
Disaggregating Stand Volume Growth to Individual Trees

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ABSTRACT. A disaggregation function, relative size-growth (*RSG*), was proposed and developed for interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Beissn] Franco) to distribute stand volume growth to a list of individual trees. The *RSG* function was formulated as a quadratic equation relating relative tree growth to relative tree size in a stand. The shape of the *RSG* function was linear, convex, or concave depending on initial stand conditions and structure. A recursive system of equations was developed to predict the three coefficients of the *RSG* function using initial stand density, mean tree size, and coefficient of variation of tree size distribution as predictor variables. This disaggregation function determines within-stand growth of individual trees and simulates stand development and dynamics. The *RSG* function provides a biologically based link between whole-stand and individual tree resolution models. FOR. SCI. 39(2):295-309.

ADDITIONAL KEY WORDS. Relative tree size, relative tree growth, stand structure and dynamics, interior Douglas-fir.

FOREST GROWTH AND YIELD MODELS of varying degrees of complexity and detail, ranging from whole-stand to individual tree resolutions, have been developed to fulfill the different information requirements for decision making. Some researchers have attempted to unify modeling approaches or link whole-stand models and size-class or individual tree models. Two general approaches have been developed: (1) aggregating diameter distribution or individual tree characters to stand yield estimates (e.g., Daniels and Burkhart 1988, Strub and Burkhart 1975), and (2) disaggregating overall stand attributes into more detailed models (e.g., Burk and Newberry 1984, Dahms 1983, Harrison and Daniels 1987). The disaggregation approach has the advantage that volumes at all levels are conditioned on whole-stand volume, which is mathematically more tractable than size-class or individual tree volumes (Burkhart 1987). However, most disaggregation approaches are based on the assumption that the distribution of tree size in a stand can be adequately characterized by a probability density function (*pdf*). Some *pdfs*, such as Weibull, have been applied only because they are flexible enough to fit a relatively broad spectrum of distribution shapes and are easily integrated, not because they are based on any biological principles. In addition, after the parameters of a *pdf* have been estimated, it is difficult to incorporate the influences and changes in stand density and/or structure due to silvicultural treatments.

Therefore, the objective of this study is to develop a new approach to disaggregate stand volume growth to a list of individual trees. This disaggregation

function is based on general concepts of competition among individual trees and dynamics of stand structure, without assuming that the distribution of tree size follows any particular probability density function.

BACKGROUND

The frequency distribution of plant weight is the link between the individual and the population biomass (Hozumi et al. 1968). Skewness is commonly found in plant size distributions of even-aged monocultures (Bliss and Reinker 1964, Ford 1975, Ford and Newbould 1970, Gates 1982, West and Borough 1983). Mohler et al. (1978) found that maximum positive skewness occurred at the time self-thinning began.

Hara (1984a, 1984b) proposed a stochastic model to investigate the dynamics of stand structure. His model described the changes in plant size distribution with time as a function of mean growth rate, variance of growth rate, and mortality. Further, the mean growth rate and variance of growth rate were expressed as quadratic functions of plant size. Westoby (1982, 1984) introduced the concept of distribution modifying function (*DMF*). He proposed a polynomial equation to describe *DMF* in which plant size increment was a dependent variable and plant size was an independent variable. The shapes of *DMF* determined changes in the shape of the frequency distribution of plant size. Westoby (1984) also pointed out that most *DMF*s were of the quadratic form, which produced skewed frequency distributions of plant size. The concepts and ideas introduced by Hara (1984a, 1984b) and Westoby (1982, 1984) were used as the basis of formulating the disaggregation function.

DATA AND METHODS

Data used in this study represent single species, second-growth, managed, even-aged Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Beissn] Franco) stands in the inland Northwest. The study area covers six geographic regions: northern and central Idaho, western Montana, northeast Oregon, central and northeast Washington. The research sites were primarily established for thinning and fertilization experiments. A total of 218 control (unfertilized) plots with a 6-yr growth period were used for data analysis and model development. Plot size ranged from 0.1 to 0.2 ac. All trees were measured for both height (to the nearest 1 ft) and diameter (to the nearest 0.01 in.). Tree volume was calculated using an individual tree cubic volume equation. A majority of the stands had been thinned 5–12 yr prior to the growth period used in this study. Selected stand attributes are summarized in Table 1.

