# Intermountain Forest Tree Nutrition Cooperative 

Supplemental Report No. 5

March 1992

Manuscript submitted to:
Forest Science

Disaggregating Stand Volume Growth
To Individual Trees

# DIBAGGREGATING BTAND VOLUNE GROWTH TO INDIVIDUAL TREES 

BY

LIANJUN ZHANG<br>JAMES A. MOORE<br>JAMES D. NEWBERRY


#### Abstract

The authors are, respectively, Research Associate and Professor, Department of Forest Resources, University of Idaho, Moscow, ID 83843, and Forest Biometrician, Potlatch Corporation, P. O. Box 1016, Lewiston, ID 83501. The support of Potlatch Corporation and the Intermountain Forest Tree Nutrition Cooperative is greatly appreciated. College of Forestry, Wildlife and Range Experiment Station contribution No. xxxx.


DIEAGGREGATING BTAND VOLUME GROWTH TO INDIVIDOAL TREES

## ABETRACT

A disaggregation function, relative size-growth (RSG) function, is proposed and developed to distribute stand volume growth to a list of individual trees. The relative size-growth (RSG) function is formulated as a quadratic equation relating relative tree growth to relative tree size in a stand. The shape of the RSG function is linear, convex, or concave depending on initial stand conditions and structure. A recursive system of equations is 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.

ADDITIONAL KEY WORDE: frequency distribution of tree size, stand dynamics, relative tree growth, Pseudotsuga menziesii var. glauca, inland Northwest.

## INYRODDCMION

Forest growth and yield models of varying degrees of complexity and detail have been developed to fulfill the different information requirements for decision making. In practice forest managers may be concerned with inconsistent growth and yield estimates from models of different resolution levels, each used for a specific set of decisions, or be forced to sacrifice efficiency and flexibility by using a single model for all projections. A number of researchers have attempted to unify modeling approaches or link whole stand models and size-class models or individual tree models. Two general approaches have been developed: (i) aggregating diameter distribution or individual tree characters to stand yield estimates (e.g. Daniels, 1981; Daniels and Burkhart, 1988; Strub and Burkhart, 1975), and (ii) disaggregating overall stand attributes into more detailed models such as individual tree models and/or size-class models (e.g. Burk and Newberry, 1984; Dahms, 1983; Harrison and Daniels, 1987; Knoebel et al., 1986; Smith and Brand, 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 classical approaches are based on the assumption that the distribution of tree sizes in a stand can be adequately characterized by a probability density function (pdf).

Some pdf's, 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. Additionally, 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, relative sizegrowth (RSG) function, is based on general concepts about 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). Many authors have studied the relationships between the frequency distribution of plant size and competitive interactions for many plant species including trees. Skewness is commonly found in stem size distributions of even-aged monocultures (Bliss and Reinker, 1964; Ford, 1975; Ford and Newbould, 1970; Gates, 1982; Harper, 1967; Koyama and Kira, 1956; West and Borough, 1983). Mohler et al. (1978) found that maximum positive skewness
occurs at the time self-thinning begins.
Hara (1984a, 1984b) and Kohyama and Hara (1989) proposed a stochastic model to investigate the dynamics of stand structure. The model describes the changes in size distribution with time as a function of mean growth rate, variance of growth rate, and mortality. The mean growth rate and variance of growth rate can be expressed as quadratic functions of plant size. They found that plant height, stem diameter, and individual plant weight each have specific size-dependent growth patterns.

Westoby $(1982,1984)$ introduced the concept of a distribution modifying function (DMF). The DMF represents the growth at a point in time of all individuals alive in a population. He proposed a polynomial equation to describe DMF in which plant size increment is a dependent variable and plant size is an independent variable. The dynamics of a stand can be delineated by a series of DMFs, and the shapes of DMF determine changes in the shape of the frequency distribution of plant size (Figure 1). Westoby (1984) also pointed out that most DMFs are of the quadratic form, which produce skewed frequency distributions of plant size. The above relationship can be related to the dynamics of an even-aged, single species stand illustrated by Long and Smith (1984). The concepts and ideas introduced by Hara (1984a, 1984b) and Westoby $(1982,1984)$ were used in this study as the basis of formulating the disaggregation function.

