
Evaluation of the Size-Density Relationships for Pure Red Alder and Douglas-Fir Stands

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ABSTRACT. Size-density trajectories were developed for pure red alder (*Alnus rubra* Bong) and Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) stands with quadratic mean diameter of the stand as the tree-size variable. The resulting self-thinning or maximum size-density line for red alder had a steeper slope (-0.64) than that for Douglas-fir (-0.52). The assumption of a common slope for all species is therefore not supported by our study. For red alder, the shape of the size-density trajectory and the elevation of the maximum line were not influenced by initial density or stand origin. Red alder and Douglas-fir mortality started at a relative density of 44% and 58%, respectively. FOR. SCI. 39(1):7-27.

ADDITIONAL KEY WORDS. Self-thinning, size-density trajectory, Stand Density Index.

YODA ET AL. (1963) found that maximum average plant size for a given plant density in even aged monospecific plant populations can be characterized by self-thinning line, expressed mathematically as

$$\log(w) = a_1 + a_2 * \log(N) \quad (1)$$

where

w = maximum average plant size,

N = plant density,

a_1 = the intercept, and

a_2 = the slope parameter.

When the size variable is volume or weight, and the density variable is number of plants per unit area, the self-thinning line has a slope of -1.5 for a variety of species (for review see White 1980), and is known as the $-3/2$ power rule. Although the universality of the parameter values of the self-thinning line (Zeide 1988, Barreto 1989) and the method used to establish this line (Weller et al. 1985, Weller 1987a, 1987b, have been questioned, the self-thinning line has been used successfully in a number of forestry applications (Reineke 1933, Drew and Flewelling 1979, Curtis 1982, Long 1985, Hyink et al. 1988, Hester et al. 1989, Smith 1989). Most applications assume that the slope of the self-thinning line is based on either the $-3/2$ power rule (Yoda et al. 1963), where w is defined as

biomass, or a Reineke (1933) slope of -0.62 , where w is quadratic mean diameter.

While the self-thinning line expresses the upper boundary of all possible size-density combinations (Yoda et al. 1963), the size-density relationship focuses on the time-trajectory of individual populations. It covers the full spectrum of stand development from phases of growth without mortality over a curved approach to a linear phase (White 1980, 1981) (Figure 1), which is commonly labeled the "maximum size-density line."

Smith and Hann (1984) developed a size-density equation using data from stands that had reached the maximum size-density line and stands that were self-thinning but still below the maximum line. This equation, therefore, describes not only the location of the maximum line but also the approach to maximum size-density and thus avoids the problem of subjectively selecting stands that are on the maximum line (Weller et al. 1985). By using a regression equation, the analysis yields the size-density trajectory that average stands would follow. Individual stands will fall above or below this line (see also Figures 2 and 3). While this "average maximum" needs to be distinguished from an "absolute maximum" (put-

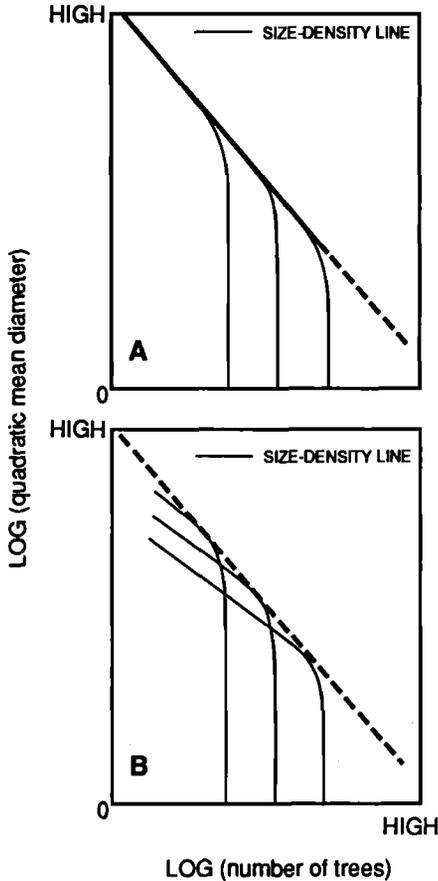


FIGURE 1. Possible size-density trajectories of stands undergoing self-thinning. A. Stands move along the maximum size-density line (Shape A). B. Stands approach a line connecting the maximum size-density points and then fall below (Shape B).

ting a line above all data points) and an "upper skin maximum" (putting a line through the upper 5% of the data points), it was chosen because it allows investigation of our objectives. In addition, the size-density relationship can be expanded into a growth model by including a growth or mortality equation (e.g., Smith and Hann 1986).

In a theoretical paper, McFadden and Oliver (1988) present two possible patterns of how stands might approach the maximum size-density line (Figure 1). The figures have been modified to show a gradual approach rather than an abrupt transition to the maximum size-density line. Figure 1A shows stands asymptotically approaching a common line, which is also the maximum size-density line. This size-density relationship with shape A represents McFadden and Oliver's (1988) type I and II shapes. Figure 1B shows stands first approaching a line representing maximum possible size-density points and then departing from the boundary to approach parallel lines, the intercepts of which are negatively correlated with initial density. This size-density relationship with shape B represents a Type III shape as defined by McFadden and Oliver (1988).

An important issue connected with the development of size-density trajectories and their application to management guides is the onset of competition-induced mortality. In Figure 1, this is the point where the trajectories leave the vertical and begin to curve left as they approach the maximum size-density line.

We chose stands of red alder (*Alnus rubra* Bong.) and Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) as test systems because those species are sympatric in the Pacific Northwest and are of economic importance. Red alder is a nitrogen-fixing pioneer, and Douglas-fir is a mature forest dominant (Franklin and Dyrness 1988). Both are common associates in early successional stages, especially in forest plantations.

