284	13.33	2.34	3.52	1.58	3.54	8.02	−0.02	1.86
Eastern white pine	66	34.8	16.77	2.10	1.52		56.01	2.4×10⁻⁵	5.87
Longleaf pine	494	44.16	1.89	2.61	1.77	3.38	51.26	−0.12	4.47
Loblolly pine									
Mississippi	96	44.42	14.41	1.04	1.80	2.12	107.00	0.03	4.88
Hawaii	64	56.87	25.54	1.04	1.80	2.12	107.00	−0.08	10.24

*Mean deviation = $\sum (y - \hat{y})$, where $\hat{y}$ is the predicted value of y m³·ha⁻¹·m⁻¹.

†Mean absolute deviation = $\sum |y - \hat{y}|$ m³·ha⁻¹·m⁻¹.

‡$100 \cdot \left[1 - \sum (y - \hat{y})^2 / \sum (y - \bar{y})^2 \right]$, where $\hat{y}$ is the mean value of y.

was considered fixed because x and c are highly correlated, and the regression would not converge when both parameters contained a random component. Goodness of fit for the best fit equation for each data set was assessed with residual statistics such as mean deviation, mean absolute deviation, and fit index. The fit index is the proportion of variance explained by the model and is analogous to the coefficient of determination. Goodness of fit was also evaluated with scattergrams of the residuals combined for all four species in relation to Dq, N, age, and site height defined as the average height of the tallest half of the trees in a plot.

Results and discussion

The best fits of eq. (5) to the red alder, eastern white pine, and longleaf pine data sets, according to the AIC, all include the intercept m (Table 3). For red alder and longleaf pine, the lowest AIC values were associated with models that also included a random component in the exponent x. For eastern white pine, the lowest AIC value was obtained with only fixed effects in the model. Fitting eq. (5) to the loblolly pine data produced the lowest AIC value when the model included the intercept m, an indicator variable for a location effect on the intercept, and u_1 (Table 4). However, the AIC values for model variants for loblolly pine that included a location effect on the exponent x were nearly eight times larger than models without that location effect.

Conceptually, the regression algorithm used in this analysis fits eq. (5) to each set of repeatedly measured plots, producing estimates of m, c, and x for each plot and generating mean values and variances for each coefficient for each species' data set (Littell et al. 2006). The values of τ_1^2 and τ_2^2 measure the variance in these fitted values of the intercept and the exponent, and the estimated values of m, c, and x reported by the regression analysis are the means of these values. According to these results, the plot-to-plot variation in the values of the intercept and the exponent are quite small if not zero, indicating that the fitted values of m and x are nearly identical for each plot time series. For eastern white pine, the lowest AIC values were obtained by assuming no variation in either the intercept or the exponent (both τ_1^2 and τ_2^2 set to 0) (Table 3). For the other species, the lowest AIC value were obtained when only u_2 was included in the model to account for plot-to-plot variation in the exponent ($\tau_2^2 > 0$) (Tables 3 and 4); however, the estimated values of τ_2^2 were three orders of magnitude less than the estimated value of the exponent (Table 5).

The fit of eq. (5) to the loblolly pine data, however, is not independent of the wide geographic variation in sites. The model variant with the lowest AIC did not contain a location effect for the exponent; however, it did contain a location effect on the intercept. The model indicated that the intercept for loblolly pine in Hawaii was 12.45 m³·ha⁻¹·m⁻¹ higher than the intercept for loblolly pine in the east-central Mississippi study. The difference in the intercepts corresponds with the observed productivity differences between the sites (Table 1).

Residual statistics for the variants of eq. (5) with the lowest AIC values within each species indicate that the fits are unbiased. The mean deviations of the residuals were close to zero for all fits and averaged −0.05 m³·ha⁻¹·m⁻¹ across the four species (Table 5). The lack of bias indicated by the mean deviation values is corroborated by the uniform scatter of residual values around zero when plotted against Dq, N, age, and site height (Fig. 1). The lack of bias is also indicated by the even scatter of the observed values around

1:1 lines between observed and predicted values of $\sum \left(\dfrac{i_V}{i_H} \right)$ when

the data points near the origin for the red alder and loblolly pine data are excluded (Fig. 2). The reason why points close to the origin fall below the 1:1 line is unclear. While the cause could be ascribed to young ages (these points are associated with measurement periods beginning at ages 4 or 5 years), measurements of the longleaf pine stands initiated at age 4 years do not fall below the line.