## DATA AND ANALYBIS METEODS

## I. Data Base for Model Development

Data used in this study represent single species, secondgrowth, managed, even-aged Douglas-fir (Pseudotsuga menziesii var. glauca (Beissn) Franco) stands (> $65 \%$ Douglas-fir by basal area) in the inland Northwest of the United States. The data were collected from 107 installations (sites) which were primarily established for thinning and fertilization experiments throughout six geographic regions (northern Idaho, western Montana, central Idaho, northeast Oregon, central Washington, and northeast Washington). A total of 206 control and/or thinning plots were utilized from four sources: the University of Idaho's McIntire-Stennis study, Intensive Timber Culture (a cooperative study between the University of Idaho and the Forest Service, USDA, Intermountain Forest and Range Experiment Station), Potlatch Corporation, and the Intermountain Forest Tree Nutrition Cooperative (IFTNC). Plot size ranged from 0.1 to 0.2 acre. No fertilized plots were used in the analysis. All trees were measured for both height (to the nearest 1 foot) and diameter (to the nearest 0.01 inch) at various growth periods (from 4 years to 14 years). Tree volume was calculated using the individual tree cubic foot volume equation for Douglas-fir in the Stand Prognosis Model (Wykoff et al., 1982). A majority of the stands had been operationally thinned at least five years prior to the growth
period used in this study. Some stands were thinned mechanically, and others were thinned from above and below to various residual densities.

Since ninety percent of the data had a common growth period of six years, six years was used for data analysis and model development. All data sets were converted to this specific growth period, e.g. a 14-year period was divided into two 6-year periods (year 0 to year 6 and year 8 to year 14), if the measurements at year 8 were available, resulting in the addition of 12 growth periods to the data base. Some mensurational attributes of the 218 Douglas-fir plots at the beginning of the 6-year growth period are summarized in Table 1.

## II. Analysis Methods

Ordinary least squares regression was utilized to estimate the parameters for linear models. Residual analysis and multicollinearity diagnostics (e.g. variance inflation factors (VIF)) 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 employed for parameter estimation. Residual analysis was conducted to detect model under-specification, departure from statistical assumptions, and existence of suspect data points. In addition, local minimum problems were checked by using different starting values for parameter estimates to ensure correct convergence.

## MODEL DEVELOPMENY

## I. Definition of The Relative Bize-Growth Function

We assume that overall development of even-aged stands follows a self-thinning process mathematically described by the -3/2 power "law". The dynamics of stand structure is affected by competitive interactions among individuals. Further, 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 general quadratic function was used to describe the relative size-growth (RSG) relationship:

$$
\begin{equation*}
R T G=\beta_{0}+\beta_{1} * R T S+\beta_{2} * R T S^{2} \tag{1}
\end{equation*}
$$

where $\beta_{0}, \beta_{1}$, and $\beta_{2}$ are coefficients to be estimated for each plot.
II. Characteristics of The Relative size-Growth Function
fit to 6-year growth data from each of 218 Douglas-fir plot observations using ordinary least squares regression. The three coefficients, $\beta_{0}, \beta_{1}$, and $\beta_{2}$, and associated statistics of the regression models, such as coefficient of determination ( $\mathbf{R}^{\mathbf{2}}$ ), were used to characterize the RSG function.