Our overall goal was to investigate the size-density relationships of red alder and Douglas-fir by developing analytical models of their size-density relationships using quadratic mean diameter (QMD) of the stand as the size variable. To meet this goal, our specific objectives were:

1. to determine if the elevation of the size-density relationships for pure red alder stands was inversely related to initial density (i.e., to compare size-density relationships in Figures 1A and 1B);
2. to examine whether the size-density relationships of red alder stands with different initial densities exhibit the same curvature;
3. to examine whether density-dependent mortality in red alder stands starts at a constant relative density regardless of initial density;
4. to compare size-density relationships for red alder in natural stands and in plantations; and
5. to compare size-density relationships for red alder and Douglas-fir stands.

THE DATA

All data were from fixed-area plots which had no signs of past disturbance and exhibited mortality during the measurement periods. A stand was defined as pure red alder or pure Douglas-fir if at least 80% of its basal area was in that species (Worthington et al. 1960, King 1966).

The red alder data set consisted of two subsets of even-aged plots. Nine plots (80 individual measurements) were from a spacing study in a plantation located in

the Coast Range of northwest Oregon and 15 plots (81 individual measurements) were from natural stands in western Oregon and Washington and southwest British Columbia. Data from the spacing study were kept separate because these plots had information about effective planting density (excluding planting mortality) that was needed to assess the role of initial size-density effects (Objectives 1 through 3).

The data for Douglas-fir stands were from the control plots on the installations of the Regional Fertilizer and Nutritional Research Program (Opalach 1989), the Level-of-Growing-Stock study (Curtis and Marshall 1986), and a study by J.E. King (1973). To ensure geographic similarity between data sets for the two species only plots located in western Oregon, western Washington or southwest British Columbia were included. In addition, plots with an annual mortality rate $>6.16\%$ (two standard deviations above the mean mortality rate) for any measurement period were assumed to have experienced disturbance-related mortality. Fourteen Douglas-fir plots were dropped, leaving 58. All red alder plots had $<6\%$ average annual mortality rate. A detailed description of the data set is presented in Table 1.

The data were from plots with different sizes: <0.05 ha ($N = 41$); 0.05 – 0.1 ha (30); 0.1 – 0.15 ha (4); 0.15 – 0.2 ha (1); >0.2 ha (6). In small plots, estimates of stand characteristics have a higher variance because growth and mortality within the plot are influenced by adjacent, unknown stand conditions (Smith 1975, Curtis 1983). To adjust for the pattern of increased variance (Zumrawi 1990) we used plot size as weight in the regression analysis. Stand QMD was selected to represent mean tree size because it can be measured accurately and easily and is closely related to crown size (Brigleb 1952, Smith 1968) and tree biomass (Hughes 1971). Relative density values were calculated by dividing actual stand density by predicted maximum stand density from the particular equation's maximum size-density line.

The equation forms in our study were nonlinear. We used the Marquardt-algorithm (Marquardt 1963) and the DUD algorithm (Ralston and Jennrich 1978) of the nonlinear component of the SAS statistical package (SAS Institute, Inc. 1987) to estimate the parameters.

Conclusions from previous analyses were needed for succeeding ones, so we worked sequentially, starting with our first objective. The sequential analysis leads to concern about loss of degrees of freedom for hypothesis testing. A loss of an unknown amount of degrees of freedom results in testing with a higher α -level than specified, which can lead to falsely declaring models significantly different. While this has to be considered in the analysis, there are not enough data available to perform model form development and parameter estimation with independent data sets.

A second concern in our analysis is the use of repeated measures, which can lead to a lack of independence in the model errors. A high positive correlation of errors has been shown to lead to underestimation of the standard errors (Seber and Wild 1989). While the number of repeated measurements of individual plots was insufficient to determine a correlation structure (the lag-residual plots showed no trends), the high number of independent plots should break up correlation between error terms (Seber and Wild 1989). In addition, a longer time period between measurements has been shown to result in lower correlation between the errors (Gertner 1985, Seber and Wild 1989). These points lead us to conclude

that the correlation between model errors and a potential underestimation of the standard errors should be considered when evaluating the results, but that the autocorrelation is not high enough to invalidate hypothesis testing.

OBJECTIVE 1 (EFFECT OF INITIAL DENSITY ON TRAJECTORY SHAPE)

The size-density trajectory was developed from log-log transformed data (Smith and Hann 1984) and was assumed to consist of two parts: a linear portion, which is the maximum size-density or self-thinning line [Equation (1)], and a nonlinear portion in which the trajectory approaches the maximum line asymptotically. When initial density is known, the size-density trajectory is modeled as the difference of a linear and negative exponential function using the equation form of Smith and Hann (1984):

$$Y_i = a_1 + a_2 * X_i - a_1 * a_4 * \exp(a_3 * (X_0 - X_i)) \quad (2)$$

where

Y_i = logarithm of quadratic mean diameter (cm)

X_i = logarithm of density (tpha)

X_0 = logarithm of initial density (tpha)

a_1 = intercept of maximum size-density line

a_2 = slope of maximum size-density line

a_3 = shape parameter for size-density trajectory

a_4 = adjustment for relative density when mortality starts.

i = measurement identifiers (1 = initial, 2 = second, etc.)

Equation (2) represents a size-density relationship with shape A (Figure 1A). Initial values for the a_1 and a_2 parameters were calculated by fitting Equation (1) to the size-density combinations of the normal yield table for red alder (Worthington et al. 1960) ($a_1 = 7.3$, $a_2 = -0.62$).

TABLE 1.

Data description: Mean values for pure red alder and pure Douglas-fir stands (ranges in parenthesis).