The various fits of eq. (5) are also acceptably precise. The mean absolute deviation of the residuals was no more than 7.01 m³·ha⁻¹·m⁻¹ and was 4.81 m³·ha⁻¹·m⁻¹ when averaged across the four species (Table 5). When expressed as a percentage of the

mean value of $\sum \left(\dfrac{i_V}{i_H} \right)$ for each data set, the mean absolute

deviation ranged from 10% to 17%.

The value of the fitted exponents for the four species ranged from 1.58 to 1.80 and averaged 1.67 across the species (Table 5). The values of x estimated for the various species are, in most cases, quite similar to exponents estimated with statistical relationships between Dq and N. Goelz (1996), working with a longleaf pine data set that included some of the data used in this study, determined an exponent of 1.78, which is nearly identical to the value estimated for the longleaf pine data used in this study, 1.77. Vanderschaaf and Burkhart (2007) observed a range of exponents from 1.38 to 1.94 with loblolly pine data collected by the Virginia Tech University Growth and Yield Cooperative. Their range of values compared favorably to the exponent determined for the loblolly pine data used in this study. The correspondence was also quite good for red alder. Puettmann et al. (1993) observed an equivalent exponent of 1.56, whereas we observed the exponent to be 1.58. For eastern white pine, Lhotka and Loewenstein (2008) observed an exponent of 1.64 using USDA Forest Inventory and Analysis data, compared with 1.52 found in this study.

One application of density indexes is in the construction of density management diagrams, which are graphical devices for plotting actual or planned stand development on a backdrop of stand density that culminates at maximum density (Jack and Long 1996). The gradient in stand density is denoted by a set of parallel lines with a negative slope. The trajectory of mean size and tree density through time illustrates the stand's progressive site occupancy, competition, growth, and stage of development (Long and Smith 1984). A basic assumption in determining the slope of the

Fig. 1. Scattergram of combined residuals ε from the fits of the model variants of eq. (5) identified in Tables 2 and 3 as corresponding best with data for each of the species according to the value of Akaike's information criterion.
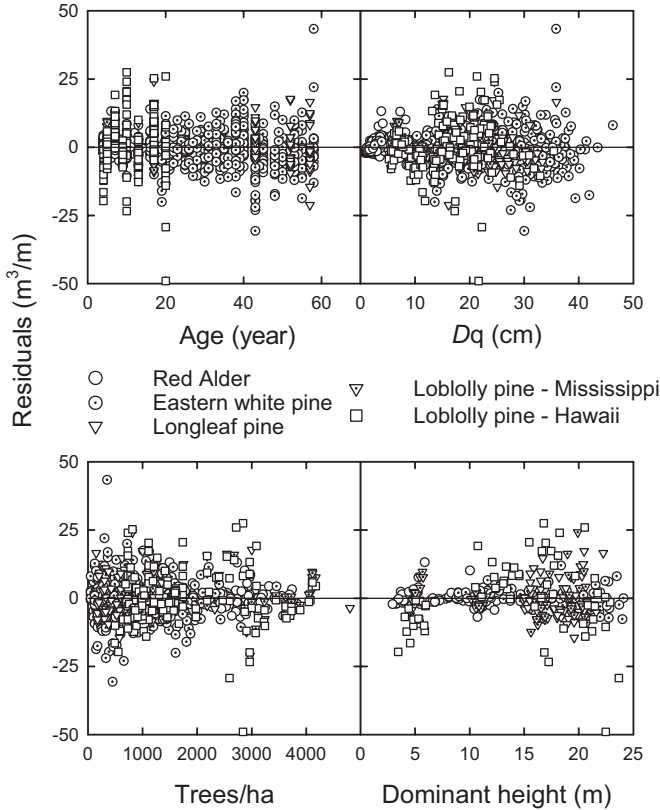