Ordinary least-squares regression was used to estimate the parameters for linear models. Multicollinearity diagnostics and residual analysis were conducted to examine the adequacy of the models and to test for violations of statistical assumptions. For nonlinear models, nonlinear least-squares regression was utilized for parameter estimation. Residual analysis was conducted to detect model underspecification, departure from statistical assumptions, and existence of suspect data points.

TABLE 1.

Averages and ranges of stand attributes at the beginning of a 6-yr growth period for Douglas-fir plots.

Attribute	Mean	Min	Max
Site index (ft @ 50 yr)	70	39	105
Stand total age (yr)	61	11	100
Number of trees (/ac)	318	90	1640
Top height (ft)	73	12	118
Basal area (ft ² /ac)	140	3	370
Quadratic mean diameter (in.)	9.8	1.2	16.9
Total volume (ft ³ /ac)	3669	33	9416
Mean tree volume (ft ³)	15	0.1	59
Relative density index*	0.20	<0.01	0.84
Coefficient of variation (%) of tree volume distribution	66	25	224

* Drew and Flewelling's (1979) relative density index.

MODEL DEVELOPMENT

DEFINITION OF THE RELATIVE SIZE-GROWTH FUNCTION

We assume that the dynamics of stand structure are affected by competitive interactions among individuals. The growth of an individual tree is size-dependent. The contribution of an individual tree's growth to stand total growth is proportional to that tree's relative size in the stand. Relative tree growth (*RTG*) is defined as the ratio of individual tree volume growth to stand total volume growth (i.e., the sum of the individual trees) on a unit area. Relative tree size (*RTS*) is defined as the ratio of individual tree volume to stand total volume on a unit area. Relative tree growth is expressed as a function of relative tree size. The following quadratic function was used to describe the relative size-growth (*RSG*) relationship:

$$RTG = \beta_0 + \beta_1 * RTS + \beta_2 * RTS^2 \quad (1)$$

where β_0 , β_1 , and β_2 are coefficients to be estimated for each plot.

CHARACTERISTICS OF THE RELATIVE SIZE-GROWTH FUNCTION

The *RSG* function [Equation (1)] was fit to the 6-yr growth data from each of 218 Douglas-fir plots using ordinary least-squares regression. The analyses showed a strong relationship between initial relative tree size and subsequent relative tree growth. Most plot regressions (93%) produced R^2 larger than 0.60. Sixty-three percent of the 218 regressions had R^2 larger than 0.80. There exist special patterns between the three coefficients of the *RSG* function as follows: when β_1 equals 1, both β_0 and β_2 are nearly equal to 0 resulting in a straight line through the origin. When β_1 is less than 1, both β_0 and β_2 are positive producing a convex curve with a positive intercept. In contrast, when β_1 is larger than 1, both β_0 and β_2 are negative, presenting a concave curve with a negative intercept. The above relationships define three basic shapes for the *RSG* function as linear, convex, and concave (Zhang 1990), determining the frequency distributions of tree size to be

normal, positively and negatively skewed, respectively, similar to Westoby's (1982, 1984) proposition.

PREDICTION MODELS FOR THE COEFFICIENTS OF THE RELATIVE SIZE-GROWTH FUNCTION

The Pearson's correlation coefficients between pairs of the three coefficients were -0.90 (β_0 versus β_1), 0.63 (β_0 versus β_2), and -0.88 (β_1 versus β_2). The relationships imply that the linear coefficient β_1 plays the most important role among the three coefficients. When β_1 is determined, the curvature and level of the *RSG* function are then defined. Therefore, a recursive system of equations was developed for predicting the three coefficients of the *RSG* function as functions of initial stand variables. Since within-stand distribution of tree growth can be influenced by the stage of stand development, stand density and structure (Pienaar and Harrison 1984, Stage 1969), prediction models for β_0 , β_1 , and β_2 of the *RSG* function can be developed accordingly as follows: (1) Stand density affects the rate and variability of tree growth, and consequently the dynamics of stand structure. (2) Mean tree size is an expression of the growth stages of even-aged stand development. The interaction between mean tree size and surviving number of trees in a stand can be expressed as a measure of relative stand density, which influences the relationship between tree volume growth and tree volume. (3) Ecological studies showed that coefficient of variation is a useful measure of inequality of plant population or "size hierarchy," which provides a robust indicator of density effects on growth and traces the effects of size-selective mortality (Bendel et al. 1989, Knox and Peet 1989).