	Red alder ^a	Douglas-fir ^a
Number of plots	24	58
Number of measurements	161	282
Tress/ha	2550 (420-11030)	1560 (290-4660)
Quadratic mean diameter (cm)	15 (3-32)	24 (9-57)
Age at first measurement (yr)	17 (1-34)	30 (6-43)
Measurement period (yr)	16 (4-30)	15 (6-35)
Site index (m) ^b	31 (19-35)	37 (23-45)

^a Pure stands are defined as having 80 to 100% basal area in red alder or Douglas-fir.

^b Red alder and Douglas-fir site indices are based on Worthington et al. (1960) and King (1966), respectively.

To compare the fits of size-density relationships with shapes A and B (Figure 1), an equation for shape B was formulated by varying the intercept term with initial density:

$$Y_i = a_1 + b_1 * X_0 + a_2 * X_i - a_1 * a_4 * \exp(a_3 * (X_0 - X_i)) \quad (3)$$

where the parameters are as in Equation (2), and

$$b_1 = \text{intercept adjustment parameter.}$$

The initial parameter values for a_2 and b_1 were set at -0.5 and -0.12 , respectively. These values were chosen to reflect a stand which first approaches a common maximum size-density line with a Reineke (1933) slope of -0.62 ($a_2 + b_1$) and then diverges from that line to asymptotically approach a line representing a basal area that would remain unchanged. The particular value for constant basal area would be inversely related to the stand's initial density.

The results of fitting Equations (2) and (3) to the spacing study data are presented in lines A and B in Table 2. The mean square error (0.0004) for Equation 2, representing shape A, was less than that for Equation 3 (0.0005). The F-test comparing the fit of those equations was significant, indicating that including the relationship between initial density and the intercept (b_1) reduces model fit ($P < 0.05$). Further analysis was therefore based on the reduced model form which assumes a size-density relationship with shape A.

OBJECTIVE 2 (CURVATURE OF THE SIZE-DENSITY TRAJECTORY)

Equation (2) assumes that the approach to the maximum size-density line is common to all stands and does not vary with initial stand conditions. A unique approach for each stand can be achieved by allowing a_3 and a_4 to vary for individual plots:

$$Y_{ij} = a_1 + a_2 * X_{ij} - a_1 * a_{4j} * \exp(a_{3j} * (X_{0j} - X_{ij})) \quad (4)$$

where parameters are as in Equation (2) and

$$j = \text{plot identifier, } j = 1, 2 \dots N.$$

By collapsing the a_3 parameter and fitting the following equation, we can test the differences between the residual sum of squares for the full (individual a_3) and the reduced (common a_3) equation:

$$Y_{ij} = a_1 + a_2 * X_{ij} - a_1 * a_{4j} * \exp(a_3 * (X_{0j} - X_{ij})) \quad (5)$$

Comparing Equations (4) and (5) determines if the shape of the asymptotic approach to the maximum size-density line is the same for all plots.

The parameter estimates for the full equation [Equation (4)] are shown in Table 3, and the estimates for the reduced equation [Equation (5)] are shown in Table 4. An F-test (Cunia 1973) on the difference in residual sum of squares between the two equations was not significantly different at $P < 0.05$ (lines C and D, Table 2) indicating that the size-density trajectory of stands with a wide range of initial densities had a common shape.

OBJECTIVE 3 (INITIATION OF MORTALITY)

To test if the onset of density-dependent mortality is associated with a constant relative density, we used Equations (5) and (2) as the full and reduced equations, respectively. Resulting parameter estimates for the full equation are given in Table 4 and for the reduced equation in line F, Table 2. An F-test on the differences between these equations (lines E and F, Table 2) was not significant, indicating that the line at which initial mortality starts is parallel to the maximum size-density line.

OBJECTIVE 4 (NATURAL STANDS VERSUS PLANTATIONS)

The preceding equations all contain a variable for initial density, which is not usually known for natural stands. Equation (2) was therefore restructured to eliminate initial density as an independent variable. First, the relationship between initial density and the density at the time of first measurement was expressed as:

$$N_{0j} = k_j * N_{1j} \quad (6)$$

where

N_{1j} = trees/ha at first measurement of the j th plot

N_{0j} = density before onset of density induced mortality of the j th plot, and

k_j = adjustment factor for the j th plot

Rewriting Equation (2) and substituting Equation (6) into it yielded

$$Y_{ij} = a_1 + a_2 * X_{ij} - a_1 * a_4 * (N_{1j} * k_j / N_{ij})^{a_3} \quad (7)$$

where N_{ij} = number of trees/ha at measurement i for the j th plot. Equation (7) can be rewritten as:

$$Y_{ij} = a_1 + a_2 * X_{ij} - (a_1 * a_4 * k_j^{-a_3}) * (N_{1j} / N_{ij})^{a_3} \quad (8)$$

Setting

$$a_{5j} = a_4 * k_j^{-a_3} \quad (9)$$

results in following equation

$$Y_{ij} = a_1 + a_2 * X_{ij} - a_1 * a_{5j} * \exp(a_{3j} * (X_{1j} - X_{ij})) \quad (10)$$

with parameters as in Equation (2), and

a_{5j} = adjustment factor, and

X_{1j} = logarithm of density at initial measurement for the j th plot.

The adjustment factor (a_{5j}) includes the adjustment for the onset of mortality (a_{4j}) and adjustment for the difference between initial density and density at the time of first measurement (k_j) for each plot. Equation (10) can therefore be used for analysis of stands with unknown initial density.

TABLE 2.
Parameter estimates for models developed and compared to meet objectives. Standard errors in parentheses.