Fig. 2. Plot sums of individual-tree values of volume increment (i_V) divided by height increment (i_H) plotted in relation to the calculated plot values of $m + c(Dq^xN)$ using the species values of m, c, and x listed in Table 5. Lines are 1:1 lines.
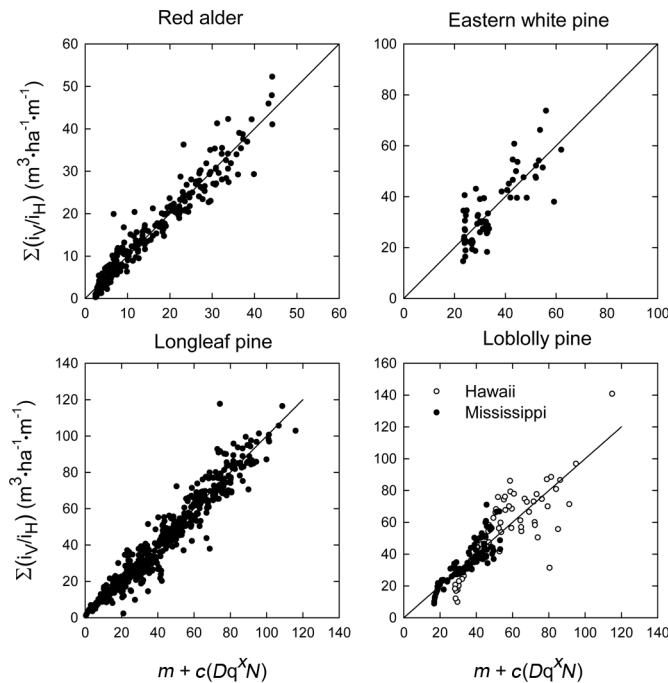

**Fig. 3.** Scattergrams of plot values of quadratic mean diameter (Dq) and trees per hectare (N) for the six data sets used in this study overlain on isolines of $\sum i_v/i_h$ calculated with $Dq = \left[\dfrac{\sum(i_v/i_H) - m}{c \times N}\right]^{\frac{1}{x}}$, a rearrangement of eq. (5). i_{V_n} and i_{H_n} are respective volume and height increments of each tree in the plot. Corresponding values of m, c, and x are in Table 5. Isolines of $\sum i_v/i_h$ in terms of m³·ha⁻¹·m⁻¹ range from 3 to 48 in increments of 5 for red alder (*a*), from 10 to 130 by 20 for longleaf pine (*b*), from 20 to 70 by 10 for eastern white pine (*c*), from 20 to 80 by 10 for loblolly pine in Mississippi (*d*), and from 30 to 150 by 20 for loblolly pine in Hawaii (*e*).
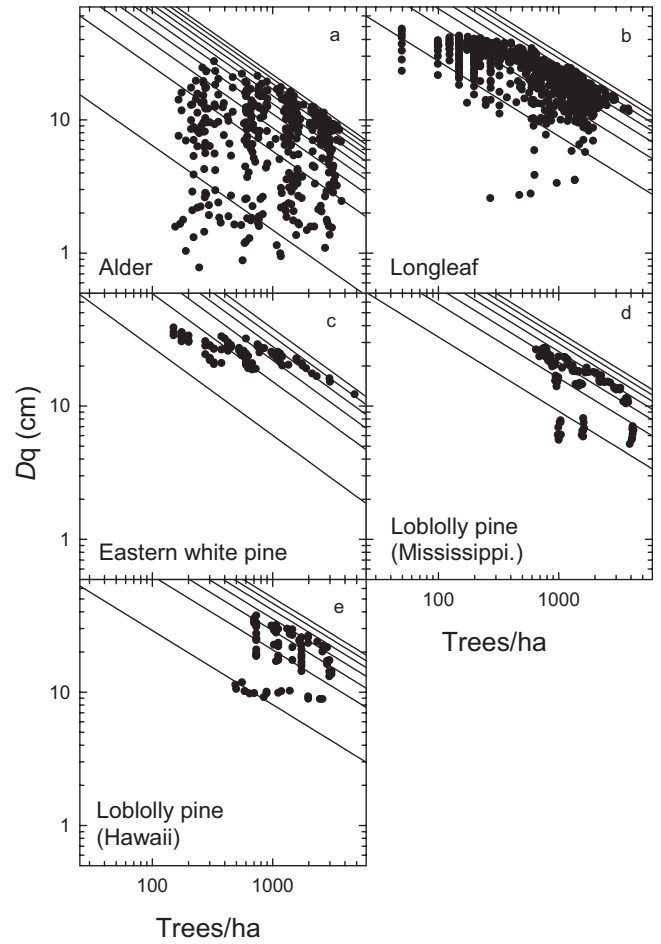
stand-density lines is that stand development asymptotes at a maximum density, allowing the slope to be determined by pairs of mean size and tree density at maximum density (e.g., Smith and Hann 1984). This is not a universal stand trajectory, however. Slash pine stands appear to reach a peak in stand density then decline, forming a curvilinear rather than a linear size-density boundary on log-transformed axes (Cao et al. 2000). A curvilinear boundary is also apparent for longleaf pine (Shaw and Long 2007). Loblolly pine plantations track maximum density for only a short time then fall away (Vanderschaaf and Burkhart 2007), giving the appearance of a curvilinear size-density boundary. Furthermore, the maximum stand density loblolly pine plantations attain may be correlated with initial planting density (Vanderschaaf 2010).

