



Silviculture

A Direct Measure of Stand Density Based on Stand Growth

Thomas J. Dean^o, Anthony W. D'Amato^o, Brian J. Palik^o, Mike A. Battaglia, and Constance A. Harrington^o

Standardizing gross volume increment on periodic height increment of the dominant trees is a means of minimizing the effects of site quality and age in growth–growing-stock relations; however, volume increment per height increment contains more information than just a normalization method for fitting growth models. This study builds on previous work suggesting that the cumulative sum of the ratios between individual-tree volume increment and height increment may be a direct measure of stand density. We used data from several levels of growing-stock studies for Douglas-fir, ponderosa pine, and red pine to explore this hypothesis. Regression analysis indicated that the sum of the ratios is proportional to $(D_q^x \cdot N)$, the underlying equation form of Reineke's stand density index. Stem growth is a function of canopy dynamics, and additional analyses showed that volume added per unit of height growth was also related to canopy architecture, increasing with decreasing live-crown ratio and increasing foliage density. The linkages between growth, canopy architecture, intermediary canopy dynamics, and $(D_q^x \cdot N)$ support the hypothesis that the sum of the tree ratios between volume increment and height increment is a direct measure of site occupancy due to its association between growth and corresponding resource use.

Study Implications: Stand density indices are fundamental to managing the development of forest stands to achieve habitat and production goals, and advanced statistical techniques are providing silviculturists with more precise tools to manage density. However, the increased precision is only available with data from self-thinning stands, rare in managed forests. Furthermore, silviculturists must assume that constant fractions of relative stand density are parallel to fitted self-thinning trajectories. The results of this study show that the slope of the stand density gradient can be determined without data from self-thinning stands and the gradient in stand density runs parallel to the trajectory of self-thinning stands.

Keywords: volume increment, height increment, canopy architecture, Reineke's stand density index

The interest in stand density management has centered on planting and maintaining the optimum spacing between trees to produce the highest number of the desired size trees. Spacing and thinning trials have been established for many species to answer this question empirically; however, given the significant lag between installing a study and obtaining results, management goals or philosophies often change in the interim, thus changing the questions to be answered. What has emerged from these studies, however, is a vague generality that total stand growth plateaus after a relatively low level of growing stock has been attained. Langsaeter (1941) proposed this idea as a hypothesis, and

it has become a general concept in silviculture, still presented in a recent silvicultural textbook (Nyland et al. 2016, p. 404). Recent evidence (e.g., Leak 1981, Curtis and Marshall 1986, Zeide 2001) showing continued growth increases with growing stock has textbook authors reevaluating its generality (Ashton and Kelty 2018). Verifying Langsaeter's proposed curve is difficult because it is not a developmental curve. Every point on the curve must come from plots with the same aged trees growing on the same quality of site. In addition, volume lost in mortality must be added back into growth estimates, requiring data to be recorded by tree number for each measurement period. Variation in site quality and age can be

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Affiliations: Thomas J. Dean (fvdean@lsu.edu), School of Renewable Natural Resources, Louisiana State University Agricultural Center, Baton Rouge, LA. Anthony W. D'Amato (awdamato@uvm.edu), Rubenstein School of Environment and Natural Resources, University of Vermont, 204E Aiken Center, Burlington, VT 05405. Brian J. Palik (brian.palik@usda.gov), USDA Forest Service, Northern Research Station, 1831 Highway 169 E, Grand Rapids, MN 55744. Mike A. Battaglia (michael.battaglia@usda.gov), USDA Forest Service, Rocky Mountain Research Station, 240 West Prospect Road, Fort Collins, CO, 80526. Constance A. Harrington (charrington@fs.fed.us), USDA Pacific Northwest Research Station, 3625 93rd Avenue SW, Olympia, WA 98512.

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standardized by dividing volume increment by the periodic height increment of the dominant trees, which are least affected by competition, and therefore, most representative of site quality and age (Smith and Long 1989, Dean and Jokela 1992).

Standardizing production and growth on the basis of height increment not only simplifies the field requirements for testing Langsaeter's hypothesized curve but also describes a direct relationship between stand structure and function. Dean et al. (2013) demonstrated one such relationship when they found that the cumulative sum of individual-tree volume increment per unit height increment is related to stand density. They fit a regression model based on the equation

$$\sum_{n=1}^N \frac{i_{V_n}}{i_{H_n}} = c(Dq^x N), \quad (1)$$

to five data sets from four North American tree species, where N = trees per hectare, i_v = individual-tree volume increment of the n th tree, i_h = individual-tree height increment of the n th tree, Dq = quadratic mean diameter, and x is an unknown. The model fit the data without bias, and the estimated values of x ranged from 1.52 to 1.8 for red alder (*Alnus rubra* Bong.), eastern white pine (*Pinus strobus* L.), longleaf pine (*Pinus palustris* Mill.), and loblolly pine (*Pinus taeda* L.). Equation (1) has several implications about how stand structure and stand function are connected. The most general implication is that tree growth is the result of coordinated changes in morphology that accompany height growth when trees are competing for light with similarly aged trees. Stand structure determines the magnitude of these changes. Another implication is that a series of stands with the same sum of the ratios of volume increment per height increment will also have the same relative stand density and occupancy.

Stand density is a concrete expression of the abstract idea of stand occupancy. As the size-density boundary is an obvious limit of stand occupancy, any mathematical combination of measurable stand dimensions that increases monotonically toward the boundary can qualify as a stand density index (SDI). Indices that are independent of stand age and site quality are most useful (Curtis 1970). The concept of stand occupancy integrates resource consumption, competition, and availability. Self-thinning occurs when the stand is fully occupying the site, meaning that all available resources are being consumed. With stand occupancy comes increased competition, seen in slower diameter increment, and increasing stand growth. In his review, Miller (1995) concluded that resource uptake is proportional to growth rate in trees. Growth rate by itself, however, does not meet the criteria for an index of stand density; however, the results of Dean et al. (2013) suggest that it does when normalized on the basis of height increment.

The tree crown provides the functional link between stand density and stand occupancy for the obvious reason that leaf area is the source of carbon compounds in the tree and the leaf is where water is lost to the atmosphere. Long et al. (2004) reviewed the literature to support the idea that leaf area is the intermediary link between density management and stand growth and between silvicultural treatments and outcomes. Although significant correlations between canopy properties such as total leaf area have been reported with both stand growth and stand density, such relationships are not universal. For example, Innes et al. (2005), working with eastern white pine, investigated the

three-way correlations of leaf area index (LAI) and growth efficiency with gross periodic volume increment and two density indexes, Reineke's SDI (Reineke 1933) and Drew and Flewelling's relative density (Drew and Flewelling 1977). They found that although both LAI and stand density (with age considered) were closely related to periodic annual increment (PAI), neither of the SDIs were related to LAI (leaf area per unit ground area). Other studies have demonstrated poor to no correlation between LAI and PAI (Dean et al. 1988) or no correlation between LAI and basal area (BA) per hectare, also a measure of stand density (McDowell et al. 2007). Furthermore, trees grow leaf area at the same time they add stem volume; consequently, neither leaf area nor volume growth can be regarded as independent variables.