Objective/ alternative	Equation form	Equation	Degrees of freedom	Weighted MSE	Critical F
1(A)	2	$Y_i = 7.84 - 0.69 * X_i - 7.84 * 0.07 * \exp(-3.92 * (X_0 - X_i))$ (0.19) (0.03) (0.001)	77	0.0004	
(B)	3	$Y_i = 7.99 - 0.07 * X_0 - 0.70 * X_i - 7.99 * 0.68 * \exp(-4.95 * (X_0 - X_i))$ (0.49) (0.26) (0.35) (1.70)	76	0.0005	3.2†
2(C)	4	(see Table 3)	61		
(D)	5	(see Table 4)	69		0.34
3(E)	5	(see Table 4)	69		
(F)	2	$Y_i = 7.84 - 0.69 * X_i - 7.84 * 0.07 * \exp(-3.92 * (X_0 - X_i))$ (0.19) (0.03) (0.001) (1.03)	76	0.0004	1.37
4(G)	10	(see Table 5)	48		
(H)	11	$Y_i = 7.11 - 0.58 * X_i - 7.11 * 0.01 * \exp(-4.23 * (X_0 - X_i))$ (0.09) (0.01) (0.003) (1.63)	76	0.0005	0.55

(O)	12	$Y_i = 7.78 - I_1 * 0.67 - (0.68 + I_1 * 0.1) * X_i - (7.78 - I_1 * 0.67) * (0.08) (0.12) (0.01) (0.02)$ $* (0.07 - I_1 * 0.05) * \exp[-5.73 + I_1 * 2.95] * [(1 - I_1) * X_0 + I_1 * X_1 - X_i] (0.002) (0.004) (0.37) (1.12)$	153	0.0005
(O)	13	$Y_i = 7.46 - 0.64 * X_i - 7.46 * (0.07 - I_1 * 0.06) * \exp[-3.88 (0.04) (0.01) (0.002) (0.003) (0.24)$ $* [(1 - I_1) * X_0 + I_1 * X_1 - X_i]]$	156	0.0005
5(K)	11	$Y_i = 6.92 - 0.52 * X_i - 6.92 * 0.03 * \exp(-22.68 * (X_1 - X_i)) (0.07) (0.001) (0.002) (4.18)$	278	0.0009
(L)	14	$Y_i = 7.33 - I_2 * 0.40 + (-0.62 + I_2 * 0.09) * X_i - (7.33 - I_2 * 0.40) (0.09) (0.11) (0.01) (0.02)$ $* (0.08 - I_1 * 0.07 + I_2 * 0.02) * \exp[-3.12 - I_2 * 13.58] * [(1 - I_1) (0.004) (0.005) (0.005) (0.49) (3.52)$ $* X_0 + I_1 * X_1 - X_i]]$	434	0.0007
(M)	13	$Y_i = 7.14 - 0.55 * X_i - 7.14 * (0.12 - I_1 * 0.09) * \exp[-1.31 (0.06) (0.01) (0.006) (0.05) (0.22)$ $* [(1 - I_1) * X_0 + I_1 * X_1 - X_i]]$	438	0.0014

† Statistically significant at $P = 0.05$.

TABLE 3.

Parameter estimates for pure red alder plantations, using individual a_3 and a_4 parameters. Standard errors in parentheses. Parameters a_1 and a_2 are common to all plots.

Plot	Parameter			
	a_1	a_2	a_{3i}	a_{4i}
1	6.79 (0.54)	-0.56 (0.07)	-6.55 (4.41)	0.08 (0.012)
2			-10.60 (3.42)	0.08 (0.008)
3			-11.71 (15.22)	0.61 (0.471)
4			-2.23 (1.31)	0.08 (0.038)
5			-7.82 (1.82)	0.13 (0.022)
6			-11.23 (0.08)	0.22 (0.033)
7			-8.89 (0.51)	0.13 (0.028)
8			-2.23 (0.12)	0.09 (0.022)
9			-7.83 (1.82)	0.18 (0.034)

MSE = 0.0016.

To simplify this equation a reduced form can be used to test whether a_{5j} and a_{3j} in Equation (10) are significantly different for each plot:

$$Y_i = a_1 + a_2 * X_i - a_1 * a_5 * \exp(a_3 * (X_1 - X_i)) \quad (11)$$

with parameters as in Equation (2), and

a_5 = adjustment factor common to all plots.

A fit of Equations (10) and (11) to the data for natural red alder stands (Table 5 and line H, Table 2, respectively) indicated that residual sum of squares for Equation (11) was not significantly different from that for Equation (10), suggesting that shape of the trajectory curve and the relative density at the initial measurement are similar for all plots in natural stands.

TABLE 4.

Parameter estimates for pure red alder plantations, using individual a_4 parameters. Standard errors in parentheses. Parameters a_1 , a_2 , and a_3 are common to all plots.

Plot	Parameter			
	a_1	a_2	a_3	a_{4i}
1	7.35 (0.35)	-0.61 (0.04)	-6.40 (0.001)	0.07 (0.011)
2				0.06 (0.009)
3				0.20 (0.031)
4				0.13 (0.056)
5				0.15 (0.019)
6				0.00 (0.0003)
7				0.08 (0.016)
8				0.08 (0.019)
9				0.13 (0.016)

MSE = 0.0002.

TABLE 5.

Parameter estimates for naturally regenerated red alder stands, using individual a_3 and a_4 parameters. Standard errors in parentheses. Parameters a_1 and a_2 are common to all plots.

Plot	Parameter			
	a_1	a_2	a_{3j}	a_{5j}
1	6.58 (0.35)	-0.50 (0.05)	-4.97 (9.24)	0.034 (0.016)
2			-7.12 (10.64)	0.019 (0.008)
3			-8.97 (8.53)	0.013 (0.004)
4			-5.23 (1.09)	0.018 (0.006)
5			-0.60 (21.36)	0.036 (0.016)
6			-6.45 (10.76)	0.024 (0.010)
7			-1.32 (7.18)	0.025 (0.010)
8			-8.32 (1.86)	0.020 (0.005)
9			-7.14 (2.71)	0.010 (0.004)
10			-2.11 (4.52)	0.016 (0.007)
11			-1.63 (8.73)	0.018 (0.007)
12			-4.33 (2.89)	0.017 (0.005)
13			-1.63 (3.69)	0.015 (0.006)
14			-10.75 (11.04)	0.008 (0.002)
15			-4.47 (3.20)	0.016 (0.005)

MSE = 0.0005.