Since stand growth is correlated with consumption of site resources (Dalla-Tea and Jokela 1994; Reich et al. 1997; Dicus and Dean 2008), and since stand density is considered an indicator of the consumption and scarcity of site resources, stand summations of tree-volume increment per metre height increment may be a more useful measure of stand density than those based on the

Fig. 4. Periodic annual increment of Lorey's tree height (ΔH_L) and estimated values of gross-volume increment (I_V) plotted as a function of $m + c(Dq^xN)$ for red alder, eastern white pine, longleaf pine, and loblolly pine. $I_V = \Delta H_L \widehat{\sum\left(\frac{i_V}{i_H}\right)}$, where $\widehat{\sum\left(\frac{i_V}{i_H}\right)}$ is the predicted value of $\sum\left(\frac{i_V}{i_H}\right)$ from best model variant of eq. (5) for each species according to the value of Akaike's information criterion in Tables 2 and 3. Corresponding values of m, c, and x are in Table 5.
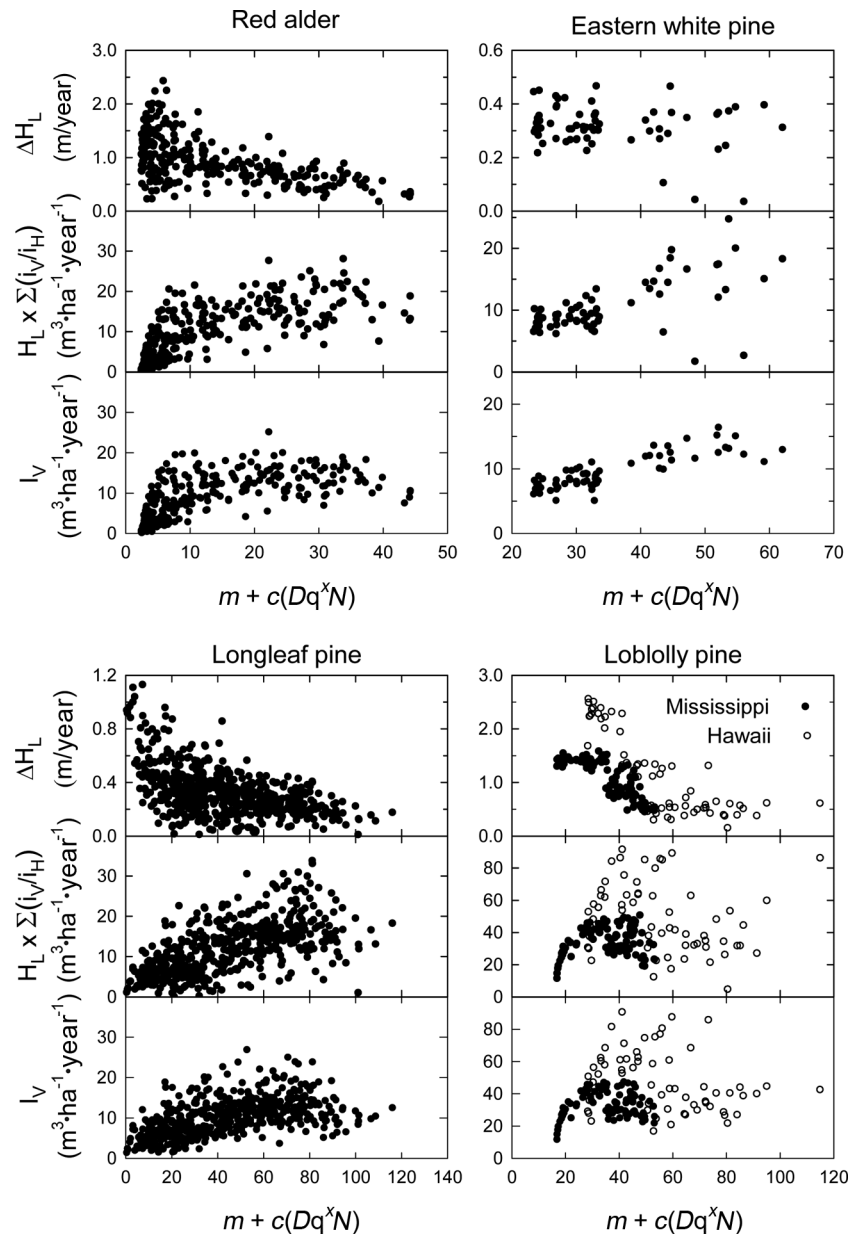
upper boundary of mean tree size and tree-density data clouds, especially for the southern pines of the US. Rather than abandoning the simplicity of measuring stand density with combinations of mean tree size and tree density, fits of eq. (5) allow set values of $\sum\left(\frac{i_V}{i_H}\right)$ to be expressed in terms of Dq and N, providing an alternative means of establishing stand-density lines on a density management diagram that represents the same degree of occupancy across a wide range of site quality, mean diameter, tree density, and age, with the exception perhaps of very young ages (Fig. 3).