The regression analysis showed a strong relationship between initial relative tree size and subsequent relative tree growth. Most plot regressions (93\%) produced $\mathrm{R}^{2}$ larger than 0.60. Sixtythree percent of the 218 regressions had $R^{2}$ larger than 0.80. Since the RSG function is a quadratic equation, the signs and magnitudes of the coefficients of the function determine the degrees and shapes of curvature. The constant coefficient $\beta_{0}$ represents the level of the curve. The linear coefficient $\beta_{1}$ delineates the rate of change, either positive or negative depending on the sign of $\beta_{1}$. The quadratic coefficient $\beta_{2}$ reflects the shape of the curve. A positive $\beta_{2}$ indicates that the curve is convex and a negative $\beta_{2}$ defines a concave curve. The slopes of the RSG function were always positive since all the linear coefficients $\beta_{1}$ had positive values. Sixty-seven percent of the 218 RSG functions had quadratic coefficients $\beta_{2}$ not significantly different than zero ( $\alpha=0.05$ ). This indicates that the relationship between RTG and RTS is usually linear. of the seventy-two RSG functions (33\%) with estimates of $\boldsymbol{\beta}_{2}$ significantly different from zero, twelve plots had a positive $\boldsymbol{\beta}_{2}$ producing convex curves and sixty plots had a negative $\beta_{2}$ representing a concave relationship.

Pearson's correlation coefficients between pairs of the three parameters were -0.90 ( $\beta_{0}$ versus $\beta_{1}$ ), 0.63 ( $\beta_{0}$ versus $\beta_{2}$ ), and $-0.88\left(\beta_{1}\right.$ versus $\left.\beta_{2}\right)$. Generally, when $\beta_{1}$ equals one, both $\beta_{0}$ and $\beta_{2}$ are nearly equal to zero resulting in a straight line through the origin. When the linear coefficient $\beta_{1}$ is less than one, both $\beta_{0}$ and $\beta_{2}$ are positive producing a convex curve with a positive intercept. In contrast, when $\beta_{1}$ is larger than one, both $\beta_{0}$ and $\beta_{2}$ have negative values which produce a concave curve with a negative intercept (Figures 2(a), (b), and (c)). Thus, three basic shapes for the RSG function exist: linear, convex, and concave. According to Westoby (1982, 1984), three basic DMF functions determine the frequency distribution of plant size to be normal, positively and negatively skewed, respectively.
III. Prediction Models for the Coefficients of The Relative Size-Growth Function

The relationship among $\beta_{0}, \beta_{1}$ and $\beta_{2}$ of the relative sizegrowth (RSG) function implies that the linear coefficient $\beta_{1}$ plays the most important role among the three coefficients. When $\beta_{1}$ 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 withinstand 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 $\beta_{0}, \beta_{1}$ and $\beta_{2}$ 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 of 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). Common statistics used to describe a frequency distribution are the mean, standard deviation, and skewness. Ecological studies showed that coefficient of variation is also 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 (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 is formulated as follows:

$$
\begin{aligned}
& \beta_{1}=f(N, D, C V), \\
& \beta_{2}=f\left(\beta_{1}, N, D, C V\right), \\
& \beta_{0}=f\left(\beta_{1}, \beta_{2}, N, D, C V\right) .
\end{aligned}
$$

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) or simple recursive system (Fomby et al., 1984). In this case, OLS provides an optimal estimating technique (Johnston, 1972; Pindyck and Rubinfeld, 1976; 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 equations in the system was estimated using the 6-year 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 $\chi^{2}$-distribution with 3 degrees of freedom. Thus, the variance-covariance matrix of the equations in the recursive system is diagonal. Therefore, each equation in this simple recursive system is appropriately
estimated by the OLS procedures we employed.
(1). Prediction model for the coefficient $\boldsymbol{\beta}_{1}$

Nonlinear relationships between the coefficient $\beta_{1}$ and three stand variables ( $N, D, C V$ ) were observed. After evaluating different nonlinear equation forms in terms of model fitting, residual analysis and biological interpretation, the following prediction model for $\beta_{1}$ resulted:

$$
\begin{equation*}
\beta_{1}=N *\left(1-e^{\frac{-0.0246 . D}{C V}}\right) . \tag{2}
\end{equation*}
$$