To examine whether plantations and natural stands follow the same trajectory, Equations (2) and (11) can be combined into a single equation and fitted to the combined data set. The following full equation uses planted red alder stands as a base equation (a_i) and an adjustment (b_i) using indicator variables for natural stands:

$$Y_i = a_1 + I_1 * b_1 + (a_2 + I_1 * b_2) * X_i - (a_1 + I_1 * b_1) * (a_4 + I_1 * b_4) * \exp\{[a_3 + I_1 * b_3] * [(1 - I_1) * X_0 + I_1 * X_1 - X_i]\} \quad (12)$$

with parameters as in Equation (11),

b_i = natural stand adjustment parameters on the red alder plantation parameters (a_1 through a_4), $i = 1, 2, 3, 4$ and

I_1 = indicator variable (0 = plantation; 1 = natural stand).

The following reduced equation, which is simplified by eliminating the stand origin adjustment parameters and indicator variables (except b_4), assumes a common size density relationship for plantations and natural stands:

$$Y_i = a_1 + a_2 * X_i - a_1 (a_4 + I_1 * b_4) * \exp\{a_3 * [(1 - I_1) * X_0 + I_1 * X_1 - X_i]\} \quad (13)$$

with parameters as in Equation (12).

A comparison between the fits of Equations (12) and (13) tests if natural stands and plantations have the same size-density relationship, making an indicator variable for origin unnecessary. The parameter estimates resulting from fitting Equation (12) and the reduced form Equation (13) to the combined plantation and

natural stand data set are presented in lines *I* and *J*, respectively, Table 2. The residual sum of squares of the reduced equation was not significantly different from the residual sum of squares of the full equation. The development of planted and natural red alder stands can be represented by a common size-density trajectory. For illustration the data used in analysis and the maximum size-density line are plotted in Figure 2. Because of the statistical concerns, the confidence intervals of individual parameters have to be viewed with caution. Thus, while the slope of -0.64 technically does not include Reineke's (1933) slope (-0.62) in its confidence interval, these values are so close that for practical use they can be assumed to be similar. The Stand Density Index (SDI) (Reineke 1933) of the maximum size-density line for a stand with a QMD of 25.4 cm is 751 (304 in English units). The relative density at the onset of mortality was 44% of the maximum density.

As a representative example, the correlation matrix for Equation (13) is presented in Table 6. While a high correlation between the intercept (a_1) and slope (a_2) parameters of the linear portion can be expected, the correlation between the a_3 and a_5 parameters is due to the mathematical derivation of a_5 [see Equation (9)]. High multicollinearity might lead to inflated confidence intervals (Kmenta 1971). However, this effect would counteract the potential underestimation of confidence intervals due to autocorrelation and sequential testing.

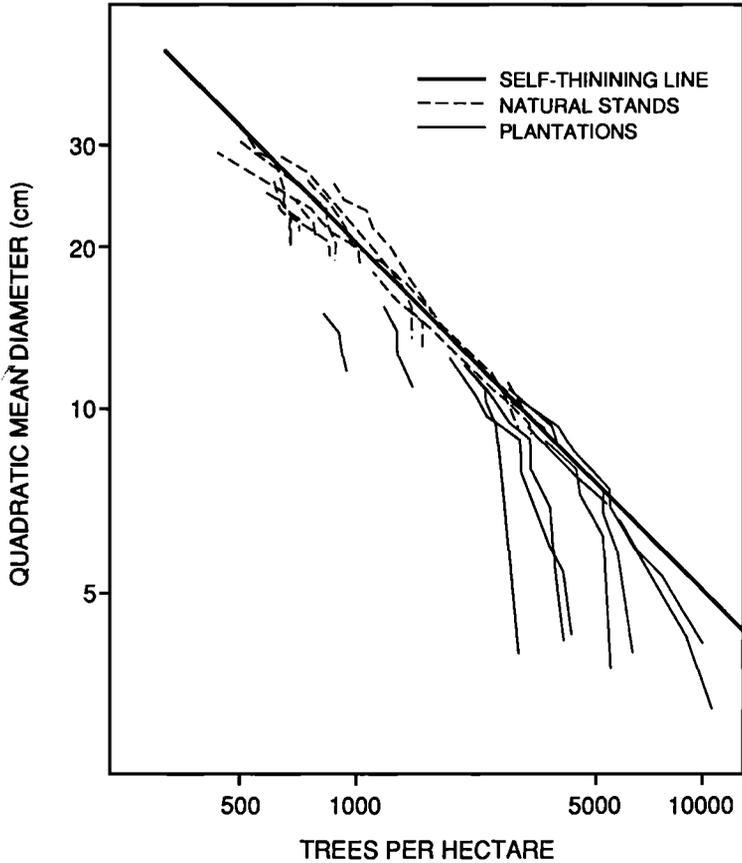


FIGURE 2. Plot measurements and asymptote of the size-density trajectory for red alder stands.

TABLE 6.