Several stand variables and the first four moments of the tree volume distribution were evaluated as predictors. Number of trees per acre (N), quadratic mean tree diameter (D), and the coefficient of variation of tree volume distribution (CV) were found to be the most statistically significant and biologically meaningful predictor variables. The recursive system was formulated as follows:

$$\beta_1 = f(N, D, CV)$$

$$\beta_2 = f(\beta_1, N, D, CV)$$

$$\beta_0 = f(\beta_1, \beta_2, N, D, CV)$$

Borders (1989) outlined systems of related equations and suggested that ordinary least-squares (OLS) can be used to obtain parameter estimates if there is no cross-equation correlation between error components of the system equations. The situation he described is a recursive system, a special case of simultaneous equation systems. If the coefficient matrix of the endogenous variables in the system is triangular and the variance-covariance matrix of the equations in the system is diagonal, the simultaneous equation system is called a *diagonally recursive system* (Kmenta 1971). In this case, OLS provides an optimal estimating technique (Johnston 1972, Pindyck and Rubinfeld 1981, Theil 1971), and the application of OLS to each of the structural equations leads to unbiased, consistent, and asymptotically efficient estimates (Kmenta 1971). To confirm that we had a diagonally recursive system, we applied the Lagrange multiplier test (Judge et al. 1988) to determine that the error components for the three equations in the system are pairwise uncorrelated. The variance-covariance matrix of the equa-

tions in the system was estimated using the 6-yr Douglas-fir growth data. The Lagrange multiplier statistic was calculated based on the estimated variance-covariance matrix and equaled 5.16, which was less than the 5% critical value (7.81) from the χ^2 -distribution with 3 degrees of freedom. Thus, the variance-covariance matrix of the equations in the recursive system is diagonal. Further, the residuals of the three equations in the above regression analyses were pairwise plotted, and no detectable trends were found, confirming the results of the Lagrange multiplier test. Therefore, each equation in this diagonally recursive system can be appropriately estimated by the OLS procedures.

1. **Prediction Model for the Coefficient β_1 .** After evaluating various equation forms in terms of model fitting, residual analysis, and biological interpretation, the linear coefficient β_1 was related to three stand variables (N , D , and CV) using nonlinear least-squares regression, resulting in:

$$\beta_1 = N * \left(1 - e^{\frac{-0.0246 * D}{CV}} \right) \quad (2)$$

The asymptotic standard error of the estimated parameter was 0.0007967. A slight trend in the plot of residuals versus the predicted β_1 existed. Adding an intercept to Equation (2) eliminated the trend in the residual plot. However, the estimated intercept was nearly equal to one, resulting in a predicted β_1 always larger than one and consequent poor model behavior. Hence, we selected Equation (2) as the prediction model for β_1 .

2. **Prediction Model for the Coefficient β_2 .** The prediction model for the quadratic coefficient β_2 was developed using the linear coefficient β_1 and two stand variables, D and CV , as predictor variables. Number of trees (N) was tested and found statistically nonsignificant in the model. The model was:

$$\beta_2 = 5.9978 - 10.4822 * \beta_1 + 2.1194 * \log(D) - 61.9929 * \left(\frac{1}{CV} \right) \quad (3)$$

All independent variables were statistically significant ($\alpha = 0.05$). The R^2 of the model was 0.75, and the root mean squared error was 2.61. The collinearity diagnostics indicated that no multicollinearity problems among the three independent variables were found (VIFs for the three variables were less than 1.2). The residual analysis showed no significant violations of ordinary least-squares assumptions.

3. **Prediction Model for the Coefficient β_0 .** The coefficient β_0 was related to both linear coefficient β_1 and quadratic coefficient β_2 of the RSG function, as well as to the three stand variables. The resulting model was:

$$\begin{aligned} \beta_0 = & 0.02765 - 0.03782 * \beta_1 - 0.001559 * \beta_2 + 0.002393 * \left(\frac{N}{1000} \right)^2 \\ & + 0.004277 * \log(D) + 0.1176 * \left(\frac{1}{CV} \right) \end{aligned} \quad (4)$$

All independent variables were statistically significant ($\alpha = 0.05$). The R^2 of the model was 0.91 and the root mean squared error was 0.0032. No multicollinearity problems among the five independent variables were diagnosed [VIFs for β_1 and β_2 were 4.1 and 4.0, respectively; VIFs were 1.5 for N^2 , 1.5 for $\log(D)$, and 1.3 for $(1/CV)$]. The residual analysis did not show a detectable pattern.