The asymptotic error of the estimated parameter was 0.0007967 . A slight trend in the residual plot versus the predicted $\beta_{1}$ existed. Adding an intercept to the equation (2) eliminated the trend in the residual plot. However, the estimated intercept was nearly equal to one, resulting in a predicted $\beta_{1}$ always larger than one and consequent poor model behavior. Therefore, we selected the equation (2) as the prediction model for $\beta_{1}$.
(2). Prediction model for the coefficient $\boldsymbol{\beta}_{2}$

The prediction model for the quadratic coefficient $\beta_{2}$ was developed using the coefficient $\beta_{1}$ and two stand variables, $D$ and $C V$, as independent variables. Number of trees (N) was statistically nonsignificant in the analysis, unlike the
prediction equation for $\beta_{1}$. The resulting model was:

$$
\begin{align*}
\beta_{2}= & 5.9978-10.4822 * \beta_{1}+2.1194 * \log (D) \\
& -61.9929 *\left(\frac{1}{C V}\right) . \tag{3}
\end{align*}
$$

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 plot of residuals against the predicted values of $\beta_{2}$ showed a random pattern around zero with no detectable trend.
(3). Prediction model for the coefficient $\boldsymbol{\beta}_{0}$

The coefficient $\beta_{0}$ was related to both linear coefficient $\beta_{1}$ and quadratic coefficient $\beta_{2}$ of the RSG function, as well as to the three stand variables. The model was:

$$
\begin{align*}
\beta_{0}= & 0.02765-0.03782 * \beta_{1}-0.001559 * \beta_{2} \\
& +0.002393 *\left(\frac{N}{1000}\right)^{2}+0.004277 * \log (D)  \tag{4}\\
& +0.1176 *\left(\frac{1}{C V}\right) .
\end{align*}
$$

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 $\beta_{1}$ and $\beta_{2}$ 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 EVALDATION AND VERIFICATION

Often model evaluation and verification are performed on data not used in model fitting process (i.e. independent data). Although using independent data has several positive aspects, we chose to test the relative size-growth (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 between 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.

## I. Evaluation of the Relative size-Growth Function

Eight plots were selected from the Douglas-fir growth data
to illustrate four stand development phases.given two different stand structures for each density class. The initial stand attributes, number of trees, quadratic mean diameter, coefficient of variation of tree volume, 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 $\beta_{1}$ of the RSG function using equation (2). Then the predicted $\beta_{1}$ and observed stand variables were input into equation (3) to predict the coefficient $\beta_{2}$. Finally the coefficient $\beta_{0}$ was obtained by equation (4) using the predicted $\beta_{1}, \beta_{2}$ and observed three stand variables. The predicted coefficients of the RSG function are given in Table 3 with corresponding coefficients estimated from regressions fit to actual Douglas-fir growth data. 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 3. Plot 50-3 is a uniform stand with little variation in tree size and represents plantation conditions (Figure $3(a)$ ). Before crown closure (< 0.15 relative density according to Drew and Flewelling (1979)) the trees are growing as a collection of individuals without inter-tree competition. The observed and predicted RSG function reflect this condition as a line with little slope, i.e. all trees contribute about the same relative growth. Plot 257-6 (Figure $3(b)$ ) 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 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 non-linear indicating that the very large individual would attain growth more than proportional to its relative size. It is noteworthy that most of the uncommon large 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, it appears that this approach has promise for modeling multi-storied or uneven-aged conditions.

Relative size-growth relationships for two stands with relative densities just past crown closure are shown in Figure 4. Plot 250-5 (Figure 4 (a)) is a uniform stand. Both the observed and predicted relationship is linear with a steeper slope than for open-grown stands (Plot 50-3 in Figure 3(a)). Each tree's relative growth is nearly proportional to its relative size (the
slope is about one) suggesting that inter-tree 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 $4(b))$, 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 $3(b)$. The predicted RSG function is more non-linear than the observed.