Instead of searching for canopy properties that relate both to growth and to SDI, equation (1) identifies relevant properties that link the functional side of the equation to the structural side of the equation. Dean and Baldwin (1996) derived an equation for Reineke's SDI based on foliage density (F) and mean live-crown ratio (C_r):

$$SDI = m \left[F \left(\frac{1}{C_r} - \frac{1}{2} \right) \right]^n \quad (2)$$

Reineke's SDI is a specific case of ($Dq^x \cdot N$). The basis for equation (2) is the constant-stress model proposed by Dean and Long (1986) that has been tested for a variety of species (Dean et al. 2002). Briefly, the constant-stress model describes stem diameter at any height on the stem (excluding butt swell) based on the leaf area above the diameter and the distance between the cross section and the middle of the leaf area above it. Tree density affects leaf area per tree and the vertical distribution of the leaf area. Algebraic manipulation of the various relationships results in equation (2), which was tested with unthinned loblolly pine data. The values of F and C_r have been used to describe canopy architecture for lodgepole pine (*Pinus contorta* Dougl. ex. Loud.) and have been shown empirically to be related closely with growth per unit of dominant height increment (Smith and Long 1989). Foliage density and C_r set the stage for how the tree canopy will change with a meter of height growth. Leaf area per tree should increase, whereas mean live-crown ratio should decrease. The magnitude of these changes is fixed due to a fixed change in height and is a function of initial canopy architecture. Dean (2001, 2004) demonstrated how the effects of canopy dynamics on growth are dependent on initial canopy architecture. A given volume increment per height increment meets the definition of an index of stand density because height increment accounts for age and site quality effects and volume increment is correlated with resource consumption and thus site occupancy.

The objective of this study was to weigh evidence for and against the hypothesis that the cumulative ratios of individual-tree volume increment and height increment can serve as a measure of stand density. A regression model based on equation (1) was fit individually to data from different levels of growing stock from studies encompassing three different species. The consistency of the fits among the different levels of growing stock were analyzed statistically by comparing the exponents within each study and visually by comparing the slopes of the predicted size-density trajectories of the various levels of growing stock on log-transformed axes of N and Dq . The sum of the ratios was also fit to canopy properties with a regression model based on equation (2) for evidence that

the sum of the ratios is related to stand occupancy. Models were fit to data from growing-stock studies for three commercially important North American coniferous species: Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* [Mirb.] Franco), ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson var. *scopulorum* Engelm.), and red pine (*Pinus resinosa* Aiton). These studies were installed in the middle part of the 20th century primarily to investigate intermediate yields in managed second-growth stands and secondarily to test Langsaeter's hypothesis under controlled conditions.

Methods

Data

The four levels of growing-stock studies used in this study were established to investigate intermediate yields from thinning and the effect of growing stock and thinning on total production. All these studies were established on forests within the US Department of Agriculture's (USDA) National Forest System.

Douglas-Fir

The procedural guidelines for the Douglas-fir levels of growing-stock study are described by [Curtis and Marshall \(1986\)](#). The principal objective of this study was to quantify the relationship between growth and growing stock for Douglas-fir for similarly aged stands growing on similar sites. We used data for the three installations established on national forests in the Pacific Northwest Region of the USDA Forest Service ([Harrington 2018](#)). These sites were located in Washington and Oregon on the Olympic (Rocky Brook installation), Gifford Pinchot (Iron Creek installation), and Umpqua (Stamper Creek installation) National Forests. Trees at the Stamper Creek installation were naturally regenerated, whereas the trees at the Rocky Brook and Iron Creek installations had been planted. At each installation, nine levels of growing stock, including an unthinned control, were randomly assigned to twenty-seven 28.3 m x 28.3 m plots. Plots designated for growing-stock control underwent a calibration thinning to condition trees to wider spacings. Plots designated as control treatments were never thinned. According to [Curtis and Marshall \(1986, table 2\)](#) tree density of the untreated controls at the beginning of the experiment was 3,376, 2,786, and 2,463 trees per hectare for the Rocky Brook, Iron Creek, and Stamper Creek installations, respectively. The initial densities of the growing-stock control plots were 986, 879, and 709, respectively. Growing-stock levels were quantified in terms of Curtis' relative density $\left(\frac{G}{\sqrt{D_i}}\right)$, where G is BA (m^2/ha) ([Curtis 1982](#)). Growing-stock treatments were defined relative to the growth of the unthinned plots. Four treatments were fixed percentages of the growth of the unthinned plots (10, 30, 50, and 70 percent). Two treatments allowed growing stock to increase from 10 to 50 percent and from 30 to 70 percent of unthinned growth, and two treatments decreased growing stock from 50 to 10 percent and from 70 to 30 percent of unthinned growth. Thinnings occurred every 3.3 m of height growth based on the average of 16 dominant trees per plot.

Trees were measured prior to thinning. Since the plots were thinned on the basis of height increment, the measurement frequency varied with installation. Diameter at breast height (dbh; 1.37 m) was measured on each tree in the plot, whereas total height and height to live crown were measured on a subsample of the trees.

Two-thirds of these trees were selected from the upper half of the dbh range, whereas the other third was selected to represent the smaller trees. The subsampling represented 34 percent of the trees overall, 56 percent in the lowest growing-stock level to 11 percent in the unthinned treatment.

Ponderosa Pine

The ponderosa pine study was established in the Black Hills Experimental Forest on the Black Hills National Forest in South Dakota in the north central region of the United States. The setting and the study are described in detail by [Graham et al. \(2019\)](#). The study was established to determine the maximum volume that ponderosa pine could produce in naturally regenerated sapling and pole-sized stands and the maximum and minimum densities that would produce this potential. Stand density was expressed in terms of GSL as defined by [Alexander \(1986\)](#), the BA desired when average stand diameter is 25 cm. Eighteen 0.1-hectare plots were established in sapling-sized stands, and eighteen 0.2-hectare plots were established in pole-sized stands. Three replications of GSLs of 5, 9, 14, 18, 23, and 28 m^2/ha were randomly assigned to the plots in each type of stand. Three replicates of unthinned plots were established in each stand type 15 years after the GSL study began. At the beginning of the study, both the saplings and poles were 65 years old. The saplings and poles averaged 9.7 cm and 17.0 cm in diameter, respectively. When the unthinned plots were included in the study, the trees averaged 14.2 cm and 16.5 cm in diameter in the plots established in the sapling-sized and pole-sized stands. Tree density in the unthinned plots in the different-sized stands was 2,122 and 1,853 trees per hectare, respectively. The maximum tree densities when the main study was initiated were 1,699 and 1,047 trees per hectares corresponding to the 28 m^2/ha GSL, and minimum tree densities when the main study was initiated were 267 and 153 trees per hectare for the 5 m^2/ha GSL for the two developmental stages. Thinning occurred every five years for the first 15 years; thereafter, thinning was sporadic, occurring at intervals of two to six years.

Tree dimensions were recorded before each thinning. The dbh (1.37 m above ground) was measured on every tree, and total height and height to live crown were measured on a subsample of trees. Across the entire study, height and height to live crown were measured on 27 percent of the trees, a maximum of 60 percent in the 5 m^2/ha treatment and a minimum of 15 percent in the unthinned plots.

Red Pine

Data for red pine were collected from two growing-stock studies conducted in northern Minnesota, bordered by North and South Dakota on the west and Lake Superior and Wisconsin on the east. One study was established in the Cutfoot Experimental Forest (CEF) located on the Chippewa National Forest, and the second study was established at the Birch Lake Plantation (BLP) located on the Superior National Forest. Initial stand conditions prior to or just after establishment of the studies were not published for either study.