MODEL EVALUATION AND VERIFICATION

Often model evaluation and verification are performed on data not used in the model fitting process (i.e., independent data). Although using independent data

has several positive aspects, we chose to test the *RSG* function differently for three reasons. First, we felt that the amount of data used in the model fitting process was somewhat limited. Therefore, we wanted to use all the data for model development. Second, independent data evaluations are most helpful when selecting among various model forms. In this situation, an independent data evaluation might give us some idea of "real" error levels when the model is used for prediction. However, with the limited data, the resulting error estimates would be questionable. Last, what we really wanted to show with the evaluation and verification is how the model responds to various stand and tree size composition structures. This, we believe, is more important than testing against independent data for the model.

EVALUATION OF THE RELATIVE SIZE-GROWTH FUNCTION

Six plots were selected from the Douglas-fir growth data to illustrate three stand development phases given two different stand structures for each density class. The number of trees, quadratic mean diameter, coefficient of variation of tree volume distribution, and relative density index (Drew and Flewelling 1979), for each example plot are provided in Table 2.

The three stand variables were used to predict the coefficient β_1 of the *RSG* function using Equation (2). Then the predicted β_1 and observed stand variables were input into Equation (3) to predict the coefficient β_2 . Finally the coefficient β_0 was obtained by Equation (4) using the predicted β_1 , β_2 and observed three stand variables. The behavior of the predicted *RSG* function was compared with that of the regression models, as well as a plot of observed data for each plot.

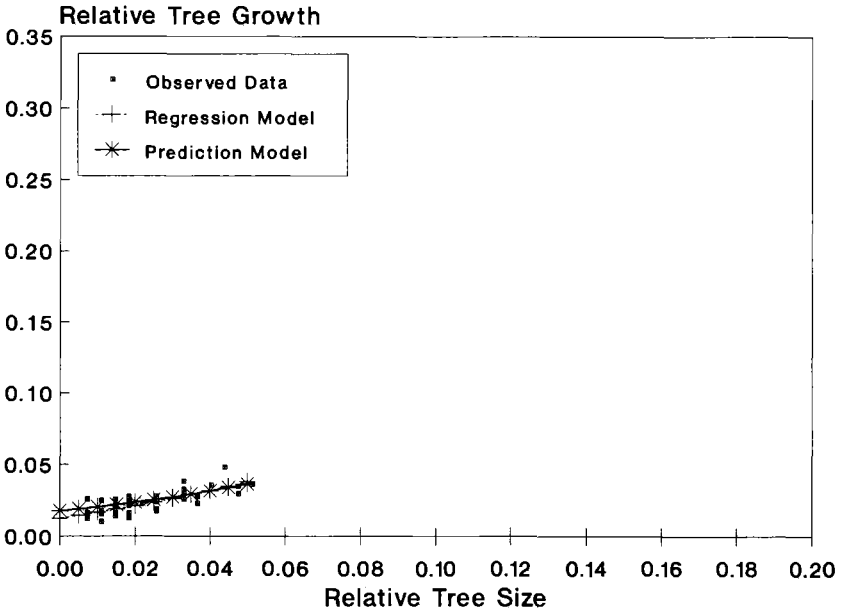
Two low density stands are illustrated in Figure 1. Plot 50-3 is a uniform stand with little variation in tree size and represents plantation conditions (Figure 1a). Before crown closure [<0.15 relative density according to Drew and Flewelling (1979)] the trees are growing as a collection of individuals without intertree competition. The observed and predicted *RSG* function reflects this condition as a line with little slope, i.e., all trees contribute about the same relative growth. Plot 257-6 (Figure 1b) is also a low density stand prior to crown closure. However, this plot shows more variation in tree size primarily due to the presence of

TABLE 2.

Stand variables and example stand conditions for six plots used in evaluation of the relative size-growth function.

Plot	Stand variables			
	Number of trees (/ac)	Quadratic mean diameter (in.)	Coefficient of variation (%)	Relative density index
50-3	470	1.16	54	0.01
257-6	93	14.63	73	0.09
250-5	350	8.23	61	0.17
224-4	100	16.94	94	0.19
14-2	1020	6.18	110	0.51
288-1	300	12.73	81	0.51