Two stands of moderate density are shown in Figure 5. The RSG relationship is linear for plot 262-3 (Figure 5(a)), and the predicted and fitted curves are nearly coincident. Crown differentiation, but not substantial density dependent mortality, has begun in this stand and the slope of the RSG function is steeper than for lower relative densities. Plot 13-6 (Figure $5(b))$ has large variation in tree size, again due to a few larger individuals. The RSG relationship, given higher density than the previous plots, is predicted to be linear even with high variation in tree size. The observed RSG function shows that the largest trees were growing less efficiently than the smaller trees. For example, the largest tree comprised about 14.5 percent of the initial volume but contributed only about 9 percent to growth.

Two high density plots near the assumed lower limit of the self-thinning zone are shown in Figure 6. 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 were larger than
average, typically high density stands had higher Cvs.
Overall, the predicted RSG functions match the observed patterns of within-stand growth well. In addition, 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 $\beta_{1}$ (steepness of the curve), but increases the value of the predicted $\beta_{2}$ (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.
II. Verification of the Relative size-Growth Function

Six plots with a 6-year 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 six plots comprised partially independent data because the growth period (from year 2 to year 8) was not directly used in 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 six plots are shown in Table 4. These plots were selected to cover a relatively broad range of stand conditions, e.g. stand density ranged from 260 to 1420 trees per acre, quadratic mean tree diameter from 4.4 to 10.7 inches, and stand total volume from 1447 to 6825 cubic feet per acre. Three of the plots (i.e. plots 13-4, 13-8, and 304) had been thinned at year 0 , the rest were unthinned (i.e. plots 13-2, 13-6 and 30-6).

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-year 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-year stand volume growth of each plot by each tree's RTG. Predicted 6-year tree volume growth was compared with the corresponding observed 6-year tree volume growth. Prediction error was defined as the difference between
observation and prediction. Positive values of error are underprediction and negative values over-prediction.

Prediction errors for the 6-year volume growth were calculated for each tree and then averaged for each plot. Since the distributions of the observed tree volume growth and prediction error for some plots were asymmetric, median prediction error may be a better measure for central tendency. Table 5 shows the means and medians of the observed 6-year volume growth and prediction error for the six plots. Overall mean and median were also calculated over the six plots. The results indicated that across all six plots, the RSG function overpredicted tree volume growth by 0.0235 cubic feet, which was about $1.1 \%$ of the observed mean tree volume growth in 6 years ( 2.20 cubic feet). If median terms were used, the RSG function over-predicted tree volume growth by 0.16 cubic feet ( $8.8 \%$ of the observed median tree volume growth).

The performance of the RSG function across diameter classes within a stand was also examined. For each of the six plots, the predicted and observed 6-year volume growth of individual trees were categorized into 2 -inch 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 (Figure 7). For most plots the distributions of the predicted volume growth are nearly identical 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 7(c)), the RSG function over-predicts tree volume growth for small diameter classes, but under-predicts tree volume growth for diameter classes larger than 6 inches 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 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.

## CONCLOEIONS

The relative size-growth (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 a whole-stand model and individual tree model. Stand volume growth predicted from a whole-stand model can be distributed among a list of individual trees if the tree list is available as input (2hang, 1990). Thus, consistent growth and yield estimates can be obtained at whole-stand or individual tree
levels as desired to fulfill different decision making. 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.

## LITERATURE CITED

Bendel, R. B., S. S. Higgins, J. E. Teberg, and D. A. Pyke. 1989. Comparison of skewness coefficient, coefficient of variation, and Gini coefficient as inequality measures within populations. Oecologia 78:394-400.

Bliss, C. I. and K. A. Reinker. 1964. A lognormal approach to diameter distribution in even-aged stands. For. Sci. 10:350-360.

Borders, B. E. 1989. Systems of equations in forest stand modeling. For. Sci. 35:548-556.

Burk, T. E. and J. D. Newberry. 1984. A simple algorithm for moment-based recovery of Weibull distribution parameters. For. Sci. 30:329-332.