The study at CEF was installed to determine feasibility of density management in 85-year-old, naturally regenerated stands. [Bradford and Palik \(2009\)](#) and [D'Amato et al. \(2010\)](#) provide some details about this study, and an unpublished intra-agency summary of the project described the purpose of the study and

contained more details about the study establishment protocols. Five levels of growing stock were replicated in three blocks. The first two experimental unit sizes were 2 hectares in size and established in 1947. The third block was 1 hectare in size and established two years later. Initially, thinnings were conducted every five years. In 1964, thinnings were synchronized across all the blocks. In 1969, the thinning interval changed to 10 years. The levels of growing stock were defined in terms of residual BA per hectare. The treatment plots were thinned to 14, 18, 23, 28, and 32 m²/ha.

Three 0.08-hectare measurement plots were established in each treatment plot. The dbh (1.37 m) was measured on all trees >8.9 cm. Height was measured on five trees per plot, which resulted in height being recorded on 24 percent of the trees in the lowest densities and 11 percent of the trees in the highest density treatment.

The study at BLP is described by Bradford et al. (2010) and D'Amato et al. (2013). The stand was planted with 2,500 trees per hectare and was 45 years old at the beginning of the experiment. The study is a completely randomized design, assigning six residual densities to eighteen 0.8-hectare blocks. The blocks were divided into thirds to add thinning method to the analyses. Stand density was defined by BA per hectare. Residual densities compared were 7, 14, 21, 28, and 34 m²/ha, plus an unthinned control. Blocks were thinned approximately every 10 years.

Tree dimensions were measured within 0.08-hectare measurement plots. The dbh was measured on all trees >10.2 cm in diameter. Tree height was measured on two to three trees within a crown class. Height to live crown was measured on an average of 57 percent of the trees over the course of the study, and it was measured on 54 percent of the trees in the unthinned plots over the course of the study.

Variables

Volume Increment per Height Increment

Volume increment per height increment is $\sum_{n=1}^N \frac{i_{v_n}}{i_{h_n}}$, which is the per hectare equivalent of N ratios between individual-tree volume increment (i_v) and height increment (i_h). Individual tree volumes were calculated with a variety of equations developed specifically for each species and region. The equation used to calculate stem volume for the Douglas-fir study was based on form factors for trees less than or greater than 18 m tall, and the form factor for each height class was a function of dbh and total height (Bruce and DeMars 1974). The form factor was then multiplied by $A_b \cdot h$, where A_b = individual-tree BA, to obtain total stem volume. The stem volume for ponderosa pine was calculated with an equation based on Flewelling and Raynes (1993). The equation is within the National Volume Equation Library of the Forest Service and applies to trees in the Black Hills of South Dakota. The stem volume equation for the two red pine studies was developed by Fowler (1997), which is $v = \frac{0.00046}{35.31} dbb^{1.86} h^{0.93}$. Volume increment at each measurement date was calculated as the difference between total stem volume for all surviving trees.

Missing heights were calculated with equations developed by regressing the subsampled height (H) on dbh and age. Since heights were measured on the same trees at each measurement, age was

added to the regression model as recommended by Curtis (1967). Parameters A_0 – A_3 were estimated by fitting the mixed model

$$H = A_0 + (A_1 + \mu_1) \cdot dbb^{(A_2 + \mu_2)} \cdot age^{(A_3 + \mu_3)} + \epsilon$$

to these data. The parameters μ_1 – μ_3 represent random effects, normally distributed with a mean of zero. For the Douglas-fir and ponderosa pine studies, the best fits as determined with Akaike's information criterion (AIC) and residual analyses were obtained with one random effect added to the fixed effect A_2 . For the two red pine studies, the best AIC and residual analyses were obtained with random effects μ_2 and μ_3 added to the fixed effects of A_1 and A_2 . The random effects were included in calculating the missing height values.

Canopy Variables

Following Smith and Long (1989), foliage density, F , was calculated by first calculating LAI per plot then dividing LAI by mean canopy depth, which was the mean of the individual-tree crown lengths. Crown length was derived from measurements of tree height and height to the base of the live crown on individual trees. Height to the base of the live crown was not measured consistently, nor was it measured every time a plot was measured, especially during the first few measurement cycles (Figure 1). At the CEF site, most sampling dates did not include measurement of height to live crown in the measurement protocols. At the Douglas-fir and ponderosa pine sites, height to live crown was not measured for the first few measurement dates. When included, it was measured along with total height on the same tree, but rarely was height to live crown measured on all the height trees. Numbers of trees measured per plot per sampling period varied from about 12 per plot to 50 per plot (Figure 1). The proportion of trees with crown measurements per plot varied 2 to 100 percent. Live-crown ratio was calculated as tree height divided by crown length; mean live-crown ratio per plot was simply the mean of the measured value or the mean of live-crown length divided by height, and no attempt was made to estimate missing heights to the live crown.

LAI is total leaf area per plot divided by plot area. For Douglas-fir, leaf area per tree was calculated with an equation developed with data collected by Maguire and Bennett (1996) for this study. This equation was based on both dbh and height: $A_l = 0.642 \cdot dbb^{2.13} h^{0.57}$, where A_l = leaf area per tree. Leaf area per tree for the red pine studies was calculated with equations from Penner and Deblonde (1996) condensed to $A_l = 759 \cdot A_b$.

The equation for leaf area per tree for ponderosa pine is based on height to the middle of the crown and sapwood cross-sectional areas. Height to the middle of leaf area could only be calculated for the subsample of trees with crown measurements. Leaf area for the subsample was expanded to the plot level by the inverse of the subsample fraction. Calculating leaf area per tree for ponderosa pine first required calculating the expected sapwood cross-sectional area of the tree with the equation $A_s = e^{(-8.56 + 0.31\sqrt{dbb})}$, where A_s is sapwood cross-sectional area in square meters and dbb is in millimeters (Simonin et al. 2006). Leaf area was then calculated with the equation $A_l = 0.17(A_s)^{1.21} \cdot S^{-0.66}$, where A_s is in square centimeters and S is distance between breast height and the middle of the live crown. This equation was developed by Ex and Smith (2014) with data collected within the Black Hills region of South Dakota.