Asymptotic correlation matrix for Equation (13) (see Table 2, G).

	a_2	a_3	a_4	a_5
a_1	0.97	0.26	0.12	0.25
a_2		-0.1	-0.03	-0.19
a_3			-0.25	0.74
a_4				-0.66

OBJECTIVE 5 (RED ALDER VERSUS DOUGLAS-FIR)

The Douglas-fir size-density trajectory could not be analyzed with the same scrutiny as that for red alder because data for initial density was not available. The equation form for natural red alder stands [Equation (11)] was applied in the analysis of Douglas-fir stands. The least square fit results are presented in line K, Table 2. The slope of the maximum size-density line for Douglas-fir (-0.52) does not include the slope determined for the red alder line (-0.64) or the slope suggested by Reineke (1933) (-0.62) in the 95% confidence interval. Even accounting for inaccuracies in calculation of this confidence interval, the difference between the values is great enough to warrant the conclusion that the slope for Douglas-fir is lower. At a QMD of 25.4 cm, the Douglas-fir maximum size-density line results in a SDI of 1196 (485 in English units). For illustration, the data in this analysis and the Douglas-fir maximum size-density line are presented in Figure 3. To determine the onset of mortality, we chose the slope of -20 as the cutoff point where the size-density trajectory starts to deviate from vertical. This resulted in a relative density of 58% of maximum for the onset of mortality. While the cutoff point was chosen subjectively, slopes in this neighborhood lead to similar relative density values, because of the high curvature.

The same general approach used to analyze objective 4 can be used to decide if different species follow the same size-density trajectory. To do this, the red alder equation is used as a base equation, and adjustments for Douglas-fir (c_i) are added to every parameter in the base equation using indicator variables (I_2) to form the following full equation:

$$\begin{aligned}
 Y_i = & a_1 + I_2 * c_1 + (a_2 + I_2 * c_2) * X_i - (a_1 + I_2 * c_1) \\
 & * (a_4 + I_1 * a_5 + I_2 * c_4) * \exp\{[a_3 + I_2 * c_3] \\
 & * [(1 - I_1) * X_0 + I_1 * X_1 - X_i]\}
 \end{aligned}
 \tag{14}$$

with parameters as in Equation (13), and

c_i = Douglas-fir adjustment parameters on the red alder parameters (a_1 through a_4), $i = 1, 2, 3, 4$, and

I_2 = indicator variable (0 = red alder, 1 = Douglas-fir).

Equation (13) is also the appropriate reduced equation form for testing whether Douglas-fir has a significantly different size-density trajectory from red alder. Therefore, a comparison between the fits of Equations (13) and (14) to the combined red alder and Douglas-fir data set will demonstrate if alder and Douglas-

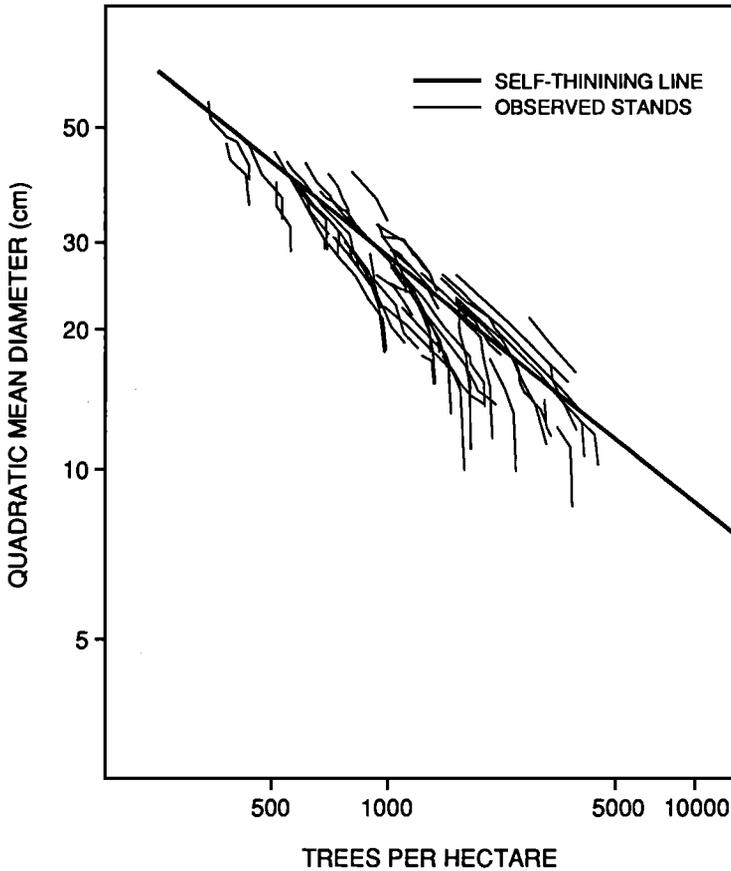


FIGURE 3. Plot measurements and asymptote of the size-density trajectory for Douglas-fir stands.

fir stands have the same size-density relationship making indicator variables for species unnecessary.

The resulting parameter estimates for the full and reduced equations are presented in lines L and M, respectively, Table 2. A comparison of the residual sum of squares of the full and reduced equations and the significance of all parameters in the full equation showed that the size-density relationship of both species differed significantly. The two-species equation could not be simplified. Species indicators and adjustments on all red alder parameters as presented in Equation (14) were needed. The projected size-density trajectories for stands with different initial densities are presented in Figure 4 and show the species differences.

DISCUSSION

The size-density trajectories for red alder and Douglas-fir were established using nonlinear regression. Concerns that the use of data from repeated measurements and sequential testing might lead to falsely declaring models significantly different seem unwarranted because, with exception of comparing trajectory shapes for red alder and the red alder and Douglas-fir model, all F-tests indicated no significant difference between models.