Burkhart, H. E. 1987. Data collection and modeling approaches for forest growth and yield prediction. p3-16, In: Proceedings of a seminar series and workshop held Jan.-Mar, 1987, Predicting Forest Growth and Yield: Current Issues, Future Prospects, Ed. by H. N. Chappell and D. A. Maguire. Coll. of For. Res., Univ. of Washington, Seattle, WA. Contribution Number 58-1987.

Dahms, W. G. 1983. Growth-simulation model for lodgepole pine in
central Oregon. USDA For. Serv., Pacific Northwest For. \& Range Exp. Stat., Portland, Oregon. Res. Pap. PNW-302, 22p.

Daniels, R. F. 1981. An integrated system of stand models for loblolly pine. Ph.D. Dissertation, Va. Polytech. Inst. and State Univ., Blacksburg, Va., 108p.

Daniels, R. F. and H. E. Burkhart. 1988. An integrated system of forest stand models. For. Ecol. and Manag. 23:159-177.

Drew, T. J. and J. W. Flewelling. 1979. Stand density management: an alternative approach and its application to Douglas-fir plantations. For. Sci. 25:518-532.

Fomby, T. B., R. C. Hill, and S. R. Johnson. 1984. Advanced econometric methods. Springer-Verlag, New York, 624p.

Ford, E. D. 1975. Competition and stand structure in some even-aged plant monocultures. J. Ecol. 63:311-333.

Ford, E. D. and P. J. Newbould. 1970. Stand structure and dry weight production through the sweet chestnut coppice cycle. J. Ecol. 58:275-296.

Gates, D. J. 1982. Competition and skewness in plantations. J. Theor. Biol. 94:909-922.

Hara, T. 1984a. A stochastic model and the moment dynamics of the growth and size distribution in plant population. J. Theor. Biol. 109:173-190.

Hara, T. 1984b. Dynamics of stand structure in plant monocultures. J. Theor. Biol. 110:223-239.

Harper, J. L. 1967. A darwinian approach to plant ecology. J. Ecol. 55:247-270.

Harrison, W. C. and R. F. Daniels. 1987. A new biomathematical model for growth and yield of loblolly pine plantations. IUFRO Forest Growth Modeling and Prediction Conference, Minneapolis, MN, Aug. 1987. USDA For. Serv. Gen. Tech. Rep. NC-120, p293-304.

Hozumi, K., K. Shinozaki, and Y. Tadaki. 1968. Studies on the frequency distribution of the weight of individual trees in forest stands: 1. A new approach towards the analysis of the distribution function and the $-3 / 2$ th power distribution. Jap. J. Ecol. 18:10-20.

Kmenta, J. 1971. Elements of econometrics. Macmillan Company, New York. 655p.

Johnston, J. 1972. Econometric methods. 2nd ed. McGraw-Hill Book Company, New York, 437p.

Judge, G. G., R. C. Hill, W. E. Griffiths, H. Lutkepohl, and T. C. Lee. 1988. Introduction to the theory and practice of econometrics. John Wiley \& Sons, New York, 1024p.

Knoebel, B. R., H. E. Burkhart and D. E. Beck. 1986. A growth and yield model for thinned stands of yellow-poplar. For. Sci. Monogr. 27, 62p.

Knox, R. G. and R. K. Peet. 1989. Population dynamics in loblolly pine stands: Changes in skewness and size inequality. Ecology 70(4): 1153-1166.

Kohyama, T. and T. Hara. 1989. Frequency distribution of tree growth rate in natural forest stands. Ann. Bot. 64:47-57.

Koyama, H. and T. Kira. 1956. Intraspecific competition among higher plants: VIII. Frequency distribution of individual plant weight as affected by the interaction between plants. J. Inst. Polytech. Osaka City Univ. Ser. D, 7:73-94.

Long, J. N. and F. W. Smith. 1984. Relation between size and density in developing stands: A description and possible mechanisms. For. Ecol. and Manag. 7:191-206.