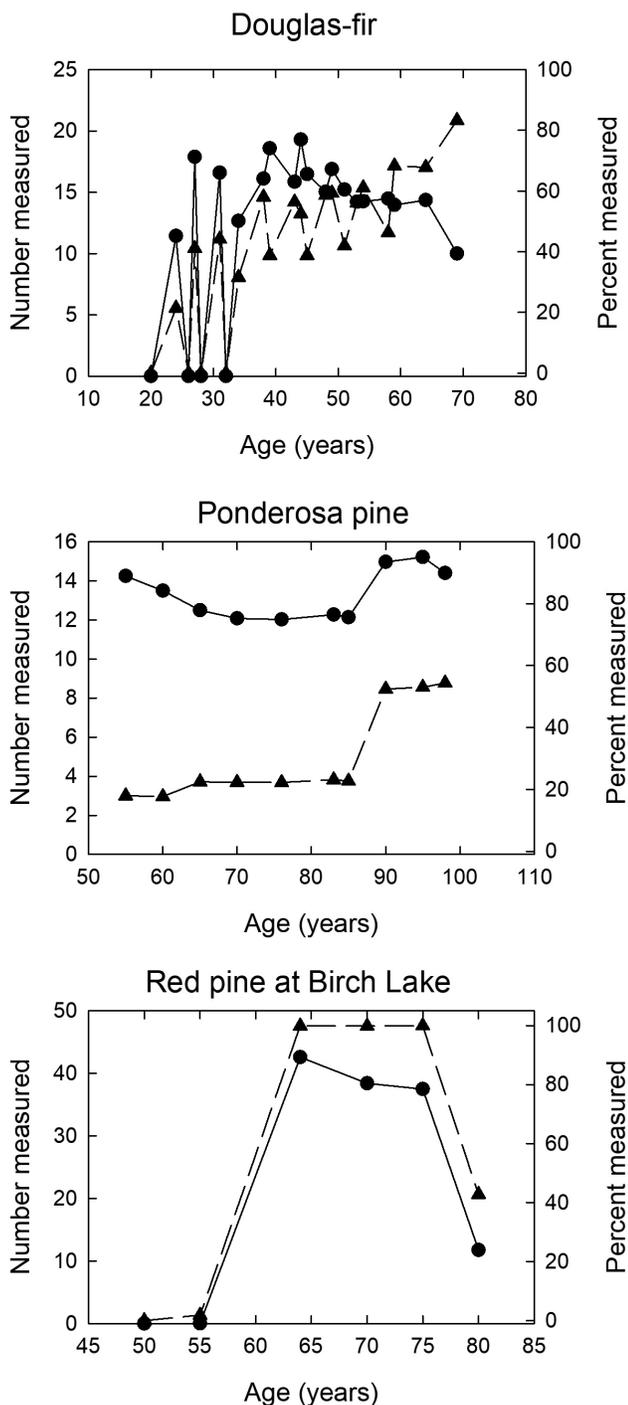


Figure 1. Number (circle) and proportion of trees (triangle) within a plot with measurements of either live-crown ratio or height to the base of the live crown by measurement age. Red pine at Cutoff Experimental Forest not shown because of insufficient numbers of measurements.

Regression Analyses

If the sum of the ratios of volume increment and height increment form a gradient congruent to the presumed gradient in stand density within a plane defined by the log of tree size and the log of tree density, any random draw of data within this plane fit to

$$\sum_{n=1}^N \frac{i_{V_n}}{i_{H_n}} = C_0 \cdot Dq^{C_1} \cdot N + \epsilon, \quad (3)$$

would produce a consistent value of the exponent C_1 , regardless of thinning treatment or age. The values of Dq and N are the initial values at the start of the growth period. For each study and each GSL, one measurement period was randomly selected from each plot. Those data were fit to equation (3), and the fitted values of C_0 and C_1 recorded. Ninety-nine additional estimates of C_0 and C_1 for each GSL were recorded with an additional 99 random selections from the plot data, resulting in 100 estimates of C_0 and C_1 for study and GSL. This resampling technique is described by Cassell (2007). This analytical approach is based on the central limit theorem and has the advantage that the serial correlation among remeasurements can be eliminated.

With the exception of the ponderosa pine data, each replicate contained eight to nine records, with the exception of the ponderosa pine data that contained 5.5 records on average. In all, equation (3) was fit to 2600 data sets randomly drawn from the original data sets, and on average, 97 percent of the regressions converged on a solution (Table 1). If the unthinned plots in the ponderosa pine study are excluded, the percentage of regressions converging to a solution increases to 99 percent. The effect of level of growing stock on C_1 was analyzed with one-way analyses of variance with the median of the replicates, which was accomplished by ranking the values of C_1 within a replicate. Since the shape of the distribution is created empirically and is not necessarily symmetrical, the median is preferable over the mean, and upper and lower percentiles substitute for confidence intervals; for this study, the confidence interval is bounded by the 10th and 90th percentiles. If the distribution is normal, the median equals the mean. Since the null hypothesis was just the absence of treatment effects, means were compared with Tukey's honestly significant difference test.

The data from the Douglas-fir study were collected across three geographically separated installations of the experimental design. To test for location effects, two indicator variables, i_1 and i_2 , were added to both C_0 and C_1 modifying equation (3) to

$$\sum_{n=1}^N \frac{i_{V_n}}{i_{H_n}} = (C_0 + C_2 \cdot i_1 + C_3 \cdot i_2) \cdot Dq^{(C_1 + C_4 \cdot i_1 + C_5 \cdot i_2)} \cdot N + \epsilon,$$

where C_2 – C_5 are location effects on the constant and the exponent. The values of i_1 and i_2 were zero if the data were collected at Iron Creek, $i_1 = 1$ if the data were collected at Rocky Creek, and $i_2 = 1$ if the data were collected at Stampede Creek. Equation (4) was fit across all levels of growing stock with the resampled data sets. The standard errors of C_4 – C_5 were calculated from the distributions of the estimated indicator variables, and the difference between the mean values of C_2 – C_5 and zero were tested with the Student's t -test. The probabilities of a greater values of t were greater than .05 (Table 2), indicating that the null hypothesis could not be rejected with these data. Consequently, installation effects for Douglas-fir were not considered in subsequent analyses.

To determine whether canopy architecture explains the sum of the ratios, this mixed regression model was fit to the data:

$$\sum_{n=1}^N \frac{i_{V_n}}{i_{H_n}} = D_0 \cdot F \left(\frac{1}{c_r} - \frac{1}{2} \right)^{(D_1 + \mu_1)} + \epsilon, \quad (4)$$

where F is foliage density, c_r is mean live-crown ratio, D_0 and D_1 are coefficients for fixed effects, and μ_1 is the coefficient for a

Table 1. Statistics for fitting the model $\sum_{n=1}^N \frac{1}{n} = C_0 \cdot Dq^{C_1} \cdot N + \epsilon$ to the four data sets by level of growing stock. The 10th and 90th percentiles for the distributions of C_0 and C_1 produced by fitting the model to 100 replicates of randomly selected record from within each level of growing stock. Selection was restricted to one remeasurement per plot. Median values of C_0 and C_1 are listed. BA, basal area; GSL, growing-stock level.

Treatment	Ponderosa pine															
	n	C_0			C_1			GSL [†] (m ² /ha)	n	C_0			C_1			
		Median	p10 [§]	p90	Median	p10	p90			Median	p10	p90	Median	p10	p90	
10% Fixed	100	9.25E-05	5.18E-05	2.14E-04	1.98	a [‡]	2.17	5	97	5.66E-04	8.64E-05	4.34E-03	1.55	d	0.79	
10%–50% Increasing	99	1.09E-04	5.69E-05	1.96E-04	1.94	a	2.14	9	99	4.60E-04	3.16E-05	1.55E-03	1.53	d	1.08	
30% Fixed	100	1.15E-04	5.32E-05	2.27E-04	1.92	a	2.15	14	99	4.26E-04	4.21E-05	2.09E-03	1.54	cd	0.94	
30%–70% Increasing	97	1.83E-04	9.71E-05	3.26E-04	1.80	b	2.01	18	98	3.53E-04	2.75E-05	1.20E-03	1.57	bcd	1.16	
50% Fixed	100	1.18E-04	4.13E-05	2.68E-04	1.92	a	2.23	23	99	2.48E-04	7.18E-05	5.48E-04	1.67	bc	1.40	
50%–10% Decreasing	99	1.25E-04	6.77E-05	2.19E-04	1.90	a	1.72	28	94	2.14E-04	2.79E-05	5.28E-04	1.70	b	1.37	
70% Fixed growing	100	2.15E-04	1.09E-04	3.41E-04	1.72	bc	1.94	Unthinned	57	1.24E-05	2.92E-08	1.15E-03	2.49	a	0.99	
70%–30% Decreasing	98	2.34E-04	8.57E-05	5.61E-04	1.70	c	2.00	Means		3.78E-04			1.72		4.58	
Control	98	1.55E-04	8.61E-05	2.90E-04	1.78	bc	1.55									
Means		1.50E-04			1.85											
Red Pine at Curfoot Experimental Forest																
BA [†] (m ² /ha)	n	Median	p10	p90	Median	C_1	p10	p90	n	Median	p10	p90	Median	C_1	p10	p90
14	98	2.08E-04	8.94E-06	6.59E-03	1.80	a	0.83	2.66	7	2.43E-03	3.57E-04	1.80E-02	1.22	cd	0.64	1.81
18	100	4.59E-04	3.92E-05	4.37E-03	1.59	ab	0.98	2.33	14	1.18E-03	4.28E-04	2.95E-03	1.22	c	1.11	1.66
23	100	4.53E-04	5.23E-05	4.28E-03	1.61	ab	0.98	2.22	21	6.62E-04	2.31E-04	2.33E-03	1.51	b	1.13	1.84
28	100	5.90E-04	1.26E-04	2.84E-03	1.53	bc	1.03	1.99	28	5.25E-04	2.23E-04	1.47E-03	1.51	b	1.21	1.77
32	99	8.81E-04	2.13E-04	3.81E-03	1.40	c	0.99	1.82	34	2.17E-04	4.56E-05	7.39E-04	1.75	a	1.37	2.25
Means		5.18E-04			1.59				Unthinned	1.89E-03	1.49E-04	2.01E-02	1.03	d	0.32	1.82
									Means	9.94E+01			1.37			