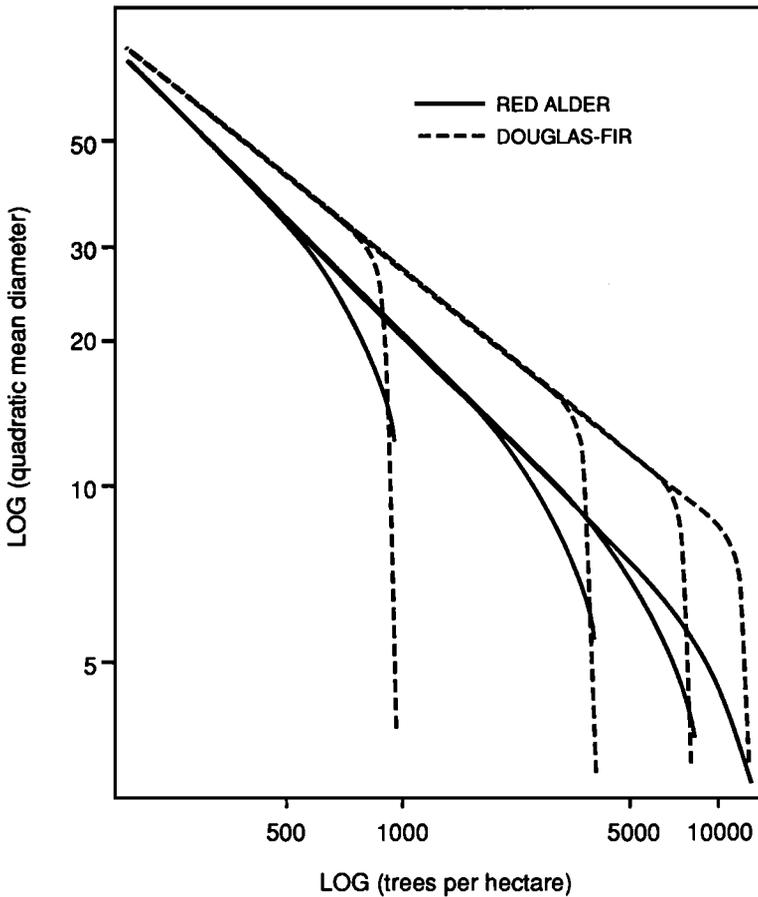


FIGURE 4. Projected size-density trajectories for red alder and Douglas-fir stands initiated at 1000, 4000, 8000, and 12,000 trees/ha, projected to 100 trees/ha.

RED ALDER

Data for the red alder spacing study, where planting density was known, were used to examine some of the different assumptions that can be built into the size-density trajectory of Smith and Hann (1984).

First, we looked at proposed forms of the size-density relationship (Figure 1A and 1B). The traditional form (shape A) showed a better fit to the data than the form representing an inverse relationship between the intercept and initial density (shape B) suggested by McFadden and Oliver (1988). However, the red alder spacing study is still young (14 yr), so the data do not cover later stages in stand development when stands move along the maximum size-density line.

Second, the spacing study data were used to see if the shape of the trajectory curves as they approach the maximum size-density line was independent of initial density. Our results agree with Smith and Hann (1984), who found a common trajectory shape for red alder seedlings and for red pine (*Pinus resinosa* Ait.) stands. A common trajectory shape seems to be implicit in a species and is not affected by stand density.

Finally, the analysis of the spacing study data indicated that the line connecting the points at which density-dependent mortality starts is parallel to the maximum line. Red alder stands start density-dependent mortality at a relative density of 0.44. This falls between Smith and Hann's (1984) value for red alder seedlings of 0.31 and Hibbs and Carlton's (1989) value of 0.5. In red pine, mortality did not start at a constant relative density, but at a lower relative density if initial density was low (Smith and Hann 1984). On the other hand, DeBell et al. (1989) found that relative density at onset of mortality in stands of loblolly pine (*Pinus taeda* L.) increased in stands with low initial density. The mortality threshold line (defined as the density at which more than 3% of the trees died) was determined by analyzing data which were measured at fairly long intervals (5 to 7 yr). Shorter intervals might have led to a different conclusion. In addition, DeBell et al. (1989) assumed the slope of the self-thinning line to be $-3/2$. The slope that we found for red alder might give different results. A more thorough investigation would require spacing studies with replicated densities on a range of sites with frequent measurements during the initial phases of growth.

An equation for size-density trajectory without initial density was fitted to natural stands. However, the equation did include an adjustment parameter that was a function of both the proportion of the initial density still alive when the first measurement was made and the relative density at which mortality starts. These two factors could, therefore, not be separated in the analysis. The adjustment parameters are specific to each data set.

As in plantations, the shape of the trajectory curve is independent of density in natural stands. In addition, the relative density at the initial measurement was similar for all plots. The plots used in the analysis were research plots that were established to observe stand growth and yield. The location was, therefore, biased toward fully stocked stand conditions, which may explain the similar relative density for the plots at time of establishment.

The red alder data set, which was a composite of planted and natural stands, provided us with the opportunity to investigate the influence of regeneration method. A common size-density trajectory characterized the development of both natural and planted stands. Stand origin does not seem to influence stand development in terms of the size-density trajectory, which agrees with results of our analysis in the first two objectives. However, research plots in natural stands are often in homogeneous areas of the stands that might be similar to plantations in evenness. Plot layout could therefore have influenced the similarity in size-density relationship. Also, all of the plantation data were from the same location. Additional studies covering a variety of sites are needed.

The slope of the maximum size-density line for red alder (-0.64) was only slightly steeper than -0.62 , which was suggested by Reineke (1933) for a variety of species and has been generally assumed to apply to red alder (Hibbs 1987, Hibbs and Carlton 1989). The average maximum SDI of red alder (751) is within the range observed by other researchers. The maximum SDI of the normal yield tables developed for red alder by Worthington et al. (1960) is 571. Hibbs and Carlton (1989) estimated the absolute maximum SDI to be 1125 from temporary red alder plots and reported a maximum SDI of 675 for data from long term studies.

DOUGLAS-FIR

Since initial density was not available for Douglas-fir plots, its effect on trajectory shape or the onset of initial mortality could not be determined in the same way as for red alder.