Mohler, C. L., P. L. Marks and D. G. Sprugel. 1978. Stand structure and allometry of trees during self-thinning of pure stands. J. Ecol. 66:599-614.

Pienaar, L. V. and W. M. Harrison. 1984. A stand table projection approach to yield prediction in unthinned even-aged stands. For. Sci. 34:804-808.

Pindyck, R. S. and D. L. Rubinfeld. 1981. Econometric models and economic forecasts. 2nd ed. McGraw-Hill. New York. 630 p .

Smith, N. J. and D. G. Brand. 1987. Compatible growth models and stand density diagrams. IUFRO Forest Growth Modeling and Prediction Conference, Minneapolis, MN, Aug. 1987. USDA For. Ser. Gen. Tech. Rep. NC-120, p636-643.

Stage, A. R. 1969. A growth definition for stocking: units, sampling, and interpretation. For. Sci. 15:255-265.

Strub, M. R. and H. E. Burkhart. 1975. A class-interval-free method for obtaining expected yields from diameter distributions. For. Sci. 21:67-69.

Theil, H. 1971. Principles of econometrics. John Wiley \& Sons Inc.,

New York, 736p.
West, P. W. and C. J. Borough. 1983. Tree suppression and the self-thinning rule in a monoculture of Pinus radiata $D$. Don. Ann. Bot. 52:149-158.

Westoby, M. 1982. Frequency distribution of plant size during competitive growth of stands: the operation of distributionmodifying functions. Ann. Bot. 50:733-735.

Westoby, M. 1984. The self-thinning rule. Adv. in Ecol. Res. 14:167-225.

Wykoff, W. R., N. L. Crookston and A. R. Stage. 1982. User's guide to the stand prognosis model. USDA For. Serv. Gen. Tech. Res. INT-133. Ogden, Utah, Intermountain For. \& Range Exp. Stn. 112p.

Zhang, L. 1990. A compatible forest growth and yield prediction system for managed Douglas-fir stands in the Inland Northwest. Ph.D. Dissertation, University of Idaho, Moscow, ID. 210p.

Table 1. Averages and ranges of stand attributes at the beginning of a 6-year growth period for 218 Douglas-fir plots

| Attribute | Mean | Min | Max |
| :--- | ---: | ---: | ---: |
|  |  |  |  |
| DF site index (ft e 50 yr) | 70 | 39 | 105 |
| Stand total age (year) | 61 | 11 | 100 |
| Number of trees (trees/ac) | 318 | 90 | 1640 |
| Top height (feet) | 73 | 12 | 118 |
| Basal area (ft ${ }^{2} / \mathrm{ac}$ ) | 140 | 3 | 370 |
| Quadratic mean diameter (in.) | 9.8 | 1.2 | 16.9 |
| Total volume (ft $/ \mathrm{ac}$ ) | 3669 | 33 | 9416 |
| Mean tree volume (ft ${ }^{3}$ ) | 15 | 0.1 | 59 |
| Relative density index | 0.20 | $<0.01$ | 0.84 |
| Coefficient of variation | 66 | 25 | 224 |
| of tree volume distribution |  |  |  |

Relative density index represents Drew-Flewelling's relative density index

Table 2. Stand variables and example stand conditions for eight plots used in evaluation of the relative size -growth function

| Plot | Stand Variables |  |  |  |
| :---: | :---: | :---: | :---: | :---: |
|  | Number of Trees | Quadratic Mean Diameter | 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 |
| 262-3 | 350 | 9.52 | 66 | 0.32 |
| 13-6 | 1640 | 3.96 | 223 | 0.34 |
| 14-2 | 1020 | 6.18 | 110 | 0.51 |
| 288-1 | 300 | 12.73 | 81 | 0.51 |