[‡] Letters next to median values of C_1 indicate results of Tukey's honestly significant difference among medians within a data set.

[†] Growing-stock level.

[‡] Residual basal area.

[§] 10th and 90th percentiles.

Table 2. Test for installation effects on the fit of equation 3 to the Douglas-fir data. Installation effects tested by fitting the equation $\sum_{n=1}^N \frac{i_{V_n}}{i_{h_n}} = (C_0 + C_2 \cdot i_1 + C_3 \cdot i_2) \cdot Dq^{(C_1 + C_4 \cdot i_1 + C_5 \cdot i_2)} \cdot N + \epsilon$ to the Douglas-fir data using resampling. The indicator variables i_1 and i_2 equal zero for data from Iron Creek, $i_1 = 1$ for data from Rocky Creek, and $i_2 = 1$ for data from Stampede Creek.

Statistic	C_0	C_2	C_3	C_1	C_4	C_5
Median	1.44E-04	-2.28E-05	-7.41E-05	1.83	0.07	0.25
Standard error		5.69E-05	5.99E-05		0.12	0.15
Prob > χ^2		0.689	0.219		0.561	0.099

$^{\circ}H_0$: effect = 0.

random effect ($N=0$). Equation (4) was fit across levels of growing stock for each data set. The red pine data from CEF were not included in this analysis because of insufficient numbers of crown measurements. Since canopy architecture is hypothesized to account for the sum of the ratios universally across levels of growing stock, no effect for GSL was included in the regression model.

Results

The highest and lowest median values of C_1 across all studies and levels of growing stock occurred for the unthinned ponderosa pine plots (2.49) and the unthinned red pine plots at BLP (1.03) (Table 1). Excluding these values, the overall average estimate of C_1 across the levels of growing stock within a study varied from 1.44 to 1.85, and the grand average is 1.62. One-way analyses of variance indicated that level of growing stock affected the estimate of C_1 at all sites. In the Douglas-fir and the red pine study at CEF, the median estimate of C_1 tended to decrease with increasing level of growing stock, with the lowest levels of growing stock exhibiting significantly higher estimates of C_1 than the higher levels of growing stock. The median values of C_1 for ponderosa pine and red pine at BLP exhibited an opposite trend with the lower levels of growing stock exhibiting significantly lower values of C_1 than the higher levels of growing stock.

The confidence intervals around the median values of C_1 indicate that fits of equation (3) are more precise with the Douglas-fir data than the fits with either the ponderosa pine or red pine data. The relative width of the interval (one-half of the difference between the percentiles divided by the median) for most of the levels of growing stock ranged from 27 to 38 percent, whereas the relative width for the Douglas-fir data ranged from 12 to 14 percent. The relative width of the interval was exceptionally high for the unthinned ponderosa pine plots and the unthinned red pine plots at BLP, both >70 percent of the median.

Visual comparison of the effects of treatment effects on the slopes between the log (N) and log (Dq) based on estimates of C_0 and C_1 can aid in comparing the consequences of level of growing stock on C_1 . Equation (1) was rearranged to calculate two data pairs to plot on log-transformed Cartesian coordinates to compare the slopes in relation to the respective size-density trajectories produced by the thinning regimes. The data pairs consisted of the measured minimum and maximum tree densities and corresponding values of Dq within a level of growing stock. The corresponding values of Dq were calculated with the median values of C_0 and C_1 and the mean value of $\sum_{n=1}^N \frac{i_{V_n}}{i_{h_n}}$ for individual levels of growing stock. The mean value of $\sum_{n=1}^N \frac{i_{V_n}}{i_{h_n}}$ was calculated with all the data for a levels of growing stock, regardless of stage of development.

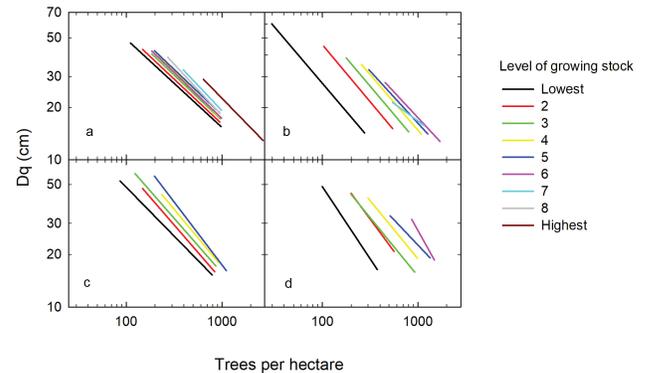


Figure 2. Lines calculated from the median values of C_0 and C_1 for each level of growing-stock within Douglas-fir (a), ponderosa pine (b), red pine at the Cutfoot Experimental Forest (CEF; c), and red pine at the Birch Lake Plantation (BLP; d). The mean value of $\sum_{n=1}^N \frac{i_{V_n}}{i_{h_n}}$ for each growing-stock level and the minimum and maximum values of trees per hectare were used to calculate two points defining the slope and the end points of the lines. Levels of growing stock within a study are ranked lowest to highest. The Douglas-fir study has nine lines corresponding to nine levels of growing stock (with the highest level represented by the brown line). The ponderosa study has seven lines with the lowest growing-stock level represented by the black line and the highest growing-stock level represented by the cyan line. The line representing the highest growing-stock level of red pine at CEF is blue, and at BLP, the line for the highest growing-stock level is pink. Levels of growing stock for each study are listed in Table 1.

For the most part, the calculated lines for each level of growing stock are parallel, moving left to right with increasing residual growing stock (Figure 2). The line representing the unthinned treatments is generally on the far right-hand side of the figures, with the exception of the unthinned plots in the ponderosa pine study. The most consistent arrangement of lines occurs within the Douglas-fir study. In addition, the effect of competition is clearly seen in the smaller maximum values of Dq in the unthinned Douglas-fir plots compared with the thinned plots. Disregarding the unthinned plots, the lines for the GSL in the ponderosa pine study also stack accordingly; however, the lines for the two highest levels of growing stock are slightly shallower than the lower levels, but the difference probably has no practical consequence for management. The lines representing the five levels of growing stock for red pine at CEF generally stack in order of growing stock and are mostly parallel; however, the line for the 14 m²/ha BA is somewhat shallower than the rest. The lines representing the levels of growing stock for the red pine study at BLP have a different pattern than the pattern seen for data from CEF. The lines move from left to right with increasing growing stock and tend to become shallower with

increasing growing stock, especially for the highest residual density. The line representing the unthinned plots is notably steeper and shorter than the other lines. The lines for 14 m²/ha, 21 m²/ha, and 28 m²/ha BA are parallel.