(a) Plot 50-3



(b) Plot 257-6

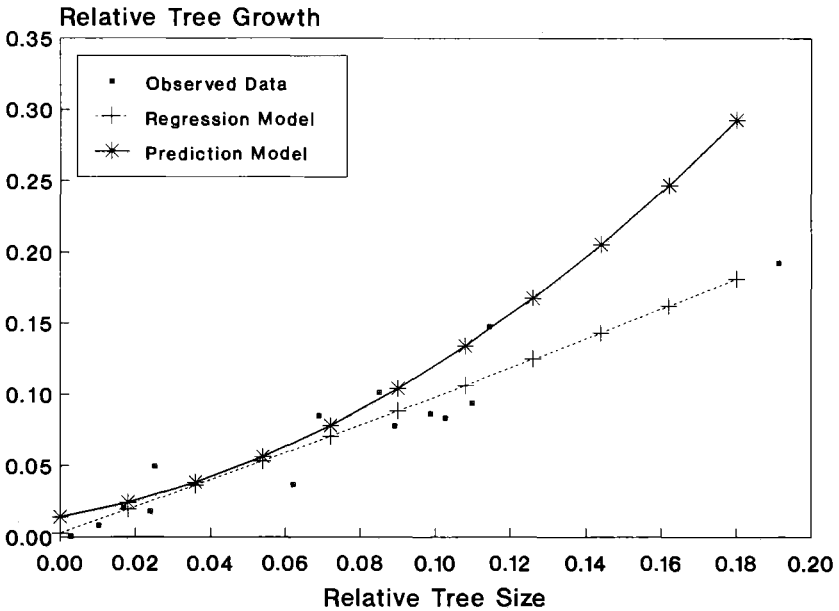


FIGURE 1. Behavior of the relative size-growth function for two low-density stands: (a) with no, and (b) with a few relatively large individual trees.

one much larger individual, likely part of an older residual age class. The observed *RSG* relationship is linear and each tree's relative growth is approximately proportional to its initial relative size. The predicted *RSG* function is nonlinear, indicating that the very large individual would attain growth more than proportional to its relative size. Most of the uncommon disagreements between observed and predicted *RSG* functions occurred in this type of situation with a few much larger residual trees in a stand. There was no particular bias apparent for these larger trees (i.e., on the average the predictions agreed with the observed), but the variation was high. Actual large trees grew more or less efficiently, as expressed by the *RTG/RTS* ratio, than smaller trees, with the shape and curvature of the actual *RSG* function depending on plot specific conditions such as age, species, and condition of the large residual trees. This type of variation in stand dynamics is not completely accounted for given the level of detail in our current modeling approach. However, we believe this indicates that this approach, with modifications, has promise for modeling multistoried or uneven-aged conditions.

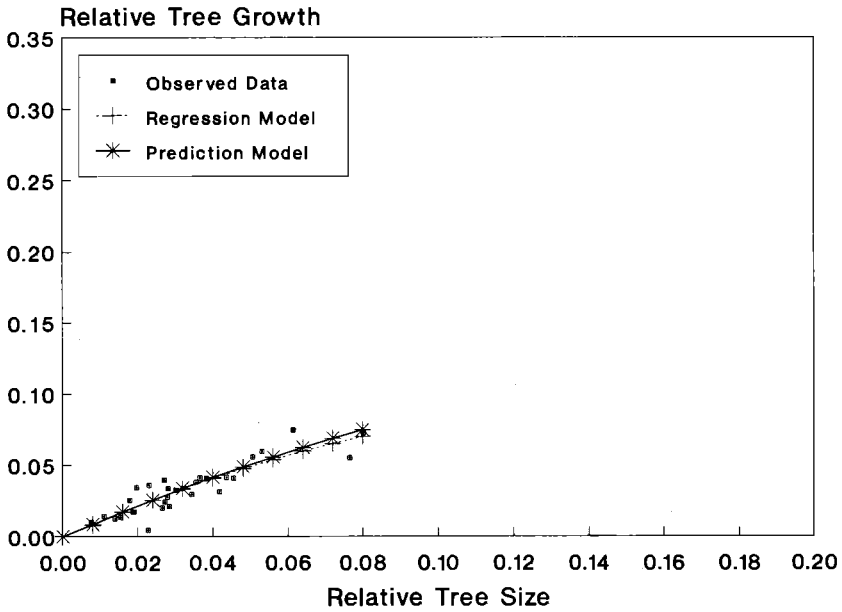
Relative size-growth relationships for two stands with relative densities just past crown closure are shown in Figure 2. Plot 250-5 (Figure 2a) is a uniform stand. Both the observed and predicted relationships are linear, with steeper slopes than for open-grown stands (Plot 50-3 in Figure 1a). Each tree's relative growth is nearly proportional to its relative size (the slope is about 1) suggesting that intertree competition and crown differentiation has begun. Plot 224-4 is about the same density as 250-5 but has more variation in tree size (Figure 2b), again primarily due to one much larger individual (17% of the initial total volume in this one tree). The result for this plot is similar to that illustrated in Figure 1b. The predicted *RSG* function is more nonlinear than the observed.