Table 3. Estimated coefficients from regressions and predicted coefficients from the prediction models of the relative size-growth function for eight example plots

| Plot | $\beta_{0}$ |  | $\beta_{1}$ |  | $\beta_{2}$ |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Regression model | Prediction model | Regression model | Prediction model | Regression model | Prediction model |
| 50-3 | 0.013 | 0.018 | 0.384 | 0.248 | 2.566 | 2.566 |
| 257-6 | 0.003 | 0.014 | 0.914 | 0.455 | 0.433 | 6.074 |
| 250-5 | -0.001 | -0.001 | 1.203 | 1.156 | -3.894 | -2.669 |
| 224-4 | 0.001 | 0.014 | 1.013 | 0.442 | -0.303 | 6.707 |
| 262-3 | -0.002 | -0.002 | 1.125 | 1.234 | -1.348 | -3.091 |
| 13-6 | 0.001 | 0.012 | 1.088 | 0.714 | -3.224 | 1.158 |
| 14-2 | -0.002 | -0.006 | 1.207 | 1.412 | -1.866 | -5.513 |
| 288-1 | -0.006 | -0.001 | 1.272 | 1.159 | -1.996 | -1.528 |

Table 4. Stand variables at year 2 for the six plots used in verification of the relative size-growth function

| Plot | Thinned | Number <br> of <br> Trees | Quadratic <br> Mean <br> Diameter | Coefficient <br> of <br> Variation | Total <br> Volume <br> $\left(\mathrm{ft}^{3} / \mathrm{a}\right)$ |
| :--- | :--- | ---: | ---: | ---: | ---: |
| $13-2$ | No | 1420 | 4.40 | 120 | 2950 |
| $13-4$ | Yes | 520 | 5.45 | 69 | 1523 |
| $13-6$ | 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 |

Table 5. Mean and median prediction errors of 6-year volume growth of individual trees for the six verification plots

|  | Mean Volume <br> Growth $\left(\mathrm{ft}^{3}\right)$ | Median Volume <br> Growth <br> $\left(\mathrm{ft}^{3}\right)$ | Mean Error <br> $\left(\mathrm{ft}^{3}\right)$ | Median Error <br> $\left(\mathrm{ft}^{3}\right)$ |
| :---: | :---: | :---: | :---: | :---: |
| $13-2$ | 1.292 | 0.715 | -0.0013 | -0.06 |
| $13-4$ | 1.925 | 1.715 | +0.0006 | -0.06 |
| $13-6$ | 1.340 | 0.740 | +0.0003 | -0.26 |
| $13-8$ | 3.985 | 3.900 | +0.0000 | -0.19 |
| $30-4$ | 3.034 | 3.070 | -0.0067 | -0.11 |
| $30-6$ | 1.611 | 0.790 | -0.1344 | -0.30 |
| Overall | 2.198 | 1.822 | -0.0235 | -0.16 |

## IIgT OF FIGURES

Figure 1: Distribution modifying function (DMF) and their effects on the shape of size frequency distribution (after Westoby, 1984).

Figure 2: Relationships between the coefficients of the relative size-growth function: (a) $\beta_{0}$ versus $\beta_{1},(b) \beta_{1}$ versus $\beta_{2}$, (c) $\beta_{0}$ versus $\beta_{2}$.

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

Figure 4: 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.

Figure 5: Behavior of the relative size-growth function for two moderate-density stands: (a) with no, and (b) with a few relatively large individual trees.

Figure 6: Behavior of the relative size-growth function for two high-density stands: (a) with no, and (b) with a few relatively large individual trees.

Figure 7: Cumulative frequency distribution of the predicted and observed 6-year tree volume growth by diameter class at year 2 for (a) plot 13-2, (b) plot 13-4, (c) plot 13-6, (d) plot 13-6, (e) plot 30-4, and (f) plot 30-6.




(a) Plot 50-3

(b) Plot 257-6

(a) Plot 250-5

(b) Plot 224-4

(a) Plot 262-3

(b) Plot 13-6

(a) Plot 14-2

(b) Plot 288-1

(a) Plot 13-2

(b) Plot 13-4

(c) Plot 13-6

(d) Plot 13-8

(e) Plot 30-4

(f) Plot $30-6$