The individual trajectories created with periodic thinning do not seem to affect the median value of the exponent C_1 (Figure 3). Equation (3) relates the sum of the ratios to current values of N and Dq . The results of these regressions indicate that thinning does not affect this relationship. Consequently, coarse or fine control of prescribed stand density results in the same relationship between stand function and stand structure. Good examples of the independence of the fit of equation (2) to the level of density control can be seen by comparing the 30 percent

and 70 percent GSLs in the Douglas-fir study; the 9 m²/ha and 28 m²/ha GSL treatment in the ponderosa pine study; the 14 m²/ha and 28 m²/ha BA treatments for the red pine study at CEF; and the 14 m²/ha and 21 m²/ha BA treatment for the red pine study at BLP.

For all three species, the sum of the tree ratios between volume increment and height increment increases with increasing foliage density and decreases with mean live-crown ratio (Figure 4). The lower end of mean live-crown ratio is constrained biologically because some minimum crown must exist for trees to survive. Consequently, a range of values of the sum of the ratios exists because foliage density can vary within a given mean live-crown ratio. Of the three possible scattergrams that can be produced for the

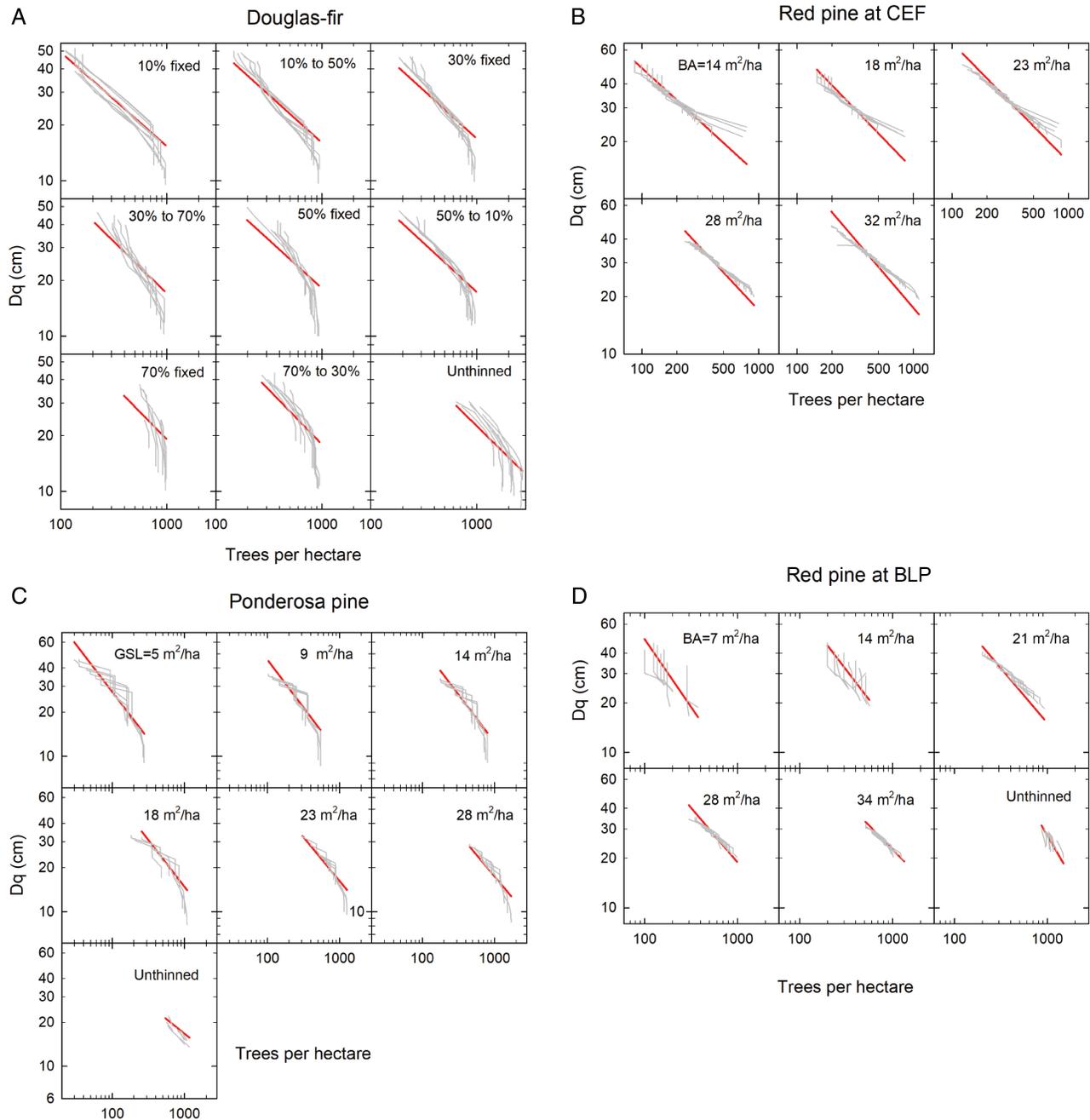


Figure 3. Each of the calculated lines in Figure 2 (represented here by the red line) was overlain by the corresponding size-density trajectories of the growing-stock levels (gray lines).