The approach of the size-density trajectory to the maximum line indicates that Douglas-fir mortality starts around a relative density of 0.58, which is higher than was found for red alder. Even though this is an extrapolation beyond the data range, it agrees closely with the commonly assumed value for Douglas-fir of 0.6 (Drew and Flewelling 1979, Long 1985).

The slope of the maximum size-density line was shallower for Douglas-fir (-0.52) than that proposed by Reineke (1933) and than that for red alder. The resulting maximum SDI for Douglas-fir (1195) would seem to be in the correct range considering the absolute maximum is 1470 (Reineke 1933). Drew and Flewelling (1979) also found that their maximum QMD was in agreement with Reineke's at high densities but that it underestimated Reineke's QMD at lower densities, indicating a shallower slope than that of Reineke (1933).

Possible explanations for the discrepancy between the slope of our maximum size-density line that generally used for Douglas-fir include differences in data analysis methods and in underlying assumptions about trajectory shapes, and the effect of clumping within the stand. They are discussed here.

Different methods have been used in determination of the self-thinning line, complicating the comparison of results. The most common methods are visual location, principal component analysis, extrapolation from other species, and regression analysis. Reineke (1933) did not locate an average line mathematically. He relied on placing a line above a number of individual stand measurements visually, and he found a common slope for a number of species. Osawa and Sugita (1989) fitted a line through data points considered to be on or near the self-thinning line. Using principal-component analysis, they determined a slope of -0.64 , which is considerably steeper than the one we found. Most other research on self-thinning in forests has assumed a slope based on the $3/2$ power rule, often because of lack of a better data (Drew and Flewelling 1979, Curtis et al. 1981, Hyink et al. 1988, Hibbs and Carlton 1989). An exception to this is the work of Von Gadow (1987), who analyzed pine species grown in plantations in South Africa. He fit regression lines through measurements considered to be on the maximum density line and separated the species into two groups in terms of self-thinning patterns. Group 1 consists of *Pinus patula*, *P. taeda*, *P. elliottii*, *P. radiata*, and *Eucalyptus grandis* with a slope of -0.51 . The second species group consists of *Pinus pinaster* and *P. roxburghii* with a slope of the self-thinning line of -0.42 . However, both the analysis by Osawa and Sugita (1989) and the work of von Gadow (1987) use a subjective selection of data points considered to be on the self-thinning line, which may have influenced the results of their analysis (Weller et al. 1985).

A size-density relationship of shape B (Figure 1) would result in individual stands following a trajectory with a slope shallower than -0.62 while the overall data set has a maximum size-density relationship that agrees with the results suggested by Reineke (1933): a collection of Douglas-fir stands are bounded by a line with the slope of -0.62 . However, our analysis of the different size-density

shapes for red alder indicated that the size-density relationship is better represented by shape A.

The apparent discrepancy between Reineke's (1933) results for Douglas-fir and ours cannot be explained by the theory that clumping leads to lower stockability and thus to a lower maximum size-density line. Studies investigating effects of clumping on stand development indicate that stands develop toward a uniform spacing over time (Stiell 1981, Hamilton 1984). This would steepen the size-density trajectory as the stand develops. Random mortality events, such as insect attacks or windthrow, would lead to increased clumping and a shallower slope of the size-density trajectory. However, earlier elimination of plots with extremely high mortality rates should have excluded most of the effects of random mortality events from this analysis.

BOTH SPECIES

A comparison of size-density trajectories for red alder and Douglas-fir indicated that each species had a different trajectory. A single asymptote could not characterize development for both species. This contradicts the theory that the slope of the self-thinning line is independent of species (Yoda et al. 1963, White 1980, Long and Smith 1983).

A number of aspects, single or in combination, might be responsible for the difference in size-density trajectories of the two species. Even though a final answer requires more detailed studies, our results raise some interesting points for discussion. The slope of the maximum size-density line reflects the relationship between mortality and growth. Stand growth, if measured as QMD, is a composite of increased diameter of the surviving trees and the increase in average size due to mortality of the smaller trees (Ford 1975). Differences in slopes might therefore be explained by different mortality patterns. However, the average yearly mortality rates of red alder were lower than the mortality rates of Douglas-fir, and, thus, the increase of the QMD due to mortality of the smaller trees is not likely a major contributor to the difference in slopes.

Suppressed trees are more likely to succumb to density dependent mortality (Dahms 1983, Hamilton 1986, Hann and Wang 1990). Those trees had been becoming less competitive with the surviving trees as suppression progressed (Ford 1975, West and Burrough 1983). Thus, a difference in slope of the size-density line is not simply related to a difference in competition intensity. Instead, the slope of the red alder maximum size-density relationship indicates that diameter growth of red alder seems to respond more efficiently to freed resources than diameter growth of Douglas-fir. This could be due to differences between the two species in how photosynthesis efficiency is affected by available resources (Perry 1984) and/or patterns of carbon allocation (Waring and Schlesinger 1985).

Red alder had a lower maximum size-density line and a lower relative density at the onset of mortality than did Douglas-fir (0.44 vs. 0.58). Welden and Slauson (1986) defined competition as the induction of strain as a direct result of resource use by other individuals, where strain is the sum of the physiochemical changes in response to stress. Species differences could, therefore, be due to different strain level or tolerances, or to different competition intensities within populations.

Shainsky (1988) found that red alder seedlings were the superior competitors over Douglas-fir, i.e., red alder influenced the growth of both species more than did Douglas-fir. This would indicate that competition and strain intensity are higher in red alder stands. Alternatively, the critical strain level at which mortality starts might be lower in red alder stands, not allowing competition intensity and stand density to become as high as in Douglas-fir stands.

As a final possibility, the competition intensity and average strain levels could be similar, but the strain distribution within a population might be different. For a similar competition intensity, trees at the lower end of the size-distribution would show more strain in red alder than in Douglas-fir stands, leading to a higher risk of mortality.

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 Manuscript received July 2, 1991

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