Two high density plots near the assumed lower limit of the self-thinning zone are shown in Figure 3. The *RSG* relationships remain nearly linear for both stands, and the observed and predicted relationships are almost identical. The relative variation (*CV*) in tree sizes for these plots was larger than average; typically, high density stands had higher *CV*s.

Overall, the predicted *RSG* functions match the observed patterns of within-stand growth well. In addition, the *RSG* function behavior conforms to findings and observations about density effects on stand growth dynamics by Hara (1984a, 1984b), Westoby (1982, 1984), and Drew and Flewelling (1979). Our results also suggest that stand structure affects growth distribution within a stand in addition to density effects. This was particularly true in low density stands where unusually large trees often attained proportionally even more growth than their initial relative size would indicate.

In summary, increasing stand density and mean tree size results in the *RSG* function changing from convex to straight, then to concave. Larger *CV* reduces the value of the predicted β_1 (steepness of the curve), but increases the value of the predicted β_2 (degree of curvature). Different stand structure, density, and tree size impact the shape of the *RSG* function, consequently, influence relative tree growth within the stand. If the *RSG* function is linear, the relative growth of individual trees is proportional to their relative sizes. If the *RSG* function is a convex curve, larger trees in the stand have larger relative growth than smaller trees. In contrast, if the *RSG* function is concave, smaller trees are more efficient than larger trees.

(a) Plot 250-5



(b) Plot 224-4

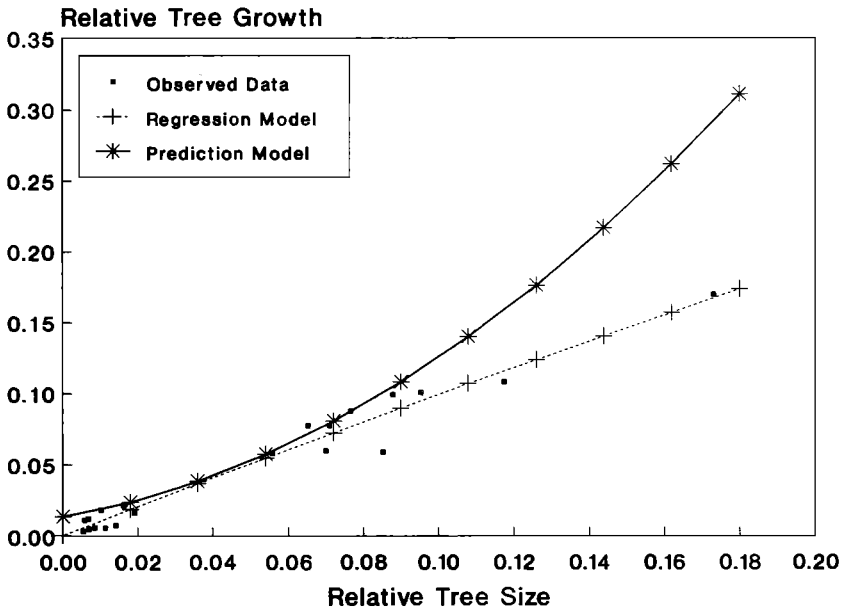
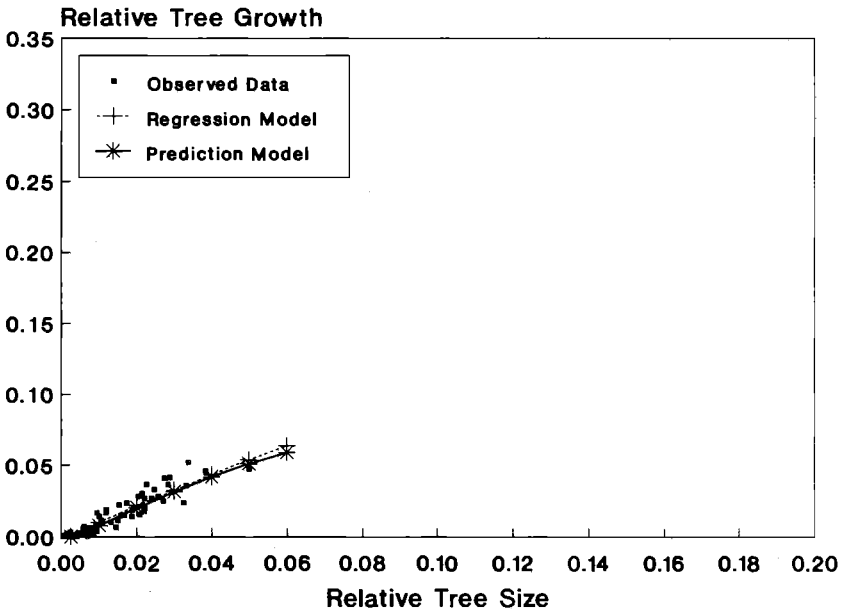


FIGURE 2. Behavior of the relative size-growth function for two stands just after approximate crown closure: (a) with no, and (b) with a few relatively large individual trees.