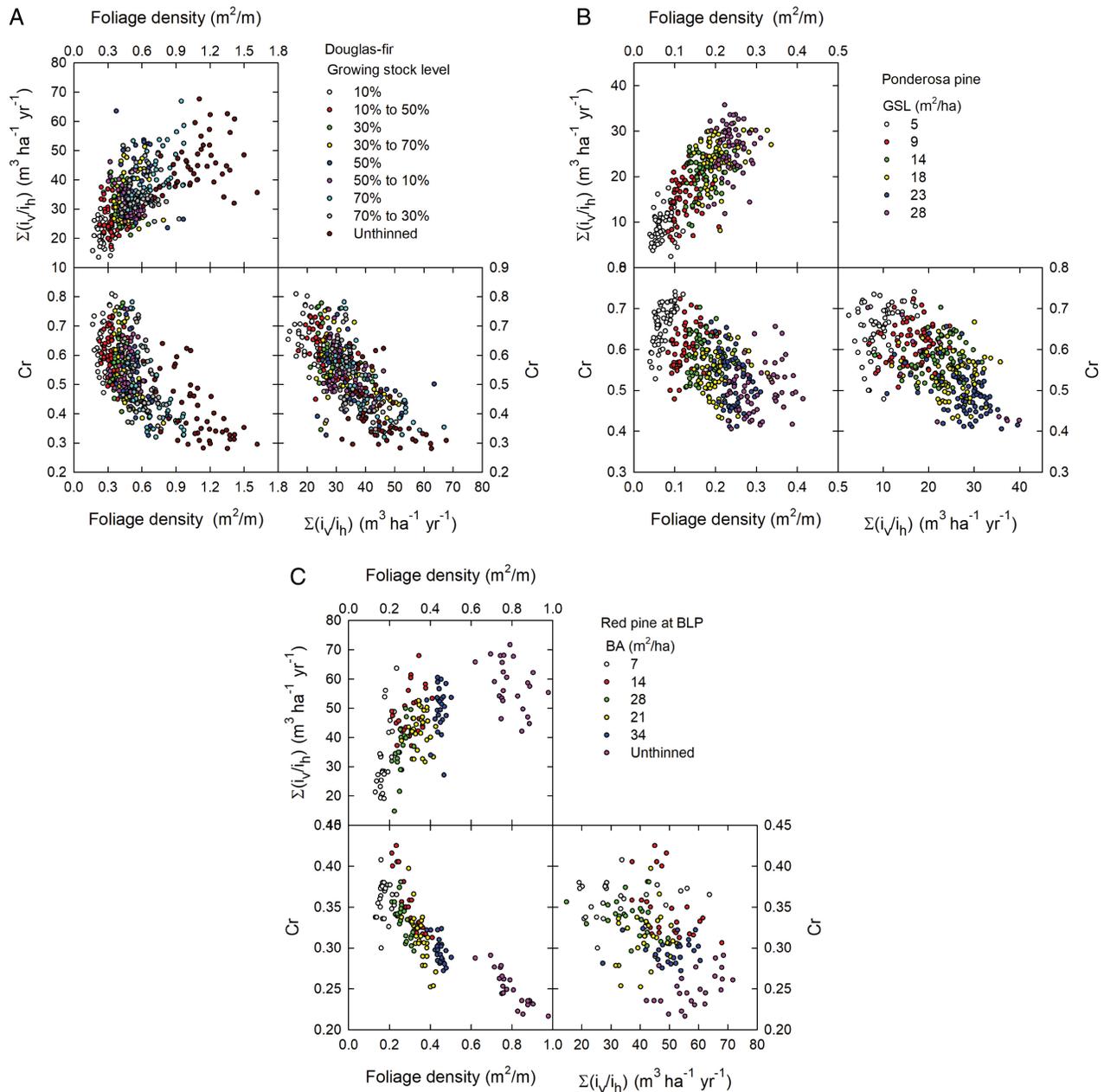


Figure 4. Projections of a three-dimensional scattergram onto three planes. The X , Y , and Z variables are foliage density, mean live-crown ratio, and $\sum_{n=1}^N \frac{i_{v_n}}{i_{h_n}}$, respectively. BLP, Birch Lake Plantation; GSL, growing-stock level.

three variables, the plot between mean live-crown ratio and the sum of the ratios shows the most variation.

Maintenance of different levels of growing stock affects foliage density and mean live-crown ratio. Furthermore, the two different approaches used in these levels of growing-stock studies also affect these canopy variables. In the Douglas-fir study, the GSLs were percentages of the unthinned control. This approach resulted in a blending of the canopy variables from low levels gradating to the highest level. In the ponderosa pine and the red pine studies, GSL was maintained at specific values of BA per hectare. This caused the foliage density and mean live-crown ratio to line up in clusters. How tightly the variables lined up depended on how closely the prescribed levels of growing stock were maintained.

Equation (4) explained up to 86 percent of the variation in the sum of tree ratios between volume increment and height increment of stem volume increment and as little as 56 percent of the variation in the sum of the ratios (Table 3). A single model was fit to all the data because if canopy architecture and dynamics were responsible for both the structure and function of a stand, the process should be consistent across the levels of growing stock. Comparing the residuals between the observed and predicted values of the sum of the ratios from the fitted equation (4) shows that the range of residuals is similar across the various levels of growing stock and is consistent with the proportion of the variation explained by the model (Figure 5). Most of the mean residuals calculated as a percent of the observed value were slightly negative, but only four values were significantly different than zero. The relative residuals

that were significantly different than zero were for the lowest level of growing stock in the studies.

Discussion

The implicit assumption in using relative density to schedule thinning treatments is that relative density is independent of average tree size and that the gradient in relative density is parallel to the trajectory of a self-thinning stand. This is one reason why so much effort has been devoted to establishing the slope of self-thinning trajectories; the slope determines when a stand reaches a

prescribed upper limit of growing stock and needs to be thinned. The assumption that the gradient in stand density runs parallel to the self-thinning trajectory has not been tested, however, with the exception of [Dean et al. \(2013\)](#). Based on the results of this current study, the assumption appears justified. Although the median exponent C_1 is not identical for each level of growing stock, when viewed graphically, the overall slope of the lines representing the various GSLs are mostly parallel and are arranged left to right with increasing level of growing stock.

The general premise of this study is that the sum of ratios between tree volume increment and height increment is a direct measure of stand density because stand occupancy is a function of the resources used in growth and that tree growth is primarily driven by height increment and associated canopy dynamics. The fits of equation (1) to the data indicate that the sum of the ratios between tree volume increment and height increment is related to the traditional measure of stand density, $D_q^x \cdot N$, for each level of growing stock with some exceptions. Furthermore, when put in terms of $\log(Dq)$ and $\log(N)$, the predicted slopes of the fitted equations stack according to level of growing stock and the slopes of the lines are generally parallel to each other. Moreover, the fitted lines correspond with the observed $\log N - \log Dq$ trajectories of the respective treatment levels.

Table 3. Regression results from fitting the model $\sum_{n=1}^N \frac{i_{v_n}}{i_{h_n}} = D_0 \cdot F\left(\frac{1}{c_r} - \frac{1}{2}\right)^{(D_1 + \mu_1)} + \epsilon$ to data from three data sets. BLP, Birch Lake Plantation; FI, fit index in percent; s.e., standard error.

Study	D_0 (s.e.)	Var (μ_1)	D_1 (s.e.)	FI ^a
Douglas-fir	36.3 (0.58)	17.7	0.30 (0.02)	86.1
Ponderosa pine	40.7 (2.01)	13.5	0.47 (0.03)	69.4
Red pine at BLP	45.1 (1.27)	20.5	0.24 (0.04)	55.7

^a $100 \cdot [1 - \sum (y - \hat{y})^2 / \sum (y - \bar{y})^2]$; \hat{y} = predicted value of y , and \bar{y} = mean value of y .