The mostly unbiased fits of eq. (5) to these data provide initial support for the hypothesis that a general equation form exists for predicting stand growth as a power function of Dq multiplied by tree density. The key step in developing the equation is summing individual-tree volume increment associated with a metre height

growth instead of the volume increment over a fixed time interval. Setting height growth to a fixed interval allows individual-tree volume growth to be predicted from stem diameter, suggesting that expanding tree dimensions follow an inherent general allometry between the stem and the crown that is common among species. Studies have supported a common allometry between the crown and the stem across conifers derived from simple beam mechanics, called the uniform–stress principle of stem formation (Dean and Long 1986; Dean et al. 2002). This principle predicts stem diameter from the product of tree leaf area and distance to the median leaf area raised to the one-third power. Discrete changes in this product over time have successfully predicted changes in stem basal area for lodgepole pine, slash pine, and loblolly pine (Dean 2004), and when combined with population effects on mean crown dimensions, have successfully predicted the

chronology of current annual increment and changes in Dq and N for loblolly pine (Dean et al. 2013).

According to the results of this study, if periodic annual gross volume increment ($\sum i_V$) exhibits a curvilinear relationship with a stand-density index, it is due to a concomitant change in periodic annual height growth with stand density. The periodic annual increment of Lorey's height (Lorey (1878) as cited by Nakai et al. 2010) is a convenient descriptor of the aggregate change in height for a stand because Lorey's height most nearly describes the height of the tree with average basal area or Dq when form height is constant. Lorey's height is mean tree height weighted by tree basal area. In general, with the exception of eastern white pine, periodic annual increment of Lorey's height (ΔH_L) decreases in a concave pattern with the computed value of $m + c(D\mathrm{q}^x N)$ (Fig. 4).

When ΔH_L is multiplied by $\sum\left(\dfrac{i_V}{i_H}\right)$, the result should be approximately equal to annual gross-volume increment for the plot and reproduce the actual pattern of periodic gross-volume increment when plotted as a function of stand density. Whereas the calculated values of gross volume increment slightly overestimate the measured values, the scatter of the values when plotted against the computed values of $m + c(D\mathrm{q}^x N)$ is quite similar for all species. Some differences between actual and measured values of gross-volume increment and patterns would be expected due to the inherent difference between a stand average and a stand total of a particular property.

Conclusions

The fits of eq. (5) to these data support our formulation of an equation relating gross-volume increment to Dq raised to a power times tree density when volume increment is based on individual-tree height increment instead the passage of time. Within each species, the fits were unbiased with respect to the independent variables, plantation age, and site height, and with the exception of the youngest ages for red alder and loblolly pine, they were unbiased with respect to the plot sums of individual-tree volume increment divided by individual height increment. The results suggest that each metre of height growth produces regular changes in stem size, regardless of initial tree size, age, or site quality and that the change in stem size is a predictable power function of stem diameter for an individual tree or Dq for a stand. The differences in the fitted exponents indicate that the change in stem volume associated with height growth is species specific; however, the change in volume that accompanies a metre of height growth seems quite similar between these species as their exponents for Dq vary only from 1.58 to 1.80. The similarity of these exponents suggests that a fundamental stem morphology not only exists within a species but also across species, supporting the hypothesis that a general relationship exists between stand growth and stand density.

Acknowledgements

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