(a) Plot 14-2



(b) Plot 288-1

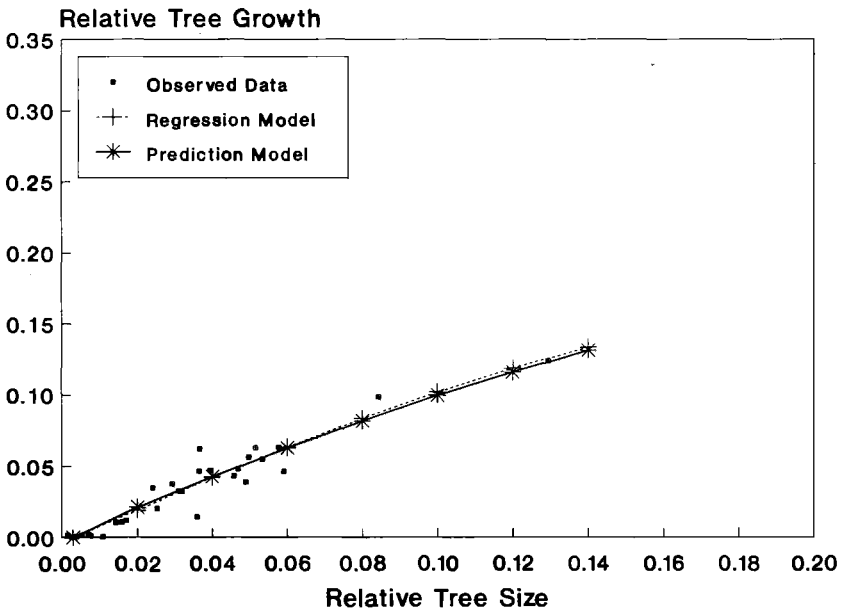


FIGURE 3. Behavior of the relative size-growth function for two high-density stands: (a) with no, and (b) with a few relatively large individual trees.

VERIFICATION OF THE RELATIVE SIZE-GROWTH FUNCTION

Four plots with a 6-yr growth period from year 2 to year 8 were selected from the Douglas-fir growth data to verify the behavior of the *RSG* function. These four plots comprised partially independent data because the growth period (from year 2 to year 8) was not directly used in the model fitting process, thus providing a set of initial conditions somewhat different than those used in model development. Stand variables at year 2 of the four plots are shown in Table 3. Two of the plots (plots 13-8 and 30-4) had been thinned, the rest (plots 13-6 and 30-6) were unthinned.

The stand variables at year 2 were input into Equations (2), (3), and (4) to predict the three parameters of the *RSG* function for each plot. Relative tree growth (*RTG*) was calculated for each alive tree during the 6-yr growth period according to its relative tree size (*RTS*), applying the plot-specific *RSG* function. Predicted tree volume growth was obtained by multiplying the actually observed 6-yr *stand* volume growth of each plot by each tree's *RTG*. Predicted 6-yr tree volume growth was compared with the corresponding observed 6-yr tree volume growth.

Prediction errors for the 6-yr volume growth were calculated for each tree and then averaged for each plot. The results indicated that, across all four plots, the *RSG* function overpredicted tree volume growth by 0.035 ft^3 , which was about 1.4% of the observed mean tree volume growth (2.5 ft^3) in 6 yr. The prediction error ranged from 0% to 8.3% of the observed mean tree volume growth. There was good agreement between observed and predicted volume growth across tree size classes within a stand, as shown in Figure 4. For each of the four plots, the predicted and observed 6-yr volume growth of individual trees were categorized into 2-in. diameter classes for initial tree dbh. A cumulative frequency distribution of the predicted tree volume growth was plotted and compared with that for the observed tree volume growth. For most plots the distributions of the predicted volume growth are very close to the distributions of the observed tree volume growth in both levels and shapes which varies from near linear to sigmoid. For plot 13-6 (Figure 4a), the *RSG* function overpredicts tree volume growth for small diameter classes, but underpredicts tree volume growth for diameter classes larger than 6 in. even though the overall curve shapes are similar. The reason may be that this plot has a number of small trees and large variation in tree size (*CV*

TABLE 3.