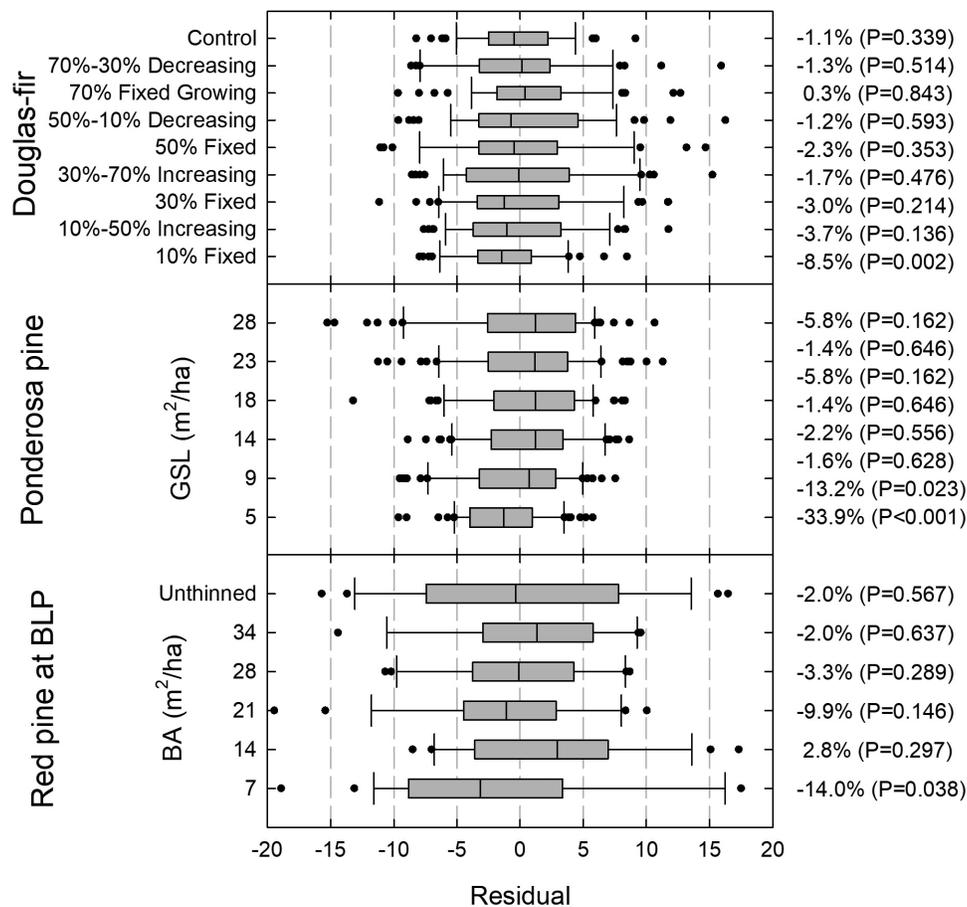


Figure 5. Box plots of the residual values from fitting $\sum_{n=1}^N \frac{i_{v_n}}{i_{h_n}} = D_0 \cdot \left[F\left(\frac{1}{c_r} - \frac{1}{2}\right) \right]^{(D_1 + \mu_1)} + \epsilon$ to the data from three data sets. Values beyond the 10th and 90th percentiles shown as whiskers, data beyond these percentiles shown as circles, 25th and 75th percentiles are the extent of the box, and the vertical line in the box is the median. Numbers on the side of the box plots show the mean value of the residual as a percent of observed and the probability of a greater value of Student's t for the hypothesis that the mean residual value is equal to zero. BLP, Birch Lake Plantation.

The data used in these analyses were collected from similarly aged trees, which is an atypical age structure for naturally regenerated ponderosa pine forests. Data from [Ex and Smith \(2014\)](#) suggest stand density relationships for single-aged stands may also apply to multiaged ponderosa forests. In their study, they calculated LAI and SDI for 21 plots in a multiaged ponderosa pine forest with the additive form of Reineke's SDI noted as SDI^* , which equals $\sum_{i=1}^N \left(\frac{dbb_i}{25}\right)^{1.6}$. [Ducey \(2009\)](#) determined that the ratio between SDI and SDI^* for a typical multiaged forest was greater than 0.9. In one sense, the similarity between SDI and SDI^* may indicate just an insensitivity to stand structure; however, [Dean \(2020, p. 464\)](#) plotted the LAI of the 21 plots against the corresponding values of SDI^* and found a clear linear relationship between the variables that was parallel to SDI^* -LAI data from 10 plots measured in a single-aged, ponderosa pine forest. Furthermore, the growth–growing-stock relationships in multiaged forests are the same as those for even-aged forests. [Lundqvist \(2017\)](#) showed that the volume growth of multiaged Norway spruce (*Picea abies* [L.] Karst.) increases with increasing residual stand volume after single-tree selection, and [Solomon and Frank \(1983\)](#) showed that overall diameter growth increases with decreasing residual density in northern hardwood forests in the New England region. This implies that the ratio of the tree sums may also measure stand density in multiaged stands.

The ability to estimate C_1 for most levels of growing stock indicates that a gradient of stand density exists and that the gradient is parallel to the self-thinning trajectory and that the slope of the gradient can be determined by fitting equation (1) to any data, regardless of stage of development. According to these results, applicable stages of development include the stand initiation stage where trees are growing without competition. The residual densities of the lowest growing-stock treatment prevented the canopies from closing, and yet, the median values of C_1 for these treatments were not significantly different from the values for treatments that allowed crowns to interact ([Table 1](#)).

A variety of statistical methods have been explored for determining the slope of size-density relationships on a log-transformed axis or the exponent for Dq or N depending which variable is set as the dependent variable. Since Reineke's SDI is based on $D_q^x \cdot N$, the exponent x is typically the variable of interest. Past analysis has been justified on a biological basis since the exponent varies according to a variety of external variables such as geographic region ([Zhang et al. 2016](#)) or initial planting density ([VanderSchaaf and Burkhart 2012](#)). The exponent also has practical consequences because it guides thinning schedules. The most acceptable analytical methods, segmented regression ([Cao and Dean 2008](#)), stochastic frontier analysis ([Bi et al. 2000](#)), and percentile regression ([Ducey and Knapp 2010](#)), have all required data from self-thinning stands. The addition of a third, intermediary variable seems to eliminate that requirement.

[Dean and Long \(1985\)](#) included foliage mass in a regression model that related average tree mass to tree density to produce a continuous function between the intercept k of the log-transformed model ($k = (\bar{w} \cdot N^p)$) and foliage mass for five genera. The data were taken from a compilation by [Cannell \(1982\)](#). Their results suggested that the slope of the size-density relationship could be determined with any set of data that included foliage mass. Foliage mass implies function, but it is still a state variable. The sum of the ratios between tree

volume increment and height increment is a functional term that is constrained within a specific change in the state variable height, which makes volume growth tractable, thus satisfying the original intention of SDIs, which is to manage stand occupancy.

The hypothesized relation between stand occupancy and the sum of the ratios is supported by the fits of equation (4) to foliage density and mean live-crown ratio. [Smith \(1986\)](#) showed that isopleths of mean live-crown ratio ran parallel to the size-density boundary for red pine and red alder, but he did not include Cr as a third variable in his size-density models. According to equation (4), however, the relationship between Cr and stand density is affected by foliage density. Thus, for a given mean live-crown ratio, the volume increment will increase with foliage density for each meter of height growth, rapidly at first and plateauing with higher values.

Although Cr varies within a given value of F , and vice versa, over the range of the sum of the tree ratios, the relationship between F and Cr is curvilinear with F increasing as Cr decreases. Concomitantly, the sum of the ratios increases with F and with $1/Cr$ ([Figure 4](#)). Mean live-crown ratio has a minimum threshold since trees require some minimum amount of foliage to survive. Intuitively, foliage density must have an ultimate upper value; however, the upper limit to foliage density apparently can vary across geographic regions. Based on data from [Harms et al. \(1994\)](#), foliage density for loblolly pine growing in Hawaii (outside its native range) was nearly three times greater than in its native range (South Carolina). The higher F at Hawaii corresponded with the higher maximum density at the Hawaii planting as well. If the differences in mean live-crown ratio are taken into account, these canopy properties account for nearly the entire difference in maximum stand densities between the two locations.

The fits of equations (3) and (4) to the levels of growing-stock data for the three species analyzed here support the hypothesis that the sum of the ratios between tree volume increment and height increment is a valid measure of stand density. The size-density lines calculated from the fitted coefficients form a parallel gradient up to the maximum value of the sum of the ratios, including treatments that prevented canopy closure. The fit of equation (3) also supports the hypothesis that the sum of the ratios between tree volume increment and height increment is a measure of stand density since equation (4) represents resource use via growth as a function of canopy properties. Together the fitted equations support the concept that stand growth is the cumulative expression of coordinated changes in crown and stem structure that become evident when the changes are standardized on the basis of height increment. The species in this study and the ones in [Dean et al. \(2013\)](#), although spanning multiple genera and functional forms, seem to have similar feedback mechanisms between height increment and changes in stem size that operate in the canopy. The relevant canopy properties that regulate this feedback appear to be foliage density and mean live-crown ratio.

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