Stand variables at year 2 for the four plots used in verification of the relative size-growth function.

Plot	Thinned	Number of trees (/ac)	Quadratic mean diameter (in.)	Coefficient of variation (%)	Total volume (ft^3/ac)
13-6	No	1340	4.44	190	3093
13-8	Yes	260	6.90	71	1447
30-4	Yes	300	10.69	58	5230
30-6	No	620	8.53	102	6825

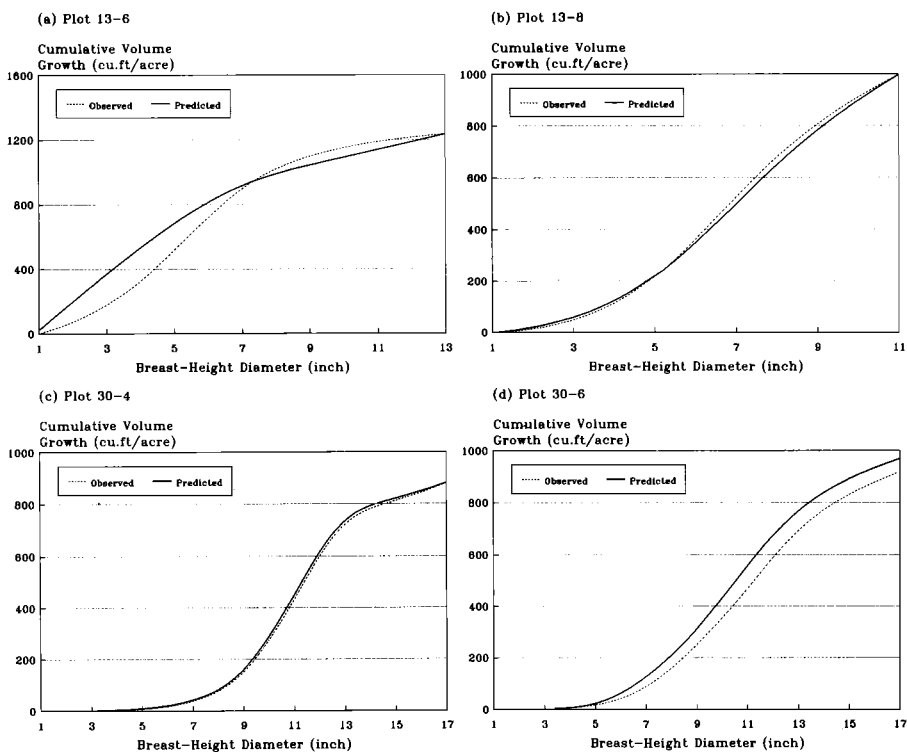


FIGURE 4. Cumulative frequency distribution of the predicted and observed 6-yr tree volume growth by diameter class at year 2 for (a) plot 13-6, (b) plot 13-8, (c) plot 30-4, and (d) plot 30-6.

is 190), due to a few larger individuals. This stand is approaching a storied condition, a situation that is relatively uncommon in the development data. The similarities in shapes between the observed and predicted volume growth distributions indicated that the *RSG* function reasonably represents the different patterns of within-stand volume growth across diameter classes.

CONCLUSIONS

The *RSG* function developed in this study provides a biologically meaningful way to represent stand dynamics and development. The characteristic shape of the *RSG* function is determined by initial stand density, mean tree size, and stand structure and describes the distribution of tree growth within a stand. Therefore, the *RSG* function can be used as a link between whole-stand and individual tree models. Stand volume growth predicted from a whole-stand model can be distributed to a list of individual trees if the tree list is available as input (Zhang 1990). Thus, consistent growth and yield estimates can be obtained at whole-stand or individual tree levels as desired to fulfill different decision-making requirements. Further, this disaggregation approach should also apply to other stand attributes (such as stand basal area growth), other tree species and/or geographic areas, and with appropriate modifications may apply to more complex stand structures.

Silvicultural interventions such as thinning directly alter the variables used for predicting the coefficients of the *RSG* function. Further, the *RSG* function performed equally well for thinned and unthinned stands. Therefore, we feel that the disaggregation function should reasonably represent the effects of density management manipulations on stand dynamics.

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